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.

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Abstract

The simple-Petersen estimator is a well known mark-recapture method to estimate animal abundance. Two key assumptions are equal catchability in both samples and complete mixing of tagged and untagged animals. If these are violated, severe bias can occur. The stratified-Petersen estimator can be used to account for some of the heterogeneity in catchability or mixing. In this paper, we first review recent developments in the stratified-Petersen experiment for fisheries audiences and demonstrate some of the practical problems that can occur that have not been discussed in the theoretical literature. Second, we present a case-study to estimate the gross escapement of Fraser River pink salmon (*Oncorhynchus gorbuscha*) in 1991. The motivation for this study is a discrepancy of over 5 million fish between the estimates as derived by the Pacific Salmon Commission (PSC) (7.5 million fish based on a hydroacoustic method) and the Department of Fisheries and Oceans (DFO), Canada (13.0 million fish based on a mark-recapture method). One hypothesis put forward was that the discrepancy may be due to the use of a pooled-Petersen estimator when there is differential migration over time. The stratified-Petersen model suggests that little of this discrepancy can be explained by differential migration.
1. **Introduction**

The Petersen-Lincoln estimate for the size of a population is well known and widely used. A total of $n_1$ fish are tagged and released at time 1, and $n_2$ fish are recovered at time 2 of which $m_2$ are marked. The estimate of the population size is:

$$\hat{N}_{petersen} = \frac{n_1n_2}{m_2}$$

(a small sample bias correction is often applied - Chapman, 1951).

The Petersen estimator is a consistent estimator of the population size under the following conditions:

1. Either or both of the samples is a simple random sample, i.e. all fish in the population have the same probability of being tagged or all fish have the same probability of being captured in the second sample; or tagged fish mix uniformly with untagged fish.
2. The population is closed.
3. There is no tag loss.
4. The tagging status of each fish is determined without error.
5. Tagging has no effect on the subsequent behavior of the fish.

Assumption 1 allows considerable latitude in planning an experiment. For example, both the initial capture or the final capture stations may sample fish in a fairly haphazard fashion but as long as tagged fish mix uniformly with untagged fish the Petersen estimator will be consistent. Or, tagged fish may not mix uniformly with untagged fish, but as long as the second sample is a random sample and all fish have equal probability of capture, the Petersen estimator will again be consistent. There are many experiments in which Assumption 1 is likely to be violated. For example, in surveys of spawning populations, fish are caught and tagged as they pass a common point prior to the spawning grounds over the
course of several days or weeks. It is unlikely that the tagged fish are a simple random sample - this would require, at a minimum, that a constant proportion of the fish are tagged each day. Similarly, the recaptures may be obtained by searching carcasses on selected spawning area. The recapture probabilities likely vary by recovery area and over time - and some spawning areas may not be sampled at all. Lastly, it is unlikely that fish passing the tagging site early in the run mix completely with fish that pass the tagging site late in the run. Under these circumstances, the simple Petersen estimator formed by pooling over time and space all of the tags applied and all of the recoveries may not be a consistent estimator, i.e., it may be biased, and this bias can be considerable (Arnason et al. 1996b).

In 1991, there was over a 5 million fish discrepancy between the estimates of the gross escapement of pink salmon (Oncorhynchus gorbuscha) returning to the Fraser River as derived by the Pacific Salmon Commission (PSC, 7.5 million fish) and the Department of Fisheries and Oceans, Canada (DFO, 13.0 million fish). The PSC estimate was based on a hydroacoustic count of fish as they pass Mission, B.C., while the DFO estimate was based on variant of a Petersen mark-recapture experiment. The Pacific Salmon Commission (1994, p.61) suggested that all of these assumptions may have been violated to some degree in the survey. In particular, the report noted that tagged:untagged ratios were higher in the early segment of dead recoveries than in later segments which could be caused by differences in the tagging rates over time, differences in the movements over time, and differences in the recovery rates in time and space. All of these may introduce bias into the Petersen estimator.

One method of reducing this bias is to stratify by time or space. This was first considered by Schaeffer (1951), Chapman and Junge (1956), and Darroch (1961); the latter partially developed the maximum likelihood theory. A summary of the work on the stratified-Petersen and some extensions is found in Seber (1982, Chapter 11). Recently,
Plante (1990) and Plante and Rivest (1995) developed general maximum likelihood theory for the cases where the number of release strata did not match the number of recapture strata. Banneheka (1995) and Banneheka et al. (1997) developed a least squares estimator and found its properties. Arnason et al. (1996a, 1996b) examined under what conditions stratified estimators were superior to the usual Petersen estimator and have developed a user-friendly computer package that implements all of these recent advances.

The purpose of this paper is two-fold. The first is to review recent developments in the stratified-Petersen experiment for fisheries audiences and to demonstrate some of the practical problems that can occur that have not been discussed in the theoretical literature. The second is to assess the degree of bias that may have been introduced into the DFO estimates by using a pooled-Petersen estimator and to see if this accounts for a substantial portion of the discrepancy.

2. Methods

2.1 The Statistical Model and its Assumptions

In the stratified-Petersen experiment, the population and sample are stratified into $s$ non-overlapping strata at the time of tagging and into $t$ non-overlapping strata at the time of recovery. Stratification may take place in space and/or time. For example, in geographic stratification, tagging strata may be different stocks of fish caught on different breeding areas and recovery strata may be different fishing areas. [Schwarz, Schweigert, and Arnason (1993) considered the case where tagging and recovery strata were the same.] In temporal stratification, tagging and recovery may take place over several weeks and individual strata correspond to time intervals (e.g. weeks). In temporal stratification, it is not necessary that the time strata at tagging and recovery correspond, i.e., it is not necessary that week 1 in the tagging strata be the same period as week 1 in the recovery strata. Nevertheless, it often happens that there is considerable overlap between the temporal periods, and consequently,
it is quite impossible for certain “movements” to occur, e.g., a fish cannot be recovered before it is tagged. In these certain statistics may be constrained to be zero.

The observed statistics from a stratified experiment are:

\[ n_i^c = \text{the number of fish that are captured and tagged in tagging stratum } i. \]
\[ n'_j = \text{the number of fish that are recovered (regardless if tagged or not) in recovery stratum } j. \]
\[ m_{ij} = \text{the total number of fish tagged in tagging stratum } i \text{ and recovered in recovery stratum } j. \]
\[ u_j = \text{the total number of untagged fish recovered in recovery stratum } j. \]

These can be arranged into a rectangular array as shown in Table 1. A total of \( n_i^c \) fish are tagged and released in each stratum. They move to the recovery strata, and some may be recovered in the recovery sample. Because each tag identifies the stratum of release, the number of tagged fish released in stratum \( i \) and recovered in stratum \( j \) \( (m_{ij}) \) can be computed. Not all fish recovered have tags; a total of \( u_j \) untagged fish are also recovered in stratum \( j \). This experiment has \( st + s + t \) statistics being the observed movements between tagging and recovery strata, \( \{ m_{ij} \} \); the number of fish tagged \( \{ n_i^c \} \) or equivalently \( n_i^c - m_{ij} \); and the number of untagged fish recovered \( \{ u_j \} \).

