Partial Stratification in Capture-Recapture Experiments and Integrated Population Modeling with Radio Telemetry

by

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Abstract

In this thesis, we develop and apply three new methods for ecological data sets. We present two new developments related to capture-recapture studies and one development related to integrated population modeling.

In the first project, we present new methods using partial stratification in two-sample capture-recapture experiments for closed populations. Capture heterogeneity is known to cause bias in estimates of abundance in capture-recapture experiments. This heterogeneity is often related to observable fixed characteristics of the animals such as sex. If this information can be observed for each handled animal at both sample occasions, then it is straightforward to stratify (e.g. by sex) and obtain stratum-specific estimates. However in many fishery experiments it is difficult to sex all captured fish because morphological differences are slight or because of logistic constraints. In these cases, a sub-sample of the captured fish at each sample occasion is selected and additional and often more costly measurements are made, such as sex determination through sacrificing the fish. We develop new methods to estimate abundance for these types of experiments. Furthermore, we develop methods for optimal allocation of effort for a given cost. We also develop methods to account for additional information (e.g. prior information about the sex ratio) and for supplemental continuous covariates such as length. These methods are applied to a problem of estimating the size of the walleye population in Mille Lacs Lake Minnesota, USA.

In the second project, we present new methods using partial stratification in k-sample ($k \geq 2$) capture-recapture experiments of a closed population with known losses on capture to estimate abundance. We present the new methods for large populations using maximum likelihood and a Bayesian method and simulated data with known losses on capture was used to illustrate the new methods.

In the third project, we present an integrated population model using capture-recapture, dead recovery, snorkel, and radio telemetry surveys. We apply this model to Chinook salmon on the West Coast of Vancouver Island, Canada to estimate spawning escapement and to describe the movement from the ocean to spawning grounds considering the stopover time, stream residence time, and snorkel survey observer efficiency.

Dedication

To the memory of my beloved father, W. A. Premarathana (1939-2006).

Acknowledgements

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Chapter 1

Introduction

Capture-recapture is a method used in Ecology to estimate abundance of an animal population. This method can be used to estimate abundance in both 'closed' and 'open' animal populations (Schwarz and Seber, 1999). The capture-recapture method can be simply described as follows. A sample of the animal population is captured, marked and then released. After some time another sample is captured from the population and the number of marked individuals marked earlier is counted along with the number of newly captured animals. New animals may be marked and released. The simplest of the capture-recapture methods is the Lincoln-Petersen method (Williams et al., 2002) which is used for closed populations (number of individuals in the population do not change through out study period) under certain assumptions. When there are two or more strata (i.e. categories of fish based on fixed attributes such as sex) in the population and there is capture heterogeneity (i.e. animals in different strata have different capture probabilities), then stratification is required at each sampling occasion to obtain unbiased estimates of abundance. Stratum specific estimates can be obtained by full stratification. However, full stratification at each sample occasion might not be possible in experiments. In that case, partial stratification at each sample occasion is considered in capture-recapture experiments.

When there are more than one type of survey data available from the same population (e.g. capture-recapture, simple counts, radio telemetry), data can be analyzed separately for each survey method to obtain estimates of abundance and other population parameters. However if we can jointly analyze these data using integrated modeling, then we can obtain more precise estimates for the population parameters. Another advantage of integrated modeling is that estimates can be obtained for certain parameters that cannot be obtained by analyzing a single survey data. For example, mean stopover time of fish (the mean length of time spent by a fish in the tagging pool before moving to the stream) cannot be estimated using capture-recapture data and snorkel data alone. However an integrated population model that combines both capture-recapture data and snorkel data allows to calculate mean stopover time. In this kind of a study, radio telemetry data perform an integral part of the integrated population modeling because radio telemetry can provide

very high detectability. For example, movements from stopover pool to the stream can be directly observed using radio telemetry but that cannot be observed using capture-recapture data or snorkel data.

The organization of this thesis is as follows. The thesis consists of three major projects and they are presented in Chapters 2, 3 and 4. Chapter 3 can be considered as an extension of the Chapter 2. Each chapter starts with an introduction, survey protocol and notations. Because notations are not shared between chapters these three chapters can be read in any order.

In Chapter 2, we develop new methods for two-sample capture-recapture studies using partial stratification. First we develop a method using maximum likelihood method and moreover, we determine optimum allocation of sampling effort for a given cost. We further develop a method using a Bayesian approach when prior information is available. A simulation study is used to compare MLE and Bayesian Methods. We also develop a method using partial stratification in two-sample capture-recapture experiments involving continuous covariates. Finally we apply these new methods to estimate the abundance of walleye in Mille Lacs Lake, MN, USA in 2013.

Chapter 3 is an extension of Chapter 2. In Chapter 3, we develop new methods for partial stratification in k-sample capture-recapture experiments for large closed populations. We develop new methods using maximum likelihood method and a Bayesian method. Because we do not have access to real life data for this kind of experiment setting, we considered simulated data when $k = 3$. Finally we use simulation studies to test the validity and the precision of the estimates provided by these new methods.

Chapter 4 considers the integrated population modeling under a Bayesian approach to estimate Chinook salmon escapement (salmon population return from the ocean to the spawning area in upstream) in Burman River on the West Coast of Vancouver Island. Data from multiple surveys (capture-recapture, snorkel, dead recovery, and radio telemetry) are available for the Burman River in 2012. A Bayesian integrated population model was developed (Beliveau, 2016) using capture-recapture, snorkel and dead recovery surveys. Burman River Chinook stay for some time (may be few days) at the stopover pool when they enter the river and then move upstream for spawning and die. Once a Chinook salmon is radio tagged at the stopover pool (where capture-recapture surveys take place), its movement can be determined until death in the upstream of the river using radio telemetry surveys. Because radio telemetry surveys can provide very high detectability and some parts of the system can only be directly observed using radio telemetry surveys, we can obtain improved estimates for population parameters and other related quantities. Therefore incorporation radio tagged data in integrated population modeling is important. This chapter focus on how the radio telemetry data provide insight on escapement, stopover times, survey life, and snorkel observer efficiency when it is included in integrated population modeling.

Chapter 2

Partial Stratification in Two-Sample Capture-Recapture Experiments

The work in this chapter is published (Premarathna, Schwarz and Jones, 2018) in Environmetrics, the official journal of the International Environmetrics Society published by Wiley.

