

An Investigation of Stratified Population Estimates

by

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AN INVESTIGATION OF STRATIFIED POPULATION ESTIMATES

BY

CHRISTOPHER WILLIAM KIRBY

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University
of Manitoba in partial fulfillment of the requirements of the degree
of
MASTER OF SCIENCE**

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Abstract

This thesis presents the results of a comparative study of the two most commonly used two-sample, mark-recapture population estimators: the unstratified pooled Petersen estimator, and the stratified Darroch estimator [Darroch, 1961], including recent maximum likelihood extensions by [Plante, 1993]. As well, the study gave brief consideration to the stratified Schaefer estimator [Schaefer, 1951], but, due to its restrictive consistency conditions and lack of a standard error estimate, it is was not included in the final results of the study.

In order to apply a stratified population estimator, a biologist must stratify, or partition, their initial and final samples into groups such that animals within a group share a similar set of parameters. Specifically, the similar parameters must be: the probability of being captured, or recaptured, and the probability of migrating from the initial stratum to a given final stratum. The stratification may be done geographically, e.g. all animals in a particular section of forest might share the same parameters, or temporally, e.g. all animals passing a marking station at a given time may share the same parameters.

The primary focus of this thesis is the study of the estimators as they are applied to temporally stratified, migrating salmon populations. The study consists of applying the estimators to a series of hypothetical populations that are constructed using six sets of capture/recapture probabilities, three migration models, three mortality models, two capture strata entry models, and two initial population sizes that are representative of those seen in migrating salmon populations.

The study focuses on the following performance measures of the estimators: the asymptotic relative bias, the coefficient of variation (CV), the bias relative to the CV (effective bias), and the root mean-square error. Using these measures, it is determined that using a stratified estimator, such as the Darroch, can provide large improvements, in terms of reducing bias, over the unstratified pooled Petersen. As

well, it is determined that while the Darroch offered improvements in bias over the pooled Petersen, the Darroch exhibited much larger CVs (and therefore much lower precision) than the pooled Petersen.

The much larger CVs of the Darroch lead to a study of the practice of pooling rows and columns of mark-recapture data to increase the precision of the Darroch estimate. Currently, there exists no definitive test for determining the optimal pooling for a given set of data. As such, biologists must perform many experimental poolings, using subjective heuristics as a guide, in order to achieve a satisfactory estimate. Using a set of hypothetical populations similar to those used in the first portion of the study, the pooling study attempts to determine the optimal, in terms of root mean-square error, level of pooling for the hypothetical populations. These experiments yield two results: the first is that there exists no clear optimum level of pooling for the populations studied, and the second is a heuristic that can be used to determine when data has been over-pooled.

As well, a simulation study is conducted to examine the properties of the estimators' standard error estimates. Using measures similar to those used in the first part of the study, it is determined that the standard error estimate for the pooled Petersen estimator is both unbiased and precise. Similarly, it is determined that standard error estimate for the Darroch estimator can exhibit the undesirable properties of high bias and low precision. Additionally, this portion of the study indicates that Darroch estimate, and in particular Plante's maximum likelihood extensions, may suffer from low reliability when applied to small sample data. This result underscores the importance of pooling as a technique for overcoming these deficiencies.

Finally, a software package developed to produce the results for the study, is presented and discussed. In brief, the software package allows for analysis of stratified, two-sample mark-recapture data, as well as simulation of mark-recapture

experiments. This includes simulations of hypothetical populations, as well as simulations of pooled populations. Both of these features can be a useful aid in planning mark-recapture experiments.

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Chapter 1

Introduction

One of the most important aspects of wildlife management is obtaining accurate estimates of the size of animal populations. Ideally, each individual animal within the population of interest would be counted and an exact population size determined. Unfortunately, due to limited resources, rugged terrain, and a host of other factors, it is usually impossible to count each individual animal. Mark-recapture attempts to alleviate this problem by using statistical methods to provide accurate estimates of population size while counting only a portion of the total population.

Some recent work ([Dempson and Stansbury, 1991], and [Warren and Dempson, 1995]) has questioned the utility of using a stratified mark-recapture estimator, such as the Darroch estimator [Darroch, 1961], over an unstratified estimator, such as the pooled Petersen estimator. To date, the answer to this question has been ambivalent. The goal of this thesis is to investigate the properties of these two estimators and to show that there is much to be gained in using a stratified estimator over one that is unstratified.

Although stratified and unstratified estimators are applicable to all types of animal populations, most recent work ([Dempson and Stansbury, 1991], [Warren and Dempson, 1995], and [Schwarz and Taylor, 1997]) has focused almost

exclusively on their application to salmon populations migrating from the ocean to inland rivers and lakes to spawn. As such, this thesis focuses on a study of the properties of the mark-recapture estimators most commonly applied to migrating salmon populations: the unstratified pooled Petersen estimator, and the stratified Darroch estimator [Darroch, 1961], including recent maximum likelihood extensions by [Plante, 1993]. As well, due to its study in [Warren and Dempson, 1995], the stratified Schaefer estimator [Schaefer, 1951] was also briefly considered in the study but, due to its strict consistency conditions and lack of a standard error estimate, it was not included.

In order to be able to apply a stratified estimator to a population, a biologist must stratify, or partition, their initial and final samples such that the animals in each partition share a similar set of parameters. Specifically, these parameters are: the probability of being captured, or recaptured, and the probability of migrating from the initial stratum to a given final stratum. To study the effect that these parameters had on the estimators, a study was conducted using a number of capture/recapture probability sets, migrations models, and initial strata entry models. As well, a number of initial population sizes, and mortality models were also included to determine their effects on the estimators.

Once an experiment has been completed, and the data collected, it is a common practice among fisheries biologists to pool, or group, strata that appear to share similar parameters in hopes of increasing the precision of the resulting estimates. In addition to the comparative study of stratified estimators, this thesis will also investigate the practice of pooling. This investigation will show that there is no optimum level of pooling for the representative set of selected populations studied. Additionally, this investigation will derive a heuristic for determining when over-pooling has occurred.

Since the precision of the estimates produced by an estimator is also of great im-

portance to a field biologist, this thesis will also study the properties of the standard error estimates for the population estimators studied.

1.1 Thesis Outline

In Chapter 2, a number mark-recapture estimators are reviewed and developed. These include the simple Petersen, and stratified estimates such as the pooled Petersen, the Schaefer, and the Darroch estimator. The primary focus of this chapter is to explain the estimators and their properties with respect to bias and precision.

Chapter 3 provides the results of a series of factorial experiments conducted in an effort to quantify the amount of bias and precision present in the pooled Petersen when it is applied to populations where there are violations of the estimator's assumptions. The pooled Petersen is compared to the Darroch moment estimator, a stratified estimate that is more tolerant of non-homogeneous sampling conditions due to a division of the samples into homogeneous strata. The comparison is made under identical conditions to provide a clear picture of the amount of precision lost when moving to the more general estimator.

The result of a similar study applied to standard error estimates of the estimators is presented in chapter 4. In addition to the pooled Petersen and Darroch moment estimate, a maximum likelihood derivation of the Darroch [Plante, 1993] is studied. As well, the validity of applying the closed population error estimates to populations where mortality is occurring is also studied.

The effects of pooling on the Darroch estimator are examined in Chapter 5. The same set of experiments discussed in Chapter 3 are repeated using various levels of pooling to determine the point where the Darroch overtakes the pooled Petersen in terms of improved precision and reduced bias (i.e. root mean-square error).

Chapter 6 describes an application program that was developed to explore the

properties of the various estimators. The features of the program are discussed, as well as two case studies, one demonstrating the analysis capabilities of the program, and another demonstrating its simulation capabilities and use as an experimental planning tool.

Finally, Chapter 7 provides a summary of the research, general conclusions, and directions for future work.

Chapter 2

Mark-Recapture Estimators

2.1 Introduction

2.1.1 Terminology

Although it is assumed that the reader has a basic understanding of statistics and statistical measures, it is necessary to define some terminology associated with estimators that may be unfamiliar. For the most part, these definitions have been drawn from [White *et al.*, 1982].

The *expected value*, or *mean*, of a random variable X , denoted $E(X)$, is the value that the mean of a random variable trends towards over many independent samples. Mathematically, the expected value of a random variable is:

$$E(X) = \sum_{j=0}^{\infty} x_j p_X(x_j) \quad \text{if } X \text{ is discrete on } 0, 1, 2, \dots$$

$$E(X) = \int_{-\infty}^{\infty} x f_X(x) dx \quad \text{if } X \text{ is continuous}$$

where $p_X(x_j)$ and $f_X(x)$ are the probability density functions for X .

Bias and *consistency* are measures of the difference between the expected value of an estimate and the true value that it is estimating. An unbiased estimator is one where the expected value of an estimator, \hat{N} , is equal to the true value N . For example, the simple two-sample Petersen estimate (section 2.2) has the formula

$$\hat{N} = \frac{m_1 n_2}{m_2} ,$$

where m_1 , the number of animals marked in the first sample, and n_2 , the number of animals recaptured in the second sample, can be treated as constants, and m_2 , the number of marked animals recovered in a second sample, is a binomial random variable that may take on values from 0 to m_1 . Working out the expected value of the function $\frac{1}{m_2}$, we get

$$E\left(\frac{1}{m_2}\right) = \sum_{i=0}^{m_1} \frac{1}{i} \text{bin}(i; m_1, p) .$$

Since it is known that the probability of obtaining the value 0 from a binomial distribution is non-zero, the sum will end up including a term of a non-zero value divided by 0, causing the sum to go to infinity, rather than the desired value of N . Hence the simple Petersen estimate, in this form, is biased.

An estimator is *Fisher consistent* if the estimate \hat{N} equals the true value N when all the random variables in the estimator are replaced by their expected values. Continuing with the above example of the simple Petersen estimate, \hat{N} will be a consistent estimate of N if

$$\hat{N} = \frac{m_1 n_2}{E(m_2)} = N .$$

From the above two examples, it should be clear that a consistent estimator need not be an unbiased estimator, or vice versa.

Bias is the difference between the expected value of an estimator for a given set of parameters, and the true value of that is being estimated. Mathematically stated,

$$\text{Bias} = E(\hat{N}) - N .$$

It is common within mark-recapture studies to measure the bias of an estimate by its *relative bias*, $\frac{E(\hat{N})-N}{N}$, which is normally expressed as a percentage of the true value, N .

Precision refers to the variability of an estimator in repeated samples drawn from the same population. It is measured by the variance of the estimate about its mean; the square root of this variance yields the *standard error* of the estimate.

Using the estimate and its standard error, a *confidence interval* (CI) may be formed for the estimate. A confidence interval is a range in which the true value being estimated is likely to fall with a given probability, or confidence. A confidence interval is formed by subtracting a multiple of the standard error from the estimate, i.e. $\hat{N} \pm xS$ where S is the standard error of the estimate. The multiplier, x , is chosen based on the normal distribution and the desired level of confidence. For example, to form the 95% confidence interval (the most commonly used confidence interval), one would use the multiplier 1.96, since the mean of the normal distributes, plus or minus 1.96 standard deviations, covers 95% of the probability density curve for the normal.

Closely tied to the confidence interval is the *coverage* of the CI, which is a measure of how often the confidence interval really covers the true value being estimated. For example, if the estimate is badly biased, it is possible that the 95% CI formed from the estimate only covers the true value 60% of the time, or never at all. The coverage of the CI can also be affected by bias in the estimated precision of the estimate. For example, if the estimated precision of the estimate is too high, the 95% CI for the estimate will be too narrow and may therefore only cover the true value 80% of the

time. Similarly, if the estimated precision of the estimate is too low, the 95% CI will be too large, and may therefore cover the true value 99% of the time.

2.2 The Simple Petersen Estimate

The Petersen estimate (also known as the Lincoln index) is a mark-recapture estimator in its simplest form. A Petersen experiment consists of two samples drawn from an animal population at two different times. An initial random sample of m_1 animals is drawn from the total population of N animals. Each animal in this initial sample is marked in some identifiable manner (e.g. a colored tag is affixed to the animal) and is re-introduced into the population. In an ideal situation, the marked animals will homogeneously mix with the unmarked members of the population.

Later, a second random sample of n_2 animals is drawn from the population. This second sample will consist of m_2 animals that were marked in the first sample, and u_2 unmarked animals that were not captured in the first sample. Assuming that the m_1 animals did indeed homogeneously mix with the unmarked members of the population, we can assume that the second sample is representative of the population as a whole. This means that the ratio of animals marked in the initial sample to the total population size N should equal the ratio of marked animals captured in the second sample to the size of the second sample, or, in expectation:

$$m_1/N = m_2/n_2$$

Since the only unknown in this equation is N we can obtain the following estimate (designated \hat{N}):

$$\hat{N} = \frac{m_1 n_2}{m_2}$$

There are several assumptions implicit in the Petersen estimate, the two most important being:

- **equal catchability:** each animal within the population is equally likely to be caught during both sample times. This does not imply that the probability of capture must be the same for both the sample times, but that the probability of capturing any given animal is the same as for any other animal at that sample time.
- **closure:** the population is closed during the interval between the first and second sample times. This means that no animals are lost through migration or mortality, and no animals are introduced into the population through immigration or birth.

If either of these assumptions is violated, the estimator may be biased. If marked animals have a lower probability of capture than unmarked animals, the estimator will have a positive bias since there will be less marks (m_2) recovered in comparison to the number of unmarked animals (n_2) recovered. Similarly, if the marked animals have a higher capture probability than those that were not marked, the estimator will have a negative bias.

In the case that the size of the population changes between the two sampling times, a positive bias can be introduced in the case of the mortality rate being higher for marked animals than for unmarked animals since the number of recovered marks will now be lower in comparison to the number unmarked animals recovered. Similarly, a positive bias can also be introduced if new, unmarked animals (called births, or recruits) are introduced into the population during the inter-sample time interval.

When changes in the population size do occur, they can also change the value that the estimator is estimating. When only mortality is occurring equally for both

marked and unmarked animals, the estimator still remains a valid estimate of the population size at capture time. When recruitment is occurring, the estimator estimates the population size at recapture time. When both recruitment and mortality are occurring, the estimator over-estimates the population size at both capture and recapture time. [Seber, 1973, pages 71–73] provides an in-depth examination of the affects of recruitment and mortality on the Petersen estimate.

2.3 Stratified Estimates

From the above, it is clear that the Petersen estimate is sufficient for two-sample experiments where sample sizes are large and a number of unlikely assumptions hold, but is insufficient for studies of migrating populations where the assumptions of equal catchability and random mixing of tagged and untagged animals are unlikely to be met. In these types of experiments, it is likely that the equal catchability assumption of the Petersen is being violated, since animals captured in one geographic area or moment in time are generally going to differ in catchability from animals captured in another area or at another time.

Stratified estimators help solve these problems by treating each of the areas or sampling times as a distinct *stratum*. By dividing the area of study, the biologist hopes to reduce any bias introduced by violations of the equal catchability assumption, and to gain insight into the structure of the population. For example, if a population under study inhabited both flat, easily accessible terrain and heavily wooded terrain, the animals in the easily accessible area might be much easier to catch than those in the wooded area. By dividing the two different types of terrain into separate strata, the effects of the assumption violation can be reduced, and the structure of the population (the number of animals in the flat terrain, and the number of animals in the wooded terrain) can be deduced.

Estimates stratified in time are commonly used by fisheries biologists in estimating the number of salmon returning inland to spawn each year. Instead of samples occurring in geographic areas, sampling is usually done in a number of weeks, or perhaps days, at single point in a river or river system. Re-sampling then occurs some time later further up the river [Dempson and Stansbury, 1991], or its tributaries. By then analyzing the collected count data, biologists can estimate the size of the returning population, and the rate at which the population moved up the river system [Schwarz and Taylor, 1997]. Geographic stratification can also be applied to migrating fish populations in order to determine the number of fish that returned to each individual river in a river system.

2.3.1 Anatomy of a Stratified Experiment

In a stratified experiment, animals are sampled and marked in s initial, or capture, *strata*. Unlike a simple Petersen experiment, where a single identifiable mark can be used to distinguish marked animals from unmarked animals, a stratified experiment requires that a unique mark be assigned to each animal, or at least to each initial stratum. This is necessary so that the *stratum* in which the animal was captured and marked is reliably identifiable. As initial marking proceeds, the number of animals marked and released in each of the initial strata is recorded.

Later, the population is re-sampled in t final, or recapture, strata. In the event that a marked animal is recaptured, its stratum of capture and the recapture stratum are recorded. As well, the number of unmarked animals captured in each of the recapture strata is also recorded. These records are then used to construct a two dimensional array, m , consisting of counts indexed by the s capture strata along the rows, and the t re-capture strata along the columns. The total animals marked in each of the s capture strata is recorded in the $s \times 1$ vector n^c , and the number of unmarked animals captured in each of the re-capture strata is recorded in the

$1 \times t$ vector u . As well, some estimators require the calculation of the number of marked animals that are never recovered, which can be calculated as $n^c_i - m_{i..}$. The resulting matrix and vectors can then be manipulated to give estimates of the number of animals present in each of the strata, as well as the rates of migration between strata. Figure 2.1 shows the typical form of the data gathered in a stratified experiment.

$$\begin{bmatrix} n^c_1 \\ n^c_2 \\ \vdots \\ n^c_s \end{bmatrix} \begin{bmatrix} m_{1,1} & m_{1,2} & \dots & m_{1,t} \\ m_{2,1} & m_{2,2} & \dots & m_{2,t} \\ \vdots & \vdots & \vdots & \vdots \\ m_{s,1} & m_{s,2} & \dots & m_{s,t} \end{bmatrix} \\ \begin{bmatrix} u_1 & u_2 & \dots & u_t \end{bmatrix}$$

Figure 2.1: The form of the data collected from a stratified experiment

Several notational conventions have been used by authors to describe stratified estimates and their derivations. Unfortunately, there is also some overlap of symbols, that can make comprehension of a model difficult if one is familiar with another, but similar notational convention. To this end, in addition to the notation already defined, the following will be used consistently throughout this manuscript:

Observable Statistics:

- m_{ij} = the number of animals marked in capture stratum i and recaptured in recapture stratum j
- n^c_i = the number of animals marked in capture stratum i , $i = 1 \dots s$
- n^r_j = the size of the sample taken in recapture stratum j , $j = 1 \dots t$
- u_j = the number of unmarked animals captured in recapture stratum j

Parameters:

- θ_{ij} = the probability that a member of stratum i at capture time is present in stratum j at recapture time
- p_i^c = probability that a member of capture stratum i is captured, marked, and released
- p_j^r = probability that a member of recapture stratum j is captured
- ψ_{ij} = the probability that an animal in capture stratum i is recaptured in j , i.e. $\psi_{ij} = \theta_{ij}p_j^r$
- u_{ij} = the number of unmarked animals that migrated from stratum i to stratum j
- U_i^c = the number of unmarked animals present in capture stratum i
- U_j^r = the number of unmarked animals present in recapture stratum j
- U = the size of the unmarked portion of the population
- N_{ij} = the total number of animals that migrated from stratum i to stratum j
- M_{ij} = the number of marked animals that migrated from stratum i to stratum j
- N = the total population size ($= \sum_i \sum_j N_{ij}$)

Dot notation will be used to indicate the summation of a vector or matrix over the indicated subscript, i.e. $m_{..}$ is the total number of marked animals recovered in all strata. Bold text will be used to indicate a vector or matrix of elements, e.g. $\mathbf{n}^c = [n_1^c \dots n_s^c]$. An estimate of a parameter will be represented by placing a caret over the parameter, e.g. the estimated total population will be denoted \hat{N} . Other notation that is required for the development of a particular result will be introduced

as needed.

2.3.2 The Pooled Petersen Estimate

The precision of mark-recapture estimators, like all statistical estimators, is heavily dependent on the quantity of data collected. In stratified experiments, since marking and re-capture occurs over a number of geographic areas or periods of time, the amount of data collected for each stratum can sometimes be inconsistent. For example, in estimating the size of a salmon run, there may be very few fish returning past the marking point during the first few marking periods. Hence, there will be very few marked fish recovered from these initial marking strata, providing little data from which to form an estimate. In order to gain greater precision, poor or minimal data can be *pooled* (summed) with data from other strata, i.e. rows of data may be pooled with other rows, or columns of data may be pooled with other columns. For example, in our salmon example, the data collected from the first few capture times could be pooled with that of a later time (i.e. pooling columns), or we may wish to pool the fish marked at earlier times with those marked later in the run (pooling rows).

The pooled Petersen estimate is formed by taking pooling to its extreme and reducing the data to a single value for m_{ij} , n^c_i , and u_j . These values can then be used in forming the simple Petersen estimate replacing m_2 , m_1 , and n_2 by $m_{..}$, $n^c_{..}$, and $m_{..} + u_{..}$ respectively. Unfortunately, by pooling in such a crude manner, the pooled Petersen is likely to exhibit bias since, by performing pooling, the biologist assumes that all of the pooled strata have the same capture/recapture probability (the equal catchability assumption); an unlikely, but not impossible, situation in migrating fish populations.

As can be seen from its development, assuming either a closed population, or mortality without recruitment, the pooled Petersen only provides an estimate of the

size of the population at capture time.

2.3.2.1 Consistency and Precision

[Seber, 1973, pages 436–437] builds on the results of [Chapman and Junge, 1956], and [Darroch, 1961], by developing a number of sufficient, but not necessary conditions for the consistency of the pooled Petersen. In proving these conditions, Seber states the form of the pooled Petersen estimate as follows:

$$\hat{N} = n^c \cdot n^r / m_{..}$$

Seber then changes the form of the estimate to

$$\hat{U} = \hat{N} - n^c = n^c \cdot u / m_{..} ,$$

the Petersen estimate of the unmarked population size. By letting n^c_i and U^r_j tend to infinity such that n^c_i/n^c , U^r_j/U^r , and n^c/U^r remain constant, Seber shows that \hat{U} is a consistent estimate of:

$$\begin{aligned} \hat{U} &= \frac{n^c E[u]}{E[m_{..}]} \\ &= \frac{n^c \sum_j U_j p^r_j}{U \sum_{i,j} n^c_i \theta_{ij} p^r_j} \cdot U . \end{aligned}$$

Although there are many solutions to the equation such that \hat{U} is a consistent estimate of U , Seber, as with [Darroch, 1961], only presents four due to their simple physical interpretations:

1. $p^r_j = p^r$ for $j = 1, 2, \dots, t$.

2. $n^c_i/U^c_i = n^c/U$ and the movement pattern for marked and unmarked is the same, meaning $U^r_j = \sum_i U^c_i \theta_{ij}$.
3. Marked and unmarked follow the same movement pattern and $\theta_{ij} = \theta_j$ for all i, j .
4. $\sum_i n^c_i \theta_{ij} = k U^r_j$.

The first condition implies that a constant proportion of each recapture stratum is sampled, i.e. the probability of recapture is the same across all recapture strata. The second condition is the marking analog of the first, saying that the marked fraction in each of the initial strata should be equal to the marked fraction for the overall population. If the third condition is true, there is complete mixing of the population, since the probability of an animal migrating to stratum j is independent from the stratum of its origin. Finally, the fourth condition states that the expected number of marked animals in the j th stratum is proportional to the number of unmarked animals present, implying that the marked fraction of the population is the same for all recovery strata.

There exists a well-known variance formula for the simple Petersen estimate [Seber, 1973, page 60], which is unbiased when the Petersen assumptions hold and sampling is performed without replacement. Namely,

$$\text{var}(\hat{N}) = \frac{(m_1 + 1)(n_2 + 1)(m_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)} .$$

This can be applied to the pooled Petersen by substituting n^c for m_1 , n^r for n_2 , and $m_{..}$ for m_2 . Unfortunately, as pointed out by [Seber, 1973, pages 59, 60], this formula is based on the assumption of hypergeometric distributions for m_2 , and u_2 . When the variance formula is applied to pooled data, where m_2 and u_2 are no longer hypergeometric, this assumption causes bias in the resulting variance estimate.

2.3.3 The Schaefer Estimate

The Schaefer estimate was developed by [Schaefer, 1951] as an alternative to the pooled Petersen. The Schaefer provides a distinct advantage over the pooled Petersen in that it provides estimates of the individual stratum sizes, which in turn makes it possible to perform *selective pooling* on the observed data. Using this estimate, a biologist can selectively pool rows and columns that appear to have similar properties, e.g. a series of columns with similar recapture probabilities could be pooled into a single column to realize gains in precision.

Although there are several different methods of deriving the Schaefer estimate (Schaefer's original paper includes two different derivations), I will follow the derivation done by [Warren and Dempson, 1995] for their "simple estimator of daily migration", another form of the Schaefer estimate.

The derivation begins by defining the variable n^c_{ij} to be the number of animals marked in stratum i that migrate to stratum j . Similarly, let n^r_{ij} denote the number of animals recaptured in stratum j that originated in capture stratum i , and u_{ij} to denote the unmarked animals that originated in i and migrated to j . Estimates of the n^c_{ij} can be obtained by equating the ratios

$$\hat{n}^c_{ij}/n^c_i = m_{ij}/m_i. .$$

Clearly, this equivalence only holds if the p^r_j are all equal since simple cross-multiplication of the ratio yields

$$\hat{n}^c_{ij}/m_{ij} = n^c_i/m_i. .$$

This equation states that the proportion of marked animals to recovered animals in each of the capture stratum must equal the proportion of marked animals to

recovered animals across all of the strata, which can only happen when the p^r_j are equal.

Estimates of the n^r_{ij} can be obtained in a similar manner by equating the ratios

$$\hat{n}^r_{ij}/n^r_j = m_{ij}/m_{.j} .$$

As with the estimates n^c_{ij} , the equality only holds if other conditions are true. In this case, the equality will only hold if one of two conditions holds:

1. the proportion of each initial stratum marked is constant across all capture strata, i.e. $p^c_i = p^c$ for all i .
2. the migration of marked and unmarked animals across recapture strata is independent of their strata of origin, i.e. $\theta_{ij} = \theta_j$.

[Warren and Dempson, 1995] then uses the preceding results to derive an estimate of the u_{ij} ($\hat{u}_{ij} = \hat{n}_{ij} - m_{ij}$), and forms an estimate for stratum-to-stratum migration as

$$\hat{N}_{ij} = \hat{n}^c_i \hat{u}_{ij} / m_{ij} + n^c_{ij} .$$

Using simple algebraic manipulation, this estimate can be expressed in the more familiar form of the Schaefer estimate

$$\hat{N}_{ij} = \frac{n^c_i m_{ij} n^r_j}{m_{i.} m_{.j}} ,$$

and $\hat{N} = \hat{N}_{..} = \sum_{ij} \hat{N}_{ij} .$

In addition to the initial population size provided by the pooled Petersen, the Schaefer estimate produces estimates of the total numbers of animals migrating

from stratum i to stratum j , i.e. the N_{ij} , and, by summing the N_{ij} , the $N_{.j}$ and the $N_{i.}$. Once these estimates are combined with the observed n^c_i and n^r_j , the Schaefer can also provide estimates of the p^c_i and p^r_j .

2.3.3.1 Consistency and Precision

Following the development done in [Warren and Dempson, 1995], it appears that the Schaefer estimate has consistency conditions far more stringent than those of the pooled Petersen estimate (constant p^c_i and constant p^r_j , or equal mixing versus only one of these for the pooled Petersen), but [Chapman and Junge, 1956, pages 379–380] show that meeting only one of these two conditions is sufficient for the Schaefer estimate to be consistent. Therefore, the Schaefer estimator is not much more restrictive than the pooled Petersen estimate, but has the advantage of being able to provide migration estimates.

In his original paper, Schaefer neglected to develop a variance for his estimate. In their work, Chapman and Junge also failed to provide a variance formula for the estimate. As it turns out, these omissions were probably purposeful rather than accidental since, in Seber's words, "the asymptotic variance of [the Schaefer estimate], ... would require considerable computation ...".

Also, the strict consistency conditions of the estimate are such that it will rarely be used in a realistic field experiment. Thus, the development of its variance estimate would be largely an academic exercise.

2.3.4 The Darroch Estimate

The Darroch estimate was developed in [Darroch, 1961]. Darroch's work was an extension to the work of [Chapman and Junge, 1956], who had developed a moment estimate for equal number of capture and recapture strata, i.e. $s = t$. Since

[Chapman and Junge, 1956] had developed their estimate on a full rank model, i.e. a model where the number of parameters is equal to the number of independent observations, Darroch was able to confirm their findings using maximum likelihood, since it is well known that when a model is of full rank, moment estimates are asymptotically equal to the maximum likelihood estimates. Also, Darroch attempted to extend Chapman and Junge's work by developing estimates for models of less than full rank, i.e. models where $s \neq t$.

2.3.4.1 Darroch's Maximum Likelihood Estimate

As with the moment estimate of [Chapman and Junge, 1956], Darroch's maximum likelihood estimate begins with a number of assumptions:

1. The population is closed, i.e. there is no mortality, which implies $\theta_{i.} = 1$ ($i = 1 \dots s$).
2. Stratification has been done such that all individuals in the j^{th} stratum, whether marked or unmarked, have the same probability p_j^c of being caught in the final sample.
3. Marked individuals behave independently of one another in regards to moving between strata and being caught.
4. The matrix $\Theta = [\theta_{ij}]$ is non-singular.

With these assumptions in mind, Darroch begins the derivation of the maximum likelihood estimate by forming the joint probability function for the random variables $\{m_{ij}\}$ and $\{n_i\}$, namely

$$f(\{m_{ij}\}|\{n_i^c\}) = \prod_{i=1}^s \left\{ \frac{n_i^c!}{(n_i^c - m_i.)! \prod_{j=1}^s m_{ij}!} (1 - \sum_j \theta_{ij} p_j)^{n_i^c - m_i.} \prod_{j=1}^s (\theta_{ij} p_j)^{m_{ij}} \right\} ,$$

the multinomial density for the number of marked animals that migrate to each of the recapture strata from a particular capture stratum, given the number of animals marked in that stratum, and

$$f(\{u_j\}) = \prod_{i=1}^s \left\{ \binom{U_j}{u_j} p_j^{u_j} (1 - p_j)^{U_j - u_j} \right\} ,$$

the binomial distribution for the number of unmarked animals taken in each of the recapture strata.