The population can be organized into a similar array as shown in Table 2. Let

\[ N_i^c = \text{the total number of fish in the population present in tagging stratum } i \text{ at the time of tagging.} \]
\[ N'_j = \text{the total number of fish in the population present in recovery stratum } j \text{ at the time of recovery.} \]
\( N^c \) = the total population size at the time of tagging. \( N^c = \sum_{i=1}^{s} N^c_i \)

\( N^r \) = the total population size at the time of recovery. \( N^r = \sum_{j=1}^{t} N^r_j \).

\( N_{ij} \) = the number of fish in the population that move from tagging stratum \( i \) to recovery stratum \( j \).

The population at the time of initial capture (\( N^c \)) is stratified into \( s \) strata each containing \( N^c_i \) fish. Then \( N_{ij} \) fish move from tagging stratum \( i \) to recovery stratum \( j \). The total number of fish now present in recovery stratum \( j \) (\( N^r_j \)) is obtained by summing the movements into the recovery stratum from all tagging strata (\( N^r_j = \sum_{i=1}^{s} N_{ij} = N_{j} \)). Some fish (\( N^c_i - N_{ij} \)) may die or move to other recovery strata not part of the experiment. If the population is closed, then \( N^c = \sum_{i=1}^{s} \sum_{j=1}^{t} N_{ij} \). On the other hand, if the fish can move to strata not subject to recovery or die before moving to a recovery stratum, then \( N^c \geq N^r \). It is implicitly assumed in Table 2 that no part of the population enter recovery strata without belonging to one of the tagging strata.

In order to link the statistics in Table 1 with the population parameters in Table 2, the usual assumptions for capture-recapture experiments are made and it is additionally assumed that:

1. Fish behave independently of one another in regard to moving among strata.
2. All tagged fish released in a stratum have the same probability distribution of movement to the recovery strata.
3. All fish in a recovery stratum behave independently in regard to being caught and all 
have the same probability of being caught.

4. No tags are lost.

5. All fish that are recovered are correctly identified as to the tagging status, and if tagged, 
the tag number is correctly recorded.

In addition, one or both of the following assumptions is usually made depending if the goal 
of the study is to estimate the number of fish in the tagging or recovery strata:

6a. [Required to estimate the total number of fish in the tagging strata.]

   The movement pattern, death, and migration rates are the same for tagged and untagged 
   fish in each tagging stratum.

6b. [Required to estimate the total number of fish at the recovery strata.]

The population is “closed” with respect to movement among strata, i.e., $\theta_{ij} = 1$ for 
$i=1,\ldots,s$. In situations like sampling of dead fish at the spawning grounds, this assumption 
means that the number of fish that die before they reach the spawning grounds is negligible 
and that all possible spawning grounds are searched. [Failing to search some spawning 
areas is indistinguishable from mortality.]

Under these assumptions, the expected value of the statistics in Table 1 can be 
written in terms of the following parameters as shown in Table 3. Let:

$\theta_{ij} = \text{the probability that a fish present in tagging stratum } i \text{ will survive and move to}$

recovery stratum $j$. If the population is closed then $\theta_{ij} = 1$. By definition, $\theta_{ij} = \frac{N_{ij}}{N_i}$,

$i=1,\ldots,s, j=1,\ldots,t$.

$pc_i = \text{the probability that a fish present in tagging stratum } i \text{ will be captured, tagged, and}$

released.

$pr_j = \text{the probability that a fish present in recovery stratum } j \text{ will be recaptured.}$
There are a total of \( st + s + t \) parameters being the movement parameters, \( \{ \theta_{ij} \} \) (the population is not assumed to be closed, i.e., \( \sum_{j=1}^{t} \theta_{ij} \leq 1 \)); the initial capture (tagging) probabilities, \( \{ pc_i \} \); and the recapture probabilities, \( \{ pr_j \} \).

At first glance it would seem that all parameters can be estimated because the number of statistics equals the number of parameters. However, as shown by Plante (1990), Plante and Rivest (1995), Banneheka (1995), and Banneheka et al. (1997), there is an indeterminacy in the experiment that does not allow all the parameters to be individually estimated. However, certain functions of the parameters may be estimated under each of two different scenarios.

First, the number of tagging strata may be less than or equal to the number of recovery strata \( (s \leq t) \). Under Assumption 6a (same movement patterns for tagged and untagged fish, but not necessarily closure over recovery strata), Plante (1990), Plante and Rivest (1996), Banneheka (1995), and Banneheka et al. (1997) showed that the number of fish in the population at the time of tagging can be estimated. The model requires an alternate parameterization in terms of \( st + 2s \) parameters:

\[
\mu_{ij} = N_i pc_i \theta_{ij} pr_j = \text{the expected number of fish that move from tagging stratum } i \text{ to recovery stratum } j \text{ that are tagged and recovered (st parameters).}
\]

\[
\beta_i = \frac{1 - pc_i}{pc_i} = \text{odds that a fish will not be captured in tagging stratum } i \text{ (s parameters).}
\]

\[
\gamma_i = \sum_{j=1}^{t} N_i pc_i \theta_{ij} (1 - pr_j) = \text{expected number of fish tagged in stratum } i \text{ but never recovered (s parameters).}
\]

Table 4 shows how this new parameterization can describe the expected values of the observed statistics and the number of fish never seen.
Second, the number of tagging strata may be greater than or equal to the number of recovery strata. Under Assumption 6b (the population is closed with respect to movement to the recovery strata), the population size at the time of recovery can be estimated. The model requires a second alternate parameterization in terms of \( st + 2t \) parameters as shown by Plante (1990).

When \( s=t \) either parameterization may be used and if both Assumptions 6a and 6b are satisfied, the population size at the time of tagging and at the time of recovery are identical and can be both estimated. The case of \( s=t \) was fully developed by Darroch (1961) and summarized by Seber (1982).

We believe that for most experiments, Assumption 6a is more tenable than Assumption 6b. In a typical spawning escapement survey, the population is not closed because there is mortality between the tagging site and the spawning areas, fish leave the “population” because of spawning in other than the recovery sites, fish may arrive and spawn before or after recovery takes place, and fish may be removed through a food-fishery that takes place during the run. For this reason we will discuss the stratified-Petersen analyses with \( s \leq t \) to estimate the number of fish that pass the primary tagging site using the parameterization presented in Table 4. [Assumption 6a will be required.] The theory for cases with \( s \geq t \) is analogous to that presented here with only minor changes.