2.1 Introduction

Capture-recapture is a method used to estimate the abundance of an animal population. Many methods have been used to estimate the parameters relating to both 'closed' and 'open' animal populations (Schwarz and Seber, 1999) and new methods are rapidly developing. The simplest of the capture-recapture methods is the Lincoln-Petersen method (Williams et al., 2002). Under the assumptions that the population is closed (the number of individuals is not changing through birth, death, immigration, or emigration), animals do not lose their marks, their marks are correctly recorded and animals act independently, the two-sample Lincoln-Petersen estimate (maximum-likelihood) for abundance is $\hat{N} = n_1 n_2 / m$. Here n_1 is the total number of animals captured, marked and released in the first sample occasion, n_2 is the total number of animals captured in the second sample occasion and m is the number of marked animals captured in the second sample occasion. Various sample protocols have been proposed to justify the Lincoln-Petersen estimate and obtain the associated standard error. The simple two-sample capture-recapture models for estimating population abundance of a closed population also assume that all animals have the same capture probability at each sample occasion. But this assumption is not satisfied in most applications and heterogeneity in capture probability is expected.

The estimate of population abundance of a closed population can be biased (negatively or positively) when there is heterogeneity in capture probability. For example consider a population of fish in a lake and the population consists of two categories of fish; male and

female. Capture probabilities for each category may vary between categories and also between the first and second sample occasions. If the sex was known at each sample occasion the problem is straightforward. Simply stratify the population into male and female, and use the Lincoln-Petersen estimate on each sex separately to calculate the estimates of abundance for each sex. Then add these stratum-specific estimates to get the estimate of total population abundance. However in some cases, each sampled fish cannot be sexed due to various reasons such as time constraints, total resources allocated for the study, or difficulty in sexing. In the situations where all the fish cannot be sexed, a partial stratification is done (a sub-sample of the captured fish at each sampling occasion is selected and sex determined).

We develop new methods for two-sample capture-recapture experiments using partial stratification and we apply these methods to estimate the abundance of walleye in Mille Lacs Lake, MN, USA in 2013. In these types of experiments, there is a cost to capture a fish in each occasion and there is a cost to categorize a fish from the sub-sample. Furthermore, given the relative costs of sampling for simple capture and for stratifying the sub-sample, the optimal allocation of effort for a given cost is determined. First we develop a method using maximum likelihood to estimate the population abundance and to find the optimal allocation of effort for given a cost. Then we develop a method using a Bayesian approach when prior information is available. Finally we develop a method using individual continuous covariates. The R programing language (R Development Core Team, 2016) was used for analysis of Mille Lacs Lake walleye data and for simulation studies discussed in this chapter.

2.2 MLE approach to Partial Stratification in Two-Sample Capture-Recapture Experiments

2.2.1 Notation

Let $t = 1, 2$ be the capture occasion. We consider that the population can be stratified into k categories. The following notation is used to represent an animal at each sample occasion.

0 - animal is not captured

U - animal is captured but not stratified

C - animal is captured and identified as category C, where
  $C = \{Category_1, \ Category_2, \ ..., \ Category_k\}$
  In practice we use a unique letter to represent each category in the population. For example, if we stratify a population as male and female, then $C = \{M, F\}$.

All the animals in the population are represented by a capture history. For example, the capture history $U0$ represents an animal caught but not stratified in the first sample occasion and not captured in the second sample occasion. CC is the capture history that represents

an animal captured and identified to category at both sample occasions. In general, the possible capture histories for partial stratification in a two-sample capture-recapture model are $U0, UU, 0U, C0, CC, 0C$ and 00. Note that the capture history 00 is unobservable. Since there are k capture histories related to each of the representations $C0, CC$, and $0C$ for the k distinct categories, there are a total of $3k + 4$ different capture histories.

Let $P_{U0}, P_{UU}, P_{0U}, P_{C0}, P_{CC}, P_{0C}$, and P_{00} denote the probabilities of the capture histories $U0, UU, 0U, C0, CC, 0C$ and 00 respectively.

Costs related to capture and stratification are denoted as follows.

C_0	-	total cost available to perform two-sample capture-recapture study
c_1	-	cost to capture an animal at the first sample occasion
c_1^*	-	cost to stratify an animal at the first sample occasion
c_2	-	cost to capture an animal at the second sample occasion
c_2^*	-	cost to stratify an animal at the second sample occasion
c_f	-	fixed cost for the study regardless of the sample size

2.2.2 Statistics

n_{U0}	-	number of animals with capture history $U0$
n_{UU}	-	number of animals with capture history UU
n_{0U}	-	number of animals with capture history $0U$
n_{C0}	-	number of animals with capture history $C0$
n_{CC}	-	number of animals with capture history CC
n_{0C}	-	number of animals with capture history $0C$
n	-	total number of animals captured in the study

$$n = n_{U0} + n_{UU} + n_{0U} + \sum_C n_{C0} + \sum_C n_{CC} + \sum_C n_{0C}$$

n_1 - total number of animals captured at the first sample occasion

$$n_1 = n_{U0} + n_{UU} + \sum_C n_{C0} + \sum_C n_{CC}$$

n_1^* - sub-sample size at the first sample occasion

$$n_1^* = \sum_C n_{C0} + \sum_C n_{CC}$$

n_2 - total number of animals captured at the second sample occasion

$$n_2 = n_{UU} + n_{0U} + \sum_C n_{CC} + \sum_C n_{0C}$$

n_2^* - sub-sample size at the second sample occasion

$$n_2^* = \sum_C n_{0C}$$

2.2.3 Model Parameters

p_{tC} -   capture probability of animals belong to category C at sample occasion t

λ_C -   proportion of category C animals in the population; $\sum_C \lambda_C = 1$

θ_t -   sub-sample proportion at sample occasion t

N -   population abundance

N_C -   population abundance of category C ; $N_C = N \times \lambda_C$

As defined above, the total number of model parameters relating to p_{tC}, λ_C, θ_t, and N is $3k + 3$. However there are only $3k + 2$ parameters to be estimated with the constraint $\sum_C \lambda_C = 1$.

2.2.4 Model Development

Sampling Protocol

Consider an animal population that can be divided into non-overlapping categories where the stratification variable has been determined. At the first sample occasion a random sample of size n_1 is captured. Then a sub-sample of size n_1^* is selected from n_1 and the stratum is determined for all animals in the sub-sample. All captured animals are tagged, usually with a unique tag number. All captured animals are released to the population after marking. Again some time later, another sample of animals of size n_2 is captured randomly from the population. The animals captured at the second sample occasion contains animals captured and marked at the first occasion (some of them might be stratified and some of them might not be stratified) as well as animals not captured at the first occasion. One of the requirements here is that some of the stratified sub-sample at the first occasion is recaptured. Furthermore, animals must not be sacrificed to determine stratification membership at the first sample occasion. Again, a sub-sample of size n_2^* is selected from the captured sample at the second sample occasion including only animals not marked at the first occasion. A pictorial view of the sampling protocol is given in Figure A.1 in Appendix A.

