ADJUSTING FOR MISSED TAGS IN SALMON ESCAPEMENT SURVEYS

by

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Abstract

A method for estimating the salmon escapement size using a mark-recapture methodology after correcting for missed tags is developed. Mark-recapture involves capturing, tagging and releasing n_1 sockeye as they return to spawn. After spawning, the sockeye die and some of the carcasses get washed onto the banks of the spawning area. A random sample of n_2 of these carcasses results in observing m_2 tags. However, tags may be missed in the initial survey. A subsample of the $n_2 - m_2$ carcasses identified as being untagged is re-examined for missed tags. It is then possible to estimate the number of tags that should have been observed in the initial sample and in turn to obtain a better estimate of the salmon escapement. The variance of the revised salmon escapement estimate is derived and the loss of efficiency compared to a Petersen estimate, where no tags are overlooked, is found. Optimal allocation of effort between the initial and second examination is considered. Finally, a numerical example using actual data from the 1994 Fraser River sockeye season is used to illustrate the results.

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1. Introduction

Salmon escapement surveys often use a mark-recapture method to obtain an estimate of the returning population size. For example, a common method used in British Columbia is to capture n_1 fish as they return to spawn, tag them with Petersen disk tags, and release them. After spawning, the fish die and some of them get washed onto the banks of the spawning area. Survey teams examine n_2 carcasses and m_2 carcasses are observed with tags present. The simple Petersen estimate (Seber 1982, p. 59) of the number of fish that return to spawn (N, the escapement) is $\hat{N} = n_1 n_2/m_2$.

One of the assumptions of all mark-recapture experiments is that all fish captured are correctly identified as to tagging status, i.e., no tags are overlooked and no untagged fish are erroneously classified as being tagged. However, field conditions for the carcass recoveries are often severe, carcasses are not in pristine condition, and so mistakes can be made. The most common error is that a tagged fish can be classified as being untagged. This results in an overestimate of N. Mistakes of the other kind are unlikely as the tag number must be recorded for each tagged fish observed. To account for these misclassification errors, a subsample of the $n_2 - m_2$ fish identified as being without tags is examined more carefully for missed tags. This second examination is assumed to be infallible and is used to correct the estimate for the number of tags that have been observed in the initial sample.

Current practice is to use a simple moment estimator to estimate a revised m_2 which is then used in the usual Petersen formula. Precision is estimated as if this revised m_2 was known exactly and does not account for the fact that m_2 has been estimated. As well, little examination of the optimal allocation of effort between the initial carcass recovery and the subsequent re-examination of carcasses has been done.

The Fraser River Sockeye Public Review Board (1995) was asked to investigate issues dealing with the 1994 sockeye salmon returns. Among its recommendations (p. 96) was:

The resampling program for missed tags should definitely be more structured. A different formula also should be developed and the uncertainty over tag loss be incorporated into a better variance estimate. In addition, the method for constructing confidence limits should be revised in light of recent developments in mark-recapture and general statistical theory.

Paulik (1961) discussed the detection of incomplete reporting of tags. He derived a preliminary guide to determine the number of fish that should be tagged, and the number that should be recaptured and examined for tags, to be reasonably sure of discovering non-reporting of a certain magnitude. His plan to estimate "incomplete reporting should not be confused with the plan of examining the catch for tags that the fisherman failed to remove" (p. 828).

Hilborn (1988) derived a method for determining the percentage of recaptured tagged fish that are represented by returned tags for cases when tags are examined sequentially, such as at the time of harvesting and then at the time of processing.

Both Hilborn and Paulik discussed ways to adjust for the non-reporting of tags but neither expanded their work to estimate the population size.

The problem of incorrectly classifying tagged fish as untagged is similar to the problem of misclassifying objects in a quality control setting. Here the object is to estimate

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the percentage of defective components, which is analogous to the percentage of fish originally tagged.

Tenenbein (1970) considered using a true and fallible device to classify sampling units into one of two categories (0, 1). The fallible device refers to an inexpensive procedure which tends to misclassify units; whereas, the true device is a more expensive procedure with no misclassification error. If only the fallible device is used on all n_2 units in a sample then a biased estimate of p, the proportion of units which belong to one of the categories, is obtained. A better estimate of p could be obtained if only the true classifier were used on all n_2 units, but the cost of this may be too high. A compromise between these two methods is a double sampling scheme where:

i) A random sample of n_2 units is selected from a population of interest.

ii) Then a subsample of n_3 units from the n_2 units is classified by both devices.

iii) And the remaining $n_2 - n_3$ units are classified by the fallible device, only.

Tenenbein developed an estimate for p with an appropriate variance formula. However, in Tenenbein's approach, a portion of fish correctly identified as having tags would be reexamined. This can be considered an unnecessary expense under the assumption that untagged carcasses cannot be incorrectly classified as having tags.

Haitovsky and Rapp (1992) expanded on Tenenbein's work. They developed a conditional resampling scheme to improve the estimators of multinomial classification probabilities in the presence of a fallible classifier. Instead of employing the same resampling rate to all categories, different sampling rates could be used on each category, which would then make it possible to exclude a category from being resampled. Using this approach, it would be possible to re-examine only those fish classified as being untagged. However, Haitovsky and Rapp only considered improving the estimate for the proportion in each class; whereas, we are interested in improving the estimate for the escapement size.

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In this paper, a general statistical theory for this type of sampling experiment will be developed. The variance for the estimate of the total escapement accounting for missed tags will be developed and the loss of efficiency compared to the simple Petersen estimate will be found. The optimal allocation of effort between the two samples will also be examined. Lastly, an example is presented, using data provided by the Fraser River Sockeye Public Review Board.

Note that other problems with the survey design, e.g., tagging and recovery occurring over a period of time rather than a single point in time, are not examined in this paper.

2. Notation

Statistics

- n₁ Number of tags applied
- n₂ Number of carcasses initially examined
- m_2 Number of tags recovered from the n_2 carcasses examined in the first survey
- n_3 Number of carcasses repitched from those initially classified as being without tags; a proportion of $n_2 m_2$
- r Repitch rate, so $r = n_3/(n_2 m_2)$
- m_3 Number of additional tags recovered from the n_3 carcasses examined in the repitch
- \tilde{m}_2 Estimated number of marks in the original sample of n_2 carcasses
- C₀ Total cost to perform recapture and repitch
- c₂ Cost per examination of a carcass in the first carcass survey
- c₃ Cost per examination of a carcass in the second survey (repitch)

Parameters

- N Population size (escapement)
- λ Miss rate; P(failing to observed a tag on a tagged fish)
- p_1 Tagging rate; P(carcass has a tag) = n_1/N
- p₂ Recapture rate (in the complete stochastic model)

3. The Sampling Experiment

As outlined by the Fraser River Sockeye Salmon Management Review Team 1994 Spawning Escapement Estimation Working Group (1994) (FRSSMRT), the method used to tag fish, recapture a sample and repitch a subsample is as follows.