Since the $\{m_{ij}\}$ and $\{u_j\}$ are independent, the maximum likelihood for the joint distribution can be found by obtaining maximum likelihood estimates $\hat{\theta}_{ij}$, \hat{p}_j from the first equation and using them to obtain the moment estimates $\hat{U}_j \hat{p}_j = u_j$. Therefore, if the matrix θ ($\theta = [\theta_{ij}]$) is non-singular, we find that

$$\hat{\theta}_{ij} \hat{p}_j = \hat{\psi}_{ij} = m_{ij} / n_i^c , \tag{2.1}$$

$$\sum_{j=1}^s \hat{\theta}_{ij} = 1 , \tag{2.2}$$

and

$$\hat{U}_j = u_j / \hat{p}_j . \tag{2.3}$$

By cross-multiplying equation 2.1, the equations can be re-written in matrix-vector form,

$$\mathbf{D}_{n^c} \hat{\Theta} \hat{\mathbf{D}}_p = [(m_{ij})] = \mathbf{M},$$

$$\theta \mathbf{1} = \mathbf{1},$$

and

$$\hat{\mathbf{U}} = \mathbf{D}_u \hat{\rho} ,$$

where $\mathbf{1}$ is a column vector of ones; $\mathbf{U} = [(U_j)]$, $\boldsymbol{\rho} = [(p_j^{-1})]$ are column vectors, and \mathbf{D}_{n^c} , \mathbf{D}_u , and \mathbf{D}_p are diagonal matrices. Assuming \mathbf{M} to be non-singular, as is likely to hold if $\boldsymbol{\Theta}$ is non-singular and the sample sizes n^r_j are large,

$$\hat{\mathbf{D}}_\rho = \hat{\mathbf{D}}_p^{-1} = \mathbf{M}^{-1}\mathbf{D}_{n^c}\hat{\boldsymbol{\Theta}}$$

and

$$\begin{aligned} \hat{\boldsymbol{\rho}} &= \hat{\mathbf{D}}_p^{-1}\mathbf{1} \\ &= \mathbf{M}^{-1}\mathbf{D}_{n^c}\hat{\boldsymbol{\Theta}}\mathbf{1} \\ &= \mathbf{M}^{-1}\mathbf{D}_{n^c} \\ &= \mathbf{M}^{-1}\mathbf{n}^c. \end{aligned}$$

This means that the \hat{p}_i^c are given by:

$$\hat{p}^{c^{-1}} = \mathbf{M}^{-1}\mathbf{n}^c$$

($\mathbf{n}^c = [(n^c_i)]$), and the $\hat{\theta}_{ij}$, \hat{U}_j then follow from equations 2.1 and 2.3, namely:

$$\hat{\boldsymbol{\Theta}} = \mathbf{D}_{n^c}^{-1}\mathbf{M}\hat{\mathbf{D}}_\rho$$

and

$$\hat{\mathbf{U}} = \mathbf{D}_u\hat{\boldsymbol{\rho}} = \mathbf{D}_u\mathbf{M}^{-1}\mathbf{n}^c .$$

With the estimate of \mathbf{U} , we can now form an estimate of \mathbf{N}

$$\begin{aligned} \hat{\mathbf{N}} &= \hat{\mathbf{U}} + \mathbf{N}^c \\ &= \mathbf{u}'\mathbf{M}^{-1}\mathbf{n}^c + \mathbf{1}'\mathbf{n}^c \\ &= (\mathbf{u}'\mathbf{M}^{-1} + \mathbf{1}'\mathbf{M}\mathbf{M}^{-1})\mathbf{n}^c \\ &= \mathbf{n}^r'\mathbf{M}^{-1}\mathbf{n}^c , \end{aligned}$$

where $n^r = [(n^r_j)]$. As noted by [Seber, 1973, page 433], this is the same result reported by [Chapman and Junge, 1956] as \hat{N}_3 .

Using the full rank model developed above, estimates are available for $N_{..}$, N_{ij} , $N_{.j}$, $N_{i.}$, and the p^c_i and p^r_j .

In addition to the full rank model, [Darroch, 1961, pages 246–248] also developed estimates when the number of strata were unequal. Since such estimates do not require an equal number of capture and recapture strata, they provide greater freedom when pooling data. Unfortunately, this freedom is not without its price. In the case of $s < t$, the parameters $\{\theta_{ij}\}$, and $\{p_j\}$ are no longer identifiable, making the U_j unestimatable. Fortunately, an estimate of the overall U , as well as the initial stratum sizes, are available if ψ_{ij} is the same for both marked and unmarked animals.

In the case of $s > t$, estimates of $\{\theta_{ij}\}$ and $\{p_j\}$ are not available, but the overall U , as well as final stratum sizes, may be estimated by imposing additional constraints on the estimate. In both cases of $s \neq t$, the required constraints effectively reduce the larger dimension (and hence the number of estimated parameters) by a set of linear combinations until the matrix is once again of full rank. Hence, in these cases, Darroch's solution is not the maximum likelihood (as it is when $s = t$), and therefore does not lead to a general solution.

2.3.4.2 Plante's Maximum Likelihood Estimator

[Plante, 1993] reformulated the likelihood and made it an explicit function of N . This was accomplished by partitioning the likelihood and making it conditional on all of the animals seen, rather than just the number of animals recaptured. Plante's likelihood formula is

$$L(N; \theta_{ij}, \beta_i, \gamma_i) = \frac{N!}{\prod_{ij} m_{ij}! \prod_i a_i! \prod_j u_j! (N-n)!} \times \prod_{ij} \left(\frac{\theta_{ij}}{N}\right)^{m_{ij}} \prod_i \left(\frac{\gamma_i}{N}\right)^{a_i} \prod_j \left(\frac{\sum_i \beta_i \theta_{ij}}{N}\right)^{u_j} \left(1 - \frac{\eta}{N}\right)^{N-n},$$

where

$$\begin{aligned} \theta_{ij} &= E(m_{ij}) \\ a_i &= \text{the number of animals marked in } i \text{ that are never recaptured} \\ \alpha_j &= \frac{1 - p_j^r}{p_j^r} \\ \beta_i &= \frac{1 - p_i^c}{p_i^c} \\ \gamma_i &= \sum_j \alpha_j \theta_{ij} = E(a_i) \\ n &= \sum_i \sum_j m_{ij} + \sum_i a_i + \sum_j u_j \\ \eta &= \sum_i \sum_j \theta_{ij} + \sum_i \gamma_i + \sum_i \sum_j \beta_i \theta_{ij} = E(n) \end{aligned}$$

Constraining $n = \eta$ to ensure parameter identifiability, [Plante, 1993] partitions this likelihood into its two component factors and then maximizes it using a constrained, iterative search, which is started using estimates obtained using a least squares estimate.

Plante's method has the advantage that it works for all of the three cases identified by [Darroch, 1961] ($s = t$, $s < t$, and $s > t$) without the need for arbitrary pooling or imposition of constraints. As well, the parameters that can be identified are similar to those produced using the Darroch method, namely estimates of N , and M_{ij} , $N_{i\cdot}$, U^r_j , p^c_i , and p^r_j when $s = t$, and estimates of N , and either $N_{i\cdot}$, or $N_{\cdot i}$

when $s < t$, or $s > t$ respectively, but without the unlikely assumptions that Darroch is forced to make to avoid the iterative search required for models of less than full rank.

As well, it is known from the principles of maximum likelihood [Burnham *et al.*, 1987], that the estimate is both consistent, and asymptotically unbiased.

Unfortunately Plante's estimator is not without a drawback in that the likelihood is parameterized on complex functions of the basic parameters (i.e. γ_i or ψ_j , where $\psi_j = \sum_i \beta_i \theta_{ij}$), which makes it difficult to constrain the likelihood or to re-parameterize the likelihood to obtain better search properties.

2.3.4.3 Consistency and Precision

Darroch demonstrates that his estimate is a consistent estimate of N , provided that θ is non-singular, and all other assumptions hold. Since Plante's estimate is similarly developed, it is also consistent under the same conditions as the Darroch.

It is upon examining the estimated variance of the two methods that differences begin to appear. Darroch provides a variance formula developed using the delta method, rather than the likelihood information, and could therefore only provide a general analytic formula for the case where $s = t$. Plante on the other hand, obtains a variance estimate from the information matrix created at the maximum likelihood estimates, requiring no specialization dependent on the shape of the data matrix.

As well, by the general properties of maximum likelihood [Burnham *et al.*, 1987], Plante's estimator is efficient, i.e. for sufficiently large samples, no other estimator is more precise. Also from the principles of maximum likelihood, we know that the standard error estimates, as with the estimate itself, are both consistent and asymptotically unbiased.

Chapter 3

Mean Value Analysis of the Pooled Petersen and Darroch Estimators

3.1 Introduction

Recently, [Warren and Dempson, 1995] of the Department of Fisheries and Oceans completed a series of simulation experiments meant to investigate the precision and bias of mark-recapture estimates under time-interval stratification.

Based upon the results of [Dempson and Stansbury, 1991], Warren models a mark-recapture experiment, stratified over time, conducted on a population of Atlantic salmon smolts migrating out of the Conne River. In this experiment, two partial counting fences were installed in the river, one approximately 11 km. upstream from the river mouth, and one approximately 1 km. upstream from the mouth. Smolts captured at the upper site were uniquely marked, had their date of capture recorded, and then released. The numbers of unmarked and marked smolts

captured at the lower fence were recorded daily for a period of time judged to cover the entire migration period.

Statistical testing rejected the hypothesis of uniform mixing of marked and unmarked animals, invalidating the pooled Petersen estimator and forcing the biologists to use a stratified estimator, namely the Darroch. After trying a number of different poolings of the collected data, Dempson and Stansbury arrived at four different estimates for the size of the migrating population. Although the largest was only 6% greater than the smallest, the precision estimates differed by as much as 25%. These results prompted Warren to design a series of experiments to attempt to determine the "best" stratum interval (i.e. row and column pooling), that would yield the most precise estimate with the lowest bias.

Warren simulated five different size populations of smolts migrating from the upper site to the lower site. To each of these five different population sizes, four different re-capture probability models were applied: constant, linearly increasing over time, linearly decreasing over time, and proportional to the number of smolts leaving the upper site on day i scaled so that an approximate average was obtained. For all of these experiments, the probability of capture, or marking, was held constant. After each realization of the model, the pooled Petersen estimate and the Schaefer estimate, derived by Warren as a "simple estimator of daily migration", were formed and their bias calculated.

Warren's results indicate that there is little to be gained, in terms of bias and precision, from using a stratified estimate. This is not surprising since, as noted earlier, all of Warren's experiments were conducted with constant capture probability, a situation where both the pooled Petersen and Schaefer estimators are known to be consistent. The more comprehensive investigation performed in this chapter will show that in situations where its consistency assumptions are violated, the pooled Petersen is subject to large biases, and that pooling of stratified estimates, namely

the Darroch, can result in substantial gains in both reduced bias over the pooled Petersen, and increased precision over the unpooled Darroch.

3.2 Methods

In order to more thoroughly investigate the amount of bias exhibited by the pooled Petersen, and the precision loss of the Darroch moment estimate, a complete factorial experiment was carried out on theoretical stratified populations, with size N and $s = t = 12$ involving all combinations of the following:

- two entry models which distribute the N over the initial strata
- three migration models (θ_{ij}) which distribute both the n_i^c and U_i^c animals from stratum i among the t recapture strata
- six capture/recapture vectors (p_c and p_r) that determine the probability that an animal is captured in each of the marking and recapture strata
- three mortality models (ϕ_{ij}) which remove animals from the migrating population

These experiments were carried out using mean value analysis, i.e. all random variables were replaced with their expected values, to provide measures of the expected estimate $\hat{N} = \hat{N}(E(s))$, and the expected precision, as measured by the mean value standard error ($\hat{S}(\hat{N}) = \sqrt{\text{var}(\hat{N}(E(s)))}$), of the two estimates. The performance measures included:

- *Asymptotic relative bias (ARB)*: the difference between the estimated population size and the true population size divided by the true population size, or $\frac{\hat{N} - N}{N}$. This is reported as the *percent ARB*, which is computed as $100 \cdot ARB$.

- The *coefficient of variation (CV)*: the ratio of the estimated standard deviation of the estimate over the estimate, or $\frac{\hat{S}}{\hat{\mu}}$. As with the ARB, this is reported as the *percent CV*, which is calculated as $100 \cdot CV$.
- *Effective bias (EB)*: the asymptotic relative bias over the CV, or $\frac{ARB}{CV}$. This measure reflects the reduction in confidence interval coverage due to bias in the estimate. It is known from [Cochran, 1977] that bias only begins to significantly reduce confidence interval coverage when the bias exceeds one half of the CV. When the effective bias is less than 0.5, coverage of the 95% CI will be 80% or greater, proportional to the size of the effective bias. Similarly, when the effective bias is greater than 0.5, the coverage of the 95% CI will be reduced proportional to the magnitude of the effective bias.

Given the definition above, the remainder of this paper will use the terms *effective*, and *effective bias* when describing asymptotic relative bias that exceeds one half of an estimate's CV, i.e. the effective bias of the estimate is greater than 0.5. Similarly, the terms *ineffective* and *ineffective bias* will be used when describing asymptotic relative bias that does not exceed one half of an estimate's CV, i.e. the effective bias of the estimate is less than or equal to 0.5.

- *Confidence loss* of the Darroch over the pooled Petersen, expressed as the CV of the Darroch estimate over the CV of the pooled Petersen, or $\frac{CV(Darroch)}{CV(PPE)}$. The term confidence loss was chosen since this measure reflects the inflation in relative confidence interval width that would be seen by a biologist when moving from the pooled Petersen to the Darroch. Confidence loss does not reflect change in the coverage of the nominal 95% CI due to bias in the estimate.
- *Error present in the pooled Petersen versus the Darroch*, expressed in terms of the ratio of the *root mean square error (RMSE)*, $\sqrt{bias^2 + \hat{S}^2}$ of the two estimates. This measure reflects total error due to the both bias and imprecision

in the estimate, and is therefore closely related to confidence interval coverage. Large values for the RMSE are likely to indicate larger reductions in confidence interval coverage.

Standard error estimates for the pooled Petersen were obtained using the formula cited in Section 2.3.2.1, while standard error estimates for the Darroch moment estimate were obtained using the formula provided in [Seber, 1973, pages 433, 434].

3.2.1 The Experimental Model

This section describes in greater detail the various factors used in the experiments.

3.2.1.1 Capture and Recapture Probabilities

As identified in [Seber, 1973], one condition under which the pooled Petersen estimator is unbiased is when all animals are equally catchable, i.e. the probability of capture is constant across the marking strata. The experiments were conducted using six different sets of capture/recapture probabilities with a fixed mean, but increasing variances. Variability in the probabilities across strata is used as a measure of the inequality of the probabilities, and hence increasing variability implies increasing inequality among the probabilities.

The probability sets were constructed by taking a discrete uniform distribution and then decreasing the middle values, while simultaneously increasing the end values to maintain a common mean. The result is a set of probability distributions that become increasingly parabolic as their variability increases. The sets used in the experiments were chosen such that their standard deviations followed a log linear trend. The six sets, along with their means and standard deviations, are presented in Table 3.1.

Table 3.1: The capture/recapture probability sets used in the experiments.

| <i>Stratum</i> | <i>Set 1</i> | <i>Set 2</i> | <i>Set 3</i> | <i>Set 4</i> | <i>Set 5</i> | <i>Set 6</i> |
|----------------|--------------|--------------|--------------|--------------|--------------|--------------|
| 1 | 0.075 | 0.075 | 0.0875 | 0.1 | 0.1 | 0.1125 |
| 2 | 0.06875 | 0.075 | 0.075 | 0.075 | 0.0875 | 0.1125 |
| 3 | 0.0625 | 0.0625 | 0.075 | 0.075 | 0.0875 | 0.0875 |
| 4 | 0.0625 | 0.0625 | 0.05 | 0.05 | 0.05 | 0.03125 |
| 5 | 0.0625 | 0.0625 | 0.05 | 0.0375 | 0.0375 | 0.01875 |
| 6 | 0.04375 | 0.0375 | 0.0375 | 0.0375 | 0.0125 | 0.0125 |
| 7 | 0.04375 | 0.0375 | 0.0375 | 0.0375 | 0.0125 | 0.0125 |
| 8 | 0.0625 | 0.0625 | 0.05 | 0.0375 | 0.0375 | 0.01875 |
| 9 | 0.0625 | 0.0625 | 0.05 | 0.05 | 0.05 | 0.03125 |
| 10 | 0.0625 | 0.0625 | 0.075 | 0.075 | 0.0875 | 0.0875 |
| 11 | 0.06875 | 0.075 | 0.075 | 0.075 | 0.0875 | 0.1125 |
| 12 | 0.075 | 0.075 | 0.0875 | 0.1 | 0.1 | 0.1125 |
| Summary | | | | | | |
| Mean | 0.0625 | 0.0625 | 0.0625 | 0.0625 | 0.0625 | 0.0625 |
| Variance | 9.94E-05 | 0.00017 | 0.000341 | 0.000568 | 0.00108 | 0.002003 |
| Std. Dev | 0.009972 | 0.013056 | 0.018464 | 0.023837 | 0.032856 | 0.044753 |
| ln(s) | -4.60802 | -4.33852 | -3.99195 | -3.73653 | -3.41561 | -3.10659 |

It should be noted that by constructing the capture/recapture sets in this way, we have assumed that the initial experimentation was conducted with sufficiently fine strata that the assumption of equal catchability within each stratum has been met. Also of note is that none of the probabilities in the table are extremely small, or extremely large, but instead cover a reasonable middle ground for migrating fish populations, as can be seen from case studies such as [Cass, 1995].

3.2.1.2 Migration Rates

The rate of migration from the initial, marking strata to the recapture strata can also have an effect on the bias of the pooled Petersen. Since temporally stratified, migrating fish populations are the primary focus of these experiments, the migration

matrices was chosen to closely parallel those observed in real experiments. As can be seen in the experiment conducted by [Dempson and Stansbury, 1991], and the numerous experiments documented by [Simpson, 1984], migrating fish populations exhibit almost no 'backward' movement, i.e. an animal marked in capture stratum i is unlikely to be recaptured in recapture stratum $i - 1$, which makes the migration matrices upper triangular with dominant diagonals. The following three migration matrices were used in the experiments:

- (A) A strongly diagonal migration matrix with little 'forward' movement. The only non-zero elements in this matrix were values of 0.75 on the diagonal (i.e. $\theta_{jj} = 0.75$, where $j = 1 \dots 12$), 0.25 on the super-diagonal (i.e. $\theta_{jj+1} = 0.25$), and a value of 1.0 on the diagonal of the final row.

This model strongly resembles the migration patterns observed by [Dempson and Stansbury, 1991] in their study of migrating Atlantic salmon smolts in the Conne River, Newfoundland.

- (B) A less strongly diagonal migration matrix with greater forward movement. In this migration model, animals migrated from stratum j through stratum $j + 3$ with probabilities 0.4, 0.3, 0.2, and 0.1, where $j = 1 \dots 12$. The last three rows of the matrix had values beginning from the diagonal of (0.4, 0.3, 0.3), (0.4, 0.6), and (1.0). All other matrix elements were zero.

The design of this migration model was drawn from the migration pattern seen in the sockeye salmon population studied by [Schaefer, 1951].

- (C) A completely upper triangular matrix with uniform forward movement. Within this migration model, animals migrated uniformly to all strata in front of their capture strata. For example, animals marked in stratum 5 would migrate uniformly across recapture strata 5 through 12.

As with the previous model, the design of this model was drawn in part from the migration pattern seen in the salmon population studied by [Schaefer, 1951], as well as the populations studied in [Pacific Salmon Commission, 1994].

3.2.1.3 Entry Models

Since migrating fish populations usually enter the marking strata in a roughly normal, or skewed, pattern, two entry models, a uniform, and normal, were used in the experiment.

Under the uniform model, animals entered the marking strata in groups of N/s . While possible, this type of entry is unlikely to occur in a migrating salmon population, but it was included as a point of comparison against the normal entry model.

Under the normal model, animals entered the marking strata in a roughly normal shape. With this model, the number of animals entering the marking strata increased with each successive initial stratum, up to a peak entry period in strata 6 and 7, and then tailed off towards the final marking strata. The exact entry proportions are presented in Table 3.2.

The normal model is a more realistic model for migrating salmon populations, such as those studied by [Dempson and Stansbury, 1991], [Schaefer, 1951], and [Pacific Salmon Commission, 1994].

3.2.1.4 Initial Population Size

Although it has no effect on the relative bias of the pooled Petersen estimate, it is clear from the standard error estimate for the pooled Petersen (presented in Section 2.3.2.1) that there is a relation between initial population size, the number of marked animals later recaptured, and the precision

Table 3.2: Distribution proportions of the normal entry model across the 12 capture strata

| <i>Stratum</i> | |
|----------------|----------|
| 1 | 0.041667 |
| 2 | 0.045833 |
| 3 | 0.060833 |
| 4 | 0.091667 |
| 5 | 0.118333 |
| 6 | 0.141667 |
| 7 | 0.141667 |
| 8 | 0.118333 |
| 9 | 0.091667 |
| 10 | 0.060833 |
| 11 | 0.045833 |
| 12 | 0.041667 |
| Summary | |
| Mean | 0.083333 |
| Variance | 0.001517 |

of the estimate. To determine the nature of this relation, two initial population sizes were used, a small population of 120,000 animals and a large population of 1,200,000 animals. These two population sizes were selected since they closely parallel the population sizes seen in [Dempson and Stansbury, 1991], and [Fraser River Sockeye Public Review Board, 1995].

3.2.1.5 Mortality Models

Another concern of biologists conducting stratified experiments is the presence of mortality within the population under study. Since one of the key assumptions of the pooled Petersen estimate is lack of mortality (as well as lack of immigration), a set of experiments was conducted to determine the effect of naturally occurring mor-

tality on the pooled Petersen estimator. It should be noted that for some stratified experiments, especially those conducted on migrating fish populations, mortality need not imply physical death of an animal, simply that the animal is not available to be recaptured in the second sample. This distinction is necessary since many experiments done on migrating fish populations, salmon in particular, use “dead pitching” as the second sample, i.e. the second sample consists of collecting dead animals from the shores of a river and checking them for tags.

There were three mortality models used in the experiments. These models were constructed in the same manner as the capture/recapture probability sets by starting with a discrete uniform distribution across recapture strata and creating subsequent survivorship models by simultaneously decreasing the middle values and increasing the values at the endpoints. This was accomplished by multiplying the row number (capture strata) by a constant fraction, adding it to the column number (recapture strata) multiplied by another constant fraction, and then subtracting the resulting value from 1 to obtain the mortality probability for the capture/recapture strata (ϕ_{ij}). Thus, the migration rate, θ_{ij} , was reduced by a survival rate, ϕ_{ij} , which was allowed to depend on both the initial and final capture strata, using:

$$\phi_{ij} = \mu_c i + \mu_r j$$

where μ_c and μ_r are the capture and recapture mortality constants, respectively.

This method was used for the first six recapture strata and the resulting vector, reversed, was used for the remaining six recapture strata. Using this method, the three models, referred to as the low, medium, and high mortality models, were created with:

- i) A low (zero) variability model with uniform mortality across recapture strata.

For this model the fractions μ_c and μ_r were not used, instead a constant survivorship probability of 0.5 was applied across all recapture strata.

- ii) A higher variability survivorship model with some variation across recapture strata. For this model, μ_c and μ_r were 0.35, and 0.05 respectively. The resulting survivorship values were then rounded to the nearest tenth.
- iii) A more extreme model with higher variation across recapture strata. μ_c and μ_r for this model were 0.1.

In all cases, mean survivorship across recapture strata was kept constant.

Although representative of the types of mortality patterns that would be seen in real data, the three mortality models are based on simplifying assumptions that may not be realistic for field experiments. Foremost among these assumptions is that the distribution of mortality across the recapture strata assumes a smooth, parabolic distribution. In reality, mortality is affected by a number of natural phenomena, such as water temperature, or flooding, that do not occur in such a smooth, predictable fashion.

When used in the experiments, these models were applied by multiplying the θ_{ij} by ϕ_{ij} , yielding row sums $\theta_i < 1$.

3.3 Results for the Closed Models

The initial set of experiments was conducted with a completely closed population, i.e. no births or deaths occurred between the marking and recapture times. This section presents the results of those experiments in two parts: a study of a single set of representative results that will demonstrate the statistical measures and their use, and a complete examination of all results that will explore the effects of the various factors on the estimates.

3.3.1 Representative Results for the Closed Models

This section presents a set of representative results for a fixed set of factor combinations. Using this set of results, we will be able to demonstrate the formation of the various measures, their meaning, their response to variability in p^c and p^r , and to establish other trends present in the measures.

For the set of results presented in this section the fixed factors are: migration model A, the small population model, and the normal entry model. The remaining factors, the capture/recapture probability sets, were allowed to vary. For each measure, the response surface for the measure over the 6×6 ($p^c \times p^r$) factor combinations was plotted and examined.

3.3.1.1 Bias of the pooled Petersen estimate

Figure 3.1 presents a graph of the bias exhibited by the pooled Petersen estimate for each combination of capture/recapture probability set and the three fixed factors. All values presented in the graph have been negated for easier presentation, i.e. the values should be negative, rather than positive.

Upon examining the graph, it is clear that as the violations of the Petersen assumptions increases, the pooled Petersen can exhibit large relative bias, with approximately a third of all factor combinations producing an asymptotic relative bias of greater than 10%, and a maximum of approximately 42%. Also, it is important to note the smooth, linear increase in the ARB as joint variability of the capture and recapture probability sets increases, i.e. the Petersen assumptions are more strongly violated.

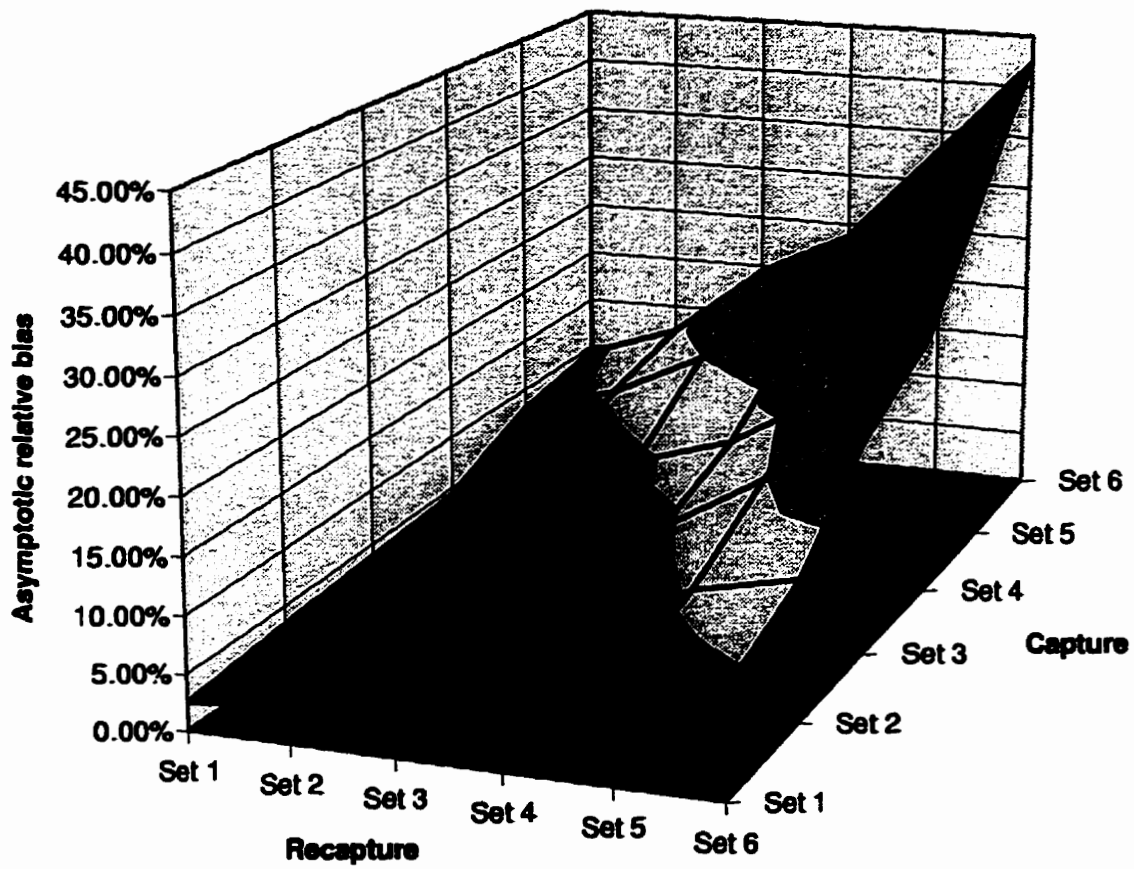


Figure 3.1: A graph of the bias present in the pooled Petersen estimate for the strongly diagonal migration model, the small population model, and the normal entry model. All values have been negated for easier presentation.

3.3.1.2 Effective bias of the pooled Petersen estimate

A graph of the effective bias for the pooled Petersen estimate is presented in Figure 3.2. As with Figure 3.1 (bias of the pooled Petersen), all of the presented results have been negated for easier presentation.

Recall that from [Cochran, 1977], it is known that bias only begins to seriously reduce confidence interval coverage when the ARB exceeds about half the CV in magnitude. Therefore, even though the pooled Petersen is subject to large relative bias, it may still be a suitable estimate if its effective bias is less than 0.5, since a confidence interval formed from the estimate and its standard error estimate would still be likely to cover the true population size. From Figure 3.2, we see that this is not the case for all of the factor combinations, although some of the less variable combinations, such as capture set 1 and recapture set 2, are close and would exhibit good confidence interval coverage.

3.3.1.3 Confidence Loss of the Darroch over the pooled Petersen

Having shown that the pooled Petersen estimate is subject to large, effective bias, the next step in the experiment was to compare the pooled Petersen against the Darroch estimate. Since the experiment was conducted in a situation where the Darroch is known to be unbiased, the only real basis of comparison for the two estimators is in their precision. Figure 3.3 presents a graph of the precision loss of the Darroch estimate over the pooled Petersen.