Model Assumptions

In addition to the assumptions related to the standard capture-recapture experiments, some additional assumptions about the subsample are required.

- The population is **closed** (geographically and demographically). The number of individuals does not change during the study through birth or immigration and/or death or emigration.

- The population can be divided into non-overlapping categories.

- Mark status is correctly identified at each sample occasion.

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- Marks are not lost between sample occasions.

- Capture and marking does not affect subsequent catchability of an animal.

- The sub-sample at each occasion is a random sample of animals that are not marked.

- The category of each animal in the sub-samples is successfully identified.

- Animal captures are independent.

Probability Statements of Capture History

Probability expressions for capture histories including the history 00 can be explicitly given using the parameters λ_C, θ_t and p_{tC} as follows.

$$
\begin{aligned}
P_{U0} &= \sum_C \lambda_C\, p_{1C}\, (1 - \theta_1)\, (1 - p_{2C}) \\
P_{UU} &= \sum_C \lambda_C\, p_{1C}\, (1 - \theta_1)\, p_{2C} \\
P_{0U} &= \sum_C \lambda_C\, (1 - p_{1C})\, p_{2C}\, (1 - \theta_2) \\
P_{C0} &= \lambda_C\, p_{1C}\, \theta_1\, (1 - p_{2C}) \\
P_{CC} &= \lambda_C\, p_{1C}\, \theta_1\, p_{2C} \\
P_{0C} &= \lambda_C\, (1 - p_{1C})\, p_{2C}\, \theta_2 \\
P_{00} &= \sum_C \lambda_C\, (1 - p_{1C})\, (1 - p_{2C})
\end{aligned}
$$

where $\qquad P_{U0} + P_{UU} + P_{0U} + \sum_C P_{C0} + \sum_C P_{CC} + \sum_C P_{0C} + P_{00} = 1$

Likelihood

Under the model assumptions, the number of animals related to each of the capture histories has a multinomial distribution with an unknown index.

$$
L = \frac{N!}{n_{U0}!\ \ n_{UU}!\ \ n_{0U}!\ \ \prod_C n_{C0}!\ \ \prod_C n_{CC}!\ \ \prod_C n_{0C}!\ \ (N - n)!} \quad \times
$$

$$
(P_{U0})^{n_{U0}} \times (P_{UU})^{n_{UU}} \times (P_{0U})^{n_{0U}} \quad \times
$$

$$
\prod_C (P_{C0})^{n_{C0}} \times \prod_C (P_{CC})^{n_{CC}} \times \prod_C (P_{0C})^{n_{0C}} \times (P_{00})^{N-n} \qquad (2.1)
$$

We use the logit-link functions to re-parameterize the model parameters p_{tC}, λ_C, θ_t, and the log-link function for N.

Model Constraints

Constraints on the parameters in the likelihood defined in equation 2.1 (e.g. equal capture probability across time or category) are implemented using design matrices. Offset values also allow additional constraints (e.g. fixed at certain values) to be placed on real parameter estimates in the model likelihood.

For example, the vector of parameters $\{p_{tC}\}$ can be constrained by using the design matrix $\mathbf{X}$, offset vector and using beta parameter vector β.

$$\text{logit}(p_{tC}) = \mathbf{X}\beta + \textit{offset}$$

Consider a model with two categories (say M and F) in which all individuals can be successfully assigned to a category. Then there are four capture probabilities relating to the two categories and two sample occasions. If there is a restriction on parameters such that $p_{1M} = p_{1F}$ and $p_{2M} = p_{2F}$, then we use design matrices and offsets as follows:

$$\text{logit}\left(\begin{bmatrix} p_{1M} \\ p_{1F} \\ p_{2M} \\ p_{2F} \end{bmatrix}\right) = \begin{bmatrix} 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

Parameter Estimation

Parameters are estimated numerically using maximum likelihood. With the use of the logit-link and the log-link functions, the parameter estimates and variance-covariance matrix are obtained in *logit* and *log* scales. The delta-method (Casella and Berger, 2002) is used to obtain the variance-covariance matrix on the back-transformed scale.

Closed form solutions under the maximum likelihood method are not available, but moment estimates (Davidson and Solomon, 1974) can be derived (see Appendix A.2.4).

Model Specification, Selection and Assessment

Model specification follows the notation used for naming models in the computer program MARK (White and Burnham, 1999).

$$
\begin{aligned}
c * t \quad &= \quad \text{parameter varies by category and time} \\
t \quad &= \quad \text{parameter varies by time but not by category} \\
c \quad &= \quad \text{parameter varies by category but not by time} \\
. \quad &= \quad \text{parameter does not vary by time or by category} \\
c + t \quad &= \quad \text{additive model: variation to be parallel between categories across time}
\end{aligned}
$$

For example, the model defined by $\{p(c * t)\, \theta(t)\, \lambda(c)\}$ is the model in which capture probabilities vary by category and time, sub-sample proportions vary by time, and category

proportions vary by category. The model defined by $\{p(c*t)\,\theta(t)\,\lambda(0.4)\}$ is the same as the previous model but the category proportions are fixed such that the category one proportion is 0.4 and the category two proportion is 0.6.

Large numbers of different models can be defined for a given data set using the appropriate design matrices and offset vectors. Model selection is based on Akaike's Information Criterion ($AICc$) (Burnham and Anderson, 2004).

There is no guarantee that the model that has the smallest $AICc$ value actually fits the data well. Therefore we need to check whether the selected model can describe the data adequately. Model fitness can be assessed using two methods. One way to assess the specified models for a data set is through residual plots using the standardized residual (Dupuis and Schwarz, 2007) for all observable capture histories as $(O_i - E_i)/\sigma_i$, where O_i and E_i are the observed and expected counts for the capture history i and σ_i is its standard deviation where $\sigma_i \approx \sqrt{E_i}$. Model fitness can also be assessed using the parametric bootstrap goodness of fit test using the deviance statistic and the Tukey statistic (Brooks, Catchpole and Morgan, 2000). Identification of violation of assumptions and a poor model fit are illustrated in Appendix A.2.1 through goodness of fit plots using simulated data.

Planning Experiments

In this partial stratified two-sample capture-recapture study, there is a cost to capturing an animal at each sample occasion, a cost to identify the category of the captured animal in the sub-samples, and also a fixed cost regardless of the sample size. If there is a fixed amount of funds (C_0) to be used in the study, then the objective is to find the optimal number of animals to capture at both sample occasions and the optimal sizes of the sub-samples to be categorized so that the variance of the estimated population abundance ($\mathrm{Var}(\hat{N})$) is minimized.