As fish return to their spawning sites, n_1 are captured using seine nets. A Petersen disk tag is attached and the fish is released. If a captured fish appears to be stressed, at an advanced stage of maturation, or physically damaged, then it is released without a tag. Tagging starts when a significant number of fish are first observed and continues through the period of spawning ground arrival. The number of fish caught and tagged on a given day is determined either by standardizing the daily application effort or by tagging in proportion to estimated daily abundance; abundance is estimated from the previous day's visual counts on or below the spawning grounds.

After spawning, the fish die and the carcasses are often washed onto the banks of the spawning area. Survey teams walk along the banks looking for carcasses. When a carcass is found, it is examined for a tag. After enumeration, all tags are cut from the carcasses, and only those carcasses are removed from the study area by cutting them into two with a machete and returning them to the river. Untagged carcasses are left where found. Recapture commences when the first dead fish is observed and continues until die-off is complete, and is conducted over the entire spawning area. More surveyors are deployed at peak of carcass abundance than at tails. A total of n_2 carcasses are examined and m_2 marks are found.

Later in the season, a second team examines some of those carcasses identified as being without tags to check for tags missed in the initial survey. A total of n_3 carcasses are re-examined (repitched) and m_3 tags are found.

Mark-recapture techniques are based on the principle that by tagging a random sample of individuals, permitting them to redistribute through the population, and by obtaining a second random sample of tagged and untagged individuals, an estimate of the population size can be calculated. The reliability and precision of the estimate is contingent upon how well the assumptions underlying the technique have been addressed.

- Assumption 1: The population is closed; i.e., the number of individuals does not change during the study through immigration and/or emigration.
- **Assumption 2**: Tag status is correctly identified at recovery.
- **Assumption 3**: Tag loss does not occur during the study.
- Assumption 4: Capture and tagging does not affect subsequent catchability or survival of a fish.
- **Assumption 5**: Each fish has a constant and equal probability of capture and recapture during the study.
- **Assumption 6**: The repitch sample is a random sample of those fish initially classified as untagged.

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Assumptions 1 is satisfied by restricting studies to terminal spawning sites, by having tagging sites close to the spawning ground and whenever possible, at the only entrance to the spawning ground. If a tagged fish could leave the spawning site prior to spawning, then this would result in a reduction in the number of tags available for recapture and an overestimate of the escapement size. The capture, holding and tagging of fish is a stressful process. If the stress is particularly severe, some individuals may die immediately, or within a few days of release and drift downstream outside the study area, prior to spawning. By choosing tagging sites near spawning grounds it is possible to reduce stress induced mortality (Assumption 4) and permit the mixing of tagged and untagged fish throughout the population. This would not be a problem if marked and unmarked fish were to behave the same.

The possibility of a tagged fish losing its tag prior to recapture has been ignored in this analysis (Assumption 3).

The assumption of equal probability of capture (Assumption 5) and simple random sampling is violated in virtually all mark-recapture studies and is generally considered to be an unattainable ideal. If possible, stratification (i.e., by gender) can be employed to reduce the effects of heterogeneity on the estimates. During the tagging period, fish are caught in seine nets, and it is assumed that all fish that pass the tagging site have an equally likely chance of being caught. Capture and tagging is not a twenty-four hour process, so those fish that pass the tagging site when the nets are not in place will be able to pass freely. After spawning, the fish die and the carcasses are often washed onto the banks. Since a carcass has no control as to whether or not it gets washed ashore, the probability of this happening can be assumed to be the same for all carcasses.

The failure to correctly identify the tag status of a carcass during the recovery period (initial examination) is common in mark-recapture studies (Assumption 2). This is usually the result of surveyor inexperience and from assigning higher priority to the speed of carcass

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processing than to the thoroughness of the examination. If left uncorrected, the proportion of tags in the population is underestimated and the escapement is overestimated. One way to correct this problem is to carefully re-examine, for missed tags, a random sample of carcasses classified as untagged. It is assumed that no tags are missed in this re-examination.

4. The Conditional Model

Because the initial tagging effort, the recovery effort, and the repitch effort are controlled by the experimenter, a conditional model for this experiment will be developed. In this conditional model, n_1 , n_2 and r are treated as fixed quantities, dependent only on the allocation of resources. The remaining random variables are m_2 and m_3 . A model that treats n_1 and n_2 as random variables has been derived in Appendix 1. Results are similar in both models.

Each of the n_2 recaptured fish can end up in one of the four categories, as shown in Figure 4.1. Under the assumptions made earlier, and given that n_1 is typically small relative to N, the number of fish in these four categories has an approximate multinomial distribution with probability

$$f(\underline{x},\underline{\theta}) = \begin{pmatrix} n_2 \\ m_2, m_3, n_3 - m_3, n_2 - m_2 - n_3 \end{pmatrix} \times (4.1)$$
$$[p_1(1-\lambda)]^{m_2} [p_1\lambda r]^{m_3} [(1-p_1)r]^{(n_3-m_3)} [(1-p_1(1-\lambda))(1-r)]^{(n_2-m_2-n_3)}$$

where

$$\underline{\mathbf{x}} = \begin{bmatrix} \mathbf{m}_2, & \mathbf{m}_3, & \mathbf{n}_3 - \mathbf{m}_3, & \mathbf{n}_2 - \mathbf{m}_2 - \mathbf{n}_3 \end{bmatrix}$$

$$\underline{\mathbf{\theta}} = \begin{bmatrix} \mathbf{p}_1(1-\lambda), & \mathbf{p}_1\lambda\mathbf{r}, & (1-\mathbf{p}_1)\mathbf{r}, & (1-\mathbf{p}_1(1-\lambda))(1-\mathbf{r}) \end{bmatrix}$$

$$\mathbf{p}_1 = \frac{\mathbf{n}_1}{N}$$



Figure 4.1: Diagram of categories that a recaptured fish can be placed in based on tag status, accuracy of identification, and probability of repitch

$$\sum_{i=1}^{4} x_i = n_2 \qquad \sum_{i=1}^{4} \theta_i = 1 \; .$$

In this distribution, N and λ are the unknown parameters.