### 2.2 The Estimators

From the parameterization in Table 4, one simple set of estimates for \( \{ \mu_{ij} \} \) and the \( \{ \gamma_i \} \) are the \( \{ m_{ij} \} \) and \( \{ n^c_i - m_* \} \) respectively. Note that \( E[u_j] = \sum_{i=1}^{t} \beta_i \mu_{ij} \) for \( j = 1, \ldots, t \) so the...
\( \{ \beta_i \} \) are the weights used to construct a linear combination of the rows of the \( \text{E}[m_{ij}] \) that equals the \( \text{E}[u_j] \). This suggests that one estimator for \( \{ \beta_i \} \) can be found as the values that weight the rows of \( \{ m_{ij} \} \) to give the best fit to the \( \{ u_j \} \). One such method is to minimize the sum of squares of the errors of predictions, i.e.,

\[
\text{choose } \{ \hat{\beta}_i \} \text{ to minimize } \sum_{j=1}^{t} \left( u_j - \sum_{i=1}^{s} \hat{\beta}_i m_{ij} \right)^2.
\]

Banneheka (1995) and Banneheka et al. (1997) investigated a least-square estimator for \( \{ \beta_i \} \):

\[
\hat{\beta}_u = (mm')^{-1} mu
\]

where

\( \hat{\beta}_u \) is the \( sx1 \) vector of estimates of \( \{ \beta_i \} \),

\( m \) is the \( sxt \) matrix of the \( \{ m_{ij} \} \), and

\( u \) is the \( tx1 \) vector of the \( \{ u_j \} \).

This estimator is consistent for the overall population size at the time of tagging and for the individual stratum sizes. The least-square estimator implicitly assumes that the \( \{ m_{ij} \} \) are precise estimates of the \( \text{E}[m_{ij}] \) and that errors in estimating the \( \{ u_j \} \) are of equal importance. In small samples, the \( \{ m_{ij} \} \) may be subject to large sampling variability and may not be very reliable. As well, the \( \{ u_j \} \) may vary considerably in size and errors in prediction may have unequal importance.

In such cases, a maximum-likelihood approach where distributional assumptions are imposed on the observed data may be preferable because then uncertainty in the \( \{ m_{ij} \} \) can be included in the estimation procedure. Plante (1990) and Plante and Rivest (1995) assumed a multinomial distribution with expected values as given in Table 4. A direct maximization of the likelihood was difficult and so they conditioned upon the observed
number of fish seen to obtain conditional maximum likelihood estimates. These estimators
do not have a closed form solution and numerical methods must be used (e.g. Plante, 1990;
Plante and Rivest, 1995; Arnason et al., 1996a). Sanathanan (1977) has shown that these
conditional maximum likelihood estimators are asymptotically equivalent to the usual
maximum likelihood estimators and experience with similar situations in multiple-recapture
settings (Schwarz and Arnason, 1996) has shown that they have good properties in small
samples. Plante’s (1990) procedure finds estimates of the \( \beta_i \) that “best” predicts the
\( \{ u_j \} \) while allowing the \( \{ m_{ij} \} \) to “vary” around their observed values in a way that is
consistent with the observed data but also improves the fit. As well, errors in prediction are
weighted differently depending upon the magnitude of the \( \{ u_j \} \).

\[ 2.3 \textbf{Assessing Model Fit} \]

A goodness-of-fit test can be applied once the model is fit. Because the underlying model is
based on a multinomial distribution, the usual \( \chi^2 \) goodness-of-fit statistic

\[
\chi^2 = \sum_{\text{all possible cells}} \frac{(\text{observed} - \text{expected})^2}{\text{expected}}
= \sum_{i=1}^{s} \sum_{j=1}^{t} \left( \frac{m_{ij} - \hat{m}_{ij}}{\hat{m}_{ij}} \right)^2 + \sum_{j=1}^{t} \left( \frac{u_j - \hat{u}_j}{\hat{u}_j} \right)^2 + \sum_{i=1}^{s} \left( \frac{n^c_i - m_{i*} - \hat{\gamma}_i}{\hat{\gamma}_i} \right)^2
\]
or the \( G^2 \) goodness-of-fit statistic:

\[
G^2 = 2 \sum_{\text{all possible cells}} \text{observed} \times \ln \left( \frac{\text{observed}}{\text{expected}} \right)
= 2 \left[ \sum_{i=1}^{s} \sum_{j=1}^{t} \frac{m_{ij}}{\hat{m}_{ij}} \ln \left( \frac{m_{ij}}{\hat{m}_{ij}} \right) \right] + \sum_{j=1}^{t} \frac{u_j}{\hat{u}_j} \ln \left( \frac{u_j}{\hat{u}_j} \right) + \sum_{i=1}^{s} \frac{(n^c_i - m_{i*})}{\hat{\gamma}_i} \ln \left( \frac{n^c_i - m_{i*}}{\hat{\gamma}_i} \right)
\]

may be computed. [The last term in both test statistics will always vanish because \( \hat{\gamma}_i \) is
always exactly equal to \( n^c_i - m_{i*} \).] Both statistics are asymptotically distributed as a \( \chi^2 \)
distribution with \((t-s)\) degrees of freedom. If a significant lack-of-fit is detected, the individual entries in the test-statistic can be examined to determine the source of the lack-of-fit.

As with all such goodness-of-fit tests, care must be taken to ensure that most expected values are reasonably large so that the \(\chi^2\) approximation to the distribution of the test statistic is adequate. This is usually only a problem with \(E[m_{ij}]\) and it is recommended that all \(E[m_{ij}]\) be at least 5 - a common practice in \(\chi^2\)-type statistics.

### 2.4 Adjusting the recovery data when problems arise in fitting the model.

Real data often presents challenges to fitting models to data. These problems have not been adequately discussed in the theoretical literature. There are two typical problems:

- values of \(m_{ij}\) close to or equal to zero;
- rows of the \(\{ m_{ij} \} \) matrix that are near or exact multiples of each other or, more generally, rows that are exactly or nearly linearly dependent (i.e., some linear combination of the rows sum to zero).

Elements of \(m_{ij}\) that are exactly equal to 0 are a problem because sampling-zeros (values of \(m_{ij}=0\) that occur just by chance) cannot be distinguished from structural-zeros (physically impossible movements, e.g. recoveries occurring before releases in time stratification). In both cases, the MLE of \(\mu_{ij}\) remains at zero and so the release group containing the “cell” cannot contribute to the predicting the \(u_j\). This is not appropriate for sampling zeros because there is some movement of the population that, just by chance, was not detected. Similarly, small non-zero values of \(m_{ij}\) are not reliable, and are subject to large
sampling fluctuations. There will be little information about the contribution of a release group to the untagged fish in these cases.

Linear dependency among the rows of the \( \{ m_{ij} \} \) matrix is a problem because the resulting estimators are no longer consistent (Darroch, 1961; Banneheka, 1996). [Linear dependency among the columns of the \( \{ m_{ij} \} \) matrix is not a problem as long as the rank of the matrix is equal to the number of rows.]

In all cases, the stratified data may have to be modified by either dropping rows or columns or by pooling two or more rows or columns and then refitting the model to this new stratification. Banneheka (1995) examined the conditions under which this pooling still leads to consistent estimators. The most extreme form of pooling where all rows and all columns are collapsed is known as the pooled-Petersen estimator and its properties are discussed in Darroch (1961), Arnason et al. (1996a, 1996b), Seber (1982, Chapter 11), and later in this paper.