The total cost (C) of the experiment can be considered as a linear function of sample sizes and it is given by

$$C \;=\; c_f + n_1 c_1 + n_1^* c_1^* + n_2 c_2 + n_2^* c_2^* \;\leq\; C_0 \qquad\qquad (2.2)$$

where,

$$n_1^* \leq n_1 \qquad and \qquad n_2^* \leq n_2 - E(n_{UU} + \textstyle\sum_C n_{CC})$$

Numerical optimization methods are used to find the optimal allocation of n_1, n_2, n_1^* and n_2^* with respect to the linear constraint defined in equation 2.2 such that $\mathrm{Var}(\hat{N})$ is minimized.

It is also important to assess the performance of the model that is going to be used in the experiment before data collection. Power, bias and precision assessments are performed using the method based on expected values given by Devineau, Choquet and Lebreton (2006).
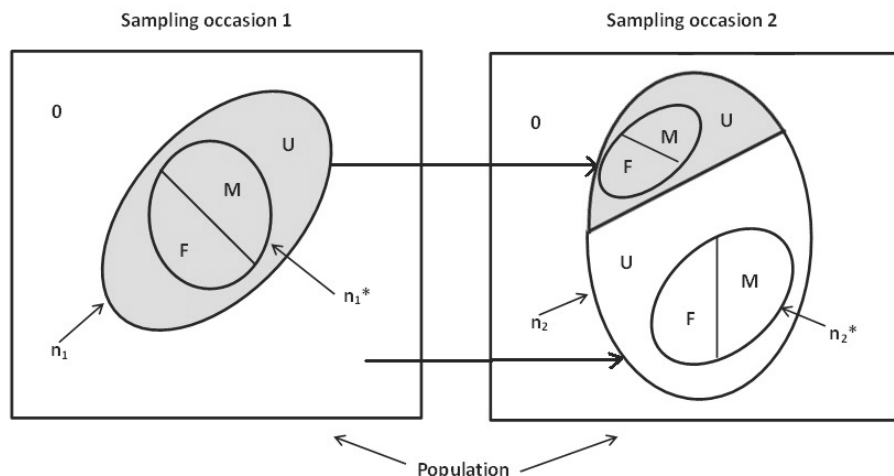
Figure 2.1: Sampling Protocol: Walleye sampled in a two-sample capture-recapture experiment, Mille Lacs Lake, MN, USA in 2013. The notations U and 0 represent a fish in each sampling time as described in Chapter 2.2.1 and $C \equiv \{M, F\}$ where M represents a fish that is captured and identified as a male and F represents a fish that is captured and identified as a female. Shaded areas represent marked fish. n_1, n_1^*, n_2 and n_2^* are as in Chapter 2.2.2.

Results of the power analysis for partial stratification in two-sample capture-recapture experiments with two categories in the population are given in Appendix A.2.2.

2.3 Example : Analysis of Mille Lacs Lake Walleye Data - MLE Approach

2.3.1 Sampling Protocol

The study took place on Mille Lacs Lake, MN, USA in 2013. Walleyes were captured on the spawning grounds. Almost all the fish were sexed in the first sample occasion. All the captured fish were tagged and released, and recapture occurred three to six weeks later using gill-nets. At the time of recapture, all of the fish could not be sexed by external examination. From a sample of fish captured at the second sample occasion with no tags, a random sample was selected and sexed internally. Figure 2.1 shows the sampling protocol of the walleye data.

Capture histories for walleye from Mille Lacs Lake are provided in Table 2.1.

2.3.2 Best Fitted Model

Six different models were fitted as given in Table 2.2. According to the AICc criteria, the best model for the walleye data is the model $\{p(c * t)\, \theta(t)\, \lambda(c)\}$. This conclusion is confirmed by examining residual plots (Figure A.6 in Appendix A), the deviance and Tukey statistic for observed data (Table 2.2), parametric bootstrap p-values, and the corresponding histograms

Table 2.1: Capture histories for walleye sampled in a two-sample capture-recapture experiment, Mille Lacs Lake, MN, USA in 2013.

Capture History	Number of Fish
$U0$	42
UU	1
$M0$	5071
MM	40
$F0$	1555
FF	32
$0M$	41
$0F$	237
$0U$	3058

for 1000 parametric bootstrap samples (Figures A.7 and A.8 in Appendix A) for each of the top four models.

The estimates for all the parameters and their standard errors using the best MLE model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ for the walleye data are shown in Table 2.3. Because there is substantial capture heterogeneity between the two sexes, the Lincoln-Peterson estimator is biased and overestimates the population abundance (N) with a larger standard error compared to the estimate given by the model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$. Usually, the effect of ignoring heterogeneity is to cause negatively bias estimates. However, we did not observe a negative bias in the Lincoln-Peterson estimate because the heterogeneity observed was mixed heterogeneity. Pure heterogeneity, which results in negative biases (Pollock et al., 1990), occurs when individuals from one category of the study animal (e.g. males) are more likely to be observed in both the initial sampling occasion and subsequent occasions. Mixed heterogeneity occurs when one category is more likely to be sampled in the first occasion, but another category is more likely to be sampled in a subsequent occasion. In the case of Mille Lacs Lake walleyes, males were more likely to be observed at the first sample occasion and less likely at the second sample occasion. Conversely, females were less likely at the first sample occasion and more likely at the second sample occasion. Mixed heterogeneity can result in positive biases in Lincoln-Peterson estimates.

Approximate closed form solutions for the parameter estimates using the best model for the walleye data are given in Appendix A.2.4.

Table 2.2: Model comparison for walleye example using MLE method.

Model	np	$\hat{N}$ '000s	$s.e.(\hat{N})$ '000s	$AICc$	$\Delta AICc$	AICc Weights	Deviance Statistic Observed	Deviance Statistic p-value	Tukey Statistic Observed	Tukey Statistic p-value
$\{p(c*t)\ \theta(t)\ \lambda(c)\}$	8	209.1	27.0	77.1	0.0	0.93	0.5	0.85	0.1	0.85
$\{p(c*t)\ \theta(t)\ \lambda(0.5)\}$	7	210.6	24.8	82.4	5.3	0.07	7.8	0.01	1.9	0.01
$\{p(c+t)\ \theta(t)\ \lambda(c)\}$	7	356.9	48.6	528.3	451.2	0.00	453.6	0.00	116.4	0.00
$\{p(t)\ \theta(t)\ \lambda(c)\}$	6	314.7	36.2	537.6	460.5	0.00	464.9	0.00	119.2	0.00
$\{p(c)\ \theta(t)\ \lambda(c)\}$	5	400.2	54.6	1657.6	1580.5	0.00	1584.9	0.00	428.1	0.00
$\{p(.)\ \theta(t)\ \lambda(c)\}$	3	352.7	40.7	1666.9	1589.8	0.00	1596.2	0.00	430.7	0.00

np = number of parameters

Table 2.3: Estimates for the parameters under MLE method, Bayesian method and individual covariate method using models $\{p(c * t) \; \theta(t) \; \lambda(c)\}$, $\{p(c * t)(0, 0.3) \;\; \theta(t)(0.7, 1)(0, 0.3) \;\; \lambda(c)(20, 40)\}$, and $\{p(length * category * time + length^2 * category * time), \; \theta(t), \; \lambda(c)\}$ respectively. $\hat{N}_{LP}$ in the last row is the Lincoln-Peterson estimate for population abundance. The model $\{p(t) \; \theta(t) \; \lambda(c)\}$ is the model related to two-sample Lincoln-Peterson method.