Maximum Likelihood Estimates

Estimates of N and λ are found by maximizing the log-likelihood function

$$\ell(\underline{x},\underline{\theta}) = \ln[L(\underline{x},\underline{\theta})] = \ln[f(\underline{x},\underline{\theta})]$$

$$= \ln \begin{pmatrix} n_{2} \\ m_{2}, m_{3}, n_{3} - m_{3}, n_{2} - m_{2} - n_{3} \end{pmatrix}$$

$$+ [m_{2} + m_{3}]\ln(p_{1}) + [n_{3} - m_{3}]\ln(1 - p_{1}) + [n_{2} - m_{2} - n_{3}]\ln(1 - p_{1}(1 - \lambda))$$

$$+ [m_{2}]\ln(1 - \lambda) + [m_{3}]\ln(\lambda) + [n_{3}]\ln(r) + [n_{2} - m_{2} - n_{3}]\ln(1 - r) .$$

$$(4.2)$$

After substituting n_1/N for p_1 and simplifying, the above equation reduces to

$$\ell(\underline{\mathbf{x}}, \underline{\theta}) = \ln \begin{pmatrix} \mathbf{n}_{2} \\ \mathbf{m}_{2}, \ \mathbf{m}_{3}, \ \mathbf{n}_{3} - \mathbf{m}_{3}, \ \mathbf{n}_{2} - \mathbf{m}_{2} - \mathbf{n}_{3} \end{pmatrix}$$

$$+ [\mathbf{m}_{2} + \mathbf{m}_{3}]\ln(\mathbf{n}_{1}) - [\mathbf{n}_{2}]\ln(\mathbf{N}) + [\mathbf{n}_{3} - \mathbf{m}_{3}]\ln(\mathbf{N} - \mathbf{n}_{1})$$

$$+ [\mathbf{n}_{2} - \mathbf{m}_{2} - \mathbf{n}_{3}]\ln(\mathbf{N} - \mathbf{n}_{1}(1 - \lambda)) + [\mathbf{m}_{2}]\ln(1 - \lambda)$$

$$+ [\mathbf{m}_{3}]\ln(\lambda) + [\mathbf{n}_{3}]\ln(\mathbf{r}) + [\mathbf{n}_{2} - \mathbf{m}_{2} - \mathbf{n}_{3}]\ln(1 - \mathbf{r}) .$$

$$(4.3)$$

The score function is found by finding the first derivatives of $\ell(\underline{x}, \underline{\theta})$ with respect to N and λ :

$$\mathbf{U}(\underline{\beta}) = \begin{bmatrix} \frac{\partial \ell}{\partial \mathbf{N}} \\ \frac{\partial \ell}{\partial \lambda} \end{bmatrix} = \begin{bmatrix} \frac{\mathbf{n}_2 - \mathbf{m}_2 - \mathbf{n}_3}{\mathbf{N} - \mathbf{n}_1(1 - \lambda)} + \frac{(\mathbf{n}_3 - \mathbf{m}_3)}{\mathbf{N} - \mathbf{n}_1} - \frac{\mathbf{n}_2}{\mathbf{N}} \\ \frac{\mathbf{n}_1(\mathbf{n}_2 - \mathbf{m}_2 - \mathbf{n}_3)}{\mathbf{N} - \mathbf{n}_1(1 - \lambda)} - \frac{\mathbf{m}_2}{(1 - \lambda)} + \frac{\mathbf{m}_3}{\lambda} \end{bmatrix}$$
(4.4)

where $\underline{\beta} = [N, \lambda]$. The maximum likelihood estimates for N and λ are obtained by solving $U(\underline{\beta}) = 0$, and are:

$$\hat{N} = \frac{n_1 n_2}{\left[m_2 n_3 + (n_2 - m_2)m_3\right]/n_3}$$
(4.5)

$$\hat{\lambda} = \frac{(n_2 - m_2)}{\left[m_2 n_3 + (n_2 - m_2)m_3\right]/m_3} .$$
(4.6)

If we let

$$\tilde{m}_2 = \frac{m_2 n_3 + (n_2 - m_2) m_3}{n_3} = m_2 + \frac{(n_2 - m_2) m_3}{n_3} = m_2 + \frac{m_3}{r}$$
(4.7)

= estimated number of tags in the original sample of n_2 fish,

found by taking the original number of tags

+ the estimated number of tags missed

then

$$\hat{\mathbf{N}} = \frac{\mathbf{n}_1 \mathbf{n}_2}{\tilde{\mathbf{m}}_2} \tag{4.8}$$

and

$$\hat{\lambda} = \frac{(n_2 - m_2)m_3}{\tilde{m}_2 n_3} = \frac{m_3/r}{\tilde{m}_2}$$

$$= \frac{\text{estimated number of tags missed}}{\text{estimated number of tags in the original sample}} .$$
(4.9)

Notice that the maximum likelihood estimate for N is similar in format to that of the Petersen estimate and is the same as the moment estimator currently in use.

The information matrix is found as

$$\mathbf{I}(\hat{\underline{\beta}}) = \mathbf{E}\begin{bmatrix} -\frac{\partial^2 \ell}{\partial \beta_i \partial \beta_j} \end{bmatrix} = \begin{bmatrix} \mathbf{I}_{11} & \mathbf{I}_{12} \\ \mathbf{I}_{21} & \mathbf{I}_{22} \end{bmatrix}$$

with

$$I_{11} = -\frac{\partial^{2} \ell}{\partial N^{2}} = \frac{n_{1} n_{2} [N(1 - \lambda(1 - r)) - n_{1}(1 - \lambda)]}{N^{2} (N - n_{1}) [N - n_{1}(1 - \lambda)]}$$

$$\begin{split} \mathbf{I}_{12} &= \mathbf{I}_{21} = -\frac{\partial^2 \ell}{\partial N \partial \lambda} = \frac{\mathbf{n}_1 \mathbf{n}_2 (1-\mathbf{r})}{\mathbf{N} \big(\mathbf{N} - \mathbf{n}_1 \big) \big[\mathbf{N} - \mathbf{n}_1 (1-\lambda) \big]} \\ \mathbf{I}_{22} &= -\frac{\partial^2 \ell}{\partial \lambda^2} = \frac{\mathbf{n}_1 \mathbf{n}_2 \big[\mathbf{N} \big(\mathbf{r} + \lambda (1-\mathbf{r}) \big) - \mathbf{n}_1 \mathbf{r} (1-\lambda) \big]}{\mathbf{N} \lambda (1-\lambda) \big[\mathbf{N} - \mathbf{n}_1 (1-\lambda) \big]} \,. \end{split}$$