### 2.4.1 Dropping or pooling recovery strata when \( s \leq t \)

If the entire column corresponding to a recovery stratum has small or zero counts, this may indicate that little movement took place to this stratum, that recovery effort was small, or that the stratification interval is too fine. Under these circumstances, it may be appropriate to either drop the recovery stratum or to pool two or more recovery strata together.

If the columns of the recovery matrix are linearly dependent, this implies that movement patterns to the corresponding recovery strata are proportional among all the tagging strata. In such cases, it is also appropriate to pool two or more recovery strata together.
As shown by Banneheka (1996), recovery strata may be arbitrarily dropped without affecting the consistency of the estimate as long as the resulting matrix of recoveries still has $s \leq t$. This result is not too surprising as the model does not assume closure and dropping a recovery stratum is exactly the same and indistinguishable from mortality or migrating out of the system. As well, in the case of $s \leq t$, it is only possible to estimate the number of fish in the release strata; the number and composition of the recovery strata is irrelevant.

Similarly, if the underlying model is appropriate, recovery strata may be arbitrarily pooled without affecting the consistency of the pooled-data estimators – as long as $s \leq t$ after pooling. [Of course, it would make sense only to pool strata that are close together in time or space.]

Unfortunately, there does not appear to be a formal statistical test to help the analyst decide if two recovery strata can be pooled (other than the goodness-of-fit test) - but any such test is unlikely to have any useful power in cases where most pooling takes place - that of small $m_{ij}$.

There are no compelling reasons to deciding between dropping or pooling strata except for the rule of thumb (from capture-recapture studies) that all the $m_{ij}$ after pooling should be at least 5 to avoid problems of sampling-zeroes. If the $m_{ij}$ in the recovery strata are all zero, it is likely preferable to drop this stratum rather than pooling with other strata.
2.4.2 Dropping tagging strata when $s \leq t$.

Dropping a tagging stratum is typically done if none or few recoveries are observed from the stratum. If the entire row corresponding to a release stratum has zero or small counts, it may indicate an inadequate tagging effort, or that fish in this stratum die before reaching the spawning grounds, or that fish migrate to strata not part of the experiment (e.g., they may arrive on the spawning grounds before or after recovery effort takes place).

In the case where fish move outside the study, the fish from this stratum do not contribute to the observed untagged recovered fish. In this case, the stratum can be dropped from the experiment; but the resulting estimate of the initial population size excludes this dropped stratum.

In some cases, a tagging stratum makes a substantial contribution to the recovery strata, but the number of recoveries is small because of limited tagging in that stratum. If the tagging stratum is dropped from the model, the estimates of $\beta_i$ for the remaining strata will be biased upwards trying to account for the contribution of the dropped stratum to the observed untagged recovered fish. Consequently, the estimates of the remaining individual stratum population sizes and the estimate of the overall population size will be biased upwards. This bias is analogous to the case of “births” or “immigration” as considered by Arnason et al. (1996a, 1996b), and indicates the importance of ensuring that all potential strata that contribute to the recovery strata are tagged in sufficient numbers.

2.4.3 Pooling tagging strata when $s \leq t$.

Pooling tagging strata may be required in the case of an exact or near singularity in the recovery matrix because one of the key assumptions required for consistency of the estimators for $\{ \beta_i \}$ is that the expected and observed recovery matrices be full rank, i.e., the
rank of the \( \{ m_{ij} \} \) and \( \mathbb{E}[m_{ij}] \) be both equal to \( s \), the number of tagging strata (Darroch, 1961; Banneheka, 1996). Unfortunately, in these situations, the only resolution available is to pool rows, but unlike pooling recovery strata, the estimator are consistent only under special circumstances.

Because pooling rows is the operation most fraught with potential problems, a series of theoretical examples (Tables 5-8) will be used to illustrate the potential pitfalls that can occur.

One of the simplest occurrences of singularity occurs when two rows of the \( \{ m_{ij} \} \) or \( \mathbb{E}[m_{ij}] \) are multiples of each other (Table 5). In this example, \( 2\text{row}_1=\text{row}_2 \), or \( 2\text{row}_1-\text{row}_2=0 \). This gives rise to an infinite number of solutions for \( \{ \beta_i \} \), namely any solution of the form \( \{ \beta_{i,\text{unpooled}} \} = \{9.00+2k, 5.67-k, 19.00\} \) will give a perfect fit to the \( \mathbb{E}[u_j] \). Fortunately, in this case, regardless of which value of \( \{ \beta_i \} \) are chosen, the “estimate” of the overall population size is the same even though none of the individual strata sizes can be estimated. When rows 1 and 2 are pooled, the pooled matrix now has full rank of 2, and a unique solution for the \( \{ \beta_{i,\text{pooled}} \} = \{6.78, 19.00\} \) is found corresponding to \( k=1.11 \). The total of the initial population in stratum 1 and 2 combined is found to be \( 9,000(6.78+1)=70,000 \) in the same fashion as in the unpooled case; note however, it is quite impossible to separate the combined total into its individual stratum totals unless it is also assumed that \( p_{c_i} = p_{c_j} \). In the latter case, the total for the pooled strata is separated into the individual stratum totals in the same ratio as the number tagged.

Unfortunately, having two rows of \( m_{ij} \) or \( \mathbb{E}[m_{ij}] \) being proportional is no guarantee that pooling will lead to consistent estimates. For example, in Table 6, two \( \theta_{ij} \) rows are
multiples of each other, two rows of the $E[m_j]$ are still multiples of each other, and there are an infinite number of solutions, $\{ \beta_{i, \text{unpooled}} \} = \{9.00+3k, 5.67-2k, 9.00\}$. However, pooling rows 1 and 2 does not lead to the correct population total, e.g. $\{ \beta_{i, \text{pooled}} \} = \{7.00, 9.00\}$ gives an exact fit to the $E[u_j]$, but doesn’t give the correct overall population value. In these cases, one is forced to pool to avoid singularity but biased is introduced into both the estimates of the individual stratum sizes and the overall population size.

Another common type of linear dependence occurs when a weighted combination of two rows adds to a third row. For example, in Table 7, $E[\text{row}_2] = E[\text{row}_1] + 2E[\text{row}_3]$. This situation common occurs when the release strata “overlap”, e.g., the second stratum has fish with migration patterns intermediate between the pattern in stratum 1 and stratum 3. [This often occurs when the tagging strata are time periods and there is no sharp change in movement patterns over time.] There are an infinite number of solutions of the form $\{ \beta_{i, \text{unpooled}} \} = \{9+k, 5.67-k, 19+2k\}$ that all give rise to a perfect fit. Pooling any two rows will still lead to consistent estimates of the overall population total ($N_c$), but not for the individual stratum totals ($N_i$).

Banneheka (1995) showed that two sufficient (but not necessary) conditions for consistency that allow two rows ($i$ and $i'$) to be pooled when $s \leq t$ are:

1. the patterns of movement are the same over all recovery strata, i.e. $\theta_{ij} = \theta_{tj}$ for $j=1,\ldots,t$.

OR

2. the initial tagging rates are the same, i.e., $pc_i = pc_{i'}$.