The values in the graph represent the increase in relative confidence interval width that would result in using the Darroch estimate over the pooled Petersen. As shown in Figure 3.3, the precision of the Darroch is less than 1.5 times worse than that of the pooled Petersen for the majority of the factor combinations, increasing slightly as the variability in the capture/recapture sets increases. It is only once we

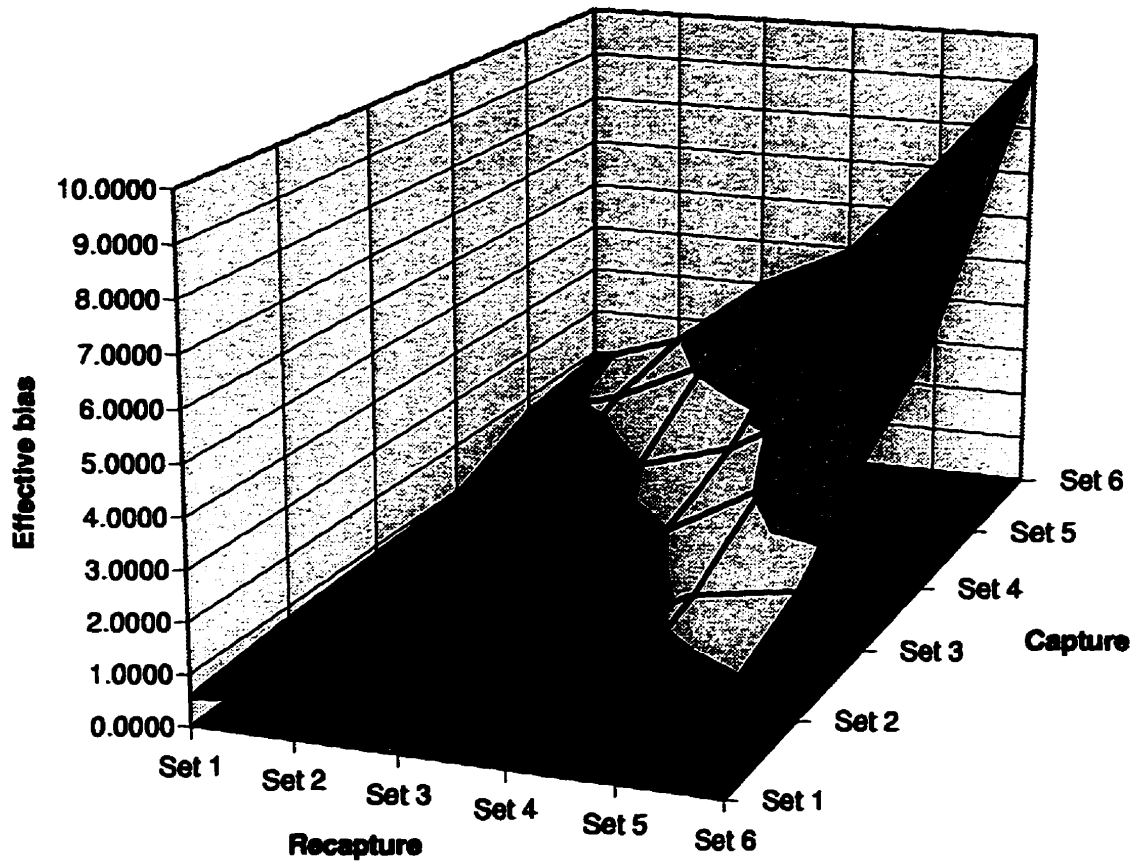


Figure 3.2: The effective bias of the pooled Petersen estimate for the strongly diagonal migration model, the small population, and the normal entry model. All values have been negated for easier presentation.

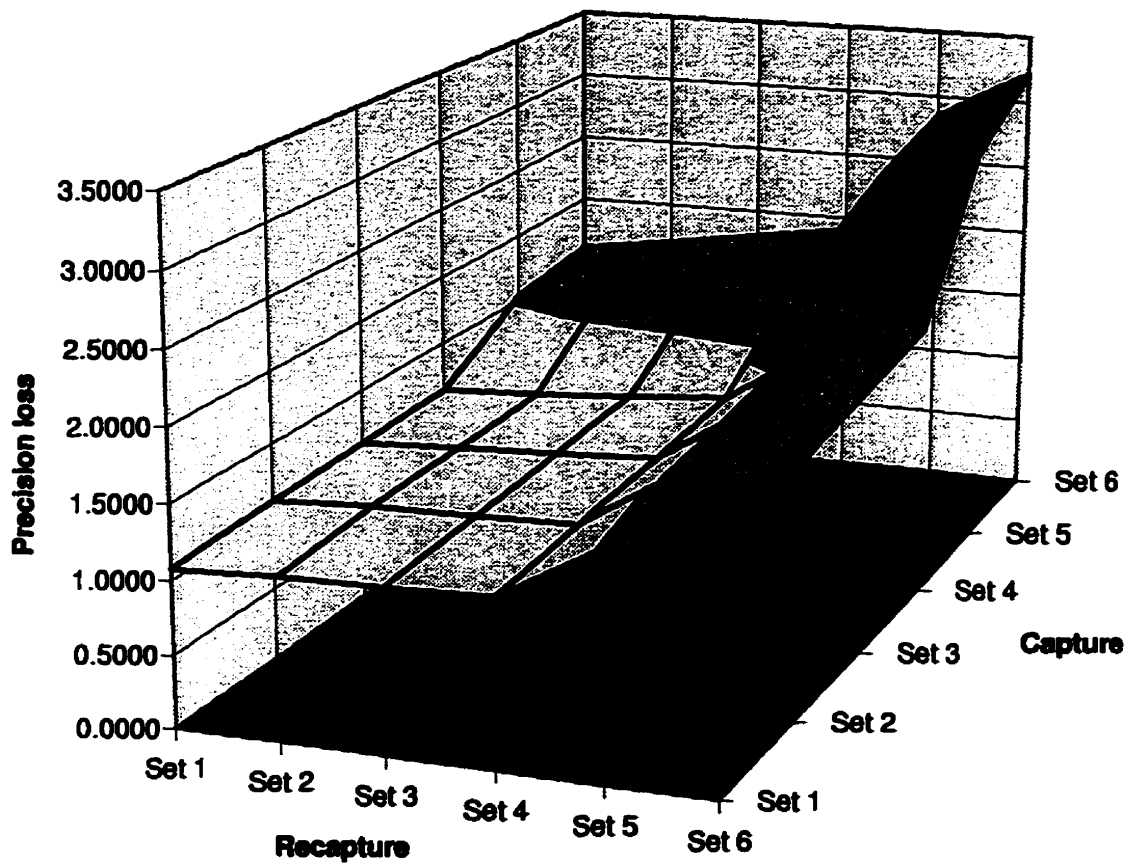


Figure 3.3: Confidence loss of the Darroch moment estimate over the pooled Petersen. Confidence loss is the increase in relative confidence interval width that would be seen in moving from the pooled Petersen to the Darroch.

move to the extreme ends of the probability sets, sets 5 and 6, that the precision of the Darroch shows a large loss, with CIs as much as 3 times wider than those of the pooled Petersen. Although, given the results presented in the previous section, a biologist would still want to use the Darroch estimate in these situations, since the effective bias of the pooled Petersen makes it highly unlikely that the estimate's confidence interval would cover the true size of the population.

3.3.1.4 RMSE Ratio of the Estimates

Combining the bias and (im)precision of the estimates, the root mean square error (RMSE) provides a measure of the suitability of an estimate in terms of overall error. The ratio of the RMSE of the Darroch and pooled Petersen estimates is graphed in Figure 3.4. When this ratio is less than 1, it indicates that the Darroch has the lowest overall error. Conversely, when the ratio is greater than 1, it indicates that the pooled Petersen has the lowest overall error, and would therefore be more suitable than the Darroch. From the graph, it is clear that this was never the case for these experiments, and the Darroch was the better estimator for the factor combinations shown. It is interesting to note for the combination of capture set 6, and recapture set 6, where the Darroch showed a precision loss of over 3 times that of the pooled Petersen, that the Darroch is still the preferable estimator by an approximate factor of 2.

3.3.2 Complete Results for the Closed Models

This section presents the complete results for each of the gathered measures. Building on the results presented in Section 3.3.1, this section will examine the effects that migration model, entry model, and initial population size have on the response surface of the estimators.

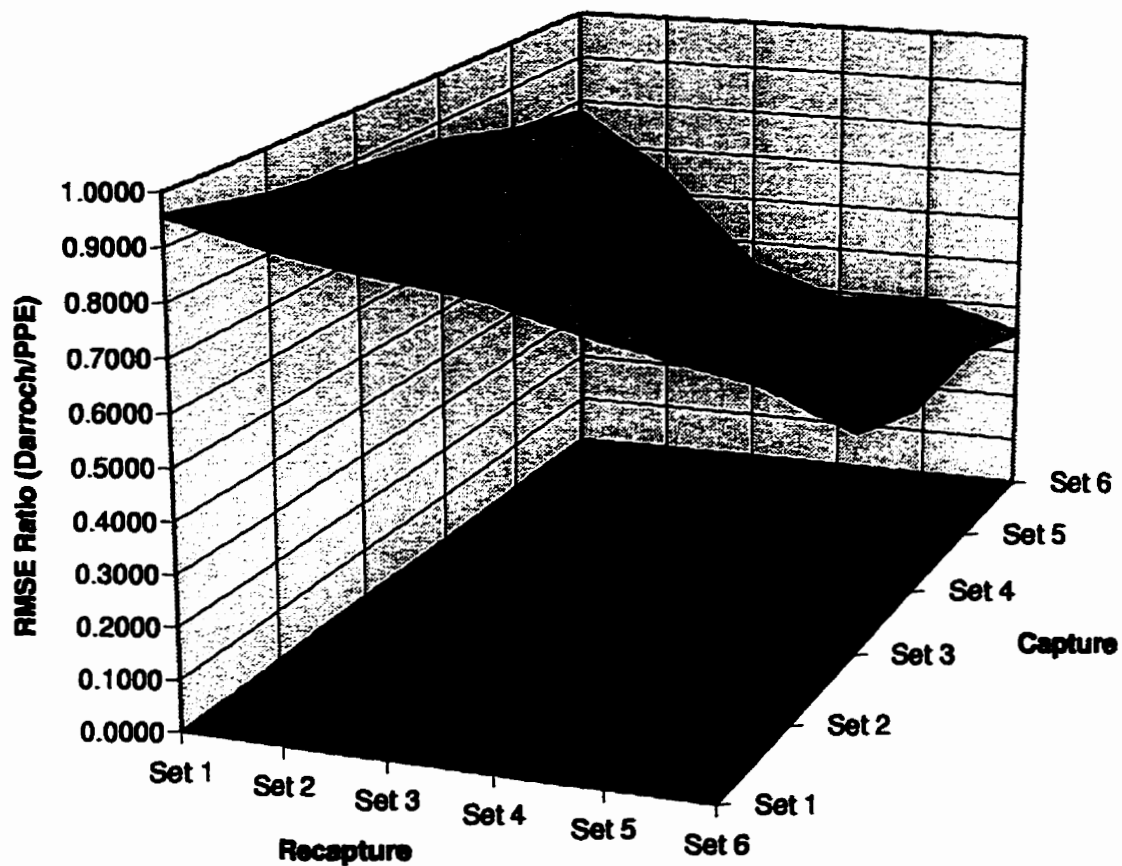


Figure 3.4: The RMSE ratio of the Darroch moment estimate versus the pooled Petersen.

The results in this section are presented in table form because it offers a more compact representation than the 48 graphs that would be required to present the complete results. As well, since Section 3.3.1 showed that the measures exhibit a smooth, monotonic increase with increasing violation of the Petersen assumptions, only the extreme and middle values for the capture/recapture sets have been reported. The other intermediate results may be interpolated from those presented.

The tables discussed in this section are presented in Appendix A.

3.3.2.1 Bias of the pooled Petersen

Table A.1 presents the percent ARB of the pooled Petersen estimate. Originally, the two population sizes were included in attempting to quantify the ARB, but it was found that population size had no effect on bias, and hence the results are general for all N .

From Table A.1, we see the relative bias of the estimate tends to increase with the joint variability of the capture and recapture probability sets. This trend can be seen in the first three rows of Table A.1, where relative bias is quite low, but trending upwards, for combinations of the capture probability set 1, and recapture probability sets 1, 3, and 6. The next three rows of the begin to give an indication of the large biases that can be produced by the pooled Petersen, with biases as large as 15% being produced by a combination of capture set 3, recapture set 6, and migration model A. Finally, the last three rows of the table demonstrate the large biases that can be produced when both the capture and recapture probability sets have high variability across strata, with a relative bias of 30.98% being produced for a combination of capture set 6, recapture set 6, and migration model A.

From the table, it is clear that three migration models have an effect on the relative bias of the estimate. Returning to table uniform entry model portion of the table, we see that for all combinations of the three capture probability sets and

recapture set 6 (the fifth column of the table), relative bias decreases with the amount of 'spread' present in the migration matrix. For example, moving from migration model A to migration model C results in nearly a 4-fold decrease in relative bias for capture set 1, recapture set 6, and just over a 3-fold decrease for capture set 6, recapture set 6. Although interesting, this result is not unexpected since the decreased spread in the migration matrix corresponds to decreased mixing of the population, or greater violation of Seber's condition 4 [Seber, 1973, page 437] for consistency of the pooled Petersen.

Finally, from a comparison of the uniform and normal entry models, we can see that the normal entry model resulted in higher relative biases than those of the uniform entry model. This result is not unexpected since the combination of the normal model's peak entry in strata 6 and 7, and the increasingly low capture/recapture rates in those strata should result in increased bias.

3.3.2.2 Precision of the pooled Petersen

Table A.2 presents the percent *coefficient of variation* (CV) of the pooled Petersen estimate for the identical sets of factors used in producing the results for the asymptotic relative bias.

Reviewing Table A.2 we see that percent CV displays remarkably different behavior from that of relative bias. While relative bias was monotonically increasing with violations of the consistency assumptions, the percent CV exhibits different behavior, in that it is relatively constant for all factor combinations. Examining the uniform entry factor combinations, we see that for the uniform entry model, percent CV exhibits marginal decreases as the joint variability of the capture and recapture probability sets increases.

Turning to normal entry factor combinations, we see that replacing the uniform entry model with the normal model results in slightly higher CVs across all factor

combinations. As with the uniform model, examination of the table columns reveals that the highest CV's for each capture/recapture combination occur with migration model A. The exception to this is those combinations involving capture set 6, where the highest CV is obtained with migration model B. Also, by examining the rows of the table, we see that the behavior of the percent CV more closely matches that of relative bias by increasing in tandem with increased joint variability of the capture and recapture probability sets.

For both the uniform and normal entry models, we see that an increased population size results in smaller CV's, due to the fact that the CV of the pooled Petersen estimate is proportional to $\frac{1}{\sqrt{m_{..}}}$ [Seber, 1973], but does not have any effect on the overall trends noted earlier. This indicates that the factors, such as the entry model, and migration model, have little effect on the precision of the estimate when compared to the effect of the sample size. This is likely the reason for the decrease in precision caused by the introduction of the normal entry model, since it concentrates animals in the middle recapture strata, which have the lowest probabilities of recapture, resulting in smaller samples.

Also of note is that for both tables, the CV's for the large population never exceed 2% and those for the small population rarely exceed 5%, indicating a very precise estimate for both population sizes.

3.3.2.3 Effective Bias of the pooled Petersen

Combining the information presented in Sections 3.3.2.1 and 3.3.2.2, Table A.3 presents the effective bias for the uniform and normal entry models.

Given the relatively constant precision of the pooled Petersen, we would expect that its effective bias would exhibit trends similar to that of its asymptotic relative bias, which is indeed the case. Combining this fact with the relatively small CV of the estimate, this implies that for the majority of situations, the bias exhibited by

the estimator will be effective. From the tables, we see that this is indeed the case and for most factor combinations, the bias of the pooled Petersen is effective (> 0.5), and in most cases effective by a large degree.

3.3.2.4 Precision of the Darroch Estimate

Table A.4 presents results for the percent CV of the Darroch moment estimate.

Reviewing the table we see that the CV of the Darroch estimate increases monotonically with increased joint variability of the capture and recapture probability sets. As well, we see that there is a decrease in percent CV with increased spread in the migration matrices.

As with the pooled Petersen estimate, we see that an increased population size results in smaller CV's, but does not alter the trends found in the smaller population model. Again, this demonstrates the effect that sample size has on the precision of the estimate, where a 10-fold increase in the number of marked animals leads to a roughly 3-fold ($3 \approx \sqrt{10}$) increase in precision (decrease in CV).

Again, as with the pooled Petersen, we see that the introduction of the normal entry model in place of the uniform model results in slightly higher CVs. As stated earlier, this is likely an artifact of the models' construction since the normal model concentrates the greatest number of animals in the middle recapture strata, which have the lowest recapture probabilities, resulting in smaller samples.

3.3.2.5 Confidence Loss of the Darroch over the pooled Petersen

Although the Darroch estimate is unbiased for all the factor combinations used in the experiments, we know from the previous section that the Darroch produces a much more imprecise estimate than the pooled Petersen. In order to quantify the amount of imprecision present in the Darroch, the pooled Petersen and Darroch precision

results were combined to determine the amount of confidence loss that results in using the Darroch estimate over the pooled Petersen. Recall from Section 3.2 that confidence loss represents the increased width in the relative confidence interval size that would be seen in moving from the pooled Petersen to the Darroch. Table A.5 presents these results. Entries in bold are the factor combinations that produced non-serious effective bias in the pooled Petersen estimate (Table A.3). Therefore, entries not in bold indicate factor combinations where a biologist would want to use the unbiased Darroch estimate, but at a cost of the indicated precision loss.

From the tables, we see that the confidence loss incurred by using the Darroch estimator follows much the same pattern as relative bias in the pooled Petersen estimate. The amount of confidence loss increases with joint variability of the capture and recapture probabilities, as well as decreasing spread in the migration matrix. Also, as with relative bias in the Petersen, the size of the initial population has negligible effect on the amount of confidence loss.

Comparing the uniform entry portion of the table with the normal entry portion, we see that the normal entry model produces slightly lower losses of confidence than the uniform entry model. Also comparing the two tables, we find that the amount of confidence loss rarely exceeds 2, but can reach losses as much as 3 times the confidence interval width.

3.3.3 RMSE Ratio of the Estimates

By combining the results of the previous sections, namely those on the bias and precision of the estimates, one can calculate the RMSE of the estimates. The RMSE can then be used as an objective measure as to which of the two estimates, when applied to the same population, yields the least overall error. The results of RMSE calculations are presented in Table A.6. When this ratio is less than 1, it indicates that the Darroch is preferable for the factor combination in question. Conversely,

when the ratio is greater than 1, the pooled Petersen is favored.

Reviewing the table we see that the RMSE measurements are as should be expected, heavily favoring the Darroch estimate as the violations of the Petersen assumptions increases, and only slightly favoring the Darroch when the Petersen assumptions are less strongly violated.

While the majority of factor combinations favor the Darroch to varying degrees, it is interesting to note that there are some factors which favor the pooled Petersen, namely those combinations involving migration model C, and the small population model. These occur because the small bias and high precision of the pooled Petersen in these situations is enough to tip the balance against the Darroch's unbiasedness but lower precision. Although, as a caution against relying solely on the RMSE for determining estimator suitability, it should be noted that the bias present in the pooled Petersen is effective for the factor combinations in question (see Table A.3).

3.4 Results for the Open Models

As well as the closed model experiments discussed in Section 3.3.2, a similar set of experiments was carried out using the three mortality models discussed in Section 3.2. At the conclusion of these experiments, it was found that the introduction of mortality did little to alter the trends noted in Sections 3.3.1 and 3.3.2, but instead only exaggerated the effects of the underlying models. As well, the amount of exaggeration introduced by mortality increased proportionately with the amount of variability in the mortality model. Therefore, rather than present the complete results of the three open model studies, this section will focus on those of the high mortality model, and will provide enough information so that the results from the other two models (uniform, and low) may be inferred from the closed model and high variance mortality model results.

The tables discussed in this section are presented in Appendix B.

3.4.1 Bias present in the pooled Petersen estimate

Table B.1 presents the percent asymptotic relative bias of the pooled Petersen estimate when it is applied to factor combinations including the high variance mortality model. Comparing the result in this table with Table A.1, the equivalent closed model table, we see that the introduction of the high variance mortality model can produce large increases in the ARB of the pooled Petersen estimate, with the largest increases occurring in those factor combinations that included migration model A, and the low variability capture/recapture sets. This is due to the interaction of the mortality model, the strongly diagonal migration matrix, and the low variability capture/recapture sets, which produced much lower estimates than the equivalent closed model factors. Similarly, the marginally increased results for the higher variability capture/recapture sets is due to the failure of the mortality model to significantly alter the violations introduced by the highly unequal capture/recapture probabilities, i.e. the introduction of mortality didn't make a bad situation much worse.

Besides the increases in percent ARB, and some reduction of the difference in percent ARB between different migration models, the introduction of mortality does not alter the trends seen in Sections 3.3.1, and 3.3.2; namely increasing percent ARB as the degree of the Petersen assumption violations increases.

For the equivalent factor combinations, the uniform and low variance mortality models yielded results that were approximately one third, and two thirds, respectively, those of the high variance mortality model.

3.4.2 Precision of the pooled Petersen estimate

The results for the percent CV of the pooled Petersen estimate when the high variance mortality model is applied are presented in Table B.2. Comparing this table with the equivalent closed model table (Table A.2), we see that the introduction of mortality can cause large decreases in the precision of the estimate (as evidenced by the large increases in percentage CV), with the largest increases occurring in those factor combinations that include migration model A, and capture/recapture set 6, i.e. increased violation of the Petersen assumptions. Besides the large decreases in precision (which are anywhere from 1.5 to nearly 16 times the equivalent closed model experiment), the introduction of the high variance mortality model does not modify the trends noted in the closed model experiments.

The uniform and low variance mortality models yielded nearly equivalent results for the pooled Petersen's percent CV, with the low variance model providing slightly less precision than the uniform model. In general, the application of the uniform, and low variance mortality models yielded percent CVs approximately two thirds less than those of the high variance model.

3.4.3 Effective Bias of the pooled Petersen estimate

Combining the results of Tables B.1, and B.2, Table B.3 presents the effective bias for the pooled Petersen estimate when it is applied to factor combinations that include the high variance mortality model. Comparing Table A.3 to Table B.3, we see that the introduction of the high variance mortality model has caused an increase in the effective bias of the estimate. As would be expected, due to the increase seen in the asymptotic relative bias, the largest increases occur in those factor combinations using migration model A, and the lower variability capture/recapture sets. This indicates that the introduction of the mortality model has, for most factor combinations, increased the bias present in the estimate without an equal,

corresponding increase in the percent CV. As a result, the estimate should exhibit effective bias for more factor combinations than the equivalent closed model, and this is indeed the case. Although, given the large number of combinations for which the pooled Petersen exhibited effective bias in the closed models, the reduction in factors that produce ineffective bias is quite small.

Experiments were also carried out using the uniform and low variance mortality models. While exhibiting the same behavior as the high variance mortality model, the results for the approximately one quarter those of the high model for the uniform model, and approximately one half those of the high model for the low variance model.

3.4.4 Precision of the Darroch estimate

As with the pooled Petersen, the percent CV of the Darroch estimate increased with the introduction of the high variance mortality model, the results of which are presented in Table B.4. Making comparisons with the equivalent closed model table (Table A.4), we see that the introduction of the high variance mortality model increases the percent CV, and subsequently decreases the precision of the estimate, by approximately 1.65 to 2 times the results for the equivalent closed model experiment, with the size of the increase growing with increasing joint variability in the capture/recapture sets, and strongly diagonal migration model. As well, it should be noted that the increase in the Darroch CV is uniform, as opposed to the large, decreasing increases seen in the percent CV of the pooled Petersen estimate (see Table B.2).

As with the pooled Petersen, the application of the uniform and low variance mortality models yielded nearly equivalent results for the Darroch's percent CV, with the results for the low model being slightly higher than those for the uniform model. In general, those results were approximately 1.5 times those for the equivalent

closed model.

3.4.5 Confidence loss of the Darroch estimate over the pooled Petersen

As in the closed model experiments, Table B.5 combines the percent CV of the Darroch estimate (Table B.4) and the percent CV of the pooled Petersen estimate (Table B.2) to determine the amount of confidence loss (i.e. increased confidence interval size) that would result from using the Darroch over the pooled Petersen. Reviewing the table and comparing it with Table A.5, we see that the introduction of the high variance mortality model results in increases in confidence loss that correspond to increases in the joint variability of the capture and recapture probability sets. More precisely, the inclusion of the high variance mortality model increases the confidence loss for factors including recapture set 1 by $\approx 30\%$, those including recapture 3 by $\approx 35\%$, and those including recapture set 6 by $\approx 50\%$.

When the uniform and low variance mortality models were applied to equivalent factor combinatorics, the uniform model yielded confidence losses equivalent to those for the closed model, and the low variance model yielded confidence losses in a pattern similar to that of the high variance model, but with increases of only 6%, 8%, and 15% for each of the respective recapture sets.

3.4.6 RMSE Ratio of the Estimates

Table B.6 presents that ratio of the root mean square error for the Darroch estimate versus that of the pooled Petersen. Unlike the closed model (Table A.6), the introduction of mortality has tilted the RMSE ratio for a number of factor combinations in favor of the pooled Petersen. This result is not surprising given the high precision relative to a large negative bias seen in the Petersen. Although interesting, this

result also serves as a further caution against relying solely on RMSE in selecting an estimator, since for the majority of factors where the RMSE ratio favors the Petersen, the estimate is also effectively biased.

When the uniform and low variance mortality models were applied to the same factor combinations, results similar to those for the high variance mortality mode were obtained.

3.5 Discussion

The results presented in Section 3.3 make it clear that the Darroch estimator is a much more robust estimator than the pooled Petersen estimate under a series of controlled conditions. Although these conditions were constructed and controlled by the experimenter, an effort was made to cover a full range of likely values for the parameter sets and to maintain the parameters within reasonable limits. For example, the extreme values of the capture and recapture probability sets was never lower than 0.0125, and no higher than 0.1125, a likely range for these parameters in real-world experiments. Also, the migration matrices were designed to reflect a full range of likely migration patterns for migrating fish populations, the primary focus of these experiments.

Based on these results, we conclude that the pooled Petersen is capable of very high, effective bias under most conditions that violate the assumptions of the estimate. Fortunately, the Darroch estimate is much more robust under these same conditions and can provide additional information, such as initial and final stratum sizes, albeit at a cost of greater imprecision than the pooled Petersen, and the requirement of a more complex sampling protocol.

As well, we have seen that the introduction of mortality, when combined with the other the other factors, both severely biases the Petersen and decreases the precision

of the Darroch so much that neither estimator is a good choice. It should be noted that it is not the introduction of mortality itself that caused the bias in the pooled Petersen, since, recalling Section 2.2, when only mortality is occurring, the Petersen is still a valid estimate of the initial population size. In addition, it should be noted that mortality does not need to be present for the estimators to produce these types of results. Similar results could be produced by poor experiment planning (ending an experiment too early, or beginning recapture too late), or tag loss.

Although these results clearly show the robustness of the Darroch estimator over the pooled Petersen in closed models, these two estimators are really two ends of a spectrum, completely unpooled data versus completely pooled. By performing less extreme pooling, it is possible that the precision of the Darroch estimate could be increased without introducing significant bias. As well, this chapter has only dealt with the bias and precision of the estimators themselves, while completely ignoring any bias, or imprecision that may be present in the standard error estimates. These topics, the standard error estimates, and pooling, respectively, will be investigated in the following chapters.

Chapter 4

Bias and Precision of the Standard Error Estimates

In Chapter 3, a number of issues were raised regarding the pooled Petersen and Darroch estimators. Specifically, the validity of applying the standard error estimates to mean-value data, and the amount of bias and imprecision in the estimates' variance estimates was questioned.

As well, the validity of using the closed population Darroch variance estimate when mortality was present was questioned. Although it is possible to derive an estimate of the Darroch's variance when mortality is present [Seber, 1973, pages 439–432], it involves non-estimable parameters and the unlikely assumption that survivorship is constant across recapture strata. In addition to the complexity of the open population variance estimate, a biologist is unlikely to know whether mortality is occurring or not, and is therefore left with little choice but to use the closed population variance estimate.

This chapter will serve four purposes: to verify the mean-value analysis performed in the preceding chapter, to investigate the amount of bias and imprecision

present in the pooled Petersen and Darroch variance estimates, to provide a comparison of the variance estimates for the iterative and moment Darroch estimates, and to attempt to prove, or disprove the validity of using the closed population variance estimate when mortality is present.

4.1 Methodology

This investigation was carried out using a subset of the factor combinations used in in Chapter 3. Since most of the 'interesting' results presented in 3 occurred at the extremes of the factor combinations, it is possible to reduce the number of factors and still maintain both the interesting extreme values, as well as some of the middle combinations that allow us to spot trends in the transitions from one extreme combination to another. To this end, capture/recapture probability sets 2, 4, and 5 were eliminated from these experiments.

For each of the remaining factor combinations, a stochastic analysis was carried out using an application program designed for the purpose (Chapter 6). Each analysis was carried out for 1000 good replications, i.e. a replication where each of the estimates produced an estimate, with a limit of 5000 attempts.

For this study, a good replication was defined as a replication where all three estimators were able to form an admissible estimate. This was done to ensure that the results for the estimators were comparable, since they were formed using the exact same simulated populations. In general, bad replications were due to failure of the iterative Darroch to converge, followed closely by the generation of singular migration matrices.

For each set of good replications, the following statistics were gathered:

1. the average percent CV, i.e. $100 \cdot \frac{\bar{S}(\hat{N})}{\bar{X}(\hat{N})}$, of the maximum likelihood Darroch, the Darroch moment estimate, and the pooled Petersen estimate

2. the percent asymptotic relative bias of the standard error estimate, i.e. $100 \cdot \frac{(\bar{X}(\hat{S}) - \bar{S}(\hat{N}))}{\bar{S}(\hat{N})}$, of the three estimates
3. the percent CV of the standard error estimate, i.e. $100 \cdot \frac{\bar{S}(\hat{S})}{\bar{X}(\hat{S})}$, for the three estimates
4. the effective bias of the standard error estimate, i.e. statistic 2 over statistic 3

where the notation $\bar{X}(s)$ and $\bar{S}(s)$ is used to denote, respectively, the mean and standard deviation of the statistic s over the good replications. In particular, $\bar{X}(\hat{N})$ and $\bar{S}(\hat{N})$ are simulation estimates of the true mean and standard deviation of \hat{N} and, similarly, $\bar{X}(\hat{S})$ and $\bar{S}(\hat{S})$ are the simulation estimates of the true mean and standard deviation of the estimated standard error for \hat{N} . If the standard error formula is unbiased, it is expected that $\bar{X}(\hat{S})$ should approximate $\bar{S}(\hat{N})$.

In this study the formulae used for the pooled Petersen and Darroch moment estimates were the same as those used in Chapter 3, while the iterative Darroch estimate was formed using the formulae presented in [Plante, 1993].

Due to the cap of 5000 attempts, it was not possible to obtain 1000 good replications for some parameter sets. Results obtained from an incomplete simulation (i.e. a simulation where less than 1000 valid estimates could be obtained) are indicated in one of two ways:

- Results in *italicized* text were obtained from simulations that completed 500 or more replications. Although these results are not directly comparable to those from simulations that ran to completion, they are formed from a sufficient number of estimates to provide for reasonable comparison with other results.
- Results that have been replaced by a – are from simulations that failed to complete 500 or more replications. Although these results may be as valid as those from simulations that completed more than 500 replications, they were,

in general, clearly problematic (e.g. estimates of 1 trillion) and were therefore excluded.

Perusing the results for this study (Appendices C, D, and E), it is clear that the majority of incomplete simulations occurred for parameter sets that included the small population model. For this reason, the discussion that follows will focus solely on those results obtain using the large population model.

4.2 Verification of the Mean-Value Analysis

To sufficiently validate the mean-value analysis performed in Chapter 3, it must be shown that the bias of the mean-value analysis matches those of the replicated results, and, similarly, the CV results for the estimators must also match. If these two conditions are met, it can then be stated that the mean-value analysis was based on valid values for the estimators and their standard error estimates, and hence the analysis is valid.

The tables containing the mean-value analysis verification results are presented in Appendix C.

Table C.1 presents the average percent ARB of the pooled Petersen estimate over replications. Comparing this table with Table A.1 from Chapter 3, we can see that there is a close correspondence between the mean-value and replicated results for all factor combinations. Although the results are not entirely equal, the inequality is likely due to a combination of two reasons: an insufficient number of replications were performed for the simulation estimate to approximate the expected estimate to the precision of the tables, and the manner in which the simulations were conducted.