And the variance-covariance matrix for the estimates is found to be

$$\operatorname{VarCov}\left(\underline{\hat{\beta}}\right) = \mathrm{I}^{-1}\left(\underline{\hat{\beta}}\right) = \begin{bmatrix} \mathrm{V}(\hat{\mathbf{N}}) & \mathrm{C}(\hat{\mathbf{N}}, \hat{\lambda}) \\ \mathrm{C}(\hat{\mathbf{N}}, \hat{\lambda}) & \mathrm{V}(\hat{\lambda}) \end{bmatrix}$$

with the following variances and covariance:

$$V(\hat{N}) = \frac{N^{2}(N - n_{1})[N\lambda + (N - n_{1})(1 - \lambda)r]}{n_{1}n_{2}r[N - n_{1}(1 - \lambda)]}$$
(4.10)

$$V(\hat{\lambda}) = \frac{N(1-\lambda)[N\lambda r + (N-n_1)(1-\lambda)]}{n_1 n_2 r[N-n_1(1-\lambda)]}$$
(4.11)

$$C(\hat{N},\hat{\lambda}) = \frac{-N^{2}\lambda(N-n_{1})(1-\lambda)(1-r)}{n_{1}n_{2}r[N-n_{1}(1-\lambda)]}.$$
(4.12)

Estimates of these variances and covariance are obtained by replacing parameters with their maximum likelihood estimates:

$$\hat{V}(\hat{N}) = \frac{n_1^2 n_2 (n_2 - m_2) (n_3 - m_3) [n_2 m_3 (n_2 - m_2) + n_3 m_2 (n_3 - m_3)]}{\tilde{m}_2^4 n_3^3}$$
(4.13)

$$\hat{V}(\hat{\lambda}) = \frac{m_2 m_3 (n_2 - m_2) [n_2 n_3 m_3 + m_2 (n_2 - m_2) (n_3 - m_3)]}{\tilde{m}_2^4 n_3^3}$$
(4.14)

$$\hat{C}(\hat{N},\hat{\lambda}) = \frac{-n_1 n_2 m_2 m_3 (n_2 - m_2)(n_3 - m_3)(n_2 - m_2 - n_3)}{\tilde{m}_2^4 n_3^3} .$$
(4.15)

Variance Inflation Factor

If all carcasses were correctly classified when initially examined, the variance for the Petersen estimate (assuming that exactly \tilde{m}_2 tags were present) could be written as (Ricker 1975, p. 78)

$$V(\hat{N}_{Petersen}) = \frac{N^2(N - n_1)}{n_1 n_2}$$
(4.16)

after replacing random variables with their expected values. The increase in variance caused by misclassification and subsequent repitching is

$$VIF = \frac{V(\hat{N})}{V(\hat{N}_{Petersen})} = \frac{N\lambda + (N - n_1)(1 - \lambda)r}{[N - n_1(1 - \lambda)]r} = 1 + \frac{N\lambda(1 - r)}{[N - n_1(1 - \lambda)]r}$$
(4.17)

or

$$\mathbf{V}(\hat{\mathbf{N}}) = \left[1 + \frac{\mathbf{N}\lambda(1-r)}{\left[\mathbf{N} - \mathbf{n}_{1}(1-\lambda)\right]\mathbf{r}}\right] \mathbf{V}(\hat{\mathbf{N}}_{\text{Petersen}}) .$$

(•)

Equality between the two variances occurs when no tags are missed in the recapture ($\lambda = 0$) or all carcasses identified as being without tags are repitched (r = 100%); in these two cases,

VIF = 1. Also for a fixed values of $\lambda \ (\neq 0)$, if the repitch rate increases, VIF monotonically approaches 1 and V($\hat{N}_{Petersen}$) approaches V(\hat{N}). Similarly, for a fixed value of r ($\neq 100\%$), if the miss rate decreases, VIF monotonically approaches 1 and V($\hat{N}_{Petersen}$) approaches V(\hat{N}).

For large N, if the following approximation is assumed

$$N - n_1(1 - \lambda) \approx N$$

then equation (4.17) can be written as:

$$VIF_{approx} = 1 + \frac{\lambda(1-r)}{r}$$
(4.18)

a function only of the miss rate (λ) and the repitch rate (r). Figure 4.2 is a plot of VIF_{approx} for various combinations of miss rate and repitch rate.



Figure 4.2: Plot of approximate variance inflation factor (VIF_{approx}) versus miss rate (λ) for various repitch rates (r)

5. Optimal Allocation

There is a cost associated with catching and examining carcasses at the initial examination and a cost associated with re-examining a portion of the carcasses identified as being without tags for missed tags. If there is a fixed allocation of funds then how many carcasses should be recaptured and re-examined so that the variance of the escapement, $V(\hat{N})$, is minimized? In other words, for a fixed cost, what optimal values of n_2 and r result in minimizing $V(\hat{N})$?

The total cost of the experiment can be approximated by a linear cost function because carcasses are spread throughout the watershed and the number of carcasses examined is roughly proportional to the total effort expended. Assuming that the number of tags applied (n_1) is fixed, the total cost of the experiment can be written as

$$C = c_2 n_2 + c_3 (n_2 - m_2) r \le C_0$$
(5.1)

and can be solved for r to give

$$\mathbf{r} = \frac{\mathbf{C}_0 - \mathbf{c}_2 \mathbf{n}_2}{\mathbf{c}_3 (\mathbf{n}_2 - \mathbf{m}_2)} \,. \tag{5.2}$$

If this is then substituted for r, m_2 replaced by its expected value, $E(m_2) = n_2 p_1 (1 - \lambda)$, and n_1 replaced by Np₁, then equation (4.10) can be written as

$$V(\hat{N}) = \frac{N^{2}c_{3}(1-p_{1})\left[\lambda + \frac{(1-p_{1})(1-\lambda)(C_{0}-c_{2}n_{2})}{c_{3}n_{2}(1-p_{1}(1-\lambda))}\right]}{p_{1}(C_{0}-c_{2}n_{2})}$$
(5.3)

which is now a function of n_2 . An optimal value for n_2 can be obtained by solving the following equation

$$\frac{\partial \mathbf{V}(\hat{\mathbf{N}})}{\partial \mathbf{n}_2} = 0$$

for n_2 . This then results in the following optimal values for n_2 and r:

$$\mathbf{n}_{2,\text{optimal}} = \left(\frac{\mathbf{C}_0}{\mathbf{c}_2}\right) \left[\frac{1}{1 + \sqrt{\left(\frac{\mathbf{c}_3}{\mathbf{c}_2}\right)\left(\frac{\lambda}{1-\lambda}\right)\left[\frac{1-\mathbf{p}_1(1-\lambda)}{1-\mathbf{p}_1}\right]}}\right]$$
(5.4)

$$\mathbf{r}_{\text{optimal}} = \sqrt{\left(\frac{\mathbf{c}_2}{\mathbf{c}_3}\right) \left(\frac{\lambda}{1-\lambda}\right) \left[\frac{1}{(1-\mathbf{p}_1)\left(1-\mathbf{p}_1(1-\lambda)\right)}\right]}$$
(5.5)