These conditions are analogous to those required for complete pooling of all the rows as outlined in Seber (1982, p. 437).
A test for condition (1) is constructed by examining the $2 \times (t+1)$ contingency table:

<table>
<thead>
<tr>
<th>Tagging stratum</th>
<th>Recovery stratum</th>
<th>not seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>$i$</td>
<td>$m_{i,1}$</td>
<td>$n_i^c - m_{i,1}$</td>
</tr>
<tr>
<td>$i'$</td>
<td>$m_{i',1}$</td>
<td>$n_{i'}^c - m_{i',1}$</td>
</tr>
<tr>
<td></td>
<td>$m_{i,2}$</td>
<td>$n_i^c - m_{i,2}$</td>
</tr>
<tr>
<td></td>
<td>$m_{i',2}$</td>
<td>$n_{i'}^c - m_{i',2}$</td>
</tr>
<tr>
<td></td>
<td>$\ldots$</td>
<td>$\ldots$</td>
</tr>
<tr>
<td></td>
<td>$m_{i,t}$</td>
<td>$n_i^c - m_{i,t}$</td>
</tr>
<tr>
<td></td>
<td>$m_{i',t}$</td>
<td>$n_{i'}^c - m_{i',t}$</td>
</tr>
</tbody>
</table>

A small $\chi^2$ test statistic for equality of the row proportions may indicate that condition (1) is satisfied. Note that the contingency table includes those fish marked but never subsequently recovered; the $2 \times t$ sub-table formed by dropping the last column would test for the proportionality of the movement probabilities but not for their equality.

Table 5 was constructed so that condition (1) above held, while in Table 6, condition (1) did not hold. In conditions similar to Table 7 where more than two rows are collinear, any two rows can always be pooled without affecting the consistency of the overall estimate, but unless condition (1) also hold for the pooled rows, the estimates of the individual strata total will be biased.

Allowance should be made for sampling variation of the $m_{ij}$ when examining the recovery matrix for linear dependencies. If the $m_{ij}$ are small, then their distribution can be well approximated by a Poisson distribution, and consequently, an approximate measure of their standard deviation is $\sqrt{m_{ij}}$. A search for colinearity should then allow the observed $m_{ij}$ to “vary” by about $\pm 2\sqrt{m_{ij}}$ from their actual value to account for this potential variability from their expected value.

Pooling may also be done when the second condition of Banneheka (1995) holds and this leads to consistent estimates of the $\{ \beta_i \}$ regardless of the movement patterns in the rows as shown in Table 8. After pooling, it is still possible to separate the total number of
fish in each of the individual stratum by partitioning the total for the pooled strata into the individual stratum totals in the same ratio as that of the initial number marked. A test for condition (2) can be done by examining the estimated \( \{ \beta_i \} \). If values are similar for two rows, this could indicated that the two rows could be pooled. Unfortunately, in the case of small observed counts, the individual estimates of the \( \{ \beta_i \} \) will have a large SEs and so in many instances, a formal test for the validity of the pooling will have poor power to detect cases where it is inappropriate to pool. The analyst must usually make strong, untestable assumptions about the initial stratum capture probabilities.

The above results can also be extended to the case of pooling multiple rows. Multiple rows may be pooled without affecting the consistency of the strata total if they all have the same movement pattern. This can be tested with real data by examining the \( k \times (t+1) \) contingency table which is a direct extension of that presented earlier. Multiple rows can also be pooled if they all have the same initial tagging rate - examination of the individual \( \{ \beta_i \} \) may be useful. In both cases, sparse data make it difficult to test these assumptions.

### 2.5 The completely-pooled Petersen estimator

The most extreme form of pooling ignores strata completely and computes a simple-Petersen estimate based on the total releases and total recaptures. Darroch (1961) and Seber (1982), summarized three common circumstances under which the completely-pooled Petersen remains a consistent estimator:

1. The tagging probabilities are the same in all release strata, i.e., \( pc_i = pc^* \) for all \( i \).

2. The recovery probabilities are the same in all recovery strata, i.e., \( pr_j = pr^* \) for all \( j \) and the same degree of closure of movement occurs, i.e., \( \theta_i = \theta^* \) for all \( i \).
3. There is complete mixing of fish from all the release strata before fish are recovered, i.e.,
\[ \theta_{ij} = \theta_{ij}^* \] for all \( i \), and the movement pattern for tagged and untagged fish is the same.

Arnason et al. (1996a, 1996b) report on simulation studies that show the pooled-Petersen estimator can be substantially biased (either positively or negatively) when none of these common conditions holds. A close approximation to the size of the relative bias can be derived using the first term of a Taylor-series expansion, and can be expressed as:

\[
\text{relative bias} \cong -C \text{(tagging probabilities, recapture probabilities)} \times \frac{\sqrt{V\text{(tagging probabilities)}V\text{(recapture probabilities)}}}{E[\text{tagging probabilities } \times \text{ recapture probabilities}]}
\]

where \( C, V, \) and \( E \) refer to the correlation, variance, and expectation taken over all individual fish in the population.

If the capture or recapture probabilities are equal in all strata, then there is a 0 correlation between the tagging and recapture probabilities, and if there is complete mixing, there is again 0 correlation among the tagging and recapture probabilities resulting in no bias.

In many real situations, the correlation between the capture and recapture probabilities is likely to be positive. For example, a temporal stratification, with relatively constant effort in each tagging stratum, leads to capture probabilities that are inversely related to the size of the run in each stratum, e.g., strata with larger numbers of fish have a lower tagging rate. If all fish move to the recovery strata in a fairly uniform fashion, then the recovery rates will also be inversely related to the size of the recovery strata. This will lead to a positive correlation between the capture and recapture probabilities and to a negative bias in the pooled-Petersen estimate.
Substantial bias is likely to occur if there is a large variability in both the capture and recapture rates and there is little mixing of the fish as they move from the tagging to the recovery strata, i.e. the \( m_{ij} \) matrix is diagonally dominant. This was confirmed in Arnason et al. (1996a, 1996b). An estimate of the bias of the pooled-Petersen can be found by comparing the estimate of the stratified-Petersen with the comparable estimate formed by complete pooling.

Darroch (1961) discussed formal statistical tests that can be used to examine if the pooled-Petersen estimate is consistent. In particular he discussed two simple contingency tables which have been implemented by Arnason et al. (1996a).