Although the replicated results are formed from a large number of replications (1000), this may not be a sufficiently large number of replicates for the results to

approximate the true values to the precision of the tables. This is borne out by the fact that the replicated results differ from the mean-value results by, on average, less than 0.1, and in most cases less than 0.05.

The other possible source of inequality between the mean-value and replicated results is the manner in which the replicated experiments were conducted. Since a replication was not considered complete, and therefore not included in the statistics, until all three estimators formed valid estimates, a bias was likely introduced into the estimates since they were only formed on those data sets that yielded non-singular migration matrices (a condition required for the Darroch moment estimate to form a valid estimate).

As with the mean-value analysis experiments, the Darroch moment estimator was unbiased for all factor combinations.

Table C.2 presents the average percent CV of the pooled Petersen estimate. Comparing Table C.2 with Table A.2 from Chapter 3, we see a close match between the results for all factor combinations, although the results obtained via averaging over replications differ slightly from those obtained by mean-value analysis. This discrepancy is likely due to the approximation and selection problems discussed in the preceding paragraphs. Although somewhat worrisome, the difference between the mean-value and replicated results is less than 3% in all cases, making the results, for all intents and purposes, equal.

As with the pooled Petersen estimate, comparing the replicated results for the Darroch moment estimate, presented in Table C.3, with the results obtained in Chapter 3 via mean-value analysis, presented in Table A.4, also shows little appreciable difference between the two analysis methods. Although there are some differences, the discrepancies are likely due to the approximation and bad replicates problems described in the preceding paragraphs. As well, the differences never exceed 0.41 at the extremes of the factor combinations, and with the majority of the

results differing by less than 0.1, making the results essentially equal.

From the above results and accompanying discussion, it is clearly valid to apply mean-value analysis (and is in fact preferable, due to the lack of bad replicates) to obtain the expected variance of the pooled Petersen and Darroch moment estimates, validating the results, and observations made in Chapter 3, as well as the conclusions drawn from those observations.

4.3 An Investigation of the Standard Error Estimates

Chapter 3 presented the results of a study that examined the properties of the pooled Petersen and Darroch moment estimators with regards to the bias and precision of the estimates produced. Although the properties of the estimates themselves are important, the standard error estimates of the population estimates, and their properties are equally important. For example, in Chapter 3, it was shown that the pooled Petersen estimate exhibited high precision in almost all situations, but as a result almost any bias present in the estimate would be effective (see Table A.3). But, given that the estimate is subject to high, negative bias, is it not possible that the standard error estimate is also subject to such bias? If this were so, it would be important to know, as it could seriously affect the coverage of the estimate's confidence interval. The aim of this section is to answer this question.

Similar to the study conducted in Chapter 3, this section presents the results of a study into the properties of the standard error estimates for each of the pooled Petersen, Darroch moment, and iterative Darroch estimates. For each estimate, the standard deviation of the estimate over replications, the average standard error estimate over replications, and the standard deviation of the standard error estimate over replications were gathered and the asymptotic relative bias, the percent CV, and the effective bias of the standard error estimate were calculated using the formulae

defined in Section 4.1.

As with the complete results of the study presented in Chapter 3, the results in this section are presented in table form to allow for a more compact presentation than that provided by graphs.

4.3.1 Complete Results for the Closed Model

This section presents the results of a study conducted using the closed population model, i.e. no mortality. The tables containing the results discussed in this section are presented in Appendix D.

4.3.1.1 Bias of the Standard Error Estimates

Table D.1 shows the amount of bias present in the standard error estimate for the pooled Petersen applied to a series of populations generated using the indicated factor combinations and no mortality, i.e. a closed population. Unlike the estimate itself, the standard error estimate does not show monotonically increasing bias with increased violation of the Petersen assumptions, but instead exhibits varying trends depending on the parameter sets used. For those parameter sets constructed using capture set 1, the bias is generally decreasing, with the exception of those factor combinations using migration model C, where the bias is increasing in skewed pattern with the peak bias occurring with recapture set 3. For most other factor combinations, bias tends to decrease with increasing violation of the estimate's assumptions, but there are a number of instances where this trend is less pronounced, or simply not present.

One possible explanation for the seeming randomness of the distribution of bias in the pooled Petersen's standard error estimate lies in the manner in which the simulations were conducted. Since a replication was not considered complete, and

therefore not added to the statistics, until all three estimates were valid, a bias could have been introduced into the Petersen since it was only formed for populations for which the two Darroch estimates converged, and the resulting migration matrix was non-singular, causing significant bias in the pooled Petersen estimate. But, reviewing Table D.3 we see that this is not the case since, for at least the large population model, there were very few bad replications (as evidenced by the number of simulations that ran for 1000, or slightly more, replications) and therefore if any selection effect were present, it would be very slight.

Therefore, the results would seem to indicate that the standard error estimate for the pooled Petersen is sensitive to changes in joint variability of the capture/recapture probabilities, and the population migration model, with the capture/recapture probabilities predominating.

Unlike the pooled Petersen, the percent asymptotic relative bias of the Darroch moment estimate's standard error estimate, the results of which are presented in Table D.2, follow a more regular trend. Reviewing the rows of the table, we initially see a trend of monotonically decreasing bias, but this turns into a monotonic increase as the extent of the assumption violations increases. For factor combinations using the uniform entry model, this trend is clearly visible in the results obtained using capture sets 1, and 6. Of the remaining rows, most either exhibit increasing bias with increased violation of the Petersen assumptions, or a skewed progression where the most extreme bias occurs in those factor combinations using recapture set 3, rather than set 6. This trend is also predominant when comparisons are made between values along columns for a given migration model and recapture set. For most combinations including recapture set 3, its inclusion produces more negative bias in the standard error estimate, although there are some instances (e.g. normal entry, capture set 3, migration model A) where recapture set 3 produces a more positive bias than the other recapture sets.

Comparing the results for the moment estimate (Table D.2) with those of the pooled Petersen (Table D.1), we see that, in general, the standard error of the moment estimate is greater than that of the pooled Petersen. Although, it is worthwhile to note that while the bias is often non-negligible, they are mostly positive and will therefore cause larger confidence intervals, and correspondingly increase the coverage of the CI.

The percent asymptotic relative bias of the iterative Darroch estimate's standard error estimate is presented in Table D.4. From this table we note trends similar to those exhibited by the moment standard error estimate. Comparing the results presented in this table with those of the pooled Petersen (Table D.1) and the Darroch moment estimate (Table D.2), we see, as with the moment estimate, the iterative Darroch's standard error estimate exhibits generally greater bias than that of the pooled Petersen, but less than that of the moment estimate's standard error. This latter observation is not surprising since, as was noted earlier, the moment estimate derives its standard error estimate using the delta method, as opposed to deriving it from the information matrix produced as part of the estimate, resulting in a slightly more biased estimate. As well, as with the moment estimate, the bias in the standard error estimate of the iterative Darroch tends to be on the positive side, which does not adversely affect the confidence interval coverage of the estimate.

4.3.1.2 Precision of the Standard Error Estimates

The percent coefficient of variation of the pooled Petersen standard error estimate for the selected factor combinations is presented in Table D.5. Reviewing the results of the large population using both the uniform and normal entry models, we see that the percent CV of the standard error estimate remains relatively constant for all factor combinations. Using the uniform entry model as an example, the extreme values are 2.10 for factor combination 6/6/A (capture set 6, recapture set 6, migration

model A), and 2.18 for combination 1/6/A, and an average value of approximately 2.0.

Turning to Table D.6, the percent CV of the moment estimate's standard error estimate, we see a different trend than that of Table D.5. Instead of the relative flatness of the pooled Petersen, the percent CV of the moment estimate's standard error estimate exhibits a somewhat exponential growth. Examining the results for a given capture set and migration model, we see a nominal difference between the percent CVs for recapture sets 1 and 3, followed by a large increase in the percent CV for recapture set 6. As with the estimate itself, the percent CV of the standard error estimate tends to increase with increasing violation of the Petersen assumptions.

Comparing the results of the uniform entry model with those of the normal entry model shows that the normal model tends to produce smaller CVs than the uniform model. For example, comparing the results for the two entry models for the 1/6/A factor combination, the uniform model yielded a percent CV of 9.54, while the normal model yielded a percent CV of only 7.79. Although interesting, this result is more than likely an artifact of the construction of the parameter sets, since the normal model concentrates animals in the middle of the capture strata. This concentration of animals coincides with the lowest capture probabilities, resulting in a comparatively greater numbers of animals appearing in these strata, and therefore more precise estimates.

Finally, reviewing the percent CV of the iterative Darroch estimate's standard error estimate in Table D.7, we again note that it exhibits the same trend as the moment estimate. Surprisingly, the standard error estimate for the iterative Darroch appears to produce slightly larger CVs than those of the moment estimate's standard error estimate (Table D.6), although the differences are so small as to make the results for the two estimates equivalent. As with the moment estimate, we see that the iterative Darroch's standard error estimate produces larger CVs than those of

the pooled Petersen estimate, and that the substitution of the uniform entry model with the normal entry model produces smaller CVs which, again, is likely an artifact of the parameter sets' construction.

4.3.1.3 Effective Bias of the Standard Error Estimates

Combining the results of Tables D.1 and D.5, Table D.8 presents the effective bias of the pooled Petersen's standard error estimate. Due to the seeming randomness of the bias of the estimate, the effective bias exhibits no strong trend but shows that, generally the bias of the pooled Petersen standard error estimate is effective. This is due to the high precision of \hat{S} , which makes even very small biases effective.

The effective bias for the Darroch moment estimates' standard error estimate is presented in Table D.9. It is interesting to note, as we review the rows of the table, that the effectiveness of the bias in the standard error estimate tends to decrease with increased violation of the Petersen assumptions. As with the percent asymptotic relative bias of the estimate, the effective bias exhibits a skewed trend where the most extreme values, both across capture strata, and recapture strata occurs in factor combinations using capture/recapture set 3, as opposed to set 6.

As with the percent asymptotic relative bias, the effective bias of the iterative Darroch's standard error estimate exhibits the same trend as the moment estimate. Due to the reduced bias found in the iterative estimate, the effective bias of the standard error estimate is less than that of the moment estimate.

4.3.2 Open Population

In addition to the closed model validation, simulations were carried out using the three mortality models described in Chapter 3.

As with the experiments performed in 3.4, it was found that the addition of mortality does little to alter the trends noted in the closed population experiments, but simply exaggerates any bias present in the estimates, or their standard error estimates. Since this is true, the tables presented include only the high variance mortality model, and the large population with normal entry, since it was the combination of population size and entry model that demonstrated the least number of bad replicates. The remaining results for the uniform entry model, and the uniform and low variance mortality models may be inferred from those presented and the closed model results presented in Section 4.3.1.

The tables containing the results discussed in this section are presented in Appendix E.

4.3.2.1 Asymptotic Relative Bias of the Standard Error Estimates

As with the closed population, the bias of the pooled Petersen standard error estimate exhibits no strong trend towards either monotonically increasing or decreasing bias as the extent of the Petersen assumption violations increases. When compared to the closed population results, the addition of mortality, presented in Table E.1, tends to shift the direction of the bias (i.e. a positive bias with the closed population becomes negative with the addition of unequally occurring mortality) rather than add a constant increase or decrease. This is likely due to the bias introduced by the approximation and replicate selection problems described earlier, and an inherent sensitivity in the estimate itself.

In sharp contrast to pooled Petersen estimate, the introduction of unequal mortality generally increased the bias of the iterative Darroch and Darroch moment standard error estimates. This is likely not a property of the estimator itself, but is more likely due to replicate selection (i.e. only replicates that formed valid estimates were included in the statistics), as is borne out by comparing the estimates for

a given factor combination (Table E.1) and the number of rejected replicates for the same combination (Table E.2). Performing this comparison, we see that the Darroch estimate only exhibits high ARB when the number of rejected replicates is high.

4.3.2.2 Percent CV of the Standard Error Estimates

The percent CV of the three estimate's standard error estimates are presented in Table E.3. From the tables presented in the closed population discussion, we have seen that the introduction of mortality has little effect on the precision of the standard error estimates. Comparison of results for both the iterative and Darroch moment estimate shows decreases in the precision of the standard error estimates ranging from as low as 0.2 (uniform entry, factor 3/3/A) to an extreme of 6.23 for the uniform entry model, factor 6/6/B. The same is also true for the pooled Petersen, where the precision of the standard error estimate decreases by a relatively constant 1.5 times.

It is also interesting to note the high percentage CV results for the two Darroch estimators when there is a large number of rejected replicates. Although the high results are mostly due to the selection effect mentioned earlier, they also indicate that there is a tendency for the estimate to 'blow up' when it is formed using marginal data (e.g. the migration matrix is near singular).

4.3.2.3 Effective Bias of the Standard Error Estimates

Table E.4 presents the results for the effective bias of the three estimates when highly unequal mortality is introduced. Although there is little difference in the trends noted in the closed population experiments, the addition of mortality is enough to move some results from being not effective to effective.

4.4 Discussion

From the results presented in the preceding sections, we see that the standard error estimates for the pooled Petersen and Darroch estimators exhibit properties that differ from those of the estimates themselves. While the pooled Petersen estimate is subject to large, effective bias when applied to the majority of the sample populations, its standard error estimate is not effectively biased when applied to those same populations.

Unlike the pooled Petersen, the two Darroch standard error estimators exhibit effective bias, where as the estimators themselves exhibit none when applied to the same populations. Although interesting, this result, at least for the iterative Darroch, is likely due to the replication and selection problems described earlier.

While the bias of the standard error estimates differs from the estimates themselves, the precision of the standard error estimates was remarkably similar to that of the estimates themselves. The pooled Petersen standard error estimate exhibits high, nearly constant precision, while the two Darroch estimators exhibit lower precision for those combinations where replicate rejection is not a factor. As well, while it exhibits similar precision to the iterative Darroch standard error estimate, the standard error estimate for the Darroch moment estimate is subject to much higher bias. This results in the moment estimate standard error being much more susceptible to effective bias than the iterative Darroch, as was documented in Tables D.9 and D.10.

As an aside, it is interesting to note that both the Darroch moment estimator, and the iterative Darroch standard error estimates can be very sensitive to the acceptability of the data on which they are formed. In particular, a review of Tables D.3 and E.2 shows that the iterative Darroch can be subject to reliability (more specifically, convergence) problems when it is formed over ill-fitting data. These reliability problems have a marked affect on the results for the estimates since, as

the data became less acceptable, the estimators exhibited higher bias and lower precision.

As with the estimators, the introduction of mortality did not alter the relative properties of the standard error estimators, but, due to the reduced number of recovered animals, simply scaled the results. Therefore, the presence of mortality in a sample population would not preclude the use of either estimator (the pooled Petersen or the Darroch), but a biologist must be aware of the potential bias introduced into both the estimates and their standard error estimates.

From these results, we conclude that while the standard error estimators were developed under the assumptions of closure, they still work reasonably well when mortality is present.

As mentioned earlier, the pooled Petersen and Darroch estimators, as presented, are really two ends of a spectrum, fully pooled and completely unpooled data, respectively. The next chapter examines the intermediate portions of this spectrum, and the effect that pooling has on the estimators.

Chapter 5

Pooling

From Chapter 3, we have seen that the pooled Petersen estimate can be far more precise than the Darroch estimate, but is subject to very high, effective bias when its consistency conditions fail to hold. This leaves a biologist with a very unsatisfactory choice: use the pooled Petersen estimator and obtain more precise, but possibly biased estimates, or use the less precise, but unbiased, Darroch estimate. Since neither choice is satisfactory, the biologist is tempted to perform less extreme pooling to increase the precision of the Darroch estimate, while attempting to keep its bias to a minimum. As well, a biologist may be forced into pooling data in order to deal with small sample sizes, convergence, or identifiability problems. This chapter investigates the effect of various levels of pooling on the bias and precision of the Darroch estimator in order to determine the best, in terms of relative root mean-square error, level of pooling for the Darroch estimator.

5.1 Methods

The investigation was carried out using a mean-value analysis similar to that used in Chapter 3, and then later verified using stochastic simulation, as was done in

Chapter 4. For the majority of this section, the results presented are from the mean-value experiments, since they are not affected by the problem of datasets that do not lead to convergent or admissible estimates. It will be clearly indicated where presented results are from the simulation study.

Since there were many factor combinations where the Darroch estimate was only marginally more imprecise than the pooled Petersen estimate, only those factor combinations where the precision of the Darroch was significantly less than that of the pooled Petersen were selected for use in these experiments. For the purposes of this study, a significant difference in precision was defined as at least 1.45 times greater than the pooled Petersen. This value was chosen for two reasons:

- It was felt that an increase in relative confidence interval width of 45% or less would be acceptable given the unbiasedness of the Darroch estimator, and there would be little incentive to pool.
- A value of 1.45 covered the majority of the 'interesting' factor combinations where the pooled Petersen exhibited large, effective biases.

Furthermore, since the use of differing entry models and population sizes produces little appreciable difference in confidence loss of the Darroch estimate (Table A.5), the number of factor combinations was further reduced to include only those with the large population and normal entry model. The selected factors were then combined to form a complete factorial experiment. The selected subset was then expanded to a 24 stratum model to provide an additional level of pooling. This expansion was achieved by simply duplicating each row/column of the capture/recapture probability sets, and extending the migration model formulae to 24 strata.

5.2 Results

For each factor combination, successive poolings were made by grouping sets of 2, 3, 4, 6, 8, 12, and 24 adjacent rows and columns. Recalling the development of the Darroch moment estimate (Section 2.3.4), we know that the 24 stratum grouping is equivalent to the pooled Petersen estimate, thus covering both ends of the pooling spectrum.

For each pooling level, the expected ARB, ERB, and percent CV were calculated for the Darroch estimate. As well, the *relative root mean square error* of the estimate was calculated as

$$100 \cdot \frac{\sqrt{S(\hat{N})^2 + bias(\hat{N})^2}}{\hat{N}} .$$

During stochastic verification of the mean-value results, it was found that those for the iterative Darroch estimate were to all intents and purposes identical to those for the moment estimate. Hence, the discussion that follows applies equally to the iterative Darroch estimate as it does to the moment estimate.

The tables discussed in this section are presented in Appendix F.

5.2.1 Bias

As with the previous experiments, the percent ARB for the estimate was computed for each level of pooling, the results of which are presented in Table F.1. Pooling level 2 was dropped from the table because, due the method used to expand the selected factors to 24 columns, pooling the data into sets of 2 resulted in a perfect pooling (i.e. no increase in heterogeneity within strata) and therefore resulted in unbiased estimates.

Reviewing Table F.1, we see that successive levels of pooling tend to have large multiplicative effects on the amount of bias exhibited by the estimate, but in absolute terms, the increases are less pronounced. For example, examining the seventh line of Table F.1 (capture set 1, recapture set 6, migration model A), we see that moving from groups of 3 to groups of 4 results in a greater than 50% increase in the ARB of the estimate, but an absolute increase of only 0.49%. Similarly, moving from groups of 4 to 6 results in an increase of over 100%, but an absolute increase of only 1.84%.

Examining the following rows of the table, we see that this is generally true for all factor combinations and groupings of less than 12. Upon moving from a groupings of 8 to groups of 12 or greater, there is typically a large increase in the amount of bias present in the estimator. For example, returning to the seventh line of the table, moving from groups of 8 to 12 results in an increase of 7.12%, or a percentage increase of 74%.

Also of interest in Table F.1 is the fact that the amount of bias present in the estimate does not increase monotonically with the size of the poolings. Again, reviewing the results of capture set 1, recapture set 6, migration model A, this is exemplified by the move from groupings of 6 to groups of 8, which results in nearly a 25% decrease in relative bias. Although interesting, and indicative of what can be expected of 'real' data, this is not surprising when one considers the construction of the capture/recapture vectors. Because the method used to expand the vectors, pooling in groups of 3, 6, and 12 introduced more heterogeneity into both the capture and recapture strata, resulting in the higher biases. Of course, the size of the increase is not consistent, since other factors, namely the migration models, were at play that would either contribute to, or counter the increased heterogeneity.

5.2.2 Precision

Table F.2 presents the percent CV for the Darroch moment estimate for each of the levels of pooling.

Unlike the asymptotic relative bias, the percent CV of the Darroch estimate is not prone to large percentage increases as the level of pooling increases, but remains more or less constant with each successive pooling. For example, consider the factor combination of capture set 1, recapture set 6, and migration model A, on the seventh row of Table F.2. Moving from groups of 2 to groups of 8 results in only a 0.19% increase in the precision of the estimate (although moving from 2 to 6 results in a 0.32% increase). For the final row of the table (capture set 6, recapture set 6, migration model A), a similar move results in only a 0.04% increase in the precision of the estimate.

Large gains in the precision of the estimate are only seen once we move to groupings of 12 or more strata. Returning to the example factor combination (1/6/A), moving from groups of 2 to groups of 12 results in an increase of 0.95% in the precision of the estimate, while a similar move for the factor combination of capture set 6, recapture set 6, migration model A, results in an increase of 3.23%.

As with the asymptotic relative bias, the precision of the estimate is not monotonically increasing with increasing pooling levels, but exhibits higher precision at pooling levels 3, and 6, which is, as with ARB, an artifact of the construction of the capture/recapture vectors.

5.2.3 Effective Bias

Combining the results of Tables F.1 and F.2, the effective relative bias of the estimate was formed for each level of pooling. Table F.3 presents those results, with estimates producing ineffective bias (i.e. bias less than half the CV) shown in bold type.

As one would expect, the effective relative bias of the estimate follows a trend similar to that of the asymptotic relative bias. As relative bias increases, as seen in Section 5.2.1, with percent CV remaining constant (Section 5.2.2), we would expect the effective relative bias to track quite closely to the ARB. To validate this expectation, again consider the factor combination of capture set 1, recapture set 6, and migration model A. Comparing the results for this combination in Table F.1 against Table F.3, it is clear that as bias increases, so does effective bias.

Of particular interest in Table F.3 is the point at which bias ceases to become ineffective. Reviewing the table we see that the level of pooling that may be safely performed on a given set of data is highly dependent on the shape of its migration model, since, from the table, we find the following:

1. Populations exhibiting a strongly diagonal migration pattern (migration model A) began to exhibit significant effective bias very early on into the pooling process, introducing effective bias when pooling beyond groups of 3.
2. Populations exhibiting an upper triangular migration pattern (migration model C) could be safely pooled the most, up to groupings of 8, before the introduced bias becomes effective.
3. Populations exhibiting a migration pattern between the two extremes (migration model B), discounting artifacts of the data's construction, could be pooled to a point between the lower and upper limits.

5.2.4 Accuracy

Besides the effective relative bias presented in Table F.3, the results of Tables F.1 and F.2 can be combined to form the root relative mean squared error (RRMSE) for the estimate at each level of pooling. Combining the bias and precision of the estimate, the RRMSE is an indicator of the balance between these two properties

and by minimizing it, we hope to minimize bias while maximizing precision. Table F.4 presents those results.

Examining the table, we see that in general, the RRMSE for the estimate is minimal at pooling level 3 for all factor combinations. This indicates that for almost all factor combinations, groupings of 3 rows and columns provides the best combination of minimal bias with high precision. Unfortunately, when comparing this table with Table F.3, we find that sometimes the best combination as indicated by the RRMSE includes significant effective bias. For example, the best pooling for the seventh row of the table (capture set 1, recapture set 6, migration model A) is groupings of 3, but turning back to Table F.3 we see that groupings of 3 produce significant effective bias (although not very significant), so selecting a pooling based solely on the RRMSE may cause significant effective bias that will prejudice confidence intervals for the estimate.

These results were not what was expected at the outset of the study. Instead, it was expected that at low pooling levels, the RRMSE of the estimator would be high due to low precision. As pooling levels increased, it was expected that precision would increase accordingly and that any bias introduced would be negligible enough that the RRMSE would drop to a minimal optimum. For pooling past this optimal point, it was felt that even as precision continued to increase, the bias introduced would be large enough to cause increases in the RRMSE. While the results presented do not preclude the existence of such an optimum pooling level, one was not found in the populations studied.

5.3 Conclusion

From the above results, we have seen that for the selected factor combinations, groupings of 3 rows and columns offers the best combination of low bias and high

precision. Although there is no one level of pooling that consistently provided the best combination of bias and precision, for most factor combinations groups of 8 appeared to be the upper limit of acceptable results.

As well, the above results offer a potential heuristic for determining a suitable level of pooling. As can be observed from the reported results, successive levels of pooling tend to cause small changes in the percent ARB and percent CV of the estimate, until a certain point is reached where there is a large jump in the percent ARB, and a corresponding, but smaller, reduction in the percent CV. Using this knowledge, it can be stated that data may be successively pooled until a large drop in the estimate, and corresponding decrease in the percent CV is seen. This change indicates that there is excessive pooling and the previous pooling is likely a more suitable one. Of course, as was seen in the the study done by [Warren and Dempson, 1995], if any of the pooled Petersen consistency conditions hold (Section 2.3.2.1), no appreciable change will be seen in the estimate.

Therefore, from these results, we draw the conclusion that pooling does indeed offer a better alternative, in terms of root relative mean square error, than either the pooled Petersen (complete pooling), or the Darroch (completely unpooled) estimates. Unfortunately, there appears to be no definitive test to determine when the disadvantages of pooling (increased RRMSE) begin to exceed the benefits, i.e. adversely affect the estimate and its confidence interval. Although the results presented in this chapter offer some assistance in determining a suitable level of pooling, numerous experimental poolings are required to find an adequate level.

Therefore, without a conclusive test for determining a suitable pooling, a biologist is forced to pool subjectively, based on their experience and knowledge of the experimental conditions. Without a tool to allow a biologist to adequately plan experiments, or perform poolings on analyzed data, this could lead to poor estimates. The next chapter discusses a tool developed for this purpose.

Chapter 6

An Application to Analyze Stratified Populations

6.1 Introduction

As we have seen from Chapter 5, Plante's iterative, maximum likelihood Darroch estimator provides a number of advantages over both the Darroch moment estimate and the pooled Petersen estimate. As well, the preceding chapters have also shown that in many situations, there is little to be gained from moving to a stratified estimator. What is clearly lacking is a means for biologists to compare these estimates and their properties to determine when each is most suitable, and to aid in the planning of mark-recapture experiments. This chapter presents the Stratified Population Analysis System (SPAS) [Arnason *et al.*, 1996], an application designed to allow biologists to both analyze collected mark-recapture data, and to perform hypothetical analyses, using stochastic simulation, to aid in the design and execution of mark-recapture experiments.

6.2 The Software

SPAS¹ was developed in order to analyze the properties of the estimators discussed in the previous chapters, and allows a user to specify and simulate the results of a mark-recapture experiment conducted on a hypothetical population. In addition, SPAS provides facilities to analyze and manipulate data collected from experiments conducted in the real world.

SPAS was developed in a series of steps, beginning with a series of routines written in FORTRAN, running on an Intel 486 PC, and using a proprietary graphics package (later converted to curses [Strang, 1986]). The next iteration of SPAS was written in the C programming language and used the SUIT² portable interface library, which enables SPAS to run on both Intel based PCs running Microsoft Windows, as well as UNIX based workstations using the X11 windowing protocol. In its final form, SPAS was ported to the wxWindows³ interface toolkit and the vast majority of its interface re-written using the C++ programming language.

Although SPAS is available for multiple windowing systems, it was developed to run efficiently and intuitively on a 486 PC running Microsoft Windows, the computing platform that is commonly available to field biologists. For this reason, the following discussion will focus on the Windows version of SPAS, although there is very little difference between the X11 and Windows versions.

6.3 SPAS Features

As a part of the analysis capabilities mentioned above, SPAS reads its data from a plain ASCII text file that can easily be produced from a spreadsheet application or

¹Available via http at <http://www.cs.umanitoba.ca/popan>

²Available via ftp from [uvax.cs.uvirginia.edu](ftp://uvax.cs.uvirginia.edu)

³Available via the World Wide Web from <http://web.ukonline.co.uk/julian.smart/wxwin>

another mark-recapture analysis package. Once read into SPAS, the user may analyze the data using any of the three estimators described in the preceding chapters, as well as the Schaefer estimate, and a least-squares estimate for stratified data. Furthermore, the user may perform arbitrary poolings on the data by selectively grouping adjacent strata, or removing strata from the analysis completely. The user also has the ability to expand pooled strata back to their component strata, or to completely revert the data back to its original form.

In addition to these analysis capabilities, SPAS also provides users with a completely general simulator that allows a user to specify the parameters of a hypothetical population using a file format similar to the one used by the analysis methods. Once loaded, a user can perform a number of operations on the hypothetical simulation. These operations include: (1) generating a set of 'real world' data using the theoretical means of the sampling distributions, (2) generating a set of 'real world' data by drawing a single set of samples from the hypothetical population, (3) the ability to perform a replicated simulation of the population with no strata alterations, and (4) the ability to perform a replicated simulation of the population with selective pooling and deletion of strata.

To provide the user with a better understanding of SPAS and its abilities, the remainder of this chapter is divided into two sections: a study of the Schaefer [Schaefer, 1951] salmon data to demonstrate SPAS's analysis capabilities, and a number of simulation studies to demonstrate SPAS's simulation and planning capabilities. Further examples and tutorials can be found in the SPAS manual [Arnason *et al.*, 1996].

6.4 Performing Data Analyses with SPAS

Figure 6.1 shows the SPAS main screen after the Schaefer salmon data has been loaded into an analysis window (all work in SPAS is accomplished through either an analysis window, for performing analyses on collected or simulated data, or a simulation window, for performing stochastic simulations and generating simulated data for analysis). Throughout this section, a series of analyses will be performed on the data (provided as part of the SPAS distribution) to showcase SPAS's analysis and pooling capabilities. First, we begin with a simple analysis of the data.

6.4.1 Analysis of the Schaefer Salmon Data

An initial analysis, using all available estimators and accepting the default values for the iterative Darroch's iteration and criterion values, was conducted on the Schaefer data (present in Figure 6.2), the results of which are presented in Figure 6.3. Beginning at the top of the figure, the first piece of analysis produced by SPAS is the values for the complete mixing and equal proportions tests. These tests are the test for complete mixing of the population, and the test for equal proportions of marked and unmarked animals in the recapture strata described in [Seber, 1973, pages 436, 437]. Upon initial examination of the results produced by SPAS (reproduced in Figure 6.3), one immediately notices that the complete mixing test fails with a significance of 0.01, and that the equal proportions test fails with a significance of 0.00, indicating possible bias in the pooled Petersen and Schaefer estimates.

Continuing to examine the results shows that the iterative Darroch failed to produce an estimate, the reasons for which can be determined by examining the least-squares results that follow. Examining the results of this estimate initially show an admissible estimate, but further examination shows that it is based on

Schaefer Sockeye Data
8 rows x 9 columns

| | Marks | 1 | 2 | 3 | |
|---|--------|------|-------|-------|-----|
| 1 | 15.00 | 1.00 | 0.00 | 2.00 | 0. |
| 2 | 59.00 | 1.00 | 3.00 | 7.00 | 0. |
| 3 | 410.00 | 1.00 | 11.00 | 33.00 | 24. |
| 4 | 695.00 | 0.00 | 5.00 | 29.00 | 79. |
| 5 | 773.00 | 0.00 | 0.00 | 11.00 | 67. |

Figure 6.1: The initial SPAS screen after loading the Schaefer salmon data. The top window, referred to as the data window, holds the currently loaded data, while the results of the last performed analysis appear in the bottom window, referred to as the results window.