The optimal quantities depend on the cost ratio (c_2/c_3) , the miss rate (λ) and the initial tagging rate (p_1) . If p_1 is small then $r_{optimal}$ can be approximated by

$$r_{\text{optimal, approx}} = \sqrt{\left(\frac{c_2}{c_3}\right)\left(\frac{\lambda}{1-\lambda}\right)}$$



Figure 5.1: Plot of optimal repitch rate $(r_{optimal})$ versus miss rate (λ) at various cost ratios $(c_2:c_3)$ with a tagging rate (p_1) of 0.01

If no tags are missed, $(\lambda = 0)$, then the optimal strategy is to recapture the maximum possible $(n_{2,optimal} = C_o/c_2)$ and repitch nothing $(r_{optimal} = 0)$. For a fixed cost ratio and tagging rate, if the miss rate increases then we should decrease the number of fish recaptured and increase the proportion repitched. For a fixed total cost, miss rate and tagging rate, if the cost ratio increases then the repitch rate can be increased (because it is cheaper to repitch); and surprisingly, the recapture number can also be increased (because resources saved in the repitch can be diverted to the recapture). Lastly, for fixed values of cost ratio and miss rate, optimal values of recapture number and repitch rate appear to be insensitive to changes in the initial tagging rate when p_1 is small. Figure 5.1 is a plot of the effect of various miss rates and cost ratios on the optimal repitch rates for a typical tagging rate (p_1) of 0.01.

6. Examples

Using actual data generously provided by Neil Schubert, Department of Fisheries and Oceans, the equations derived in the previous sections are used to estimate escapement size and standard error values. These standard error values are then compared to those of the Petersen estimate by comparing the ratio of the standard errors to $\sqrt{\text{VIF}_{approx}}$. Also, optimal recapture number and repitch rate values are compared to those actually used.

In addition, two scenarios are examined for their effect on the variance of the escapement at various levels of cost ratio (c_2/c_3) and miss rate (λ) .

Data Analysis

The following information was provided by sex for sockeye on the Chilko River and the Horsefly River for the 1994 escapement: the number of tags applied (n_1) , carcasses recaptured (n_2) , tags observed in the recapture (m_2) , carcasses repitched (n_3) , and tags observed in the repitch (m_3) .

As described by the FRSSMRT (p. 2), the Chilko River (Figure 6.1) is part of the Chilkotin River system, which drains a large portion of the west-central Fraser River watershed. Spawning occurs immediately downstream from the lake in a spawning channel on the upper Chilko River, and on the shores along the north and south ends of Chilko Lake. Sockeye first arrive in August with peak spawning in late September; die-off is complete by late October. The tagging site is located near Lingfield Creek, 5 kilometres below the spawning grounds. Recovery surveys were conducted every two to three days in the river and north lake, and every week in the south lake. Boat access to the south lake was restricted by weather and the fact that fish in this area spawn in a remote area which is logistically difficult to sample.

The Horsefly River (Figure 6.1), a tributary of the main section of Quesnel Lake, is part of the Quesnel River system which drains a large portion of the east-central Fraser River watershed. Sockeye start arriving in August with a peak in early to mid September; die-off is complete by mid October. The tagging site is located in the lower river approximately 2 kilometres above the lake. Recovery surveys were conducted in the lower and upper river every four to six days.

From the information provided, the following values have been calculated: repitch rate (r), miss rate (λ), estimated number of tags in the original sample (\tilde{m}_2), Petersen and Conditional model escapement estimates and standard errors, and ratio of standard errors for these two estimates. These values are listed in Table 6.1.

For the four data sets, repitch rates range from approximately 19% (Chilko River, male sockeye) to 38% (Horsefly River, female sockeye). Estimated miss rates range from approximately 9% (Chilko River, female sockeye) to 22% (Horsefly River, male sockeye). The estimated values for escapement size, \hat{N} , are the same for the Petersen and the Conditional model estimates since we are assuming for the Petersen estimate that carcasses were correctly classified when initially examined; i.e., $\hat{N} = n_1 n_2 / \tilde{m}_2$.

Given the repitch and miss rates, an increase of between 12% and 23% is observed in the standard error between the Conditional model and Petersen estimates. For this data set, the correct standard error is about 20% larger than that for the Petersen estimate. Hence, previous estimates of precision found by treating \tilde{m}_2 as a know quantity were too small, and a nominal 95% confidence interval for the total escapement had serious undercoverage. The values obtained for the change in standard error between the two models,

 $\hat{S}E(\hat{N}_{Conditional})/\hat{S}E(\hat{N}_{Petersen})$, is observed to be close in value to that of $\sqrt{VIF_{approx}}$, for all four data sets because $p_1 = n_1/N$ is small in equation (4.10).

For arbitrary cost ratios (c_2 : c_3), it is possible to calculate the amount of effort required to obtain the given data values by using the cost equation (equation 5.1). From the cost ratios, the optimal repitch rates can be found since these are not dependent on the total cost but are dependent on cost ratio, miss rate and tagging rate. Then given the total cost required for each data set and the optimal repitch rates, the number of sockeye that should be recaptured is compared to the number that were recaptured (n_2). Finally the standard error estimates of the escapement under optimal allocation have been compared to the observed standard error. Results are summarized in Table 6.2 for various cost ratios.

For example, consider a cost ratio of 4 to 1 (4:1, 4 times as much to recapture than repitch). For the male sockeye on the Horsefly River, a total of 46,772.25[#] units of effort was required. Approximately 30% of those carcasses identified as being without tags were repitched, whereas the optimal would have been to repitch 100%, given a miss rate of 0.22; the highest miss rate for the four data sets. From the total cost and optimal repitch rate, a total of 37,056 carcasses should have been recaptured, compared to 43,557 that were. By using these optimal values, the standard error of the estimate of the escapement size would have reduced by 14%. For a 1 to 1 cost ratio (1:1, equal cost for recapture and repitch) a total of 56,418 units was incurred to recapture 43,557 sockeye and repitch 30%. Optimal values would have been to recapture 37,009 sockeye and repitch 53%; which would still have given the same total cost of 56,418 units. This would have reduced the standard error by 4%. In general, the optimal repitch rates for all cost ratios are much greater than those observed and

^{# 46,772.25 = 43,557 + (0.25)12,861}

decrease as cost ratio decreases. Given total cost and optimal repitch rates, the number of sockeye that should have been recaptured are slightly less than the number actually recaptured. Also, as the cost ratio decreases, the reduction in standard error, under optimal allocation, decreases.