Parameter	MLE model		Bayesian model		Covariate model	
	Estimate	SE	Posterior Mean	SD	Estimate	SE
p_{1M}	0.076	0.015	0.082	0.013		
p_{1F}	0.011	0.002	0.013	0.002		
p_{2M}	0.008	0.001	0.008	0.001		
p_{2F}	0.020	0.004	0.023	0.003		
λ_M	0.323	0.060	0.336	0.042	0.293	0.068
λ_F	0.677	0.060	0.664	0.042	0.707	0.068
θ_1	0.994	0.001	0.993	0.001	0.993	0.001
θ_2	0.083	0.005	0.083	0.005	0.083	0.005
N	209,067	27,032	192,229	22,923	279,230	57,034
N_M	67,527	13,335	64,327	9,990	81,833	25,398
N_F	141,540	24,771	127,902	18,631	197,397	44,625
$\hat{N}_{LP}$	314,673	36,232				

2.3.3 Optimal Allocation of Sampling Effort

We consider the problem of how to optimally allocate sampling effort at the two sample occasions. We need to find optimal values for n_1, n_1^*, n_2, and n_2^* for given c_f, c_1, c_1^*, c_2, c_2^*, and C_0 such that the variance for the estimate of abundance is minimized (i.e. minimize $\text{Var}(\hat{N})$).

The following costs were considered for the analysis of optimal allocation: $c_f = 0$, $c_1 = 4$, $c_1^* = 0.4$, $c_2 = 6$, $c_2^* = 0.4$, and $C_0 = 90,000$. In this study cost can be considered as the time in minutes. $C_0 = 90,000$ is the total number of minutes (i.e. 1500 hours) available for this study. Then the total cost (C) of the experiment can be considered as a linear function of sample sizes and it is given by equation 2.2.

Optimal allocation is carried out before collecting the data with suitable guesstimates for the parameters using the previous studies or researcher's experience. For the Mille Lacs Lake walleye data, we found the estimates for the parameters (Table 2.3) using the MLE method for the best fitted model $\{p(c * t) \;\; \theta(t) \; \lambda(c)\}$ out of the candidate models. We considered these estimates as our guesstimates for the optimal allocation to see how much

the precision of the estimate of population abundance can be improved compared to the current allocation. We used the guesstimates for the parameters as follows considering the model $\{p(c*t)\ \theta(t)\ \lambda(c)\}$.

$$N = 209,000, \qquad \lambda_M = 0.33, \qquad r_1 = 6.5, \qquad r_2 = 0.4$$

where r_1 is the guesstimate of the ratio of p_{1M}/p_{1F} and r_2 is the guesstimate of the ratio of p_{2M}/p_{2F}. It is difficult to give guesstimates for capture probabilities for each category at each sample occasion. But in practice we can give a ratio of the capture probabilities at each sample occasion. For example, if detection probability of males is half that of females at the first sample occasion then the ratio r_1 is 0.5. The guesstimates of the ratios r_1 and r_2 given above are calculated using the estimates for capture probabilities given in Table 2.3 under the MLE model.

Optimal allocation of sample sizes and sub-sample sizes produced by numerical methods (general-purpose optimization with L-BSGS-B method (Byrd, Lu, Nocedal, & Zhu, 1995) was used for numerical optimization and Rsolnp package (Ghalanos & Theussl, 2015) was used for optimization the cost function with constraints in R programing language) for the given costs are $n_1 = 8,929$, $n_1^* = 8,908$, $n_2 = 8,359$, and $n_2^* = 1,412$. At these optimal values $SE(\widehat{N})$ is 13,657. This standard error is 50% lower than the $SE(\widehat{N})$ obtained from the current allocation (Table 2.3).

Different solutions are available for n_1, n_2, n_1^*, and n_2^* at optimal allocation. Conditional contour plots were used to see these different solutions. A conditional contour plot in this situation is a contour plot for standard error of $\widehat{N}$ where two values of n_1, n_2, n_1^*, or n_2^* are fixed at the optimal values. Conditional contour plots for standard error of $\widehat{N}$ when n_1^* and n_2^* are fixed at the optimal values and when n_1 and n_2 are fixed at the optimal values are given in Figure A.9 and Figure A.10 respectively in Appendix A. These contour plots show that many solutions are possible for optimal allocation.

2.3.4 Precision of the Estimates when Additional Information is Available

Now consider how well the precision of the estimate of population abundance can be improved in the presence of additional information. For example, we can compare the precision of the estimate under the best fitted model to the model where the sex ratio is known.

In the case of walleye in Mille Lacs Lake, let the first model be $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ and the second model be $\{p(c*t)\,\theta(t)\,\lambda(MLE)\}$. The first model is the best fit model to the walleye data and the second model can be considered as the model where the sex ratio is known and fixed at the MLE values obtained from the first model. Therefore λ_M is fixed at 0.323 (i.e. λ_F is 0.677) for the second model. The first model has 8 parameters to be estimated and the second model has only 7 parameters to be estimated since male and female proportions are fixed. Estimates for the parameters produced by the model $\{p(c*t)\,\theta(t)\,\lambda(MLE)\}$ are the

same as the estimates given in the Table 2.3 under the model $\{p(c*t)\theta(t)\lambda(c)\}$. However the standard errors for the population estimates produced by these two models are different. Standard errors for the estimates of the parameters N, N_M and N_F are 27,032, 13,335 and 24,771 under the model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ and 26,103, 8,431 and 17,632 under the model $\{p(c*t)\,\theta(t)\,\lambda(MLE)\}$. According to these standard errors there is little improvement of the precision of the estimate of population abundance (N) when the second model is used. However the precision of the estimates of population abundance for each category N_M and N_F is considerably better (around 35% improvement) when the second model is used compared to the best fitted model. Standard errors for all the estimates produced by these two models are given in Table A.5 in Appendix A.

2.4 Bayesian Analysis

The previous analysis shows that prior knowledge about the parameters in the model may have a substantial impact on the precision of the estimate of the population abundance and especially the precision of the estimates for each category. This motivates the use of a Bayesian analysis approach to develop models of partial stratification in two-sample capture-recapture experiments. In this section we use Bayesian methods to develop such models and apply them to the walleye data from Mille Lacs Lake.