Schaefer Sockeye Data
8 rows x 9 columns

| | Marks | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Unseen |
|-----------|--------|--------|--------|---------|---------|--------|---------|--------|--------|------|--------|
| 1 | 15.00 | 1.00 | 0.00 | 2.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 12.00 |
| 2 | 59.00 | 1.00 | 3.00 | 7.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 48.00 |
| 3 | 410.00 | 1.00 | 11.00 | 33.00 | 24.00 | 5.00 | 1.00 | 0.00 | 1.00 | 0.00 | 334.00 |
| 4 | 695.00 | 0.00 | 5.00 | 29.00 | 79.00 | 52.00 | 3.00 | 2.00 | 7.00 | 3.00 | 515.00 |
| 5 | 773.00 | 0.00 | 0.00 | 11.00 | 67.00 | 77.00 | 2.00 | 16.00 | 7.00 | 3.00 | 590.00 |
| 6 | 335.00 | 0.00 | 0.00 | 0.00 | 14.00 | 25.00 | 3.00 | 10.00 | 6.00 | 2.00 | 275.00 |
| 7 | 59.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 5.00 | 0.00 | 53.00 |
| 8 | 5.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 | 0.00 | 0.00 | 4.00 |
| Unmarked | 16.00 | 113.00 | 718.00 | 2664.00 | 3317.00 | 635.00 | 1217.00 | 904.00 | 368.00 | | |
| Recovered | 19.00 | 132.00 | 800.00 | 2848.00 | 3476.00 | 644.00 | 1247.00 | 930.00 | 376.00 | | |

Figure 6.2: The Schaefer salmon data as presented by SPAS after loading the data into the data window.

negative initial strata estimates, which were in turn caused by negative capture probability estimates. Since the iterative Darroch's search is initially 'seeded' with a least-squares estimate, the search likely remained stuck in an area of inadmissible estimates. Further examination of these results show little difference between the estimated m_{ij} s and the observed numbers (Figure 6.2), but that there is significant (as indicated by the significant G^2 goodness-of-fit test) difference between the observed and estimated numbers of unmarked animals recovered, especially in the early and final recapture strata.

Examining the last two estimators, we see that the Schaeffer estimator yielded an estimate of 47,886 animals, and the pooled Petersen estimator yielded an estimate of 47,428 animals, with a standard error of 1779.84. In light of the capture and recapture probabilities estimated by the Schaeffer estimate and the results presented in chapter 3, it is likely that these two estimates contain a small negative bias since there is some inequality among the capture and recapture probabilities, with likely violations of the complete mixing and equal proportions assumptions.

In the next section, we deal with the inadmissibility problems exhibited by the iterative Darroch and least-squares estimators by pooling the data set.

```

>>>Schaefer Sockeye Data

Chi-square Test Statistics

Complete Mixing :      18.71 (7 df)
Significance...   :      0.01
Equal Proportions:    141.93 (8 df)
Significance...   :      0.00

>> ML Darroch Estimate

Failed to form an estimate

>> Least squares Estimate

Estimate (std. err) :  61210.48 (  -1.00)
G-square           :    5.55 (1 df)
Significance...   :    0.02
Chi-square        :    3.17 (1 df)
Significance...   :    0.08
> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)

      Stratum Si  P(Capture)  1      2      3      4      5      6      7      8      9
1      1977.61    0.01    0.99    0.00    2.01    0.00    0.00    0.00    0.00    0.00    0.00
2     -9075.08   -0.01    1.01    3.02    6.97    0.00    0.00    0.00    0.00    0.00    0.00
3     19409.37    0.02    1.00   10.97   33.05   23.98    5.00    1.00    0.00    1.00    0.00
4     10843.42    0.06    0.00    5.00   29.01   78.98   52.00    3.00    2.00    7.00    3.01
5    -28448.91   -0.03    0.00    0.00   10.99   67.03   76.99    2.01   16.00    7.00    2.98
6     70505.47    0.00    0.00    0.00    0.00   13.96   25.01    2.95   10.00    6.00    2.08
7     -2734.25   -0.02    0.00    0.00    0.00    0.00    0.00    0.00    1.00    5.00    0.00
8     -1268.25    0.00    0.00    0.00    0.00    0.00    0.00    0.00    1.00    0.00    0.00

Unmarked                22.37   118.30   714.82  2665.40  3316.76  642.93  1217.00  904.00  349.32

> End of Table

>>>Schaefer Estimate

Estimate :  47885.91

> Table of Stratum Estimates: N(cap), N(cap,rec), N(rec)
      Stratum Si  P(Capture)  1      2      3      4      5      6      7      8      9
1      129.23    0.12    31.67    0.00    97.56    0.00    0.00    0.00    0.00    0.00    0.00
2      512.06    0.12    33.97   111.79   366.30    0.00    0.00    0.00    0.00    0.00    0.00
3     5355.99    0.08    34.17  412.27  1736.84  2004.03  589.69  386.02    0.00   192.97    0.00
4     12998.18    0.05    0.00   134.12  1092.41  4721.30  4389.33  828.85  320.99  966.76  544.42
5     17011.36    0.05    0.00    0.00   453.31  4380.52  7110.53  604.51  2809.27  1057.64  595.59
6     9503.87    0.04    0.00    0.00    0.00  1209.88  3051.52  1198.56  2320.81  1198.27  524.83
7     2167.39    0.03    0.00    0.00    0.00    0.00    0.00    0.00    408.74  1758.65    0.00
8      207.83    0.02    0.00    0.00    0.00    0.00    0.00    0.00    207.83    0.00    0.00

Stratum Si                99.80   658.18  3746.42 12315.73 15141.07 3017.94 6067.64 5174.29 1664.84
P(Re-captu                0.19    0.20    0.21    0.23    0.23    0.21    0.21    0.18    0.23

> End of Table

>>>Pooled Petersen Estimate

Estimate (std. err) :  47278.26 ( 1779.84)

95 % normal C I      :( 43789.78,  50766.75)
95 % transform C I  :( 43954.59,  50945.65)

```

Figure 6.3: Analysis results produced by SPAS for the Schaefer salmon data after selecting the *All...* option from the *Analysis* menu.

6.4.2 Analyses with Pooling

As was done by Darroch, the data was pooled by grouping the first three weeks and last three weeks of tagging into a single stratum (this pooling is actually suggested by the estimated capture probabilities of the Schaefer estimate), and grouping the first three weeks and last four weeks of recovery into a single stratum. While this pooling forms a square matrix, and therefore allows Darroch to apply the moment estimate (55,621 with a standard error of 6103.73), the iterative Darroch still fails to find an estimate. This can be corrected by restoring the original data and re-pooling it by grouping the weeks of tagging as before, and re-examining the column (recovery) pooling. Although the first week of recovery is indeed small, grouping it with the next two weeks of recovery seems like overkill, since combining it with the next column should yield a sufficiently large sample. Finally, pooling week 7 with the next 2 weeks gives a data set that will produce an estimate for the iterative Darroch estimator, the results of which are presented in Figure 6.4.

Reviewing 6.4 we see that the pooling has increased both the complete mixing and equal proportions tests relative to their degrees of freedom, indicating the introduction of heterogeneity into the data. As well, we see that while the iterative Darroch converges and provides valid estimates, 54,080 animals with a standard error of 4,659.82, the G^2 goodness-of-fit test indicates a poor fit, which is due to the large discrepancies between the observed and estimated values for the number of unmarked animals captured in the first and final two recovery strata.

Through the use of pooling, we have been able to obtain estimates from all four estimators, but without obtaining a convincing fit. This is mostly due to the estimators' inability to predict the number of unmarked animals in each recovery stratum. Although it is hard to say why this happens without greater detail about the capture methods and conditions, perusal of Figure 6.2 suggests that the experiment was terminated too early in the run. Since there were still returns from tagging

```

>>>Schaefer Sockeye Data

Chi-square Test Statistics

Complete Mixing :      16.91 (3 df)
Significance...   :      0.00
Equal Proportions:  141.55 (5 df)
Significance...   :      0.00

>> ML Darroch Estimate

Total Number of iterations is 1 (Max iterations is 25 )
Estimate (std. err) :  54079.59 ( 4659.82)
Log likelihood      :  68126.42

95 % normal C I    : ( 44946.34, 63212.83)
G-square           :    722.20 (2 df)
Significance       :      0.00
Chi-square        :    309.20 (2 df)
Significance...    :      0.00

> Table of Stratum Estimates & Predicted counts N(cap), n(cap,rec), u(rec)

      Stratum Si  P(Capture)      1-2      3      4      5      6      7-9
1-3    3733.77    0.13      17.00    42.00    24.00    5.00    1.00    1.00
4      9355.21    0.07      5.00    29.00    79.00    52.00    3.00    12.00
5      3976.14    0.19      0.00    11.00    67.00    77.00    2.00    26.00
6-8    36776.51  0.01      0.00    0.00    14.00    25.00    3.00    25.00

Unmarked                                176.45    688.95    2699.58    3279.89    325.90    2543.27

> End of Table

```

Figure 6.4: Results produced by SPAS after pooling of the Schaefer salmon data and analyzing it using the iterative Darroch.

strata 4 through 6, and none from strata 7, and 8 in final week of the experiment, it appears likely that there were still a number of animals in transit at the time of the experiment's completion.

6.5 Simulation

As was described earlier, SPAS also provides users with a general simulator, allowing users to perform experiments and "what-if" analyses on hypothetical migrating populations. Using this capability, a biologist, armed with guesstimated parameters for the population to be studied, could perform multiple simulated experiments on the population. From the results of those experiments, he would be able to accurately predict the estimates, and their bias and precision, that will be seen when the experiment is conducted.

In addition to providing predictions of estimates, the simulation capability can be used to plan resource allocation for an experiment. For example, suppose a biologist prepares a simulation parameter set using a combination of experience and the results of an earlier experiment. Now, suppose that upon completion of the simulation, the biologist finds with the guesstimated capture and recapture rates, the properties of the resulting estimates are unacceptable. Seeing this, the biologist guesses that the addition of another person to the marking crew would increase capture and recapture rates by 5%, or perhaps working longer days would increase capture and recapture rates by 10%. Using the simulation capabilities of SPAS, the biologist is able to determine the effects that the addition of two more people, and working 10-hour days would have on the results of the experiment.

This section explores and demonstrates these capabilities of SPAS in greater detail.

6.5.1 Simulation Parameters

Before performing any sort of simulation, a user must first specify the parameters for their hypothetical population. In SPAS, these consist of the following:

1. a title for the parameter set
2. the number of capture (s) and recapture strata (t)
3. a series of labels for the capture strata
4. a series of labels for the recapture strata
5. a vector describing the number of animals available to be marked in the initial capture strata (N_i)
6. a vector describing the probability that an animal will be marked in each of the capture strata (p^c_i)
7. a matrix describing the probability that an animal migrating from a given capture stratum migrates to a given recapture stratum (θ_{ij})
8. a vector describing the probability that an animal present in a given recapture stratum is captured (p^r_j)

SPAS reads these parameters from a comma, tab, or space delimited text file, expecting them to appear in a form similar to that used to present analysis and simulation results. A sample simulation parameter file is shown in Figure 6.5.

Expanding on the example of the biologist in the introduction of this section, a biologist is forced to come up with guesstimates for each of the simulation parameters. Fortunately, sources for these guesstimates are plentiful, including: results from earlier studies conducted in the same area, published reports of similar studies

```

"Simulation test data"
4 4
      "Column 1" "Column 2" "Column 3" "Column 4"
"Row 1" 5000 0.3    0.25    0.25    0.25    0.25
"Row 2" 5000 0.5    0.01    0.33    0.33    0.33
"Row 3" 5000 0.7    0.0    0.0    0.5    0.5
"Row 4" 5000 0.9    0.0    0.0    0.0    1.0
      0.5    0.5    0.5    0.5

```

Figure 6.5: A sample simulation parameter set provided with SPAS

conducted elsewhere, and the biologist's own experience. As well, given that estimates are available from previous studies, a biologist can 'bootstrap' their way to fairly accurate guesstimates by creating a parameter set to approximate the previous results and then successively refining the parameter set until the simulated and previous results match. Once this is accomplished, the biologist will have a solid basis on which to predict and plan for the upcoming experiment.

6.5.2 Mean Values Simulation

Once an acceptable parameter set has been arrived at, the next action a biologist is likely to perform is a mean-values analysis of the parameter set. As was shown in Section 4.2, the expected values of the estimate provide a good indication of the bias and precision that is likely to be seen in estimates. To enable users to perform this sort of mean-value analysis using a simulation parameter set, SPAS allows a user to form a mean-value data set from the simulation data set (as was done for the work presented in Chapters 3 and 5). For example, the mean-value dataset presented in Figure 6.6 was generated using the sample simulation data included with SPAS (Figure 6.5).

Reviewing the two figures, the process of generating a mean-value dataset from a simulation parameter set becomes clear. For example, the 1500 animals marked in the first capture stratum (Row 1) is calculated as the number of animals that

originate in the stratum (5000, from Figure 6.5) multiplied by the probability of an animal being marked in the stratum (0.3). Similarly, the 187.50 animals that originated in Row 1 and were recaptured in Column 1 is calculated by multiplying the number of marked animals, 1500, by the probability that an animal in Row 1 migrates to Column 1, in this case 0.25, and then multiplying the result by the probability that an animal is captured in Column 1, 0.5.

Simulation test data
4 rows x 4 columns

| | Marks | Column 1 | Column 2 | Column 3 | Column 4 | Unseen |
|-----------|---------|----------|----------|----------|----------|---------|
| Row 1 | 1500.00 | 187.50 | 187.50 | 187.50 | 187.50 | 750.00 |
| Row 2 | 2500.00 | 12.50 | 412.50 | 412.50 | 412.50 | 1250.00 |
| Row 3 | 3500.00 | 0.00 | 0.00 | 875.00 | 875.00 | 1750.00 |
| Row 4 | 4500.00 | 0.00 | 0.00 | 0.00 | 2250.00 | 2250.00 |
| Unmarked | | 450.00 | 850.00 | 1225.00 | 1475.00 | |
| Recovered | | 650.00 | 1450.00 | 2700.00 | 5200.00 | |

Figure 6.6: The mean-value dataset generated by SPAS from the sample simulation data of Figure 6.5

Once generated, the mean-value dataset can be used to perform a a range of analyses to get the expected values of the estimators (as was done in Chapter 3). The results of such an analysis are presented in Figures 6.7 and 6.8.

Reviewing the two figures, we see that all of the estimators are unbiased when applied to the generated population. The reason for this is clear when we review the sample parameter set in Figure 6.5 and note that the recapture probabilities are constant across the four recapture strata. Recalling from Chapter 2 that this is one of the consistency conditions for the pooled Petersen and Schaefer estimators, the unbiasedness is not surprising. As was seen in earlier chapters, the pooled Petersen is clearly more precise (as indicated by the standard error estimate presented in parentheses next to the estimates) than the iterative Darroch, which in turn is more precise than the Darroch moment estimate.

```

>>>Simulation test data

Chi-square Test Statistics

Complete Mixing :      0.00 (3 df)
Significance...   :      1.00
Equal Proportions:  766.63 (3 df)
Significance...   :      0.00

>> ML Darroch Estimate

Total Number of iterations is 1 (Max iterations is 25 )
Estimate (std. err) : 20000.00 ( 139.16)
Log likelihood      : 58586.78

95 % normal C I    :( 19727.25, 20272.75)
G-square          :      0.00 (0 df)
Significance      :      2.00
Chi-square       :      0.00 (0 df)
Significance...   :      2.00

> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)

      Stratum Si  P(Capture)  Column 1  Column 2  Column 3  Column 4
Row 1    5000.00      0.30      187.50    187.50    187.50    187.50
Row 2    5000.00      0.50       12.50    412.50    412.50    412.50
Row 3    5000.00      0.70       0.00     0.00     875.00    875.00
Row 4    5000.00      0.90       0.00     0.00     0.00    2250.00

Unmarked                                450.00    850.00    1225.00    1475.00

> End of Table

>> Darroch moment Estimate

Estimate (std. err) : 20000.00 ( 213.13)
> Table of Stratum Estimates: N(cap), N(cap,rec), N(rec)

      Stratum Si  P(Capture)  Column 1  Column 2  Column 3  Column 4
Row 1    5000.00      0.30     1250.00    1250.00    1250.00    1250.00
Row 2    5000.00      0.50       50.00    1650.00    1650.00    1650.00
Row 3    5000.00      0.70       0.00     0.00    2500.00    2500.00
Row 4    5000.00      0.90       0.00     0.00     0.00    5000.00

Stratum Si                                1300.00    2900.00    5400.00    10400.00
P(Re-captu                                0.50     0.50     0.50     0.50

> End of Table

>> Least squares Estimate

Estimate (std. err) : 20000.00 ( -1.00)
G-square          :      0.00 (0 df)
Significance...   :      2.00
Chi-square       :      0.00 (0 df)
Significance...   :      2.00

> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)

      Stratum Si  P(Capture)  Column 1  Column 2  Column 3  Column 4
Row 1    5000.00      0.30      187.50    187.50    187.50    187.50
Row 2    5000.00      0.50       12.50    412.50    412.50    412.50
Row 3    5000.00      0.70       0.00     0.00     875.00    875.00
Row 4    5000.00      0.90       0.00     0.00     0.00    2250.00

Unmarked                                450.00    850.00    1225.00    1475.00

> End of Table

```

Figure 6.7: The results produced by SPAS after analyzing a mean-value dataset generated from the sample simulation parameter set.

```

>>Schaefer Estimate
Estimate : 20000.00
> Table of Stratum Estimates: N(cap), N(cap,rec), N(rec)
      Stratum Si  P(Capture)  Column 1  Column 2  Column 3  Column 4
Row 1      3334.93      0.45      1218.75      906.25      686.44      523.49
Row 2      4736.85      0.53      81.25      1993.75      1510.17      1151.68
Row 3      5646.34      0.62      0.00      0.00      3203.39      2442.95
Row 4      6281.88      0.72      0.00      0.00      0.00      6281.88
Stratum Si
P(Re-captu      1300.00      2900.00      5400.00      10400.00
                0.50      0.50      0.50      0.50
> End of Table
>>Pooled Petersen Estimate
Estimate (std. err) : 19999.33 ( 115.44)
95 % normal C I : ( 19773.07, 20225.60)
95 % transform C I : ( 19774.76, 20227.32)

```

Figure 6.8: The results produced by SPAS after analyzing a mean-value dataset generated from the sample simulation parameter set (continued).

Of note in Figure 6.8 is that while the Schaefer estimate \hat{N} is unbiased, the initial stratum estimates, the $\hat{N}_{i\cdot}$, are not (the true values, from Table 6.5, are all 5000). This is because the Schaefer estimator requires both the p^c_i and the p^r_j to be constant in order for the \hat{N}_{ij} to be unbiased.

6.5.3 Stochastic Simulation

Once the biologist is satisfied with the mean-value analyses, i.e. the expected bias and precision for his selected estimator is within an acceptable range, the next step in the planning process is to perform stochastic simulation of the population parameter set. This is necessary since the mean-value results are only asymptotic, i.e. they are the expected values as the sample size goes to infinity, while real samples will be typically be much smaller. As was seen from the simulation results presented in Section 4.3.1, once small and variant sample sizes are introduced, the two Darroch estimators became subject to convergence and singularity problems, which seriously affects their reliability. By performing stochastic simulations prior to conducting an

experiment, the biologist will be better able to judge the reliability of the estimator selected.

Continuing with the sample simulation data set, the results presented in Figures 6.9, 6.10, and 6.11 were generated by SPAS with for a replicated simulation with 100 replications, and a limit of 500 attempted replications.

Beginning at the top of the results in Figure 6.9, SPAS first prints the initial and final random number seeds for the simulation. This is necessary so that comparative studies can be done between the various estimators with controlled variability, i.e. the experimenter can ensure that the same series of replications is analyzed by the estimators.

Next, SPAS presents the number of replications requested, and the maximum number of allowed attempts, followed by the number of completed, good replications and the total number of attempted replications. As explained in Chapter 4, a good replication is one where all of the estimators under study form valid, though not necessarily admissible, estimates. If any of the estimators fail to form a valid estimate, e.g. the iterative Darroch estimate fails to converge, or the Schaefer estimate encounters a zero divide, during a replication, that replication is considered to be a bad replication and its results are not added to the statistics.

Following the replication counts is the mean-values over replications of the generated populations. Since the sample simulation was generated with 100 replications, and there were no failed replications, these values should closely match those of the mean-values data set generated in the previous section, presented in Figures 6.7 and 6.8. Examination of these two figures reveals that there is a close match. As well, the standard deviations over replications of the generated populations are presented.

Following the simulated population statistics are the estimates and their standard errors. Presented in tabular format are the average estimate for each estimator

```

Simulation test data
Initial seeds      = 123456789 123456789
Final seeds       = 2042003007 1813050821
Good replications required : 100   Max attempts allowed : 500
Good replications executed : 100   Total attempts executed : 100
All statistics based on 100 good replications

> Table of sample sizes : n(cap), m(cap,rec), u(rec)
Means of table values (over replications)

      Captures      Column 1      Column 2      Column 3      Column 4
Row 1      1500.69      185.56      185.80      186.55      191.01
Row 2      2499.82      12.37      415.68      411.91      413.77
Row 3      3501.67      0.00      0.00      875.26      872.54
Row 4      4499.35      0.00      0.00      0.00      2249.03
Recovered                647.58      1447.23      2699.56      5199.01

Standard Deviation of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      31.75      14.64      12.79      12.96      16.85
Row 2      36.36      3.85      17.62      19.02      21.01
Row 3      32.15      0.00      0.00      25.51      27.57
Row 4      21.58      0.00      0.00      0.00      36.31
Recovered                23.04      36.94      46.02      60.55

> End of Table

> Table of Estimates and Standard Errors
Means and Standard Deviations over replications

      Estimates      Mean      Std. Dev.
      -----      ----      -
      ML Darroch      19994.13      142.17
      Std. Error      141.09      6.71
      Darroch Moment      19994.13      142.17
      Std. Error      215.40      9.51
      Least Squares      19994.13      142.17
      Std. Error      -1.00      0.00
      Schaefer      19991.57      112.24
      Std. Error      0.00      0.00
      Pooled Petersen      19990.88      104.60
      Std. Error      115.37      1.95

> End of Table

>>ML Darroch
> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)
Means of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      5061.75      185.56      185.80      186.55      191.01
Row 2      4940.98      12.37      415.68      411.91      413.77
Row 3      5023.89      0.00      0.00      875.26      872.54
Row 4      4967.51      0.00      0.00      0.00      2249.03
Unmarked                449.65      845.75      1225.84      1472.66
    
```

Figure 6.9: The results of a replicated simulation performed using the sample data set (part 1 of 3).


```

Standard Deviation of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      342.44      14.64      12.79      12.96      16.85
Row 2      388.67      3.85      17.62      19.02      21.01
Row 3      257.35      0.00      0.00      25.51      27.57
Row 4      152.08      0.00      0.00      0.00      36.31
Unmarked
19.98      31.47      30.88      37.91

> End of Table

>>Darroch Moment
> Table of Stratum Estimates: N(cap), N(cap,rec), N(rec)
Means of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      5061.75      1269.34      1237.50      1263.83      1291.07
Row 2      4940.98      50.06      1618.05      1635.19      1637.68
Row 3      5023.89      0.00      0.00      2517.67      2506.21
Row 4      4967.51      0.00      0.00      0.00      4967.51
Stratum Si
1319.40      2855.55      5416.70      10402.48

Standard Deviation of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      342.44      166.03      153.43      141.16      160.07
Row 2      388.67      17.99      148.67      173.96      165.96
Row 3      257.35      0.00      0.00      133.81      172.36
Row 4      152.08      0.00      0.00      0.00      152.08
Stratum Si
172.83      209.87      195.87      140.24

> End of Table

>>Least Squares
> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)
Means of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      5061.75      185.56      185.80      186.55      191.01
Row 2      4940.98      12.37      415.68      411.91      413.77
Row 3      5023.89      0.00      0.00      875.26      872.54
Row 4      4967.51      0.00      0.00      0.00      2249.03
Unmarked
449.65      845.75      1225.84      1472.66

Standard Deviation of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      342.44      14.64      12.79      12.96      16.85
Row 2      388.67      3.85      17.62      19.02      21.01
Row 3      257.35      0.00      0.00      25.51      27.57
Row 4      152.08      0.00      0.00      0.00      36.31
Unmarked
19.98      31.47      30.88      37.91

> End of Table
    
```

Figure 6.10: The results of a replicated simulation performed using the sample data set (part 2 of 3).

```

>>Schaefer
> Table of Stratum Estimates: N(cap), N(cap,rec), N(rec)
Means of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      3332.00      1217.13      896.13      684.79      533.94
Row 2      4730.51      80.62      1994.38      1504.47      1151.04
Row 3      5651.30      0.00      0.00      3212.34      2438.96
Row 4      6277.75      0.00      0.00      0.00      6277.75
Stratum Si      1297.76      2890.51      5401.61      10401.70

Standard Deviation of table values (over replications)
      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1      69.94      54.29      57.67      44.60      44.36
Row 2      67.34      24.24      62.71      61.60      54.18
Row 3      59.66      0.00      0.00      71.77      63.87
Row 4      49.84      0.00      0.00      0.00      49.84
Stratum Si      52.20      80.40      88.41      102.40
> End of Table
    
```

Figure 6.11: The results of a replicated simulation performed using the sample data set (part 3 of 3).

($\bar{X}(\hat{N})$ from Chapter 4), the standard deviation for each of the average estimates ($\bar{S}(\hat{N})$ from Chapter 4), the average standard error estimate for each estimator ($\bar{X}(\hat{S})$ from Chapter 4), and the standard deviation of the standard errors ($\bar{S}(\hat{S})$ from Chapter 4).

Examining this table, we see that all of the estimates are relatively unbiased since all are within 2 standard errors of the true population size of 20,000 animals, as expected in a well behaved population such as the sample. Comparing the precision (standard deviations, $\bar{S}(\hat{N})$) of the estimates we see that while the Darroch estimates (iterative, moment, and least squares) all exhibit the least amount of bias, they also have the most imprecise estimates with standard deviations of 142.17, while the Schaefer and pooled Petersen estimates exhibit slightly more bias, but with higher precision of 112.24, and 104.60 respectively.

What is interesting to note is the bias present in the standard error estimates, which is calculated as the difference between the standard deviation of the average estimate, $\bar{S}(\hat{N})$, and the average standard error, $\bar{X}(\hat{S})$. We see that the iterative

Darroch estimate is both very precise and unbiased, with $\bar{S}(\hat{N})$ equaling only 6.71, while the Darroch moment estimate also exhibits a very precise standard error estimate but it includes a large, effective bias ($\bar{X}(\hat{S})$ is 215.40 with a standard deviation of 9.51, while $\bar{S}(\hat{N})$ is 142.17). As well, the pooled Petersen estimate exhibits a very precise standard error estimate of 115.37 with a standard deviation of 1.95, but unfortunately it is effectively biased from the true value of $\bar{S}(\hat{N})$, 104.60.

Following the estimates and their standard errors, are the averages and standard deviations over replications for the initial and final stratum sizes, and the counts for each estimate that are available from each estimator. Using these values we can determine the amount of bias and imprecision present in these estimates by comparing them with the true values presented at the top of the simulation results. Note that the formulae used for the estimators, and their standard error estimates, are those described in Chapter 2.

6.5.4 Simulations with Data Manipulation

Continuing with the example described at the beginning of Section 6.5, suppose that after completing a stochastic simulation, the biologist finds that the estimators are subject to very low reliability. As seen in Chapter 5, it is possible to work around such reliability problems by pooling homogeneous rows and columns, thereby increasing stratum sample sizes and reducing the number of parameters in the model.

Since it is common to pool data from a field experiment to obtain better model fits, or estimator convergence, SPAS allows a biologist to explore the effects of various poolings on a simulated population. Pooling and deletion of data columns and rows is performed much as it is for an analysis. When a simulation with pooling is requested by the user, SPAS generates and presents the user with a mean-value data set (as discussed earlier) which can then be manipulated to obtain the desired pooling. Once the user is satisfied with the pooling, he may perform the simulation

in the same manner as a straight (i.e. non-pooled) simulation.

The mean-value data set is used to obtain the desired pooling from the user because of the difficulty of allowing the user to directly pool the simulation data set and still present meaningful parameters. This difficulty arises since by pooling, for example, two rows, the user does not mean that they wish to combine the row parameters, i.e. they do not wish the capture probability for the two rows to be $p_{row_i} + p_{row_{i+1}}$, but rather that the two rows should be first simulated, and then the simulated results combined. The results of pooling the first two rows of the sample data set and then performing 100 replications are presented in Figures 6.12 and 6.13.

Reviewing the parameter set in Figure 6.5, we would expect that pooling the two rows would result in an increase in the precision of the iterative Darroch and least-squares estimators, since the two rows have similar capture probabilities and migration rates. Turning to the results of the simulation, we see that, as expected, pooling did increase the precision of the iterative Darroch, and least-squares estimators, since they exhibit $\bar{S}(\hat{N})$ values of 128.97, and 124.56 respectively, compared to their unpooled values (from Figure 6.9) of 142.17, and 142.17. As well, the average standard error estimate for the iterative Darroch estimator is reduced from 141.09 to 137.87, but this unfortunately introduces a bias into the standard error estimate, since the 137.87 value of $\bar{X}(\hat{S})$ now over-estimates the true value for $\bar{S}(\hat{N})$, 128.97, by 8.9.

6.6 Discussion

Having completed his simulation studies, a biologist is now well equipped to perform his experiment and then bring his data back to be analyzed with SPAS.