Figure 6.1: Map of Chilko and Horsefly Rivers

	Chilko I	River	Horsefly River		
	Males	Females	Males	Females	
n ₁ .	1,510	2,074	2,140	2,669	
n ₂	45,595	63,752	43,557	49,382	
m ₂	279	467	355	424	
n ₃	8,462	12,708	12,861	18,363	
m ₃	6	9	29	28	
r (%)	19%	20%	30%	38%	
λ.	0.10	0.09	0.22	0.15	
m ₂	311	512	452	499	
Petersen					
Ñ	221,284	258,337	206,032	264,314	
$\hat{V}(\hat{N}_{Petersen})$	156,419,577	129,438,020	93,063,107	138,898,743	
$\hat{S}E(\hat{N}_{Petersen})$	12,507	11,377	9,647	11,786	
Conditional model					
Ñ	221,284	258,337	206,032	264,314	
$\hat{V}(\hat{N}_{conditional})$	227,045,606	174,758,535	140,408,269	173,579,155	
$\hat{S}E(\hat{N}_{Conditional})$	15,068	13,220	11,849	13,175	
$\frac{\hat{S}E(\hat{N}_{\text{Conditional}})}{\hat{S}E(\hat{N}_{\text{Petersen}})}$	1.21	1.16	1.23	1.12	
$\sqrt{\text{VIF}_{approx}}$	1.20	1.16	1.23	1.12	

 Table 6.1: Standard errors and VIF values of mark-recapture conducted on the Chilko and

 Horsefly Rivers

	Chilko River		Horsefly River		
	Males	Females	Males	Females	
p ₁	0.006	0.008	0.010	0.010	
r (%)	19%	20%	30%	38%	
λ	0.10	0.09	0.22	0.15	
c ₂ : c ₃	4:1	4:1	4:1	4:1	
Cost (C)	47,710.50	66,929.00	46,772.25	53,972.75	
r _{optimal} (%)	68%	62%	100%1	85%	
n_2 (given $r_{optimal}$)	40,787	57,950	37,056	44,607	
$SE(\hat{N})_{optimal}$	13,533	12,241	10,385	12,559	
Improvement in SE from	n				
using optimal design	1.11	1.08	1.14	1.05	
$c_2 : c_3$	2:1	2:1	2:1	2:1	
Cost (C)	49,826.00	70,106.00	49,987.50	58,563.50	
r _{optimal} (%)	48%	44%	75%	60%	
n_2 (given $r_{optimal}$)	40,181	57,505	36,465	45,156	
$\hat{SE(N)}_{optimal}$	14,039	12,625	10,910	12,923	
Improvement in SE	1.07	1.05	1.08	1.02	
$c_2 : c_3$	1.33 : 1	1.33 : 1	1.33 : 1	1.33 : 1	
Cost (C)	51,941.50	73,283.00	53,202.75	63,154.25	
r _{optimal} (%)	40%	36%	61%	49%	
n_2 (given $r_{optimal}$)	40,140	57,777	36,586	46,312	
$SE(\hat{N})_{optimal}$	14,348	12,848	11,218	13,085	
Improvement in SE	1.05	1.03	1.06	1.00	
$c_2 : c_3$	1:1	1:1	1:1	1:1	
Cost (C)	54,057.00	76,460.00	56,418.00	67,745.00	
r _{optimal} (%)	34%	31%	53%	42%	
n_2 (given $r_{optimal}$)	40,357	58,371	37,009	47,710	
$SE(\hat{N})_{optimal}$	14,559	12,990	11,420	13,155	
Improvement in SE	1.03	1.02	1.04	1.00	

Table 6.2: Optimal allocation of repitch rates and recapture number given various cost ratios and total costs assuming estimated values of miss rate and tagging rate are close to actual for the Chilko and Horsefly Rivers

¹ Formula gave 106%.

Sensitivity Analysis - Varying The Cost Ratio

First, consider the case where for a fixed total cost and miss rate, the cost ratio may vary.

Suppose the tagging rate, p_1 , is set at 0.006, the estimated tagging rate for male sockeye on the Chilko River. Using a fixed total cost of 50,000 units and a miss rate of $\lambda =$ 0.10, the repitch rate and recapture number as well as the variance estimate for the escapement at the following cost ratios were computed, using equations derived in section 5:

$$c_2: c_3 = \{4:1, 2:1, 1.33:1, 1:1\}.$$

Figure 6.2 is a plot of the variance estimate versus repitch rate for each of the four cost ratios. Given the cost ratios mentioned and miss rates ranging from 0.05 to 0.20, Table 6.3 is a summary of the optimal repitch rates and recapture numbers that minimize the variance estimates; i.e., the lowest point on the plot in Figure 6.2 for each cost ratio. Values were not assigned to the vertical axis in Figure 6.2 because the value of the repitch rate that is associated with the lowest point on the line for each cost ratio is of interest and not what the variance estimate is at that point. Also, recall that the optimal repitch rate is not dependent on the total cost; whereas, the variance estimate is dependent on the total cost which has been chosen arbitrarily. Notice that as the cost ratio decreases, the variance estimate increases, and the repitch rate as well as the recapture number decrease; this was observed for various miss rates. This implies that for a fixed miss rate, if the cost per repitch approaches the cost per recapture then it is best to decrease both the number recaptured and proportion repitched. Also, for a cost ratio of 4 to 1 ($c_2/c_3 = 4$), the optimal repitch rate is 67%, for a miss rate of 0.10, but a greater repitch rate would not substantially increase the variance estimate.



Figure 6.2: Plot of variance estimate versus repitch rate (r) for various cost ratios $(c_2:c_3)$ at a miss rate (λ) of 0.10 and tagging rate (p_1) of 0.006

			cost ratio	$(c_2 : c_2)$	
miss rate (λ)		1:1	1.33 : 1	2:1	4:1
0.05	r	23%	27%	33%	46%
	n_2	40,650	41,700	43,050	44,850
0.10	r	34%	39%	47%	67%
	n_2	37,500	38,800	40,500	42,900
0.15	r	42%	49%	60%	85%
	n_2	35,250	36,600	38,550	41,250
0.20	r	50%	58%	71%	100%
	n ₂	33,300	34,950	36,900	40,050

Table 6.3: Optimal repitch rates (r) and recapture numbers (n_2) for various miss rate (λ) and cost ratio $(c_2:c_3)$ combinations, with total cost fixed at 50,000 units and a tagging rate (p_1) of 0.006

Sensitivity Analysis - Varying The Miss Rate

Consider now, the case of fixing the cost ratio and the total cost and observing the effect of differing miss rates on the number of carcasses recaptured and the repitch rate; as well, as its effect on the variance estimate for the escapement size.