2.4.1 Model Development

Prior Selection

We consider sensible prior distributions for each of these parameters. Since the parameters p_{tC}, θ_t are probabilities between 0 and 1, Beta prior distributions are suitable for them. Because we re-parameterize these parameters using the logit-link function, we use Normal distributions on the logit-scale as prior distributions with suitable means and variances to closely represent these Beta distributions. The Dirichlet prior distribution is used for the category proportions because all of the category proportions sum to 1. Because population abundance (N) is an unknown large value, we use a Normal flat prior distribution (Gelman et al., 2004) on the log-scale.

$$\text{logit}(p_{tC}) \sim N(\mu_{tC},\ \sigma_{tC}^2)$$

$$\text{logit}(\theta_t) \sim N(\mu_t,\ \sigma_t^2)$$

$$\lambda_C \sim \text{Dirichlet}(m, n), \text{ where } m, n > 0$$

$$\log(N) \sim N(\mu_N, \sigma_N^2),$$

We use informative priors based on expert opinion or prior data. For example, let prior belief for capture probability for a particular category at a certain sample occasion be located in the interval (0,0.3) with an average around 0.15. A Beta$(2, 10)$ would be a good

prior distribution to represent this information. Because we model the capture probabilities on the logit-scale, $N(-2, 1)$ would closely represent this prior information. However when informative priors are not available, $U(0, 1)$ can be used. Because we use priors on the logit-scale, $N(0, 1.78)$ distribution is considered as the prior distribution because it closely represents $U(0, 1)$ on the logit-scale.

Model Specification, Selection and Assessment

Models are defined using the notation as described in Chapter 2.2.4 and also using prior information. For example, the model defined by $\{p(c*t)(0, 0.3)\,\theta(t)(0.7, 1)(0, 0.3)\,\lambda(c)(2, 4)\}$ is the model where the capture probabilities vary by category and time, sub-sample proportions vary by time, and category proportions vary by category. Prior information is given within the parenthesis for each parameter. $p(c*t)(0, 0.3)$ means prior belief for all the capture probabilities that are in the interval (0,0.3). In this case $N(-2, 1)$ prior distributions are used on the logit-scale. $\theta(t)(0.7, 1)(0, 0.3)$ means two different prior beliefs are used for sub-sample proportions at two sampling occasions. The sub-sample proportion at the first sample occasion is in the interval (0.7,1), the sub-sample proportion at the second sample occasion is in the interval (0,0.3). $N(2, 1)$ and $N(-2, 1)$ prior distributions on the logit-scale are suitable for the sub-sample proportions at these two occasions respectively. $\lambda(c)(2, 4)$ means that the prior distribution of category proportions is Dirichlet$(2, 4)$. In this case, we need to specify only one Normal prior distribution on the logit-scale because there are only two categories; defining one category automatically also defines the second. A $N(-0.7, 0.95)$ on the logit-scale is a good prior distribution for the first category proportion. The model defined by $\{p(c*t)(0, 0.3)\theta(t)(0.7, 1)(0, 0.3)\lambda(0.5)\}$ is the same model described above except the category proportions are fixed at 0.5.

Model selection is performed using the deviance information criterion (DIC) for finite sample sizes where the posterior distributions of the model have been obtained by MCMC simulations using the Metropolis-Hasting method. Two methods are considered for the DIC calculation, the first using pD (Spiegelhalter et al., 2002), and the second using pv (Gelman et al., 2004). The model which has the smallest DIC value is considered the best fitted model for the data.

For a likelihood $p(y|\theta)$, we define the deviance as $D(\theta) = -2log(p(y|\theta))$ where y are the data and θ are the unknown parameters. Posterior mean deviance is defined as $\bar{D}$ where $\bar{D} = E[D(\theta)]$. Then we define pD and pv as follows.

$$pD = \bar{D} - D(\bar{\theta}) \qquad pv = \frac{1}{2}\text{Var}(D(\theta))$$

where $\bar{\theta}$ is the expectation of θ. Then the DIC values are

$$DIC = pD + \bar{D} \qquad or \qquad DIC = pv + \bar{D}$$

Model assessment of fit is done using the Bayesian p-value (Brooks, Catchpole and Morgan, 2000). Two discrepancy statistics; (a) Deviance statistic and (b) Freeman Tukey Statistic (FT) are used. Bayesian p-value close to 0.5 implies that the distribution of the discrepancy statistics for the observed and the simulated data are similar and the given model can describe the data well.

2.4.2 Example : Bayesian Analysis of Mille Lacs Lake Walleye Data

For the Mille Lacs walleye data given in Table 2.1, a MCMC Metropolis-Hasting method was used with 3 chains, 60,000 iterations for burn-in, and 100,000 iterations for post burn-in samples. The MCMC output was thinned by a factor of 50. This produced a sample of 6,000 (3 chains each with 2,000) to approximate the posterior distribution.

Table A.6 in Appendix A shows the DIC values and related information for six different models denoted by $M1$ to $M6$ using two methods; one involving the value pD and the other involving the value pv as described in Chapter 2.4.1. Informative prior distributions for capture probabilities and sub-sample proportions were considered for the first three models $M1$ to $M3$. Under the pv method, the model with the lowest DIC value is $M1 \equiv \{p(c*t)(0,0.3)\,\theta(t)(0.7,1)(0,0.3)\,\lambda(c)(20,40)\}$. This model also has a DIC value very close to the lowest value under the pD method.

Figure A.11 in Appendix A shows the Bayesian p-value goodness of fit plots (King, Morgan, Gimenez, & Brooks, 2010) using two discrepancy statistics, the deviance statistic and the Freeman Tukey statistic for the best four models according to the DIC criteria. Bayesian p-value using both discrepancy statistics for the model $M1 \equiv \{p(c*t)(0,0.3)\,\theta(t)(0.7,1)(0,0.3)\,\lambda(c)(20,40)\}$, which was selected from the DIC criteria, was close to 0.5. Hence the selected model fit the Mille Lacs Lake walleye data well.

Trace plots, autocorrelation plots, and potential scale reduction plots ($\hat{R}$ plots) of the beta parameters for the best fitted model showed that the convergence of the posterior distributions is rapid and dependence between iteration is small.