Throughout this chapter, it is shown that SPAS is a powerful tool that enables

```

Simulation test data
Initial seeds      = 123456789 123456789
Final seeds       = 2042003007 1813050821
Good replications required : 100   Max attempts allowed : 500
Good replications executed : 100   Total attempts executed : 100
All statistics based on 100 good replications

> Table of sample sizes : n(cap), m(cap,rec), n(rec)
Means of table values (over replications)

      Captures      Column 1      Column 2      Column 3      Column 4
Row 1-2      4000.51      197.93      601.48      598.46      604.78
Row 3        3501.67        0.00        0.00        875.26      872.54
Row 4        4499.35        0.00        0.00        0.00        2249.03
Recovered                    647.58      1447.23      2699.56      5199.01

Standard Deviation of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2          51.07      15.22      21.74      20.13      25.55
Row 3            32.15        0.00        0.00      25.51      27.57
Row 4            21.58        0.00        0.00        0.00      36.31
Recovered                    23.04      36.94      46.02      60.55

> End of Table

> Table of Estimates and Standard Errors
Means and Standard Deviations over replications

      Estimates          Mean      Std. Dev.
-----
      ML Darroch      19984.07      128.97
      Std. Error      137.48        4.37

      Least Squares      19880.83      124.56
      Std. Error        -1.00        0.00

      Schaefer          19989.66      109.85
      Std. Error          0.00        0.00

      Pooled Petersen      19990.88      104.60
      Std. Error          115.37        1.95

> End of Table
    
```

Figure 6.12: The results of a pooled simulation using the sample data set

```

>>ML Darroch
> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)
Means of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2      10488.79      247.12      552.29      598.46      604.78
Row 3        4522.58        0.00        0.00      875.26      872.54
Row 4        4972.70        0.00        0.00        0.00      2249.03
Unmarked                                400.46      894.94      1225.84      1472.66

Standard Deviation of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2        273.02        10.43        19.48        20.13        25.55
Row 3          240.71         0.00         0.00        25.51        27.57
Row 4          144.30         0.00         0.00         0.00        36.31
Unmarked                                16.82        29.65        30.88        37.91

> End of Table

>>Least Squares
> Table of Stratum Estimates & Predicted counts N(cap), m(cap,rec), u(rec)
Means of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2      9965.73      249.86      549.55      598.46      604.78
Row 3        4835.96        0.00        0.00      875.26      872.54
Row 4        4974.78        0.00        0.00        0.00      2249.03
Unmarked                                295.17      895.88      1225.84      1472.66

Standard Deviation of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2        278.92        10.32        19.64        20.13        25.55
Row 3          239.48         0.00         0.00        25.51        27.57
Row 4          139.56         0.00         0.00         0.00        36.31
Unmarked                                26.68        29.41        30.88        37.91

> End of Table

>>Schaefer
> Table of Stratum Estimates: N(cap), N(cap,rec), N(rec)
Means of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2      8060.60      1293.74      2891.41      2190.01      1685.45
Row 3        5651.30         0.00         0.00      3212.34      2438.96
Row 4        6277.75         0.00         0.00         0.00      6277.75
Stratum Si                                1293.74      2891.41      5402.35      10402.17

Standard Deviation of table values (over replications)

      Stratum Si      Column 1      Column 2      Column 3      Column 4
Row 1-2         90.39         46.89         81.15         66.22         64.66
Row 3           59.66         0.00         0.00         71.77         63.87
Row 4           49.84         0.00         0.00         0.00         49.84
Stratum Si                                46.89         81.15         88.13        102.58

> End of Table
    
```

Figure 6.13: The results of a pooled simulation using the sample data set (continued)

biologists to better analyze real data gathered through mark-recapture experiments, and can serve as an aid to biologists in planning mark-recapture experiments.

As was noted in Chapter 5, a particular feature of SPAS that is potentially very useful to biologists is the ability to perform free-form poolings of rows and columns of data. When analyzing real world data, this feature allows biologists to perform, and save the results of, many different poolings of their data as they search for the pooling that will give them the most acceptable estimates. When used in simulation studies, the pooling capabilities of SPAS allow a biologist to simulate the effects of their poolings, prior to ever conducting the experiment. This allows a biologist to better plan experiments so that they can realize the estimates, amount of bias, and level of precision they desire once they go out into the field.

As well, as was demonstrated by the studies presented in Chapters 3, 4, and 5, SPAS is a useful tool for exploring the theoretical properties of the estimators.

Chapter 7

Conclusions

This thesis presents the results of a study on the bias and precision of a number of stratified population estimates when applied to migrating populations that violate the assumptions of the pooled Petersen estimator. Although not comprehensive, the study found that for a number of populations representative of migrating fish populations, the pooled Petersen estimate exhibits large bias (Section 3.3.2.1). Additionally, while the pooled Petersen is capable of large bias, it was also shown to exhibit high, nearly constant precision (Section 3.3.2.2). Combining these two results, it was shown that the bias of the pooled Petersen is, for the majority of the populations studied, effective, and will therefore affect confidence interval coverage (Section 3.3.2.3).

As well, throughout this thesis, the bias and precision of the pooled Petersen estimate are compared to those of the Darroch moment estimate. Through these comparisons, it is found that while unbiased, the Darroch estimate typically exhibits much lower precision than the pooled Petersen. This is exemplified in Section 3.3.2.5, where it is shown that the Darroch moment estimate's precision is such that as much as a 3-fold increase in relative confidence interval width can be seen when moving from the pooled Petersen to the Darroch.

These two results, the large, effective bias of the pooled Petersen, and the low precision of the Darroch moment estimate, are particularly important to field biologists because they indicate that there is a tradeoff to be made between bias and precision when selecting an estimator for an experiment. If a biologist highly values precision in an estimate, without regard for bias, or confidence interval coverage, the pooled Petersen is a likely choice. Similarly, if a biologist values unbiasedness, at the expense of high precision, the stratified Darroch estimate is a likely choice.

Fortunately, the biologist is not restricted to such a limited choice, since it is shown that they may have the option of increasing the precision of the Darroch, at the expense of unbiasedness, through pooling (Chapter 5). It is shown that, for the representative populations studied, the precision of the Darroch estimate can be increased, without effective change in the bias of the estimate, by pooling 'like' rows and columns (i.e. rows and columns with similar capture/recapture probabilities, and similar migration probabilities).

This result is also important to a field biologist since it impacts both experiment planning and estimator selection. Based on the results of the pooling study, we conclude that it is always better to perform a stratified experiment, and use the Darroch moment, or iterative Darroch estimator, rather than performing a pooled experiment and using the pooled Petersen estimator. This implies that the biologist must plan their experiment, and distribute their marks, so that they sufficiently stratify the population under study to eliminate heterogeneity within sample strata.

Although the pooling study shows that the Darroch estimators are robust to heterogeneity in the strata, it also shows that increasing heterogeneity can cause large drops in the resulting estimate, and corresponding drops in the percent CV of the estimate. Using this property as a guide, a biologist can try a variety of poolings on their gathered data, until a pooling that produced satisfactory results is found. Again, such experimentation is only possible if the population is sufficiently stratified

to reduce, or eliminate heterogeneity within sample strata. This is necessary since by stratifying the studied population finely enough, the biologist will hopefully gather data that lends itself to many different poolings (i.e. the biologist would start with data at pooling level 2 in Chapter 5, instead of pooling level 12). As well, the biologist need not worry about over-stratification because, as is shown in the pooling study, any over-stratification in the sample, and its resulting low precision, can later be eliminated by pooling.

In addition to the results for closed populations, it is shown that the introduction of mortality into the sample populations further biased the pooled Petersen, and further lowered the precision of the Darroch moment estimator. This result simply underscores the previous conclusion that it is always better to perform a stratified experiment, and use one of the Darroch estimators, since they are unbiased in the presence of mortality, and their resulting low precision can be increased through pooling.

Chapter 4 presents the results of a study, similar to that conducted on the estimators, for the estimator's standard error estimates. This study shows that the standard error estimators exhibit properties that at once differ and are similar to the estimators themselves. In particular, it is shown that the pooled Petersen standard error estimate generally exhibits low bias and high precision, even when the estimate is itself biased. Similarly, it is shown that the standard error estimates for the moment and iterative Darroch estimates exhibit high, generally positive, bias, and low precision.

There are two results presented in Chapter 4 that are of particular note to a field biologist; namely that the standard error estimate for the Darroch moment estimate typically exhibits much higher bias than that of the iterative Darroch estimate, and that the iterative Darroch estimate shows that it is subject to reliability problems when formed on ill-fitting data. The first result indicates that, given the option, a

biologist would likely prefer to use the the iterative Darroch estimator over the Darroch moment estimator, since it provides the same unbiased population estimates, but the low bias in the standard error estimate provides better coverage than would be provided by the moment estimate. The second result indicates that the biologist may not have the option of selecting the iterative Darroch, since the biologist can potentially run into convergence problems when applying it to populations similar to those studied.

Fortunately, recalling the results of Chapter 5, the convergence problems of the iterative Darroch can be worked around by pooling data to obtain a better fit without adversely affecting the bias of the estimate.

Finally, the SPAS analysis and simulation package described in Chapter 6 demonstrates capabilities that can potentially be a great help to biologists in both analyzing experimental data, and in planning mark-recapture experiments.

In summary, the results presented in this thesis indicate that there is potentially much to be gained in using either the iterative Darroch, or Darroch moment estimator over the pooled Petersen. This is true for a number of reasons, namely:

1. the unbiasedness of the Darroch estimators,
2. the robustness of the Darroch estimators in the presence of mortality,
3. the additional estimates available from the Darroch estimators (e.g. stratum estimates, migration rates, etc.) that cannot be derived from the pooled Petersen, and
4. the flexibility of that the Darroch estimates provide by allowing a biologist to selectively pool data until a satisfactory result, in terms of bias and precision, is found.

7.0.1 Future Work

The results presented in this thesis suggest a number of areas for future investigation. It is shown in Chapter 3 that the Darroch estimator out-performs the pooled Petersen for the set of hypothetical populations studied, future research should be directed towards finding a general analytical result that a biologist can use to, given only collected data, determine the suitability of the Darroch over the pooled Petersen.

It is shown in Chapter 5 that there is no optimum level of pooling for the set of hypothetical populations studied. Future research should be directed towards determining whether this a general property of stratified populations, or if this result is particular to the populations studied. If it is discovered that this is a particular result, future research should be directed towards developing the general conditions necessary to obtain an optimum level of pooling. Additionally, provided this result is not general, a test should be developed to aid biologists in determining the optimum level of pooling for their data.

Bibliography

- [Arnason *et al.*, 1996] A.N. Arnason, C.W. Kirby, C.J. Schwarz, and J.R. Irvine. Computer analysis of data from stratified mark-recovery experiments for estimation of salmon escapements and other populations. Technical Report 2106, Canadian Technical Report of Fisheries and Aquatic Sciences, 1996.
- [Box *et al.*, 1969] M. J. Box, D. Davies, and W. H. Swann. *Non-Linear Optimization Techniques*, volume 5 of *I.C.I Monographs*. Oliver and Boyd, 1969.
- [Burnham *et al.*, 1987] K. P. Burnham, D. R. Anderson, and G. C. White. Design and analysis methods for fish survival experiments based on release-recapture. Monograph 5, American Fisheries Society, 1987.
- [Cass, 1995] A. Cass. Pink salmon escapement in the Fraser River. In J.R. Irvine and T.C. Nelson, editors, *Proceedings of the 1994 Salmon Escapement Workshop plus an Annotated Bibliography on Escapement Estimation*, pages 37–38. Minister of Supply and Services Canada, 1995.
- [Chapman and Junge, 1956] D.G. Chapman and C.O. Junge. The estimation of the size of a stratified population. *Annals of Mathematical Statistics*, 27:375–389, 1956.
- [Cochran, 1977] G. Cochran. *Sampling Techniques*. John Wiley and Sons, 3rd edition, 1977.

- [Darroch, 1961] J. N. Darroch. The two-sample capture-recapture census when tagging and sampling are stratified. *Biometrika*, 48:241-260, 1961.
- [Dempson and Stansbury, 1991] J. B. Dempson and D. E. Stansbury. Using partial counting fences and a two-sample stratified design for mark-recapture estimation of Atlantic salmon smolt population. *North American Journal of Fisheries Management*, 11:27-37, 1991.
- [Edwards, 1972] A. W. F. Edwards. *Likelihood*. Cambridge University Press, 1972.
- [Everitt and Dunn, 1983] B. S. Everitt and G. Dunn. *Advanced Methods of Data Exploration and Modelling*. Heinemann Educational Books, 1983.
- [Fraser River Sockeye Public Review Board, 1995] Fraser River Sockeye Public Review Board. *Fraser River Sockeye 1994: Problems & Discrepancies*. Canada Communication Group - Publishing, 1995.
- [Mardia *et al.*, 1979] K. V. Mardia, J. T. Kent, and J. M. Bibby. *Multivariate Analysis*. Academic Press, 1979.
- [Pacific Salmon Commission, 1994] Pacific Salmon Commission. *Report of the Fraser River Panel to the Pacific Salmon Commission on the 1991 Fraser River Sockeye and Pink Salmon Fishing Season*. Vancouver, B.C., 1994.
- [Plante, 1993] N. Plante. Estimation de la taille d'une population animale à l'aide d'un modèle de capture-recapture avec stratification. Master's thesis, Université Laval, 1993.
- [Schaefer, 1951] M. B. Schaefer. Estimation of size of animal populations by marking experiments. *Fishery Bulletin of the Fish and Wildlife Service*, 69:191-203, 1951.
- [Schwarz and Taylor, 1997] C.J. Schwarz and C.G. Taylor. The use of the stratified-Petersen estimator in fisheries management with an illustration of estimating

the number of pink salmon (*Oncorhynchus gorbuscha*) that return to spawn in the Fraser River. *Canadian Journal of Fisheries and Aquatic Sciences*, 1997. To appear.

[Seber, 1973] G. A. F. Seber. *The Estimation of Animal Abundance*. Charles Griffin and Company Ltd., 1973.

[Simpson, 1984] Kent Simpson. The accuracy of mark-recapture estimates of escapements. In *Proceedings of the Workshop on Stream Indexing for Salmon Escapement Estimation*, pages 209–223, 1984.

[Strang, 1986] J. Strang. *Programming with curses*. O'Reilly and Associates, Sebastopol, CA, 1986.

[Warren and Dempson, 1995] W. G. Warren and J.B. Dempson. Does temporal stratification improve the accuracy of mark-recapture estimates of smolt production: a case study based in the Conne River, Newfoundland. *North American Journal of Fisheries Management*, 15:126–136, 1995.

[White *et al.*, 1982] G.C. White, D.R. Anderson, K.P. Burnham, and D.L. Otis. *Capture-Recapture and Removal Methods for Sampling Closed Populations*. Los Alamos National Laboratory, 1982.

Appendix A

Tables for the Closed Model, Mean-Value Analyses

Table A.1: Percent absolute asymptotic relative bias (ARB) of the pooled Petersen.

| <i>Capture</i> | <i>Migration Model</i> | <i>Recapture</i> | | |
|----------------|------------------------|------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 2.06 | 3.38 | 7.28 |
| | <i>B</i> | 1.48 | 2.75 | 6.14 |
| | <i>C</i> | 0.53 | 0.95 | 1.87 |
| <i>Set 3</i> | <i>A</i> | 3.38 | 6.98 | 15.16 |
| | <i>B</i> | 2.79 | 5.65 | 12.33 |
| | <i>C</i> | 0.99 | 2.01 | 4.01 |
| <i>Set 6</i> | <i>A</i> | 7.28 | 15.16 | 30.98 |
| | <i>B</i> | 6.37 | 12.60 | 25.73 |
| | <i>C</i> | 2.29 | 4.63 | 9.41 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Recapture</i> | | |
|----------------|------------------------|------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 2.53 | 3.85 | 9.46 |
| | <i>B</i> | 1.64 | 3.01 | 7.61 |
| | <i>C</i> | 0.54 | 0.94 | 1.94 |
| <i>Set 3</i> | <i>A</i> | 3.83 | 7.70 | 19.37 |
| | <i>B</i> | 2.95 | 6.05 | 14.97 |
| | <i>C</i> | 0.98 | 1.97 | 4.16 |
| <i>Set 6</i> | <i>A</i> | 9.45 | 19.45 | 42.39 |
| | <i>B</i> | 7.91 | 15.87 | 34.54 |
| | <i>C</i> | 2.70 | 5.54 | 11.61 |

(b) Normal entry

Table A.2: Mean-value percent CV of the pooled Petersen estimate.

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------|-------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 4.26 | 4.23 | 4.13 | 1.35 | 1.34 | 1.31 |
| | B | 4.27 | 4.23 | 4.15 | 1.35 | 1.34 | 1.32 |
| | C | 4.22 | 4.13 | 3.92 | 1.34 | 1.31 | 1.24 |
| Set 3 | A | 4.23 | 4.14 | 3.93 | 1.34 | 1.31 | 1.25 |
| | B | 4.23 | 4.16 | 3.99 | 1.34 | 1.32 | 1.27 |
| | C | 4.21 | 4.11 | 3.87 | 1.34 | 1.30 | 1.23 |
| Set 6 | A | 4.13 | 3.93 | 3.48 | 1.31 | 1.25 | 1.10 |
| | B | 4.15 | 3.98 | 3.63 | 1.32 | 1.26 | 1.15 |
| | C | 4.18 | 4.04 | 3.75 | 1.33 | 1.28 | 1.19 |

(a) Uniform entry

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------|-------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 4.53 | 4.65 | 5.02 | 1.44 | 1.48 | 1.60 |
| | B | 4.51 | 4.60 | 4.86 | 1.43 | 1.46 | 1.55 |
| | C | 4.40 | 4.34 | 4.20 | 1.40 | 1.38 | 1.33 |
| Set 3 | A | 4.66 | 4.71 | 4.88 | 1.48 | 1.50 | 1.55 |
| | B | 4.64 | 4.68 | 4.81 | 1.48 | 1.49 | 1.53 |
| | C | 4.55 | 4.47 | 4.30 | 1.44 | 1.42 | 1.37 |
| Set 6 | A | 5.05 | 4.91 | 4.54 | 1.61 | 1.56 | 1.44 |
| | B | 5.06 | 4.94 | 4.67 | 1.61 | 1.57 | 1.48 |
| | C | 5.05 | 4.91 | 4.61 | 1.61 | 1.56 | 1.47 |

(b) Normal entry

Table A.3: Mean-value effective bias of the pooled Petersen estimate. Values in bold indicate no effective bias (i.e. < 0.5).

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.48 | 0.80 | 1.76 | 1.52 | 2.52 | 5.55 |
| | <i>B</i> | 0.35 | 0.65 | 1.48 | 1.09 | 2.05 | 4.66 |
| | <i>C</i> | 0.13 | 0.23 | 0.48 | 0.39 | 0.72 | 1.50 |
| <i>Set 3</i> | <i>A</i> | 0.80 | 1.69 | 3.86 | 2.52 | 5.31 | 12.17 |
| | <i>B</i> | 0.66 | 1.36 | 3.09 | 2.08 | 4.29 | 9.73 |
| | <i>C</i> | 0.24 | 0.49 | 1.04 | 0.74 | 1.54 | 3.27 |
| <i>Set 6</i> | <i>A</i> | 1.76 | 3.86 | 8.90 | 5.55 | 12.17 | 28.08 |
| | <i>B</i> | 1.54 | 3.17 | 7.09 | 4.84 | 9.98 | 22.37 |
| | <i>C</i> | 0.55 | 1.15 | 2.51 | 1.73 | 3.61 | 7.92 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.56 | 0.83 | 1.88 | 1.76 | 2.61 | 5.92 |
| | <i>B</i> | 0.36 | 0.65 | 1.57 | 1.14 | 2.06 | 4.93 |
| | <i>C</i> | 0.12 | 0.22 | 0.46 | 0.37 | 0.68 | 1.45 |
| <i>Set 3</i> | <i>A</i> | 0.82 | 1.63 | 3.97 | 2.59 | 5.14 | 12.49 |
| | <i>B</i> | 0.63 | 1.29 | 3.11 | 2.00 | 4.07 | 9.79 |
| | <i>C</i> | 0.21 | 0.44 | 0.97 | 0.68 | 1.39 | 3.05 |
| <i>Set 6</i> | <i>A</i> | 1.87 | 3.97 | 9.34 | 5.88 | 12.48 | 29.42 |
| | <i>B</i> | 1.56 | 3.21 | 7.40 | 4.92 | 10.11 | 23.30 |
| | <i>C</i> | 0.53 | 1.13 | 2.52 | 1.68 | 3.54 | 7.92 |

(b) Normal entry

Table A.4: Mean-value percent CV of the Darroch estimate.

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------|-------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 4.54 | 4.72 | 6.78 | 1.43 | 1.49 | 2.15 |
| | B | 4.50 | 4.68 | 6.67 | 1.42 | 1.48 | 2.11 |
| | C | 4.39 | 4.46 | 5.87 | 1.39 | 1.41 | 1.86 |
| Set 3 | A | 4.72 | 4.98 | 7.34 | 1.49 | 1.57 | 2.32 |
| | B | 4.69 | 4.92 | 7.16 | 1.48 | 1.55 | 2.26 |
| | C | 4.54 | 4.63 | 6.15 | 1.44 | 1.46 | 1.94 |
| Set 6 | A | 6.78 | 7.34 | 11.77 | 2.15 | 2.32 | 3.72 |
| | B | 6.67 | 7.16 | 11.13 | 2.11 | 2.26 | 3.52 |
| | C | 6.34 | 6.52 | 8.94 | 2.01 | 2.06 | 2.83 |

(a) Uniform entry

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------|-------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 4.87 | 5.20 | 8.08 | 1.54 | 1.64 | 2.56 |
| | B | 4.79 | 5.09 | 7.72 | 1.52 | 1.61 | 2.44 |
| | C | 4.59 | 4.70 | 6.36 | 1.45 | 1.49 | 2.01 |
| Set 3 | A | 5.20 | 5.60 | 8.81 | 1.64 | 1.77 | 2.79 |
| | B | 5.12 | 5.47 | 8.39 | 1.62 | 1.73 | 2.65 |
| | C | 4.89 | 5.02 | 6.83 | 1.55 | 1.59 | 2.16 |
| Set 6 | A | 8.11 | 8.84 | 14.59 | 2.56 | 2.79 | 4.61 |
| | B | 7.92 | 8.56 | 13.64 | 2.50 | 2.71 | 4.31 |
| | C | 7.46 | 7.70 | 10.69 | 2.36 | 2.44 | 3.38 |

(b) Normal entry

Table A.5: Mean-value confidence loss of the Darroch over the pooled Petersen. Values in bold indicate factor combinations where the pooled Petersen exhibited no effective bias.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1.06 | 1.12 | 1.64 | 1.06 | 1.11 | 1.64 |
| | <i>B</i> | 1.06 | 1.11 | 1.61 | 1.05 | 1.10 | 1.60 |
| | <i>C</i> | 1.04 | 1.08 | 1.50 | 1.04 | 1.08 | 1.49 |
| <i>Set 3</i> | <i>A</i> | 1.12 | 1.20 | 1.87 | 1.11 | 1.20 | 1.86 |
| | <i>B</i> | 1.11 | 1.18 | 1.79 | 1.10 | 1.18 | 1.79 |
| | <i>C</i> | 1.07 | 1.13 | 1.59 | 1.08 | 1.12 | 1.58 |
| <i>Set 6</i> | <i>A</i> | 1.64 | 1.87 | 3.38 | 1.64 | 1.86 | 3.37 |
| | <i>B</i> | 1.61 | 1.80 | 3.07 | 1.60 | 1.79 | 3.06 |
| | <i>C</i> | 1.52 | 1.61 | 2.38 | 1.51 | 1.61 | 2.38 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1.07 | 1.12 | 1.61 | 1.07 | 1.11 | 1.60 |
| | <i>B</i> | 1.06 | 1.11 | 1.59 | 1.06 | 1.10 | 1.58 |
| | <i>C</i> | 1.04 | 1.08 | 1.51 | 1.04 | 1.08 | 1.51 |
| <i>Set 3</i> | <i>A</i> | 1.12 | 1.19 | 1.80 | 1.11 | 1.18 | 1.80 |
| | <i>B</i> | 1.11 | 1.17 | 1.74 | 1.10 | 1.16 | 1.74 |
| | <i>C</i> | 1.08 | 1.12 | 1.59 | 1.07 | 1.12 | 1.58 |
| <i>Set 6</i> | <i>A</i> | 1.60 | 1.80 | 3.22 | 1.60 | 1.79 | 3.20 |
| | <i>B</i> | 1.56 | 1.73 | 2.92 | 1.56 | 1.72 | 2.91 |
| | <i>C</i> | 1.48 | 1.57 | 2.32 | 1.47 | 1.56 | 2.31 |

(b) Normal entry

Table A.6: Mean-value RMSE of the Darroch over the pooled Petersen. Values in bold indicate factor combinations where the pooled Petersen exhibited no effective bias.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.97 | 0.89 | 0.86 | 0.59 | 0.41 | 0.32 |
| | <i>B</i> | 1.01 | 0.94 | 0.96 | 0.71 | 0.48 | 0.38 |
| | <i>C</i> | 1.04 | 1.06 | 1.28 | 0.97 | 0.87 | 0.84 |
| <i>Set 3</i> | <i>A</i> | 0.89 | 0.62 | 0.54 | 0.41 | 0.22 | 0.18 |
| | <i>B</i> | 0.95 | 0.71 | 0.63 | 0.49 | 0.27 | 0.21 |
| | <i>C</i> | 1.06 | 1.03 | 1.13 | 0.88 | 0.62 | 0.51 |
| <i>Set 6</i> | <i>A</i> | 0.86 | 0.54 | 0.51 | 0.32 | 0.18 | 0.16 |
| | <i>B</i> | 0.97 | 0.63 | 0.56 | 0.39 | 0.21 | 0.18 |
| | <i>C</i> | 1.27 | 1.14 | 1.14 | 0.88 | 0.55 | 0.43 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.96 | 0.88 | 0.81 | 0.53 | 0.40 | 0.29 |
| | <i>B</i> | 1.01 | 0.95 | 0.94 | 0.70 | 0.50 | 0.36 |
| | <i>C</i> | 1.04 | 1.06 | 1.31 | 0.97 | 0.90 | 0.84 |
| <i>Set 3</i> | <i>A</i> | 0.88 | 0.63 | 0.52 | 0.40 | 0.23 | 0.17 |
| | <i>B</i> | 0.95 | 0.73 | 0.61 | 0.48 | 0.28 | 0.20 |
| | <i>C</i> | 1.07 | 1.04 | 1.15 | 0.90 | 0.66 | 0.52 |
| <i>Set 6</i> | <i>A</i> | 0.81 | 0.52 | 0.46 | 0.29 | 0.17 | 0.15 |
| | <i>B</i> | 0.95 | 0.63 | 0.53 | 0.37 | 0.21 | 0.17 |
| | <i>C</i> | 1.29 | 1.17 | 1.14 | 0.89 | 0.58 | 0.43 |

(b) Normal entry

Appendix B

Tables for the Open Model, Mean-Value Analyses

Table B.1: Mean-value percent asymptotic relative bias of the pooled Petersen with the high variance mortality model. All values have been negated for simpler presentation.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 6.71 | 7.54 | 9.45 | 6.42 | 7.28 | 9.24 |
| | <i>B</i> | 5.48 | 6.31 | 8.04 | 5.19 | 6.04 | 7.82 |
| | <i>C</i> | 2.10 | 2.36 | 2.76 | 1.82 | 2.11 | 2.55 |
| <i>Set 3</i> | <i>A</i> | 12.54 | 14.75 | 18.79 | 12.30 | 14.53 | 18.62 |
| | <i>B</i> | 10.45 | 12.24 | 15.58 | 10.19 | 12.01 | 15.39 |
| | <i>C</i> | 3.95 | 4.60 | 5.56 | 3.69 | 4.36 | 5.37 |
| <i>Set 6</i> | <i>A</i> | 25.37 | 29.24 | 36.41 | 25.19 | 29.09 | 36.30 |
| | <i>B</i> | 21.72 | 24.99 | 30.97 | 21.53 | 24.82 | 30.85 |
| | <i>C</i> | 8.64 | 10.03 | 12.39 | 8.40 | 9.82 | 12.23 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 8.37 | 9.52 | 12.83 | 7.99 | 9.15 | 12.49 |
| | <i>B</i> | 6.47 | 7.62 | 10.43 | 6.10 | 7.27 | 10.11 |
| | <i>C</i> | 2.14 | 2.38 | 2.83 | 1.82 | 2.10 | 2.59 |
| <i>Set 3</i> | <i>A</i> | 15.17 | 18.26 | 25.11 | 14.82 | 17.94 | 24.84 |
| | <i>B</i> | 12.10 | 14.53 | 19.76 | 11.75 | 14.21 | 19.49 |
| | <i>C</i> | 4.01 | 4.67 | 5.76 | 3.69 | 4.38 | 5.52 |
| <i>Set 6</i> | <i>A</i> | 33.94 | 39.52 | 50.45 | 33.68 | 39.30 | 50.31 |
| | <i>B</i> | 28.46 | 33.15 | 42.25 | 28.18 | 32.91 | 42.07 |
| | <i>C</i> | 10.45 | 12.18 | 15.22 | 10.10 | 11.87 | 14.98 |

(b) Normal entry

Table B.2: Mean-value percent CV of the pooled Petersen estimate with the high variance mortality model.

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.00 | 7.99 | 8.51 | 13.23 | 2.53 | 2.69 |
| | <i>B</i> | 4.18 | 7.92 | 8.44 | 13.00 | 2.51 | 2.67 |
| | <i>C</i> | 4.11 | 7.22 | 7.57 | 11.09 | 2.28 | 2.39 |
| <i>Set 3</i> | <i>A</i> | 3.51 | 8.55 | 9.17 | 14.45 | 2.70 | 2.90 |
| | <i>B</i> | 4.57 | 8.44 | 9.03 | 14.08 | 2.67 | 2.86 |
| | <i>C</i> | 4.45 | 7.53 | 7.91 | 11.66 | 2.38 | 2.50 |
| <i>Set 6</i> | <i>A</i> | 3.69 | 13.57 | 14.72 | 24.22 | 4.29 | 4.66 |
| | <i>B</i> | 7.66 | 12.95 | 14.00 | 22.61 | 4.10 | 4.43 |
| | <i>C</i> | 7.15 | 10.84 | 11.46 | 17.20 | 3.43 | 3.62 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 5.44 | 9.33 | 10.06 | 16.32 | 2.95 | 3.18 |
| | <i>B</i> | 5.16 | 9.01 | 9.70 | 15.46 | 2.85 | 3.07 |
| | <i>C</i> | 4.89 | 7.74 | 8.16 | 12.15 | 2.45 | 2.58 |
| <i>Set 3</i> | <i>A</i> | 3.84 | 10.13 | 10.96 | 17.87 | 3.20 | 3.47 |
| | <i>B</i> | 5.65 | 9.76 | 10.53 | 16.88 | 3.09 | 3.33 |
| | <i>C</i> | 5.34 | 8.29 | 8.75 | 13.07 | 2.62 | 2.77 |
| <i>Set 6</i> | <i>A</i> | 4.13 | 16.81 | 18.27 | 30.50 | 5.31 | 5.78 |
| | <i>B</i> | 9.65 | 15.81 | 17.14 | 27.99 | 5.00 | 5.42 |
| | <i>C</i> | 8.85 | 12.92 | 13.69 | 20.71 | 4.09 | 4.33 |

(b) Normal entry

Table B.3: Mean-value effective bias of the pooled Petersen estimate with the high variance mortality model. Values in bold indicate no effective bias. All values have been negated for simpler presentation.