Suppose, once again, that the tagging rate is set at 0.006 and total cost is fixed at 50,000 units. Consider a cost ratio of 2 to 1 and vary the miss rate from 0.05 to 0.20. Table 6.3 shows the effect of varying the miss rate on the optimal repitch rate and recapture number. Figure 6.3 is a plot of the variance estimate versus repitch rate for each value of miss rate considered; again, values have not been assigned to the vertical axis. It is evident that as the miss rate increases, the repitch rate increases as does the variance estimate (observed in plot), and the recapture number decreases. This implies that for high values of miss rate, it is best to decrease the number of sockeye recaptured and increase the proportion re-examined.



Figure 6.3: Plot of variance estimate versus repitch rate (r) for various miss rates (λ) at a cost ratio of 2:1, and tagging rate (p_1) of 0.006

7. Summary

The estimate of salmon escapement size using mark-recapture methodology can be improved by carefully re-examining a portion of the carcasses identified as not having tags for missed tags. This re-examination provides a better estimate of the number of tags in the recaptured sample. Using this estimate in a simple Petersen estimate results in a better estimate of the escapement size but a biased estimate of its standard error. This estimate of the standard error is approximately $\sqrt{1 + \lambda(1 - r)/r} = \sqrt{\text{VIF}_{approx}}$ times smaller than the correct estimate of standard error that treats the number of tags found as an estimated value of the total number of tags in the recapture. Confidence intervals using the biased standard error can have severe undercoverage.

Given values for total cost, the cost per examination of a carcass in the initial survey and in the repitch (c_2 and c_3), it has been shown that optimal values for the number of carcass recaptured (n_2) and the repitch rate (r) are dependent on the cost ratio (c_2 : c_3), the miss rate (λ) and the tagging rate (p_1); in addition, the optimal recapture number is dependent on the total cost. If no tags are missed (λ =0), the optimal strategy is to recapture the maximum possible ($n_2 = C_o/c_2$) and repitch nothing (r=0). For a fixed cost ratio and tagging rate, if the miss rate increases then it is advisable to decrease the number of carcasses recaptured and increase the proportion repitched. And for a fixed miss rate and tagging rate, if the cost ratio increases then both the number of carcasses recaptured and the repitch rate should be increased. Optimal values of recapture number and repitch rate appear to be insensitive to changes in the tagging rate when p_1 is small.

Appendix The Complete Stochastic Model

This model does not condition upon n_1 and n_2 , but treats them as random variables. Figure A1.1 is a diagram of the five categories that sockeye can be placed in based on tag status, probability of recapture, tag identification and repitch rate.

From Figure A1.1, we see that n_1 sockeye are captured, tagged and released back into the population, with tagging rate p_1 . After spawning, the fish die and some get washed onto the banks of the spawning area. From these carcasses, n_2 are examined for tags; $N - n_2$ are not examined or did not get washed onto the banks. Tags are observed on m_2 carcasses and the remaining $n_2 - m_2$ carcasses either do not have a tag or the tag has not been observed. A portion, n_3 , of the $n_2 - m_2$ carcasses are re-examined and m_3 additional tags are recorded.

As in the conditional model, n_1 and n_2 are typically small relative to N. Here, the likelihood can be approximated by the product of a binomial and multinomial distribution. The binomial distribution refers to the tagging portion and the multinomial model contains all events that occur after the recapture period.

$$f(\underline{x}, \underline{\theta}) = {\binom{N}{n_1}} [p_1]^{n_1} [1 - p_1]^{N - n_1} \times$$

$$\binom{N}{m_2, m_3, n_3 - m_3, n_2 - m_2 - n_3, N - n_2} \times$$

$$[p_1 p_2 (1 - \lambda)]^{m_2} [p_1 p_2 \lambda r]^{m_3} [(1 - p_1) p_2 r]^{(n_3 - m_3)} \times$$

$$[(1 - p_1 (1 - \lambda)) p_2 (1 - r)]^{(n_2 - m_2 - n_3)} [1 - p_2]^{N - n_2}$$
(A1.1)

where

$$\begin{split} \underline{\mathbf{x}} &= \begin{bmatrix} \mathbf{m}_2, \ \mathbf{m}_3, \ \mathbf{n}_3 - \mathbf{m}_3, \ \mathbf{n}_2 - \mathbf{m}_2 - \mathbf{n}_3, \ \mathbf{N} - \mathbf{n}_2 \end{bmatrix} \\ \underline{\boldsymbol{\theta}} &= \begin{bmatrix} \mathbf{p}_1 \mathbf{p}_2 (1 - \lambda), \ \mathbf{p}_1 \mathbf{p}_2 \lambda \mathbf{r}, \ (1 - \mathbf{p}_1) \mathbf{p}_2 \mathbf{r}, \ (1 - \mathbf{p}_1 (1 - \lambda)) \mathbf{p}_2 (1 - \mathbf{r}), \ 1 - \mathbf{p}_2 \end{bmatrix} \\ \sum_{i=1}^5 \mathbf{x}_i &= \mathbf{n}_2 \qquad \sum_{i=1}^5 \mathbf{\theta}_i = 1 \; . \end{split}$$

In this distribution, N, λ , p_1 , and p_2 are the unknown parameters. And n_1 and n_2 , are treated as random variables, in addition to m_2 and m_3 .

Maximum Likelihood Estimates

Estimates of N, λ , p_1 , and p_2 are found by maximizing the log-likelihood function

$$\ell(\underline{x},\underline{\theta}) = \ln[L(\underline{x},\underline{\theta})] = \ln[f(\underline{x},\underline{\theta})]$$
(A1.2)
$$= \ln\binom{N}{n_1} + \ln\binom{N}{m_2, m_3, n_3 - m_3, n_2 - m_2 - n_3, N - n_2}$$
(A1.2)
$$+ [n_1 + m_2 + m_3]\ln(p_1) + [N - n_1 + n_3 - m_3]\ln(1 - p_1)$$
$$+ [n_2 - m_2 - n_3]\ln(1 - p_1(1 - \lambda)) + [n_2]\ln(p_2) + [N - n_2]\ln(1 - p_2)$$
$$+ [m_2]\ln(1 - \lambda) + [m_3]\ln(\lambda) + [n_3]\ln(r) + [n_2 - m_2 - n_3]\ln(1 - r) .$$

First derivatives (first difference for N) of $\ell(\underline{x}, \underline{\theta})$, with respect to