The results obtained by the MCMC Metropolis-Hasting simulations for the best fitted model $\{p(c*t)(0,0.3)\,\theta(t)(0.7,1)(0,0.3)\,\lambda(c)(20,40)\}$ are given in Table A.7 in Appendix A. Means and standard deviations of the posterior distributions produced from this best fitted Bayesian model are given in Table 2.3. The means of the posterior distributions for all the parameters were similar to the estimates of the MLE model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ given in Table 2.3 with improved standard deviation for the parameters. Variance estimates reveal that the Bayesian method gives improved precision over the MLE method when estimating population abundance N and population category totals N_M and N_F. Bayesian analysis provides models with improved precision for estimates if we can provide informative prior distributions for the parameters. Consider the two models $M1$ and $M3$ given in Table A.6 in Appendix A. The prior distributions are the same for these two models except for the category proportions. Model $M1$ has a Dirichlet$(20, 40)$ prior and the model $M3$ has a

Dirichlet$(2, 4)$ prior. Model $M1$ produced improved precision for estimates compared to the model $M3$ because the Dirichlet$(20, 40)$ prior distribution has less variance than the Dirichlet$(2, 4)$.

Posterior distributions for the population abundance and category totals are given in Figure 2.2. Posterior distributions for the capture probabilities, category proportions and the sub-sample proportions are given in Appendix A.3.4.
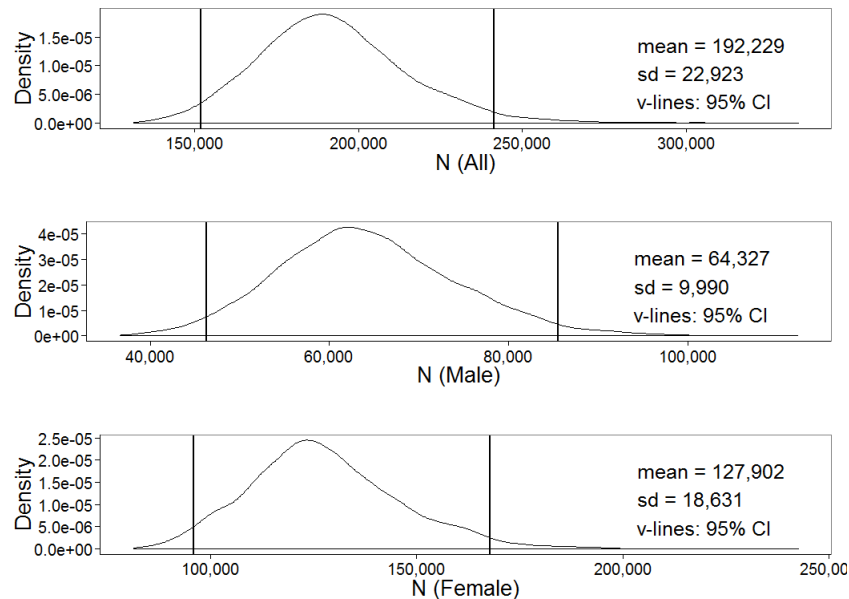
Figure 2.2: Posterior distributions for population abundance (N) and for each category total for males (N_M) and females (N_F) using a sample of 6000 (3 chains each with 2000) observations from the posterior distribution using the best model $\{p(c * t)(0, 0.3)\ \theta(t)(0.7, 1)(0, 0.3)\ \lambda(c)(20, 40)\}$. Vertical bars are the 95% credible interval.

2.5   Simulation Studies for MLE and Bayesian Methods

Bayesian methods produced estimates for population abundance and category totals with improved precision compared to the MLE method when walleye data were used. The sample size (n) of walleye data is about 10,000, which is a large sample. To investigate the effect of sample size, we conducted two simulation studies to test the performance of MLE and Bayesian models development.

We simulated 1,000 samples (total sample size was around 10,000) from a large population with a true population size of 212,000. We also simulated 1,000 samples (total sample size was around 300) from a small population with a true population size of 1,000. Results of simulation studies from both situations are given in Table 2.4. Estimates of the parameters are similar to the true parameter values under the both MLE and Bayesian method.

However the Bayesian method produced improved precision for population abundance and category totals for both large and small populations.

Table 2.4: Simulation study considering a large population and a small population where 1000 samples were simulated from each population. The model { $p(c *$ $t)$ $\theta(t)$ $\nu(t)$ $\lambda(c)$} was fitted to samples under the MLE method. The model {$p(c *$ $t)(0, 0.3)$ $\theta(t)(0.7, 1)(0, 0.3)$ $\lambda(c)(20, 40)$} was fitted to the samples from the large population and the model {$p(c * t)(0, 0.3)$ $\theta(t)(0.7, 1)(0.25, 0.0.55)$ $\lambda(c)(30, 20)$} was fitted to the samples from the small population under the Bayesian method. Under the both MLE and Bayesian methods, the SE matches the actual mean SD of estimates over the simulated samples.

Parameter	Samples from a large population					Samples from a small population				
	True value	MLE Method		Bayesian Method		True value	MLE Method		Bayesian Method	
		Mean	SE	Mean	SD		Mean	SE	Mean	SD
p_{1M}	0.07	0.069	0.010	0.075	0.009	0.15	0.151	0.029	0.153	0.017
p_{1F}	0.01	0.010	0.002	0.011	0.001	0.10	0.106	0.043	0.111	0.019
p_{2M}	0.01	0.010	0.001	0.010	0.001	0.25	0.253	0.045	0.253	0.024
p_{2F}	0.02	0.020	0.004	0.022	0.003	0.15	0.155	0.057	0.174	0.020
λ_M	0.35	0.352	0.057	0.359	0.028	0.6	0.588	0.111	0.615	0.025
λ_F	0.65	0.648	0.057	0.641	0.028	0.4	0.411	0.111	0.384	0.025
θ_1	0.9	0.900	0.004	0.900	0.004	0.9	0.898	0.026	0.899	0.021
θ_2	0.2	0.200	0.007	0.199	0.006	0.4	0.400	0.035	0.399	0.024
N	212,000	218,797	30,126	198,174	20,616	1,000	1,073	289	967	80
N_M	74,000	76,301	12,028	70,669	8,239	600	611	118	594	64
N_F	138,000	142,496	28,520	127,505	15,434	400	462	271	372	40

2.6 Analysis with Individual Covariates

In this section we develop a method to estimate the abundance of a closed population with partial stratification in two-sample capture-recapture experiments using observable individual covariates. For example, the individual covariates for a fish population can be age, weight, length etc. To develop the method with partial stratification in capture-recapture experiments, we used methods described in Huggins (1989), Huggins (1991), and Alho (1990) for estimating population abundance in capture-recapture experiments in a closed population with heterogeneous capture probabilities.