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------------|-------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 1.15 | 1.34 | 1.83 | 3.48 | 4.09 | 5.65 |
| | B | 0.94 | 1.13 | 1.56 | 2.82 | 3.40 | 4.78 |
| | C | 0.38 | 0.44 | 0.57 | 1.03 | 1.25 | 1.68 |
| Set 3 | A | 2.24 | 2.75 | 3.88 | 6.91 | 8.54 | 12.12 |
| | B | 1.85 | 2.27 | 3.17 | 5.70 | 7.01 | 9.87 |
| | C | 0.72 | 0.88 | 1.18 | 2.11 | 2.62 | 3.59 |
| Set 6 | A | 4.95 | 6.06 | 8.65 | 15.49 | 19.02 | 27.22 |
| | B | 4.15 | 5.06 | 7.07 | 12.98 | 15.84 | 22.21 |
| | C | 1.61 | 1.98 | 2.74 | 4.95 | 6.10 | 8.52 |

(a) Uniform entry

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------------|-------------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 1.24 | 1.42 | 1.96 | 3.72 | 4.30 | 6.00 |
| | B | 0.98 | 1.17 | 1.67 | 2.91 | 3.52 | 5.09 |
| | C | 0.36 | 0.42 | 0.54 | 0.97 | 1.16 | 1.57 |
| Set 3 | A | 2.26 | 2.78 | 4.02 | 6.94 | 8.59 | 12.52 |
| | B | 1.83 | 2.25 | 3.24 | 5.58 | 6.93 | 10.05 |
| | C | 0.66 | 0.80 | 1.09 | 1.91 | 2.36 | 3.28 |
| Set 6 | A | 5.15 | 6.31 | 9.05 | 16.10 | 19.76 | 28.43 |
| | B | 4.28 | 5.23 | 7.39 | 13.34 | 16.34 | 23.18 |
| | C | 1.59 | 1.95 | 2.71 | 4.83 | 5.97 | 8.40 |

(b) Normal entry

Table B.4: Mean-value percent CV of the Darroch estimate with the high variance mortality model.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| <i>Set 1</i> | <i>A</i> | 7.99 | 8.51 | 13.23 | 2.53 | 2.69 | 4.18 |
| | <i>B</i> | 7.92 | 8.44 | 13.00 | 2.51 | 2.67 | 4.11 |
| | <i>C</i> | 7.22 | 7.57 | 11.09 | 2.28 | 2.39 | 3.51 |
| <i>Set 3</i> | <i>A</i> | 8.55 | 9.17 | 14.45 | 2.70 | 2.90 | 4.57 |
| | <i>B</i> | 8.44 | 9.03 | 14.08 | 2.67 | 2.86 | 4.45 |
| | <i>C</i> | 7.53 | 7.91 | 11.66 | 2.38 | 2.50 | 3.69 |
| <i>Set 6</i> | <i>A</i> | 13.57 | 14.72 | 24.22 | 4.29 | 4.66 | 7.66 |
| | <i>B</i> | 12.95 | 14.00 | 22.61 | 4.10 | 4.43 | 7.15 |
| | <i>C</i> | 10.84 | 11.46 | 17.20 | 3.43 | 3.62 | 5.44 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| <i>Set 1</i> | <i>A</i> | 9.33 | 10.06 | 16.32 | 2.95 | 3.18 | 5.16 |
| | <i>B</i> | 9.01 | 9.70 | 15.46 | 2.85 | 3.07 | 4.89 |
| | <i>C</i> | 7.74 | 8.16 | 12.15 | 2.45 | 2.58 | 3.84 |
| <i>Set 3</i> | <i>A</i> | 10.13 | 10.96 | 17.87 | 3.20 | 3.47 | 5.65 |
| | <i>B</i> | 9.76 | 10.53 | 16.88 | 3.09 | 3.33 | 5.34 |
| | <i>C</i> | 8.29 | 8.75 | 13.07 | 2.62 | 2.77 | 4.13 |
| <i>Set 6</i> | <i>A</i> | 16.81 | 18.27 | 30.50 | 5.31 | 5.78 | 9.65 |
| | <i>B</i> | 15.81 | 17.14 | 27.99 | 5.00 | 5.42 | 8.85 |
| | <i>C</i> | 12.92 | 13.69 | 20.71 | 4.09 | 4.33 | 6.55 |

(b) Normal entry

Table B.5: Mean-value confidence loss of the Darroch versus the pooled Petersen with the high variance mortality model. Values in bold indicates situations where the pooled Petersen was not subject to effective bias.

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1.37 | 1.52 | 2.57 | 1.37 | 1.51 | 2.56 |
| | <i>B</i> | 1.36 | 1.51 | 2.52 | 1.36 | 1.50 | 2.51 |
| | <i>C</i> | 1.30 | 1.42 | 2.31 | 1.29 | 1.42 | 2.30 |
| <i>Set 3</i> | <i>A</i> | 1.53 | 1.71 | 2.98 | 1.52 | 1.71 | 2.97 |
| | <i>B</i> | 1.50 | 1.67 | 2.86 | 1.49 | 1.67 | 2.86 |
| | <i>C</i> | 1.37 | 1.51 | 2.47 | 1.36 | 1.50 | 2.46 |
| <i>Set 6</i> | <i>A</i> | 2.65 | 3.05 | 5.75 | 2.64 | 3.04 | 5.74 |
| | <i>B</i> | 2.48 | 2.83 | 5.16 | 2.47 | 2.83 | 5.15 |
| | <i>C</i> | 2.03 | 2.26 | 3.80 | 2.02 | 2.25 | 3.79 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1.38 | 1.50 | 2.49 | 1.37 | 1.49 | 2.48 |
| | <i>B</i> | 1.36 | 1.49 | 2.47 | 1.36 | 1.49 | 2.46 |
| | <i>C</i> | 1.31 | 1.43 | 2.34 | 1.30 | 1.43 | 2.33 |
| <i>Set 3</i> | <i>A</i> | 1.51 | 1.67 | 2.86 | 1.50 | 1.66 | 2.85 |
| | <i>B</i> | 1.47 | 1.63 | 2.76 | 1.47 | 1.62 | 2.75 |
| | <i>C</i> | 1.36 | 1.50 | 2.46 | 1.36 | 1.50 | 2.46 |
| <i>Set 6</i> | <i>A</i> | 2.55 | 2.92 | 5.47 | 2.54 | 2.91 | 5.45 |
| | <i>B</i> | 2.38 | 2.70 | 4.89 | 2.37 | 2.69 | 4.88 |
| | <i>C</i> | 1.97 | 2.19 | 3.69 | 1.96 | 2.18 | 3.67 |

(b) Normal entry

Table B.6: Mean-value RMSE ratio of the Darroch and pooled Petersen estimates with the high variance mortality model. Values in bold indicate situation where the pooled Petersen was not subject to effective bias.

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------------|-------------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 0.93 | 0.93 | 1.26 | 0.38 | 0.36 | 0.45 |
| | B | 1.02 | 1.03 | 1.39 | 0.46 | 0.43 | 0.52 |
| | C | 1.24 | 1.33 | 2.05 | 0.91 | 0.89 | 1.19 |
| Set 3 | A | 0.64 | 0.59 | 0.75 | 0.22 | 0.20 | 0.24 |
| | B | 0.73 | 0.69 | 0.87 | 0.26 | 0.24 | 0.29 |
| | C | 1.14 | 1.16 | 1.64 | 0.59 | 0.54 | 0.66 |
| Set 6 | A | 0.53 | 0.50 | 0.66 | 0.17 | 0.16 | 0.21 |
| | B | 0.59 | 0.55 | 0.73 | 0.19 | 0.18 | 0.23 |
| | C | 1.09 | 1.04 | 1.32 | 0.40 | 0.37 | 0.44 |

(a) Uniform entry

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|-------------|-------|-------------------------------|-------|-------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 0.90 | 0.89 | 1.16 | 0.36 | 0.34 | 0.41 |
| | B | 1.01 | 1.00 | 1.31 | 0.44 | 0.41 | 0.48 |
| | C | 1.25 | 1.35 | 2.10 | 0.94 | 0.94 | 1.26 |
| Set 3 | A | 0.63 | 0.58 | 0.70 | 0.21 | 0.19 | 0.23 |
| | B | 0.73 | 0.68 | 0.83 | 0.26 | 0.23 | 0.27 |
| | C | 1.17 | 1.21 | 1.71 | 0.63 | 0.59 | 0.72 |
| Set 6 | A | 0.49 | 0.46 | 0.60 | 0.16 | 0.15 | 0.19 |
| | B | 0.55 | 0.51 | 0.66 | 0.18 | 0.16 | 0.21 |
| | C | 1.08 | 1.02 | 1.30 | 0.40 | 0.36 | 0.44 |

(b) Normal entry

Appendix C

Tables for the Mean-Value Analysis Verification

Table C.1: Percent ARB of the pooled Petersen estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 2.02 | 3.23 | 7.41 | 2.02 | 3.34 | 7.27 |
| | <i>B</i> | 1.65 | 3.11 | 6.28 | 1.44 | 2.69 | 6.17 |
| | <i>C</i> | - | - | - | 0.60 | 0.91 | 1.85 |
| <i>Set 3</i> | <i>A</i> | 3.45 | 6.95 | 15.28 | 3.38 | 6.96 | 15.15 |
| | <i>B</i> | 3.04 | 5.99 | 12.45 | 2.87 | 5.62 | 12.27 |
| | <i>C</i> | - | - | - | 1.03 | 2.04 | 4.09 |
| <i>Set 6</i> | <i>A</i> | 7.16 | 15.38 | 31.18 | 7.29 | 15.13 | 30.98 |
| | <i>B</i> | 6.53 | 12.84 | - | 6.38 | 12.61 | 25.74 |
| | <i>C</i> | - | - | - | 2.34 | 4.61 | 9.46 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | Small Population | | | Large Population | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 2.38 | 3.89 | 9.45 | 2.59 | 3.87 | 9.56 |
| | <i>B</i> | 2.15 | 3.22 | 7.92 | 1.59 | 3.02 | 7.65 |
| | <i>C</i> | - | - | - | 0.58 | 1.02 | 1.99 |
| <i>Set 3</i> | <i>A</i> | 3.83 | 7.64 | 19.63 | 3.77 | 7.72 | 19.31 |
| | <i>B</i> | 3.26 | 6.38 | 15.26 | 2.96 | 6.02 | 14.97 |
| | <i>C</i> | - | - | - | 1.03 | 2.03 | 4.16 |
| <i>Set 6</i> | <i>A</i> | 9.21 | 19.52 | 42.41 | 9.45 | 19.45 | 42.37 |
| | <i>B</i> | 8.40 | - | - | 7.91 | 15.86 | 34.57 |
| | <i>C</i> | - | - | - | 2.73 | 5.53 | 11.68 |

(b) Normal entry

Table C.2: Percent CV of the pooled Petersen estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 4.34 | 4.19 | 4.16 | 1.31 | 1.37 | 1.37 |
| | <i>B</i> | 4.34 | 4.27 | 4.03 | 1.35 | 1.36 | 1.33 |
| | <i>C</i> | - | - | - | 1.34 | 1.30 | 1.24 |
| <i>Set 3</i> | <i>A</i> | 4.27 | 4.13 | 3.91 | 1.33 | 1.31 | 1.25 |
| | <i>B</i> | 4.42 | 4.12 | 3.96 | 1.34 | 1.32 | 1.30 |
| | <i>C</i> | - | - | - | 1.30 | 1.30 | 1.24 |
| <i>Set 6</i> | <i>A</i> | 4.15 | 3.93 | 3.50 | 1.32 | 1.23 | 1.10 |
| | <i>B</i> | 4.08 | 3.97 | - | 1.31 | 1.26 | 1.13 |
| | <i>C</i> | - | - | - | 1.29 | 1.31 | 1.21 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 4.65 | 4.67 | 5.04 | 1.43 | 1.47 | 1.54 |
| | <i>B</i> | 4.42 | 4.79 | 4.74 | 1.41 | 1.51 | 1.53 |
| | <i>C</i> | - | - | - | 1.39 | 1.36 | 1.29 |
| <i>Set 3</i> | <i>A</i> | 4.89 | 4.63 | 4.89 | 1.53 | 1.55 | 1.60 |
| | <i>B</i> | 4.61 | 4.73 | 4.80 | 1.51 | 1.46 | 1.52 |
| | <i>C</i> | - | - | - | 1.46 | 1.42 | 1.32 |
| <i>Set 6</i> | <i>A</i> | 4.81 | 5.08 | 4.86 | 1.67 | 1.52 | 1.38 |
| | <i>B</i> | 4.92 | - | - | 1.65 | 1.65 | 1.50 |
| | <i>C</i> | - | - | - | 1.52 | 1.59 | 1.48 |

(b) Normal entry

Table C.3: Percent CV of the Darroch moment estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 4.96 | 5.38 | 9.24 | 1.42 | 1.52 | 2.26 |
| | <i>B</i> | 5.23 | 5.24 | -2787.47 | 1.44 | 1.52 | 2.28 |
| | <i>C</i> | - | - | - | 1.51 | 1.48 | 1.98 |
| <i>Set 3</i> | <i>A</i> | 5.51 | 5.73 | 11.03 | 1.51 | 1.56 | 2.45 |
| | <i>B</i> | 5.53 | 5.72 | -2549.51 | 1.54 | 1.60 | 2.49 |
| | <i>C</i> | - | - | - | 1.52 | 1.58 | 2.16 |
| <i>Set 6</i> | <i>A</i> | 10.32 | 10.44 | 11.41 | 2.19 | 2.37 | 4.53 |
| | <i>B</i> | 8.18 | 8.88 | - | 2.25 | 2.33 | 4.17 |
| | <i>C</i> | - | - | - | 2.27 | - | - |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 5.35 | 5.87 | 10.78 | 1.55 | 1.66 | 2.61 |
| | <i>B</i> | 5.39 | 5.95 | -2787.47 | 1.51 | 1.66 | 2.54 |
| | <i>C</i> | - | - | - | 1.53 | 1.57 | 2.10 |
| <i>Set 3</i> | <i>A</i> | 5.87 | 6.03 | 12.90 | 1.68 | 1.79 | 3.04 |
| | <i>B</i> | 5.82 | 6.01 | 11.00 | 1.69 | 1.78 | 2.90 |
| | <i>C</i> | - | - | - | 1.66 | 1.69 | 2.34 |
| <i>Set 6</i> | <i>A</i> | 10.34 | 13.37 | 17.87 | 2.59 | 2.98 | 5.02 |
| | <i>B</i> | 9.15 | 10.61 | - | 2.66 | 2.88 | 4.74 |
| | <i>C</i> | - | - | - | 2.44 | 2.68 | - |

(b) Normal entry

Appendix D

Tables for the Closed Model, Standard Error Estimate Study

Appendix D. Tables for the Closed Model, Standard Error Estimate Study130

Table D.1: Percent asymptotic relative bias of the pooled Petersen standard error estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | -1.49 | 1.27 | -0.35 | 3.23 | -1.83 | -4.45 |
| | <i>B</i> | -1.33 | -0.81 | 3.36 | 0.27 | -1.32 | -1.13 |
| | <i>C</i> | - | - | - | 0.09 | 0.52 | 0.44 |
| <i>Set 3</i> | <i>A</i> | -0.70 | 0.60 | 0.53 | 0.84 | 0.39 | -0.11 |
| | <i>B</i> | -4.12 | 1.22 | 1.21 | 0.18 | 0.16 | -2.49 |
| | <i>C</i> | - | - | - | 2.77 | 0.12 | -1.23 |
| <i>Set 6</i> | <i>A</i> | 0.03 | 0.18 | -0.60 | -0.37 | 1.47 | 0.34 |
| | <i>B</i> | 1.93 | 0.49 | - | 0.77 | 0.24 | 1.35 |
| | <i>C</i> | - | - | - | 2.65 | -1.85 | -1.76 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | -2.18 | -0.09 | 0.17 | 0.41 | 0.41 | 3.38 |
| | <i>B</i> | 2.21 | -3.70 | 2.82 | 1.69 | -3.38 | 1.01 |
| | <i>C</i> | - | - | - | 0.76 | 1.21 | 3.37 |
| <i>Set 3</i> | <i>A</i> | -4.27 | 2.26 | 0.05 | -2.97 | -3.57 | -3.02 |
| | <i>B</i> | 0.96 | -0.68 | 0.58 | -2.56 | 2.13 | 0.74 |
| | <i>C</i> | - | - | - | -1.34 | -0.30 | 3.22 |
| <i>Set 6</i> | <i>A</i> | 5.82 | -2.98 | -6.26 | -3.99 | 2.86 | 4.66 |
| | <i>B</i> | 3.04 | -3.88 | - | -2.22 | -4.76 | -1.10 |
| | <i>C</i> | - | - | - | 5.42 | -1.41 | -0.83 |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study131

Table D.2: Percent asymptotic relative bias of the Darroch moment standard error estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 3.40 | 2.34 | 11.28 | 4.53 | 0.95 | -0.91 |
| | <i>B</i> | 19.25 | 27.12 | -100.00 | 5.96 | 4.91 | 3.96 |
| | <i>C</i> | - | - | - | 8.55 | 14.75 | 25.43 |
| <i>Set 3</i> | <i>A</i> | 0.94 | 4.17 | 11.88 | 2.36 | 4.14 | -0.06 |
| | <i>B</i> | 20.44 | 30.04 | -100.00 | 3.95 | 5.10 | 4.32 |
| | <i>C</i> | - | - | - | 14.35 | 13.00 | 28.57 |
| <i>Set 6</i> | <i>A</i> | 7.41 | 16.64 | 47.35 | 5.36 | 5.27 | -1.22 |
| | <i>B</i> | 49.97 | 59.29 | - | 9.20 | 13.30 | 16.78 |
| | <i>C</i> | - | - | - | 21.12 | -92.21 | -89.01 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1.23 | -0.85 | 1.57 | 2.05 | 1.44 | 0.14 |
| | <i>B</i> | 17.72 | 13.42 | 37.24 | 7.18 | 3.25 | 3.99 |
| | <i>C</i> | - | - | - | 9.51 | 9.46 | 18.49 |
| <i>Set 3</i> | <i>A</i> | -0.25 | 4.92 | -1.20 | 1.06 | 1.69 | -5.02 |
| | <i>B</i> | 19.96 | 23.20 | -77.49 | 2.50 | 3.72 | -0.24 |
| | <i>C</i> | - | - | - | 7.86 | 10.33 | 16.57 |
| <i>Set 6</i> | <i>A</i> | 6.96 | -3.37 | 35.49 | 4.46 | -1.24 | 1.00 |
| | <i>B</i> | -54.56 | 45.69 | - | 5.66 | 5.79 | 12.06 |
| | <i>C</i> | - | - | - | 21.15 | 16.82 | -81.62 |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study132

Table D.3: Good replications versus total replications for all factor combinations, with no mortality. The number of good replications was limited to 1000, and the total replications limited to 5000. Total replications of 1000 or slightly more indicate very low rejection rates.

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|--------------|--------------|-------------------------------|--------------|--------------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 1000 1008 | 1000 1014 | 1000 1238 | 1000 1000 | 1000 1000 | 1000 1000 |
| | B | 1000 1997 | 1000 2217 | 792 5000 | 1000 1000 | 1000 1000 | 1000 1047 |
| | C | 193 5000 | 165 5000 | 32 5000 | 1000 1102 | 1000 1132 | 1000 2072 |
| Set 3 | A | 1000 1015 | 1000 1022 | 1000 1337 | 1000 1000 | 1000 1000 | 1000 1000 |
| | B | 1000 2271 | 1000 2472 | 654 5000 | 1000 1000 | 1000 1000 | 1000 1063 |
| | C | 208 5000 | 182 5000 | 27 5000 | 1000 1130 | 1000 1174 | 1000 2128 |
| Set 6 | A | 1000 1258 | 1000 1330 | 1000 3709 | 1000 1000 | 1000 1000 | 1000 1011 |
| | B | 800 5000 | 601 5000 | 111 5000 | 1000 1032 | 1000 1065 | 1000 1512 |
| | C | 240 5000 | 118 5000 | 8 5000 | 1000 1626 | 1000 1771 | 998 5000 |

(a) Uniform entry

| Capture | Migration Model | Small Population Recapture | | | Large Population Recapture | | |
|---------|-----------------|-------------------------------|--------------|--------------|-------------------------------|--------------|--------------|
| | | Set 1 | Set 3 | Set 6 | Set 1 | Set 3 | Set 6 |
| Set 1 | A | 1000 1077 | 1000 1003 | 1000 1077 | 1000 1000 | 1000 1000 | 1000 1000 |
| | B | 1000 2327 | 1000 2396 | 932 5000 | 1000 1002 | 1000 1003 | 1000 1012 |
| | C | 189 5000 | 173 5000 | 81 5000 | 1000 1061 | 1000 1072 | 1000 1424 |
| Set 3 | A | 1000 1003 | 1000 1006 | 1000 1139 | 1000 1000 | 1000 1000 | 1000 1000 |
| | B | 1000 2810 | 1000 2786 | 755 5000 | 1000 1002 | 1000 1002 | 1000 1028 |
| | C | 177 5000 | 172 5000 | 69 5000 | 1000 1077 | 1000 1104 | 1000 1583 |
| Set 6 | A | 1000 1123 | 1000 1164 | 1000 2094 | 1000 1000 | 1000 1000 | 1000 1000 |
| | B | 652 5000 | 546 5000 | 141 5000 | 1000 1052 | 1000 1067 | 1000 1367 |
| | C | 169 5000 | 161 5000 | 10 5000 | 1000 1551 | 1000 1733 | 1000 3869 |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study133

Table D.4: Percent asymptotic relative bias of the iterative Darroch standard error estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1.60 | 0.90 | 11.56 | 2.41 | -0.84 | -0.93 |
| | <i>B</i> | 16.61 | 24.77 | 59.31 | 1.99 | 1.33 | 2.77 |
| | <i>C</i> | - | - | - | 3.83 | 10.03 | 23.29 |
| <i>Set 3</i> | <i>A</i> | -0.81 | 2.70 | 12.09 | 0.18 | 2.24 | -0.18 |
| | <i>B</i> | 17.84 | 27.93 | 49.29 | 0.05 | 1.57 | 3.19 |
| | <i>C</i> | - | - | - | 9.44 | 8.44 | 26.61 |
| <i>Set 6</i> | <i>A</i> | 6.20 | 15.29 | 47.19 | 2.52 | 2.91 | -1.73 |
| | <i>B</i> | 47.93 | 57.78 | - | 5.20 | 9.73 | 15.79 |
| | <i>C</i> | - | - | - | 16.64 | -36.01 | - |

(a) *Uniform entry*

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | -0.51 | -2.14 | 1.98 | 0.04 | -0.12 | 0.46 |
| | <i>B</i> | 15.02 | 11.12 | 37.27 | 3.20 | -0.06 | 3.08 |
| | <i>C</i> | - | - | - | 4.54 | 4.75 | 16.31 |
| <i>Set 3</i> | <i>A</i> | -2.10 | 3.41 | -0.96 | -1.13 | -0.04 | -4.91 |
| | <i>B</i> | 17.15 | 20.74 | 531860.07 | -1.36 | 0.35 | -1.16 |
| | <i>C</i> | - | - | - | 2.94 | 5.63 | 14.45 |
| <i>Set 6</i> | <i>A</i> | 4.87 | -4.74 | 35.28 | 1.51 | -3.54 | 0.46 |
| | <i>B</i> | 37.00 | 43.98 | - | 1.59 | 2.35 | 10.98 |
| | <i>C</i> | - | - | - | 16.04 | 12.37 | - |

(b) *Normal entry*

Appendix D. Tables for the Closed Model, Standard Error Estimate Study134

Table D.5: Percent CV of the pooled Petersen standard error estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 6.88 | 6.64 | 6.58 | 2.08 | 2.15 | 2.18 |
| | <i>B</i> | 6.86 | 6.73 | 6.37 | 2.14 | 2.15 | 2.11 |
| | <i>C</i> | - | - | - | 2.11 | 2.07 | 1.97 |
| <i>Set 3</i> | <i>A</i> | 6.80 | 6.53 | 6.26 | 2.11 | 2.09 | 1.98 |
| | <i>B</i> | 6.96 | 6.51 | 6.33 | 2.11 | 2.08 | 2.06 |
| | <i>C</i> | - | - | - | 2.05 | 2.05 | 1.98 |
| <i>Set 6</i> | <i>A</i> | 6.59 | 6.28 | 5.67 | 2.10 | 1.95 | 1.78 |
| | <i>B</i> | 6.47 | 6.30 | - | 2.06 | 2.01 | 1.82 |
| | <i>C</i> | - | - | - | 2.04 | 2.07 | 1.93 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 7.33 | 7.38 | 7.93 | 2.26 | 2.32 | 2.43 |
| | <i>B</i> | 6.99 | 7.57 | 7.52 | 2.21 | 2.36 | 2.41 |
| | <i>C</i> | - | - | - | 2.20 | 2.15 | 2.04 |
| <i>Set 3</i> | <i>A</i> | 7.68 | 7.38 | 7.72 | 2.39 | 2.44 | 2.52 |
| | <i>B</i> | 7.25 | 7.50 | 7.56 | 2.39 | 2.30 | 2.40 |
| | <i>C</i> | - | - | - | 2.32 | 2.26 | 2.10 |
| <i>Set 6</i> | <i>A</i> | 7.61 | 8.01 | 7.79 | 2.65 | 2.38 | 2.20 |
| | <i>B</i> | 7.76 | 8.15 | - | 2.59 | 2.59 | 2.38 |
| | <i>C</i> | - | - | - | 2.39 | 2.49 | 2.33 |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study135

Table D.6: Percent CV of the Darroch moment standard error estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 15.19 | 21.96 | 59.48 | 3.04 | 3.53 | 9.54 |
| | <i>B</i> | 26.99 | 30.09 | 58.98 | 3.62 | 4.26 | 13.05 |
| | <i>C</i> | - | - | - | 7.35 | 8.72 | 21.63 |
| <i>Set 3</i> | <i>A</i> | 23.72 | 24.72 | 66.01 | 3.48 | 3.94 | 10.87 |
| | <i>B</i> | 31.19 | 34.72 | 61.05 | 4.46 | 4.96 | 15.07 |
| | <i>C</i> | - | - | - | 9.43 | 10.09 | 33.61 |
| <i>Set 6</i> | <i>A</i> | 64.96 | 61.22 | 42.33 | 9.25 | 9.89 | 31.91 |
| | <i>B</i> | 51.80 | 58.85 | - | 13.49 | 12.72 | 40.02 |
| | <i>C</i> | - | - | - | 23.82 | - | - |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 13.21 | 17.10 | 59.60 | 3.13 | 3.53 | 7.79 |
| | <i>B</i> | 19.11 | 20.67 | 47.12 | 3.49 | 4.06 | 9.98 |
| | <i>C</i> | - | - | - | 5.98 | 6.44 | 15.74 |
| <i>Set 3</i> | <i>A</i> | 15.06 | 16.06 | 69.71 | 3.45 | 3.85 | 9.31 |
| | <i>B</i> | 23.41 | 23.51 | 2765.86 | 4.03 | 4.54 | 11.02 |
| | <i>C</i> | - | - | - | 6.11 | 8.13 | 18.99 |
| <i>Set 6</i> | <i>A</i> | 47.33 | 67.30 | 51.78 | 7.52 | 8.59 | 21.43 |
| | <i>B</i> | 2543.62 | 65.04 | - | 10.00 | 10.34 | 25.88 |
| | <i>C</i> | - | - | - | 14.80 | 19.23 | - |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study136

Table D.7: Percent CV of the iterative Darroch standard error estimate with no mortality. Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 15.48 | 22.39 | 59.59 | 3.10 | 3.60 | 9.61 |
| | <i>B</i> | 28.13 | 31.37 | 59.69 | 3.75 | 4.42 | 13.32 |
| | <i>C</i> | - | - | - | 7.79 | 9.22 | 22.37 |
| <i>Set 3</i> | <i>A</i> | 24.16 | 25.15 | 66.11 | 3.53 | 4.01 | 10.94 |
| | <i>B</i> | 32.48 | 35.96 | 61.90 | 4.63 | 5.14 | 15.36 |
| | <i>C</i> | - | - | - | 9.94 | 10.66 | 34.62 |
| <i>Set 6</i> | <i>A</i> | 66.12 | 62.02 | 42.34 | 9.45 | 10.08 | 32.10 |
| | <i>B</i> | 53.13 | 60.08 | - | 14.04 | 13.16 | 40.57 |
| | <i>C</i> | - | - | - | 25.07 | 31.53 | - |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 13.44 | 17.33 | 59.55 | 3.18 | 3.59 | 7.80 |
| | <i>B</i> | 19.57 | 21.43 | 47.65 | 3.61 | 4.18 | 10.11 |
| | <i>C</i> | - | - | - | 6.27 | 6.79 | 16.27 |
| <i>Set 3</i> | <i>A</i> | 15.33 | 16.29 | 69.71 | 3.51 | 3.91 | 9.33 |
| | <i>B</i> | 24.39 | 24.36 | - | 4.17 | 4.69 | 11.18 |
| | <i>C</i> | - | - | - | 6.43 | 8.56 | 19.57 |
| <i>Set 6</i> | <i>A</i> | 48.34 | 68.32 | 51.93 | 7.70 | 8.75 | 21.56 |
| | <i>B</i> | 52.00 | 66.57 | - | 10.39 | 10.67 | 26.24 |
| | <i>C</i> | - | - | - | 15.60 | 20.19 | - |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study 137

Table D.8: Effective bias of the pooled Petersen standard error estimate with no mortality. Entries in bold indicate no effective bias (< 0.5). Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | Small Population <i>Recapture</i> | | | Large Population <i>Recapture</i> | | |
|----------------|------------------------|--------------------------------------|--------------|--------------|--------------------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | -0.22 | 0.19 | -0.05 | 1.55 | -0.85 | -2.04 |
| | <i>B</i> | -0.19 | -0.12 | <i>0.53</i> | 0.13 | -0.62 | -0.53 |
| | <i>C</i> | - | - | - | 0.04 | 0.25 | 0.22 |
| <i>Set 3</i> | <i>A</i> | -0.10 | 0.09 | 0.09 | 0.40 | 0.18 | -0.05 |
| | <i>B</i> | -0.59 | 0.19 | <i>0.19</i> | 0.09 | 0.08 | -1.21 |
| | <i>C</i> | - | - | - | 1.35 | 0.06 | -0.62 |
| <i>Set 6</i> | <i>A</i> | 0.00 | 0.03 | -0.11 | -0.17 | 0.75 | 0.19 |
| | <i>B</i> | <i>0.30</i> | <i>0.08</i> | - | 0.37 | 0.12 | 0.74 |
| | <i>C</i> | - | - | - | 1.30 | -0.89 | -0.91 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | Small Population <i>Recapture</i> | | | Large Population <i>Recapture</i> | | |
|----------------|------------------------|--------------------------------------|--------------|--------------|--------------------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | -0.30 | -0.01 | 0.02 | 0.18 | 0.18 | 1.39 |
| | <i>B</i> | 0.32 | -0.49 | <i>0.37</i> | 0.77 | -1.43 | 0.42 |
| | <i>C</i> | - | - | - | 0.35 | 0.56 | 1.65 |
| <i>Set 3</i> | <i>A</i> | -0.56 | 0.31 | 0.01 | -1.24 | -1.47 | -1.19 |
| | <i>B</i> | 0.13 | -0.09 | <i>0.08</i> | -1.07 | 0.93 | 0.31 |
| | <i>C</i> | - | - | - | -0.58 | -0.13 | 1.54 |
| <i>Set 6</i> | <i>A</i> | 0.76 | -0.37 | -0.80 | -1.50 | 1.20 | 2.12 |
| | <i>B</i> | <i>0.39</i> | -0.48 | - | -0.86 | -1.83 | -0.46 |
| | <i>C</i> | - | - | - | 2.26 | -0.56 | -0.35 |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study138

Table D.9: Effective bias of the Darroch moment standard error estimate with no mortality. Entries in bold indicate no effective bias (< 0.5). Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | Small Population <i>Recapture</i> | | | Large Population <i>Recapture</i> | | |
|----------------|------------------------|--------------------------------------|--------------|--------------|--------------------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.22 | 0.11 | 0.19 | 1.49 | 0.27 | -0.10 |
| | <i>B</i> | 0.71 | 0.90 | -1.70 | 1.65 | 1.15 | 0.30 |
| | <i>C</i> | - | - | - | 1.16 | 1.69 | 1.18 |
| <i>Set 3</i> | <i>A</i> | 0.04 | 0.17 | 0.18 | 0.68 | 1.05 | -0.01 |
| | <i>B</i> | 0.66 | 0.87 | -1.64 | 0.89 | 1.03 | 0.29 |
| | <i>C</i> | - | - | - | 1.52 | 1.29 | 0.85 |
| <i>Set 6</i> | <i>A</i> | 0.11 | 0.27 | 1.12 | 0.58 | 0.53 | -0.04 |
| | <i>B</i> | 0.96 | 1.01 | - | 0.68 | 1.05 | 0.42 |
| | <i>C</i> | - | - | - | 0.89 | -0.03 | -0.06 |

(a) Uniform entry

| <i>Capture</i> | <i>Migration Model</i> | Small Population <i>Recapture</i> | | | Large Population <i>Recapture</i> | | |
|----------------|------------------------|--------------------------------------|--------------|--------------|--------------------------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.09 | -0.05 | 0.03 | 0.66 | 0.41 | 0.02 |
| | <i>B</i> | 0.93 | 0.65 | 0.79 | 2.06 | 0.80 | 0.40 |
| | <i>C</i> | - | - | - | 1.59 | 1.47 | 1.17 |
| <i>Set 3</i> | <i>A</i> | -0.02 | 0.31 | -0.02 | 0.31 | 0.44 | -0.54 |
| | <i>B</i> | 0.85 | 0.99 | -0.03 | 0.62 | 0.82 | -0.02 |
| | <i>C</i> | - | - | - | 1.29 | 1.27 | 0.87 |
| <i>Set 6</i> | <i>A</i> | 0.15 | -0.05 | 0.69 | 0.59 | -0.14 | 0.05 |
| | <i>B</i> | -0.02 | 0.70 | - | 0.57 | 0.56 | 0.47 |
| | <i>C</i> | - | - | - | 1.43 | 0.87 | -0.03 |

(b) Normal entry

Appendix D. Tables for the Closed Model, Standard Error Estimate Study139

Table D.10: Effective bias of the iterative Darroch standard error estimate with no mortality. Entries in bold indicate no effective bias (< 0.5). Italicized entries indicate combinations where less than 1000, but greater than 500 good replications could be obtained. Entries replaced by -'s indicate combinations where less than 500 good replications could be obtained.