 $\underline{\beta} = [N, \lambda, p_1, p_2]$, are found to give the score function, $U(\underline{\beta})$. Solving $U(\underline{\beta}) = 0$ gives the following maximum likelihood estimates:

$$\hat{N} = \frac{n_1 n_2}{\left[m_2 n_3 + (n_2 - m_2)m_3\right] / n_3} = \frac{n_1 n_2}{\tilde{m}_2}$$
(A1.3)

$$\hat{\lambda} = \frac{(n_2 - m_2)}{\left[m_2 n_3 + (n_2 - m_2)m_3\right] / m_3} = \frac{(n_2 - m_2)m_3}{\tilde{m}_2 n_3} = \frac{m_3 / r}{\tilde{m}_2}$$
(A1.4)

$$\hat{\mathbf{p}}_1 = \frac{\mathbf{n}_1}{\mathbf{N}} \tag{A1.5}$$

$$\hat{p}_2 = \frac{n_2}{N}$$
 (A1.6)

The maximum likelihood estimates for N and λ are the same as those obtained in the conditional model. Also, notice that the maximum likelihood estimate of p_1 is equal to the tagging rate and the estimate of p_2 is equal to the number of carcasses recaptured divided by the escapement size.

The variance-covariance matrix is then found by inverting the information matrix to obtain

$$\operatorname{VarCov}(\hat{\underline{\beta}}) = \mathrm{I}^{-1}(\hat{\underline{\beta}}) = \begin{bmatrix} \mathrm{V}(\hat{\mathrm{N}}) & \mathrm{C}(\hat{\mathrm{N}}, \hat{\lambda}) & \mathrm{C}(\hat{\mathrm{N}}, \hat{\mathrm{p}}_{1}) & \mathrm{C}(\hat{\mathrm{N}}, \hat{\mathrm{p}}_{2}) \\ \mathrm{C}(\hat{\lambda}, \hat{\mathrm{N}}) & \mathrm{V}(\hat{\lambda}) & \mathrm{C}(\hat{\lambda}, \hat{\mathrm{p}}_{1}) & \mathrm{C}(\hat{\lambda}, \hat{\mathrm{p}}_{2}) \\ \mathrm{C}(\hat{\mathrm{p}}_{1}, \hat{\mathrm{N}}) & \mathrm{C}(\hat{\mathrm{p}}_{1}, \hat{\lambda}) & \mathrm{V}(\hat{\mathrm{p}}_{1}) & \mathrm{C}(\hat{\mathrm{p}}_{1}, \hat{\mathrm{p}}_{2}) \\ \mathrm{C}(\hat{\mathrm{p}}_{2}, \hat{\mathrm{N}}) & \mathrm{C}(\hat{\mathrm{p}}_{2}, \hat{\lambda}) & \mathrm{C}(\hat{\mathrm{p}}_{2}, \hat{\mathrm{p}}_{1}) & \mathrm{V}(\hat{\mathrm{p}}_{2}) \end{bmatrix}$$

with the following variances and covariances

$$V(\hat{N}) = \frac{N(N - n_1) \left[N^2 \lambda + \left(\left(N^2 - n_1 (N + n_2) \right) (1 - \lambda) + N n_2 \right) r \right]}{n_1 n_2 r \left[N - n_1 (1 - \lambda) \right]}$$
(A1.7)

$$V(\hat{\lambda}) = \frac{N\lambda(1-\lambda)[N\lambda r + (N-n_1)(1-\lambda)]}{n_1 n_2 r[N-n_1(1-\lambda)]}$$
(A1.8)

$$V(\hat{p}_{1}) = \frac{n_{1}(N - n_{1})[N\lambda + (N - n_{1})(1 - \lambda)r]}{N^{2}n_{2}r[N - n_{1}(1 - \lambda)]}$$

$$V(\hat{p}_{2}) = \frac{n_{1}n_{2}[2n_{1}n_{2}(1-\lambda)r + N(2N+n_{2})\lambda r - N(N+3n_{2})r - N^{2}\lambda]}{N^{3}n_{1}r[N-n_{1}(1-\lambda)]} + \frac{n_{2}\lambda(1-r)}{n_{1}r[N-n_{1}(1-\lambda)]} + \frac{(N+n_{2})r}{Nn_{1}r[N-n_{1}(1-\lambda)]}$$

$$C(\hat{N},\hat{\lambda}) = \frac{-N^{2}\lambda(N-n_{1})(1-\lambda)(1-r)}{n_{1}n_{2}r[N-n_{1}(1-\lambda)]}$$
(A1.9)

$$C(\hat{N}, \hat{p}_1) = \frac{-(N - n_1)[N\lambda + (N - n_1)(1 - \lambda)r]}{n_2 r[N - n_1(1 - \lambda)]}$$

$$C(\hat{N}, \hat{p}_2) = \frac{-(N - n_1) \left[N^2 \lambda + \left[(N^2 - (N + n_2)n_1)(1 - \lambda) + Nn_2 \right] r \right]}{Nn_1 r [N - n_1(1 - \lambda)]}$$

$$C(\hat{\lambda}, \hat{p}_1) = \frac{(N - n_1)(1 - r)(1 - \lambda)\lambda}{n_2 r [N - n_1(1 - \lambda)]}$$

$$C(\hat{\lambda}, \hat{p}_2) = \frac{(N - n_1)(1 - r)(1 - \lambda)\lambda}{n_1 r [N - n_1(1 - \lambda)]}$$

$$C(\hat{p}_1, \hat{p}_2) = \frac{(N - n_1) [N\lambda + (N - n_1)(1 - \lambda)r]}{N^2 r [N - n_1(1 - \lambda)]} .$$

The variance for $\hat{\lambda}$ and the covariance term of N and $\hat{\lambda}$ are the same as those obtained under the conditional model. However, the variance for \hat{N} is not the same as that derived under the

conditional model because n_1 and n_2 are treated as random variables in the full model. By applying the following substitutions for large N:

$$\begin{split} \mathbf{N} + \mathbf{n}_2 &\approx \mathbf{N} \\ \mathbf{N} - \mathbf{n}_1 &\approx \mathbf{N} \end{split}$$

it can be shown that:

$$V(\hat{N}_{Full}) \approx \left[1 + p_2\left(\frac{r}{r + \lambda(1 - r)}\right)\right] V(\hat{N}_{Conditional})$$

where $V(\hat{N}_{Full})$ refers to equation (A1.7) and $V(\hat{N}_{Conditional})$ refers to equation (4.10). If p_2 , λ and r are small, the variance of the full model is very close to that of the conditional model. Results on optimal allocation are also expected to be similar to those of the conditional model.



Figure A1.1: Diagram of all categories that escapement can be placed in based on tag status, probability of recapture, accuracy of identification, and repitch rate

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