The first test is formed by examining the \( 2 \times t \) table:

\[
\begin{array}{cccc}
  m_{11} & m_{21} & \ldots & m_{t1} \\
  u_1 & u_2 & \ldots & u_t \\
  m_{11} + u_1 & m_{21} + u_1 & \ldots & m_{t1} + u_t \\
\end{array}
\]

The usual \( \chi^2 \)-test for a contingency table with \((t-1)\) degrees of freedom is computed. Failure to reject the hypothesis of equal marked proportions in the recovery strata may indicate that either the proportions tagged in each release stratum are equal \((pc_i=pc^*\) for all \(i)\) in which case the pooled-Petersen is consistent or that observable movements are proportional among strata \((\theta_{ij}/\theta_{i}*\) does not depend on \(j)\) in which case the pooled-Petersen is not consistent unless, as Darroch (1961) points out, the degree of closure is the same for all release strata (i.e., \(\theta_{i} = \theta^*\) for all \(i)\). This would occur if all spawning grounds are searched or if all release strata move to the same spawning areas in the same proportions and the same subset is searched. Consequently, a non-significant test statistic may not indicate that the pooled-Petersen may be consistent unless some biological knowledge can be used to assess the degree of closure.
The second test is formed by examining the \((sx2)\) table:

\[
\begin{array}{ccc}
  m_{1}, & n_{1}^{c} - m_{1}, & n_{1}^{c} \\
  m_{2}, & n_{2}^{c} - m_{2}, & n_{2}^{c} \\
  \vdots & \vdots & \vdots \\
  m_{s}, & n_{s}^{c} - m_{s}, & n_{s}^{c} \\
  m_{*} & n_{*}^{c} - m_{*} & n_{*}^{c}
\end{array}
\]

The usual \(\chi^2\)-test for contingency tables with \((s-1)\) degrees of freedom is computed. Failure to reject the hypothesis of equal overall recovery from each release stratum may indicate that either the proportions recovered in each recovery stratum are equal and that the total movement to recovery strata are also equal \((pr_j=pr^*\text{ for all } j \text{ and } \theta_{i*}=\theta \text{ for all } i)\), or that (again) complete mixing occurred among the release strata \((\theta_{ij}=\theta_j \text{ for all } i)\). Either condition is sufficient for the pooled-Petersen to be consistent.

Note that there are an infinite number of conditions under which the pooled-Petersen can remain consistent - the above two tests only examine three common conditions. Rejection by both tests only indicates that the common conditions under which pooling is appropriate did not hold - but there are other (biologically unlikely) conditions under which pooling is valid. Any only one test need be satisfied to allow complete pooling except that the first test may not be reliable without further outside information on the degree of closure in the experiment. Lastly, the tests should be conducted after the final pooling or dropping of rows or columns has been done as this pooling will have been necessary to obtain stratified estimates and what is of interest is whether complete pooling is further justified.
3. Case Study - Fraser River Pink Salmon

3.1 Survey protocol

Fraser River pink salmon (*Oncorhynchus gorbuscha*) exhibit a pronounced two-year population cycle with spawning populations occurring almost exclusively during old-numbered years. A review of the character of the run is found in Ward (1959).

Briefly, fish return up the Fraser River starting in mid-September and return to spawn in more than 60 different streams in the Fraser River watershed. However, roughly 95% of the spawners return to five general areas - the lower Fraser River Main Stem, the Seton, the Thompson, the Harrison, and the Vedder-Chilliwak river systems (Figure 1).

As returning fish pass Mission, samples were taken at Duncan Bar (Glen Valley). This site is downstream of all the major spawning areas in the Fraser River. Daily tag application rates were set to approximately 1% of the expected population passing the tagging site based on timings from past cycles and pre-season forecasts. Fish were sexed, tagged with individually numbered Petersen disc tags, and released.

Sampling of the five spawning areas was done by searching the spent carcasses (called dead-pitching). The gender, number, date, and location of the tagged and untagged fish was recorded. The tag number of each tag-recovery was also recorded. The distribution of sampling effort appears to be based more on an opportunity and availability of carcasses than on a systematic design (A. Cass and T. Whitehorse, pers. comm). Typically, the recovery program does not start until several weeks after tagging has started. Tag releases from the first week of tagging were only sampled during the descending limb of the recovery distribution, i.e., carcasses from fish that passed Glen Valley early in the season were not sampled until some time after they arrived, spawned, and died (A. Cass and T.
Whitehorse, pers. comm). As well, the recovery program was terminated before all the late
migrating pinks became available to the dead-pitch. The proportion sampled in the dead
pitch ranged from less than 1% in the Fraser Main Stem to over 20% in the Harrison River.
Searched carcasses were usually cut with a knife to prevent double counting in subsequent
weeks.

This study will examine the data on releases at Glen Valley and recovered on the five
spawning areas. It will provides estimates of the number of fish passing the tagging site that
is near the Mission, B.C. site of the PSC hydro-acoustic program.

Because of potential differences in the run timing of males and females, and more
importantly because of differences in behavior on the spawning grounds (females remain
near the reds and their carcasses are more likely to be recovered), they will be analyzed
separately. The results of the analyses of the female data will be given in detail; those for the
male data will be given in a summary form only.

3.2 Results for Females

Approximately 22,000 female pink salmon were tagged and released between 10 Sep 91 and
8 Oct 91 with daily application rates of over 1000 fish/day during the peak of the run falling
to less than 50 fish/day by the end of the run.

A total of approximately 300,000 female carcasses were dead-pitched from 2 Oct 91
to 12 Nov 91 (depending on the system), and about 700 tags were found in the five
systems. There were approximately 200 tags returned from other sources (spawning
channels, the food fishery, other systems, etc.) that are not included in these analysis.
The data were too sparse to stratify on a daily basis. As well, migration patterns would typically change slowly on a daily basis. These would likely lead to singular or near-singular recovery matrices. As noted earlier, pooling of recovery strata may be done in a fairly arbitrary fashion without affecting the consistency of the estimates. Because migration patterns change slowly over time, pooling daily releases is a necessity to avoid singular matrices and as long as the pooling interval is small, can be done without affecting the consistency of the final estimates. We found it necessary to stratify releases into 5-day intervals (e.g., 10 Sep 91 – 14 Sep 91; 15 Sep 91 – 19 Sep 91; …) and recoveries into 6-day intervals (e.g., 8 Oct 91 – 13 Oct 91; 14 Oct 91 – 19 Oct 91; …) before it was possible to obtain admissible estimates that were not too sensitive to small data values. The resulting 6x22 matrix of recoveries and other summary statistics are shown in Table 9. Table 9 indicates that, not unexpectedly, different segments of the run are composed of individuals with different migration patterns, e.g. fish tagged early in the run seem to spawn in the upper reaches of the Fraser (Thompson and Seton Rivers) while fish tagged later in the run seem to spawn near the mouth of the Fraser (Main Stem, Harrison, and Vedder-Chilliwack Rivers). The different release groups also appear to mix fairly well on their way to the spawning grounds because the submatrices for the individual spawning sites do not show a strong upper triangular form, that would occur, for example, if each release group had the same distribution for the time required to reach the spawning ground. This mixing was also noted by Ward (1959, p. 44).

These data can be used to obtain estimates of the abundance at the primary tagging site in a number of ways. Estimates can be obtained by considering the recoveries in each of the five spawning areas individually, or by using all the spawning sites simultaneously. In this paper, we initial found estimates based on the five individual spawning areas. Detailed procedures will be presented for the Fraser Main Stem recoveries (Table 10), but the results for the other areas are summarized only in Table 11. Based upon the results for the
individual areas, three of the spawning areas were used simultaneously to estimate the initial population totals (summarized in Table 11).