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.10 | 0.04 | 0.19 | 0.78 | -0.23 | -0.10 |
| | <i>B</i> | 0.59 | 0.79 | 0.99 | 0.53 | 0.30 | 0.21 |
| | <i>C</i> | - | - | - | 0.49 | 1.09 | 1.04 |
| <i>Set 3</i> | <i>A</i> | -0.03 | 0.11 | 0.18 | 0.05 | 0.56 | -0.02 |
| | <i>B</i> | 0.55 | 0.78 | 0.80 | 0.01 | 0.31 | 0.21 |
| | <i>C</i> | - | - | - | 0.95 | 0.79 | 0.77 |
| <i>Set 6</i> | <i>A</i> | 0.09 | 0.25 | 1.11 | 0.27 | 0.29 | -0.05 |
| | <i>B</i> | 0.90 | 0.96 | - | 0.37 | 0.74 | 0.39 |
| | <i>C</i> | - | - | - | 0.66 | -1.14 | - |

(a) *Uniform entry*

| <i>Capture</i> | <i>Migration Model</i> | <i>Small Population</i> | | | <i>Large Population</i> | | |
|----------------|------------------------|-------------------------|--------------|--------------|-------------------------|--------------|--------------|
| | | <i>Recapture</i> | | | <i>Recapture</i> | | |
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | -0.04 | -0.12 | 0.03 | 0.01 | -0.03 | 0.06 |
| | <i>B</i> | 0.77 | 0.52 | 0.78 | 0.89 | -0.01 | 0.30 |
| | <i>C</i> | - | - | - | 0.72 | 0.70 | 1.00 |
| <i>Set 3</i> | <i>A</i> | -0.14 | 0.21 | -0.01 | -0.32 | -0.01 | -0.53 |
| | <i>B</i> | 0.70 | 0.85 | 205.37 | -0.33 | 0.08 | -0.10 |
| | <i>C</i> | - | - | - | 0.46 | 0.66 | 0.74 |
| <i>Set 6</i> | <i>A</i> | 0.10 | -0.07 | 0.68 | 0.20 | -0.40 | 0.02 |
| | <i>B</i> | 0.71 | 0.66 | - | 0.15 | 0.22 | 0.42 |
| | <i>C</i> | - | - | - | 1.03 | 0.61 | 36.68 |

(b) *Normal entry*

Appendix E

Tables for the Open Model, Standard Error Estimate Study

Appendix E. Tables for the Open Model, Standard Error Estimate Study141

Table E.1: Percent asymptotic relative bias of the three estimators with high variance mortality, large population, and normal entry.

| <i>Capture</i> | <i>Migration Model</i> | <i>Recapture</i> | | |
|----------------|------------------------|------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.59 | 0.61 | 0.89 |
| | <i>B</i> | 4.73 | 4.00 | 0.04 |
| | <i>C</i> | -1.74 | 3.62 | -2.17 |
| <i>Set 3</i> | <i>A</i> | -1.33 | 1.28 | -0.82 |
| | <i>B</i> | -1.35 | -0.92 | 3.07 |
| | <i>C</i> | -1.43 | 0.90 | 2.90 |
| <i>Set 6</i> | <i>A</i> | 2.49 | 0.21 | -2.23 |
| | <i>B</i> | -0.41 | -1.40 | -0.48 |
| | <i>C</i> | -3.80 | -1.88 | -4.36 |

(a) Pooled Petersen estimator

| | | | | |
|--------------|----------|-------|-------|--------|
| <i>Set 1</i> | <i>A</i> | -0.19 | 0.30 | 0.66 |
| | <i>B</i> | 9.64 | 7.53 | 3.34 |
| | <i>C</i> | 14.21 | 17.60 | 21.19 |
| <i>Set 3</i> | <i>A</i> | -0.55 | 0.77 | -3.01 |
| | <i>B</i> | 4.60 | 2.93 | 7.34 |
| | <i>C</i> | 11.57 | 13.09 | 25.89 |
| <i>Set 6</i> | <i>A</i> | 7.00 | 2.60 | 3.49 |
| | <i>B</i> | 10.30 | 4.35 | 16.05 |
| | <i>C</i> | 11.86 | 25.30 | -58.81 |

(b) Darroch moment estimator

| | | | | |
|--------------|----------|-------|-------|-----------|
| <i>Set 1</i> | <i>A</i> | -0.27 | 0.32 | 1.50 |
| | <i>B</i> | 8.28 | 6.27 | 3.13 |
| | <i>C</i> | 12.83 | 16.10 | 20.50 |
| <i>Set 3</i> | <i>A</i> | -0.87 | 0.55 | -2.43 |
| | <i>B</i> | 3.11 | 1.57 | 7.03 |
| | <i>C</i> | 10.11 | 11.57 | 25.15 |
| <i>Set 6</i> | <i>A</i> | 5.39 | 1.32 | 3.29 |
| | <i>B</i> | 8.06 | 2.49 | 15.48 |
| | <i>C</i> | 10.35 | 23.64 | 140174.30 |

(c) Iterative Darroch estimator

Appendix E. Tables for the Open Model, Standard Error Estimate Study142

Table E.2: Good replications versus total replications for all factor combinations, with high variance mortality. The number of good replications was limited to 1000, and the total replications limited to 5000. Total replications of 1000 or slightly more indicate very low rejection rates.

| <i>Capture</i> | <i>Migration Model</i> | <i>Recapture</i> | | |
|----------------|------------------------|------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 1000 | 1000 | 1000 |
| | <i>B</i> | 1000 | 1000 | 1000 |
| | <i>C</i> | 1047 | 1038 | 1069 |
| <i>Set 3</i> | <i>A</i> | 1000 | 1000 | 1000 |
| | <i>B</i> | 1000 | 1000 | 1000 |
| | <i>C</i> | 1055 | 1051 | 1114 |
| <i>Set 6</i> | <i>A</i> | 1000 | 1000 | 1000 |
| | <i>B</i> | 1282 | 1320 | 1872 |
| | <i>C</i> | 1000 | 1000 | 561 |
| | | 3511 | 3701 | 5000 |

Appendix E. Tables for the Open Model, Standard Error Estimate Study143

Table E.3: Percent CV of the three standard error estimates with high variance mortality, large population, and normal entry.

| <i>Capture</i> | <i>Migration Model</i> | <i>Recapture</i> | | |
|----------------|------------------------|------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 3.06 | 3.27 | 3.95 |
| | <i>B</i> | 2.99 | 3.20 | 3.95 |
| | <i>C</i> | 3.42 | 3.33 | 3.77 |
| <i>Set 3</i> | <i>A</i> | 3.34 | 3.42 | 4.03 |
| | <i>B</i> | 3.35 | 3.50 | 3.89 |
| | <i>C</i> | 3.54 | 3.54 | 3.71 |
| <i>Set 6</i> | <i>A</i> | 3.89 | 4.01 | 4.16 |
| | <i>B</i> | 3.98 | 4.09 | 4.23 |
| | <i>C</i> | 4.19 | 4.13 | 4.41 |

(a) Pooled Petersen estimator

| | | | | |
|--------------|----------|-------|-------|---------|
| <i>Set 1</i> | <i>A</i> | 4.08 | 3.85 | 8.20 |
| | <i>B</i> | 5.55 | 5.39 | 10.48 |
| | <i>C</i> | 12.29 | 9.97 | 19.63 |
| <i>Set 3</i> | <i>A</i> | 3.92 | 4.10 | 9.36 |
| | <i>B</i> | 5.38 | 5.32 | 11.72 |
| | <i>C</i> | 9.85 | 9.85 | 23.13 |
| <i>Set 6</i> | <i>A</i> | 7.71 | 8.96 | 20.98 |
| | <i>B</i> | 9.46 | 11.38 | 31.10 |
| | <i>C</i> | 18.47 | 26.45 | 1786.93 |

(b) Darroch moment estimator

| | | | | |
|--------------|----------|-------|-------|---------|
| <i>Set 1</i> | <i>A</i> | 4.12 | 3.86 | 8.14 |
| | <i>B</i> | 5.67 | 5.48 | 10.53 |
| | <i>C</i> | 12.77 | 10.29 | 19.98 |
| <i>Set 3</i> | <i>A</i> | 3.94 | 4.10 | 9.31 |
| | <i>B</i> | 5.50 | 5.39 | 11.79 |
| | <i>C</i> | 10.14 | 10.10 | 23.55 |
| <i>Set 6</i> | <i>A</i> | 7.76 | 9.01 | 21.01 |
| | <i>B</i> | 9.63 | 11.57 | 31.35 |
| | <i>C</i> | 18.86 | 27.04 | 1178.29 |

(c) Iterative Darroch estimator

Appendix E. Tables for the Open Model, Standard Error Estimate Study144

Table E.4: Effective bias of the three standard error estimates with high variance mortality, large population, and normal entry. Values in bold indicate ineffective bias (i.e. < 0.5).

| <i>Capture</i> | <i>Migration Model</i> | <i>Recapture</i> | | |
|----------------|------------------------|------------------|--------------|--------------|
| | | <i>Set 1</i> | <i>Set 3</i> | <i>Set 6</i> |
| <i>Set 1</i> | <i>A</i> | 0.19 | 0.19 | 0.22 |
| | <i>B</i> | 1.58 | 1.25 | 0.01 |
| | <i>C</i> | -0.51 | 1.09 | -0.58 |
| <i>Set 3</i> | <i>A</i> | -0.40 | 0.37 | -0.20 |
| | <i>B</i> | -0.40 | -0.26 | 0.79 |
| | <i>C</i> | -0.40 | 0.25 | 0.78 |
| <i>Set 6</i> | <i>A</i> | 0.64 | 0.05 | -0.54 |
| | <i>B</i> | -0.10 | -0.34 | -0.11 |
| | <i>C</i> | -0.91 | -0.46 | -0.99 |

(a) Pooled Petersen estimator

| | | | | |
|--------------|----------|--------------|-------------|--------------|
| <i>Set 1</i> | <i>A</i> | -0.05 | 0.08 | 0.08 |
| | <i>B</i> | 1.74 | 1.40 | 0.32 |
| | <i>C</i> | 1.16 | 1.77 | 1.08 |
| <i>Set 3</i> | <i>A</i> | -0.14 | 0.19 | -0.32 |
| | <i>B</i> | 0.85 | 0.55 | 0.63 |
| | <i>C</i> | 1.17 | 1.33 | 1.12 |
| <i>Set 6</i> | <i>A</i> | 0.91 | 0.29 | 0.17 |
| | <i>B</i> | 1.09 | 0.38 | 0.52 |
| | <i>C</i> | 0.64 | 0.96 | -0.03 |

(b) Darroch moment estimator

| | | | | |
|--------------|----------|--------------|-------------|--------------|
| <i>Set 1</i> | <i>A</i> | -0.06 | 0.08 | 0.18 |
| | <i>B</i> | 1.46 | 1.14 | 0.30 |
| | <i>C</i> | 1.01 | 1.56 | 1.03 |
| <i>Set 3</i> | <i>A</i> | -0.22 | 0.13 | -0.26 |
| | <i>B</i> | 0.57 | 0.29 | 0.60 |
| | <i>C</i> | 1.00 | 1.14 | 1.07 |
| <i>Set 6</i> | <i>A</i> | 0.70 | 0.15 | 0.16 |
| | <i>B</i> | 0.84 | 0.22 | 0.49 |
| | <i>C</i> | 0.55 | 0.87 | 118.96 |

(c) Iterative Darroch estimator

Appendix F

Tables for the Pooling Study

Table F.1: Percent asymptotic relative bias of the Darroch moment estimate with increasing levels of pooling, a large population, and normal entry. All values have been negated for cleaner presentation.

| <i>Capture</i> | <i>Recapture</i> | <i>Migration Model</i> | <i>Pooling Level</i> | | | | | |
|----------------|------------------|------------------------|----------------------|------|------|------|-------|-------|
| | | | 3 | 4 | 6 | 8 | 12 | 24 |
| <i>Set 1</i> | <i>Set 1</i> | <i>A</i> | 0.92 | 1.41 | 1.86 | 1.58 | 2.71 | 2.70 |
| | | <i>B</i> | 0.53 | 0.94 | 1.24 | 0.77 | 2.31 | 2.17 |
| | | <i>C</i> | 0.10 | 0.19 | 0.17 | 0.12 | 0.87 | 0.46 |
| <i>Set 1</i> | <i>Set 3</i> | <i>A</i> | 0.73 | 1.11 | 1.53 | 1.54 | 3.99 | 3.97 |
| | | <i>B</i> | 0.40 | 0.48 | 1.03 | 0.65 | 3.79 | 3.60 |
| | | <i>C</i> | 0.08 | 0.09 | 0.14 | 0.12 | 1.61 | 0.85 |
| <i>Set 1</i> | <i>Set 6</i> | <i>A</i> | 0.94 | 1.43 | 3.27 | 2.48 | 9.60 | 9.58 |
| | | <i>B</i> | 0.50 | 0.34 | 2.46 | 1.00 | 9.43 | 9.13 |
| | | <i>C</i> | 0.09 | 0.03 | 0.47 | 0.16 | 3.72 | 1.75 |
| <i>Set 3</i> | <i>Set 1</i> | <i>A</i> | 0.73 | 1.12 | 1.52 | 1.57 | 3.98 | 3.96 |
| | | <i>B</i> | 0.41 | 0.54 | 1.02 | 0.74 | 3.73 | 3.55 |
| | | <i>C</i> | 0.08 | 0.11 | 0.14 | 0.20 | 1.61 | 0.88 |
| <i>Set 3</i> | <i>Set 3</i> | <i>A</i> | 0.61 | 1.88 | 1.28 | 2.66 | 7.98 | 7.97 |
| | | <i>B</i> | 0.32 | 0.65 | 0.86 | 1.26 | 7.43 | 7.19 |
| | | <i>C</i> | 0.07 | 0.14 | 0.12 | 0.31 | 3.18 | 1.78 |
| <i>Set 3</i> | <i>Set 6</i> | <i>A</i> | 0.70 | 3.44 | 2.65 | 4.87 | 19.85 | 19.82 |
| | | <i>B</i> | 0.37 | 1.15 | 2.04 | 2.38 | 18.79 | 18.30 |
| | | <i>C</i> | 0.07 | 0.23 | 0.38 | 0.46 | 7.52 | 3.70 |
| <i>Set 6</i> | <i>Set 1</i> | <i>A</i> | 0.94 | 1.45 | 3.22 | 2.54 | 9.59 | 9.57 |
| | | <i>B</i> | 0.47 | 0.47 | 2.27 | 1.21 | 9.41 | 9.13 |
| | | <i>C</i> | 0.09 | 0.08 | 0.25 | 0.39 | 4.41 | 2.50 |
| <i>Set 6</i> | <i>Set 3</i> | <i>A</i> | 0.70 | 3.45 | 2.62 | 4.88 | 19.89 | 19.86 |
| | | <i>B</i> | 0.35 | 1.15 | 1.89 | 2.44 | 18.96 | 18.54 |
| | | <i>C</i> | 0.07 | 0.23 | 0.16 | 0.60 | 8.64 | 5.06 |
| <i>Set 6</i> | <i>Set 6</i> | <i>A</i> | 2.08 | 6.75 | 8.55 | 9.33 | 43.15 | 43.11 |
| | | <i>B</i> | 0.87 | 2.56 | 6.06 | 4.84 | 41.17 | 40.57 |
| | | <i>C</i> | 0.17 | 0.55 | 1.27 | 0.97 | 18.63 | 10.37 |

Table F.2: Percent CV of the Darroch moment estimate with increasing levels of pooling, a large population, and normal entry.

| <i>Capture</i> | <i>Recapture</i> | <i>Migration Model</i> | <i>Pooling Level</i> | | | | | | |
|----------------|------------------|------------------------|----------------------|----------|----------|----------|----------|-----------|-----------|
| | | | <i>2</i> | <i>3</i> | <i>4</i> | <i>6</i> | <i>8</i> | <i>12</i> | <i>24</i> |
| <i>Set 1</i> | <i>Set 1</i> | <i>A</i> | 1.56 | 1.51 | 1.49 | 1.47 | 1.48 | 1.44 | 1.43 |
| | | <i>B</i> | 1.58 | 1.55 | 1.52 | 1.49 | 1.51 | 1.44 | 1.44 |
| | | <i>C</i> | 1.53 | 1.52 | 1.51 | 1.49 | 1.48 | 1.43 | 1.39 |
| <i>Set 1</i> | <i>Set 3</i> | <i>A</i> | 1.66 | 1.61 | 1.58 | 1.57 | 1.57 | 1.47 | 1.47 |
| | | <i>B</i> | 1.68 | 1.65 | 1.63 | 1.60 | 1.61 | 1.48 | 1.47 |
| | | <i>C</i> | 1.55 | 1.54 | 1.54 | 1.53 | 1.54 | 1.44 | 1.37 |
| <i>Set 1</i> | <i>Set 6</i> | <i>A</i> | 2.54 | 2.43 | 2.35 | 2.22 | 2.35 | 1.59 | 1.59 |
| | | <i>B</i> | 2.54 | 2.48 | 2.48 | 2.29 | 2.50 | 1.59 | 1.57 |
| | | <i>C</i> | 2.03 | 2.03 | 2.07 | 2.00 | 2.24 | 1.59 | 1.33 |
| <i>Set 3</i> | <i>Set 1</i> | <i>A</i> | 1.67 | 1.63 | 1.60 | 1.58 | 1.58 | 1.48 | 1.48 |
| | | <i>B</i> | 1.69 | 1.66 | 1.64 | 1.61 | 1.62 | 1.49 | 1.48 |
| | | <i>C</i> | 1.63 | 1.61 | 1.61 | 1.60 | 1.60 | 1.48 | 1.45 |
| <i>Set 3</i> | <i>Set 3</i> | <i>A</i> | 1.79 | 1.75 | 1.71 | 1.71 | 1.70 | 1.50 | 1.49 |
| | | <i>B</i> | 1.80 | 1.78 | 1.76 | 1.74 | 1.75 | 1.50 | 1.49 |
| | | <i>C</i> | 1.66 | 1.64 | 1.64 | 1.65 | 1.67 | 1.48 | 1.42 |
| <i>Set 3</i> | <i>Set 6</i> | <i>A</i> | 2.78 | 2.68 | 2.63 | 2.46 | 2.65 | 1.54 | 1.54 |
| | | <i>B</i> | 2.77 | 2.72 | 2.76 | 2.53 | 2.81 | 1.55 | 1.54 |
| | | <i>C</i> | 2.18 | 2.17 | 2.26 | 2.16 | 2.49 | 1.57 | 1.36 |
| <i>Set 6</i> | <i>Set 1</i> | <i>A</i> | 2.63 | 2.52 | 2.44 | 2.31 | 2.43 | 1.62 | 1.62 |
| | | <i>B</i> | 2.64 | 2.59 | 2.58 | 2.43 | 2.59 | 1.63 | 1.62 |
| | | <i>C</i> | 2.48 | 2.47 | 2.50 | 2.50 | 2.57 | 1.68 | 1.62 |
| <i>Set 6</i> | <i>Set 3</i> | <i>A</i> | 2.86 | 2.75 | 2.70 | 2.54 | 2.72 | 1.57 | 1.57 |
| | | <i>B</i> | 2.86 | 2.81 | 2.84 | 2.64 | 2.88 | 1.58 | 1.57 |
| | | <i>C</i> | 2.55 | 2.54 | 2.59 | 2.57 | 2.75 | 1.64 | 1.58 |
| <i>Set 6</i> | <i>Set 6</i> | <i>A</i> | 4.66 | 4.41 | 4.49 | 3.54 | 4.62 | 1.43 | 1.43 |
| | | <i>B</i> | 4.58 | 4.50 | 4.73 | 3.71 | 4.95 | 1.45 | 1.45 |
| | | <i>C</i> | 3.40 | 3.41 | 3.77 | 3.19 | 4.31 | 1.59 | 1.48 |

Table F.3: Effective relative bias of the Darroch estimate with increasing levels of pooling, a large population, and normal entry. Values in bold indicate no effective bias, i.e. < 0.5. All values have been negated for cleaner presentation.

| Capture | Recapture | Migration Model | Pooling Level | | | | | |
|---------|-----------|-----------------|---------------|-------------|-------------|-------------|-------|-------------|
| | | | 3 | 4 | 6 | 8 | 12 | 24 |
| Set 1 | Set 1 | A | 0.61 | 0.95 | 1.27 | 1.07 | 1.89 | 1.88 |
| | | B | 0.34 | 0.62 | 0.83 | 0.51 | 1.60 | 1.51 |
| | | C | 0.07 | 0.13 | 0.12 | 0.08 | 0.61 | 0.33 |
| Set 1 | Set 3 | A | 0.45 | 0.70 | 0.97 | 0.98 | 2.70 | 2.70 |
| | | B | 0.24 | 0.29 | 0.64 | 0.40 | 2.57 | 2.45 |
| | | C | 0.05 | 0.08 | 0.09 | 0.08 | 1.12 | 0.62 |
| Set 1 | Set 6 | A | 0.39 | 0.61 | 1.47 | 1.06 | 6.05 | 6.04 |
| | | B | 0.20 | 0.14 | 1.07 | 0.40 | 5.94 | 5.82 |
| | | C | 0.05 | 0.01 | 0.23 | 0.07 | 2.34 | 1.32 |
| Set 3 | Set 1 | A | 0.45 | 0.70 | 0.96 | 0.99 | 2.68 | 2.68 |
| | | B | 0.25 | 0.33 | 0.63 | 0.46 | 2.51 | 2.40 |
| | | C | 0.05 | 0.07 | 0.09 | 0.13 | 1.09 | 0.61 |
| Set 3 | Set 3 | A | 0.35 | 1.10 | 0.75 | 1.56 | 5.34 | 5.33 |
| | | B | 0.18 | 0.37 | 0.50 | 0.72 | 4.95 | 4.81 |
| | | C | 0.04 | 0.08 | 0.07 | 0.18 | 2.15 | 1.25 |
| Set 3 | Set 6 | A | 0.26 | 1.31 | 1.08 | 1.84 | 12.89 | 12.88 |
| | | B | 0.14 | 0.42 | 0.81 | 0.85 | 12.16 | 11.92 |
| | | C | 0.03 | 0.10 | 0.17 | 0.19 | 4.80 | 2.71 |
| Set 6 | Set 1 | A | 0.37 | 0.59 | 1.40 | 1.04 | 5.92 | 5.91 |
| | | B | 0.18 | 0.18 | 0.93 | 0.47 | 5.79 | 5.63 |
| | | C | 0.04 | 0.03 | 0.10 | 0.15 | 2.62 | 1.55 |
| Set 6 | Set 3 | A | 0.25 | 1.28 | 1.03 | 1.79 | 12.70 | 12.68 |
| | | B | 0.13 | 0.41 | 0.71 | 0.85 | 12.04 | 11.79 |
| | | C | 0.03 | 0.09 | 0.06 | 0.22 | 5.28 | 3.21 |
| Set 6 | Set 6 | A | 0.47 | 1.50 | 2.42 | 2.02 | 30.13 | 30.11 |
| | | B | 0.19 | 0.54 | 1.63 | 0.98 | 28.39 | 27.97 |
| | | C | 0.05 | 0.15 | 0.40 | 0.22 | 11.70 | 7.00 |

Table F.4: Root relative mean square error of the Darroch moment estimate with increasing levels of pooling, a large population, and normal entry.

| <i>Capture</i> | <i>Recapture</i> | <i>Migration Model</i> | <i>Pooling Level</i> | | | | | | |
|----------------|------------------|------------------------|----------------------|----------|----------|----------|----------|-----------|-----------|
| | | | <i>2</i> | <i>3</i> | <i>4</i> | <i>6</i> | <i>8</i> | <i>12</i> | <i>24</i> |
| <i>Set 1</i> | <i>Set 1</i> | <i>A</i> | 1.56 | 1.76 | 2.04 | 2.35 | 2.15 | 3.05 | 3.04 |
| | | <i>B</i> | 1.58 | 1.63 | 1.78 | 1.92 | 1.68 | 2.71 | 2.59 |
| | | <i>C</i> | 1.53 | 1.52 | 1.52 | 1.50 | 1.48 | 1.66 | 1.46 |
| <i>Set 1</i> | <i>Set 3</i> | <i>A</i> | 1.66 | 1.76 | 1.92 | 2.17 | 2.19 | 4.23 | 4.22 |
| | | <i>B</i> | 1.68 | 1.69 | 1.69 | 1.89 | 1.73 | 4.05 | 3.87 |
| | | <i>C</i> | 1.55 | 1.54 | 1.54 | 1.53 | 1.54 | 2.15 | 1.61 |
| <i>Set 1</i> | <i>Set 6</i> | <i>A</i> | 2.54 | 2.58 | 2.72 | 3.91 | 3.38 | 9.70 | 9.68 |
| | | <i>B</i> | 2.54 | 2.52 | 2.50 | 3.33 | 2.67 | 9.54 | 9.24 |
| | | <i>C</i> | 2.03 | 2.03 | 2.07 | 2.05 | 2.24 | 4.02 | 2.18 |
| <i>Set 3</i> | <i>Set 1</i> | <i>A</i> | 1.67 | 1.77 | 1.94 | 2.18 | 2.21 | 4.22 | 4.21 |
| | | <i>B</i> | 1.69 | 1.70 | 1.72 | 1.90 | 1.77 | 3.99 | 3.83 |
| | | <i>C</i> | 1.63 | 1.61 | 1.61 | 1.60 | 1.60 | 2.17 | 1.68 |
| <i>Set 3</i> | <i>Set 3</i> | <i>A</i> | 1.79 | 1.85 | 2.52 | 2.12 | 3.13 | 8.10 | 8.09 |
| | | <i>B</i> | 1.80 | 1.80 | 1.87 | 1.92 | 2.14 | 7.56 | 7.32 |
| | | <i>C</i> | 1.66 | 1.65 | 1.65 | 1.65 | 1.70 | 3.49 | 2.26 |
| <i>Set 3</i> | <i>Set 6</i> | <i>A</i> | 2.78 | 2.75 | 4.28 | 3.57 | 5.48 | 19.89 | 19.86 |
| | | <i>B</i> | 2.77 | 2.74 | 2.95 | 3.21 | 3.63 | 18.83 | 18.35 |
| | | <i>C</i> | 2.18 | 2.17 | 2.27 | 2.18 | 2.52 | 7.66 | 3.93 |
| <i>Set 6</i> | <i>Set 1</i> | <i>A</i> | 2.63 | 2.66 | 2.81 | 3.92 | 3.47 | 9.70 | 9.68 |
| | | <i>B</i> | 2.64 | 2.62 | 2.61 | 3.28 | 2.83 | 9.53 | 9.24 |
| | | <i>C</i> | 2.48 | 2.47 | 2.50 | 2.51 | 2.59 | 4.69 | 2.96 |
| <i>Set 6</i> | <i>Set 3</i> | <i>A</i> | 2.86 | 2.82 | 4.33 | 3.60 | 5.52 | 19.93 | 19.90 |
| | | <i>B</i> | 2.86 | 2.83 | 3.03 | 3.21 | 3.72 | 19.00 | 18.58 |
| | | <i>C</i> | 2.55 | 2.54 | 2.59 | 2.57 | 2.80 | 8.77 | 5.27 |
| <i>Set 6</i> | <i>Set 6</i> | <i>A</i> | 4.66 | 4.79 | 7.94 | 9.14 | 10.22 | 43.16 | 43.12 |
| | | <i>B</i> | 4.58 | 4.54 | 5.27 | 6.99 | 6.75 | 41.18 | 40.58 |
| | | <i>C</i> | 3.40 | 3.41 | 3.79 | 3.39 | 4.38 | 18.68 | 10.45 |