In all cases, the least-square estimates of \( \{ \beta_i \} \) were used as the initial values for the iterative procedure to obtain the MLEs. Estimates of the individual stratum totals were found as: \( \hat{N}_i = n_i \times (\hat{\beta}_{i, \text{MLE}} + 1) \) and the estimated overall total was found by summing the individual stratum estimates. Test for consistency of the pooled Petersen were also performed. Finally, the pooled-Petersen estimates for comparable segments of the run and to a pooled-Petersen estimate for the entire run were also computed.

3.2.1 Details on using the Fraser River Main Stem recoveries only.

This subset consists of the 6x5 submatrix extracted from Table 9. No recoveries were obtained from the release group dated 5 Oct 91 and so this row must be deleted. Because of the small number of fish tagged in this release group, these observed zeroes may not be structural zeroes, i.e., fish from this release group may spawn in the Fraser Main Stem, but there were too few tagged to detect such spawning.

The stratified-Petersen was then fit to the resulting 5x5 matrix and ML estimates were found to be:

\[
\hat{\beta}_{5x5} = \begin{bmatrix} 12,949 & -6,023 & -1,089 & 4,118 & 13,039 \end{bmatrix}.
\]

These are clearly inadmissible results (odds of not being captured cannot be negative). The failure of the stratified-Petersen in this case can be traced to the near-singularity of the recovery matrix where it appears that \( \text{row}_{15\text{Sep91}} \approx \text{row}_{10\text{Sep91}} + \text{row}_{20\text{Sep91}} \). [Recall that the observed \( m_{ij} \) are subject to sampling error and they can vary from sample to sample in the range of about \( \pm 2 \sqrt{m_{ij}} \); an exact linear dependence is not required.]
As outlined earlier, this type of dependency may be an indication that the tagging strata are not mutually exclusive. In this case, it would appear that fish in release group 15 Sep 91 is a mixture of fish with movement patterns similar to those in release groups 10 Sep 91 and 20 Sep 91. It may be possible to re-stratify the data to try and separate the two stocks, but this was not attempted in this paper.

As was seen earlier, pooling recoveries from two of the release groups still leads to consistent estimates for the population total but not necessarily for the individual tagging stratum totals unless the tagging rates were equal in the pooled strata. Unfortunately, there is not enough information in the data to test this latter hypothesis but pooling will not affect the consistency of the overall estimate.

After pooling release groups 10 Sep 91 and 15 Sep 91, the ML estimates were:

\[ \hat{\beta}_{4 \times 5} = \begin{bmatrix} 326 \\ -351 \\ 1,219 \\ 1,030 \end{bmatrix}. \]

Again the inadmissible results are caused by a near singularity - it appears that

\[ row_{20Sep91} = row_{25Sep91} + row_{30Sep91}. \]

Pooling these three release groups leads to admissible estimates in all the strata of \( \hat{\beta}_{2 \times 5} = \begin{bmatrix} 186.5 \\ 519.4 \end{bmatrix} \).

Final results are shown in Table 10. A chi-square goodness-of-fit of the Darroch model to the pooled data shows some evidence of a lack-of-fit in two cells, but given the relatively small \( \{ m_{ij} \} \) and large \( \{ u_{j} \} \) the lack-of-fit is assessed not to be serious. The estimated number of fish to pass the tagging sites in the first five release periods is 8.35 (se .82) million fish. The estimated \( \{ \beta_{i} \} \) and their standard errors indicate that the tagging rates in each stratum appear to be unequal and substantially less than the 1% tagging rate that was a goal of the study. Tests for the consistency of the pooled-Petersen showed some evidence...
that complete pooling may not be appropriate. The pooled-Petersen appears to have a negative bias of about 8% compared to the stratified.

3.2.2 Using recoveries from the other areas.

A similar procedure was used to obtain estimates of the abundance of fish in each tagging stratum using the recovery data from each of the remaining four recovery areas.

When using recoveries from the Harrison River, the rows corresponding to the 15 Sep 91 and 20 Sep 91 release groups are small in absolute terms, small relative to the number of recoveries from later release groups, and are almost the same leading to a near-singular matrix. These rows were deleted. The only pooling that lead to admissible estimates was to pool the remaining three rows to form a single release stratum. In cases such as this, the pooled-Petersen is always identical to the stratified estimator.

When using recoveries from the Seton River, no recoveries were obtained from the 5 Oct 91 release group and this row was deleted. The only pooling that lead to admissible estimates was to pool the first three remaining rows because they appear to be nearly co-linear. The tests for complete pooling indicated that complete pooling may be acceptable.

For the data from the Thompson River, no recoveries were obtained from the 5 Oct 91 release group and only 1 recovery was obtained from the 30 Sep 91 release group. Both of these rows were deleted. The only pooling that gave admissible estimates had the first three remaining release groups pooled. The tests for complete pooling indicate that it may be acceptable.
Lastly, for the data from the Vedder-Chilliwack River, no recoveries were obtained from the 10 Sep 91 release group and only 1 recovery was obtained from the 15 Sep 91 release group. Both of these rows were deleted. No further pooling was before admissible estimates were obtained. The tests for complete pooling indicated that complete pooling may be acceptable.

### 3.2.3 Comparing estimates from the individual spawning areas.

A summary of the population estimates for the five individual spawning areas and for the three combined areas is shown in Table 11. Because of different poolings of the tagging strata, the estimated totals cannot be compared directly.

The Harrison and Vedder-Chilliwack estimates of the total fish that passed the tagging site from 25 Sep 91 to the end of the experiment (strata 4-6) are similar (between 3-4 million fish), but the estimate from the Fraser Main Stem for the same period appears to be about 5 million fish. Note that the precision of the estimates is poor - a direct result of the small sample sizes.

Estimates from the Thompson system are extremely high. It turns out that a second pitching of the already pitched carcasses showed that a substantial number of tags were missed on the initial pitch - the estimated missing rate was almost 30%! If this rate was applied uniformly to the observed tag recoveries, each entry in the recovery matrix should be multiplied by 1/.70=1.42, each estimate of \( \beta_i \) would be divided by 1.42 to give an equivalent fit, and the estimated total would be reduced to about 13.5 million. This is still much larger than any of the estimates from the other systems.
The Seton estimates are also higher than the other three estimates and a repitch in this system showed that approximately 15% of tags were overlooked. This would reduce the Seton estimate by a factor of about 1.17 to 9.2 million fish.

It should be noted that both the Seton and Thompson River systems are well up the Fraser River. Because tagging the fish is very stressful to the fish, the observed estimates may also be affected by a handling induced mortality that is not present in the three systems closer to the mouth of the Fraser. There may have also been substantial tag loss from the tagging site to the spawning site. All of these possibilities will tend to inflate the estimates. These problems were also noted by the Pacific Salmon Commission (1994, p. 63).

For these reasons, only the recoveries from the Main Stem, Harrison, and Vedder-Chilliwack systems were used together. The initial data consists of the $6 \times 4$ submatrix from Table 9. Neither test for complete pooling indicated it may be acceptable. The estimates from three spawning areas analyzed together are comparable to the estimates reported from the three corresponding individual spawning sites and the estimates of the individual stratum totals are comparable.

### 3.3 Results for Males

Approximately 19,000 male pink salmon were tagged and released between 10 Sep 91 and 8 Oct 91. A total of approximately 180,000 male carcasses were dead-pitched from 2 Oct 91 to 12 Nov 91 (depending on the system), and about 600 tags were found in the five systems. There were approximately 300 additional tags returned from other sources (spawning channels, the food fishery, other systems, etc.) that are not included in this analysis.
The number of males tagged was approximately equal to the number of female, but only about 1/2 of the number of male carcasses were pitched. This may be due to behavioral differences between the sexes, e.g., females stay near the redds after spawning and are more prone to be left on the banks (Ward, 1959, p.44). The number of tags recovered is comparable to that from the females which indicates that the number of males returning may be substantially less than the number of females.

The same stratification intervals were used as with the female data and a summary is presented in Table 12. As with the female data, estimates were obtained using each spawning area separately, and for several systems combined. The poolings done for the male data are not exactly the same as for the female data. This is an artifact of the sample data actually observed - if the experiment was repeated in another year, it is likely that a different pooling would occur. A summary of the final results is shown in Table 13.

The estimates of the individual release stratum total are not very precise but are roughly comparable. The estimates of the overall total for the same period are generally consistent with each other except for the estimate from the Thompson River. Other data again showed substantial tag-overlooking in the original pitch. Surprisingly, the estimate for the number of males based on recoveries from the Seton River does not seem to be as inflated as it was for the females but a second repitch in the Seton system showed that fewer tags were overlooked for the males. The estimates from the Harrison data seem to be on the low side - no ready explanation is available for this.
3.4 Comparing the tagging estimates with the Pacific Salmon Commission Estimates and DFO’s spawning ground estimates

As shown in Tables 11 and 13, individual stratum estimates usually could not be found because the recovery data was too sparse or linear dependencies were detected in the recovery data. However, an estimate can be determined by fitting the various estimates into a regression problem with indicator variables for the individual strata. The estimates from the Thompson and Seton systems were not used when fitting the female data and the estimates from the Thompson system were not used when fitting the male data because of problems noted earlier. No standard error were derived because this analysis failed to account for any covariance among the estimates within each sex as a result of using the same set of recovery data.

The estimated individual stratum size and overall total are shown in Table 14. Note that only an estimate for the total of the first two release strata could be derived for the female data.

The estimated total of both sexes was compared to the PSC estimates as found from the hydroacoustic monitoring system at Mission, B.C. (Pacific Salmon Commission, 1994). The PSC estimates are approximately 1/2 of those from the marking data.

The Department of Fisheries and Oceans also computes total escapements for each of the major and minor spawning grounds upstream using a series of pooled-Petersen estimates from each of the secondary tagging programs combined with a pooled-Petersen estimator from the primary-tagging program as outlined by the Pacific Salmon Commission (1994, Appendix E) and by A. Cass and T. Whitehouse (pers. comm). These were corrected for an assumed 5% tag loss. These estimates are comparable to the stratified estimators.
4. Discussion

The Pacific Salmon Commission (1994, p. 66) concluded that “whether the bias (in the mark-recapture estimate) is due to tag loss and mortality or to non-random spatial or temporal distributions of tagged fish, or, to a combination of these factors” could not be determined from the summary data available at that time.

The results of this paper seem to indicate that the non-random time or area-distribution of tagged fish carcasses in dead recoveries accounts for little of the discrepancy between the DFO and PSC estimates of escapement. Consequently, the remaining discrepancy may be due to other violations of assumptions as discussed by the Pacific Salmon Commission (1994, Appendix E) - in particular an acute or chronic increase in mortality or differential movement of tagged fish compared to untagged fish. Alternatively, the hydroacoustic program may not sample all the fish as pink salmon have a tendency to migrate close to shore (Pacific Salmon Commission, 1994, p. 64) and its estimates may be too low even after correcting for this “known” undercount based on historical comparisons of DFO and PSC estimates.

The stratified analysis revealed potential problems with the recovery program in the Thompson and Seton systems. These systems gave estimates that were quite far from the estimates derived from the other spawning areas. This may be caused by a failure to correctly identify all tagged fish when pitching carcasses and/or by a handling induced mortality that becomes serious compared to the other systems because of the length of the migration. Both of these causes would inflate the estimates obtained.

The stratified-Petersen estimator should be used when estimates of the individual strata sizes are of direct interest. Even if the individual strata are not of interest, it can significantly reduce the bias of a pooled-Petersen estimator when there is substantial
variation in and correlation among the initial capture and final recapture probabilities. In many escapement studies, the natural pattern of returns often induces a positive correlation between these two probabilities and this results in a negative bias in the pooled-Petersen estimate.

However, despite recent theoretical advances and the availability of easy-to-use computer software, there are numerous practical problems that often make it difficult to use the stratified-Petersen estimator. For this pink-salmon data, the stratified-Petersen was not as successful in disaggregating the run into its individual daily or weekly components as originally hoped. This was due to several causes:

- Recovery data was relatively sparse. Even with the application of over 40,000 tags and the pitching of over half a million carcasses, the number of tags returned was often small after stratification by gender, time of tagging, spawning ground, and time of recovery.
- Release strata were not completely distinct. In many cases, the migration pattern is slowly changing over time and a release stratum consisted of fish with migration patterns from the previous and the next stratum. This causes near linear dependencies to exist in the observed and expected recovery matrices.
- The release strata appear to mix on their way to the recovery strata. This implies that the recovery matrices did not have an upper-triangular structure and allowed linear dependencies to occur.

In many cases, extensive pooling was required to obtain admissible estimates which partially defeated the purpose of stratification. The regression analysis was used to estimate the individual stratum sizes based on the estimates of aggregates of strata from the individual spawning areas. It appears to gives estimates consistent with those from DFO and about 70% higher than those from a hydroacoustic system operated by the Pacific Salmon Commission.
A potentially useful extension of the stratified-Petersen is for in-season estimates. As tagging and recovery programs progress over the season, estimates can be computed for individual run segments. Of course, this will only be successful if recoveries occur soon enough after releases so that estimates obtained are timely. For estimating the pink-salmon run, it may be feasible to employ a second set of gill-nets or fish wheels to sample the run looking for tags rather than waiting for spawning on the grounds.

The pooled-Petersen and stratified-Petersen provide methods at the opposite ends of the spectrum with regards to assumptions about capture and movement. The pooled-Petersen assumes that all fish have identical capture and movement probabilities while the stratified-Petersen lets each release stratum have its own distinct movement pattern. While this may be realistic for geographical stratification, it is, paradoxically, too flexible for temporal stratification. As was seen with the pink-salmon data, migration patterns likely change slowly over time leading to situations where near linear-dependencies can occur. Continuing research is being conducted in this area by fitting a smoothing parameter which will allow successive temporal strata to slowly change their migration pattern from previous strata.

ACKNOWLEDGMENTS

This work was supported by a Science Subvention Grant from the Department of Fisheries and Oceans and NSERC, and a Research Grant from NSERC.
5. References