2.6.1 Likelihood

Let the population consists of $i = 1, 2, \ldots, N$ individuals. Then the likelihood is

$$L^* = \prod_{i=1}^{N} (P_{U0i})^{\Delta_{U0i}} (P_{UUi})^{\Delta_{UUi}} (P_{0Ui})^{\Delta_{0Ui}} \prod_{C}(P_{C0i})^{\Delta_{C0i}} \prod_{C}(P_{CCi})^{\Delta_{CCi}} \prod_{C}(P_{0Ci})^{\Delta_{0Ci}}$$

$$\times (P_{00i})^{(1-\sum_h \Delta_{hi})} \quad (2.3)$$

where

$$\Delta_{hi} = \begin{cases} 1 & ; \text{if the } i^{th} \text{ individual captured has a capture history in the set } h, \text{ where} \\ & \qquad h = \{U0, UU, 0U, C0, CC, 0C\} \\ 0 & ; \text{otherwise} \end{cases}$$

$$\begin{aligned}
P_{U0i} &= \sum_C \lambda_C \, p_{1Ci} \, (1-\theta_1) \, (1-p_{2Ci}) \\
P_{UUi} &= \sum_C \lambda_C \, p_{1Ci} \, (1-\theta_1) \, p_{2Ci} \\
P_{0Ui} &= \sum_C \lambda_C \, (1-p_{1Ci}) \, p_{2Ci} \, (1-\theta_2) \\
P_{C0i} &= \lambda_C \, p_{1Ci} \, \theta_1 \, (1-p_{2Ci}) \\
P_{CCi} &= \lambda_C \, p_{1Ci} \, \theta_1 \, p_{2Ci} \\
P_{0Ci} &= \lambda_C \, (1-p_{1Ci}) \, p_{2Ci} \, \theta_C \\
P_{00i} &= \sum_C \lambda_C \, (1-p_{1Ci}) \, (1-p_{2Ci})
\end{aligned}$$

and

$$P_{U0i} + P_{UUi} + P_{0Ui} + \sum_C P_{C0i} + \sum_C P_{CCi} + \sum_C P_{0Ci} + P_{00i} = 1$$

Capture probabilities for each individual depend on the individual covariates and those probabilities can be represented by p_{tCi} where $t = \{1, 2\}$. We consider a logistic model for the capture probabilities. For example, if the individual covariate is *length*, then the capture probabilities are given by

$$logit(p_{tCi}) = log\left(\frac{p_{tCi}}{1 - p_{tCi}}\right) = \beta_0 + \beta_1 \, (length_i) + \beta_2 \, (length_i)^2 + \beta_3 \, (category) + \beta_4 \, (time)$$

In this capture probability formula *time* takes values 0 and 1 where it represents the sample time 1 and 2 respectively. If there are two categories in the population then the variable *category* takes values 0 and 1 representing each respective category. When there are more than 2 categories in the population, more indicator variables have to be defined accordingly.

We can write the likelihood given in Equation 2.3 by letting $i = 1, 2, \ldots, n$ as the captured individuals in the experiment and $i = n + 1, \ldots, N$ for animals not captured in the experiment.

$$L^* = \prod_{i=1}^{n} \left((P_{U0i})^{\Delta_{U0i}} \, (P_{UUi})^{\Delta_{UUi}} \, (P_{0Ui})^{\Delta_{0Ui}} \, \prod_C (P_{C0i})^{\Delta_{C0i}} \, \prod_C (P_{CCi})^{\Delta_{CCi}} \, \prod_C (P_{0Ci})^{\Delta_{0Ci}} \right)$$
$$\times \left(\prod_{i=n+1}^{N} (P_{00i})^{\left(1 - \sum_h \Delta_{hi}\right)} \right) \quad (2.4)$$

Now we condition on the captured individuals because we have covariate information only on the individuals captured at least once in the study. Therefore $(1 - P_{00i})$ denotes the probability that the ith individual is captured at least once in the study for $i = 1, 2, ..., n$. Then the conditional likelihood can be written as

$$L = \prod_{i=1}^{n} \left(\frac{(P_{U0i})^{\Delta_{U0i}} (P_{UUi})^{\Delta_{UUi}} (P_{0Ui})^{\Delta_{0Ui}} \prod_C (P_{C0i})^{\Delta_{C0i}} \prod_C (P_{CCi})^{\Delta_{CCi}} \prod_C (P_{0Ci})^{\Delta_{0Ci}}}{1 - P_{00i}} \right)$$

(2.5)

The conditional likelihood involves only the captured individuals. Therefore the maximum conditional estimates of the parameters can be found.

The Horvitz-Thompson estimator (Huggins, 1991) gives an estimate for population abundance N.

$$\hat{N}(\beta) = \sum_{i=1}^{n} \frac{1}{\phi_i(\beta)} \qquad \text{with} \quad \phi_i(\beta) = 1 - P_{00i}$$

where ϕ_i is the probability for the ith individual captured at least once in the study for $i = 1, 2, ..., n$ and β is the parameter vector associated with the model.

As described in Huggins (1991), when β is estimated from the data by $\hat{\beta}$, the variance of $\hat{N}(\beta)$ is

$$Var(\hat{N}(\hat{\beta})) = s^2(\hat{\beta}) + \hat{\mathbf{D}}^T \hat{\mathbf{I}}^{-1} \hat{\mathbf{D}}$$

where

$$s^2(\hat{\beta}) = \sum_{i=1}^{n} \phi_i(\hat{\beta})^{-2} \left[1 - \phi_i(\hat{\beta}) \right],$$

$\hat{\mathbf{I}}$ is a matrix of second derivatives (Hessian matrix) of the conditional log-likelihood evaluated at $\hat{\beta}$ and $\hat{\mathbf{D}}$ is a vector calculated as follows.

$$\left. \frac{dN(\beta)}{d\beta} \right|_{\hat{\beta}} = \sum_{i=1}^{n} \phi_i(\hat{\beta})^{-2} \left. \frac{d\phi_i(\beta)}{d\beta} \right|_{\hat{\beta}}$$

2.6.2 Model Fitting and Parameter Estimation for Mille Lacs Walleye Data

Now we consider the individual lengths as additional information available for all captured and recaptured walleyes in both sampling occasions for the Mille Lacs Lake walleye data given in Table 2.1. The distribution of length for males (M), females (F) and for the walleyes whose sex is not determined (U) in the captured samples in both sampling occasions is given in Figure A.15 in Appendix A.

Seven different models were fitted to walleye data as shown in Table A.8 in Appendix A. According to the AICc criteria, the best model for the walleye data is the model $\{p(length *$

$category * time + length^2 * category * time), \theta(t), \lambda(c)\}$. In the best fitted model, $\theta(t)$ means sub-sample proportions vary by time, $\lambda(c)$ means category proportions vary by category and $p(length * category * time + length^2 * category * time)$ represents the capture formula. The capture probabilities for each individual i for each category C at time t can be found by this capture formula as follows;

$$
\begin{aligned}
logit(p_{tCi}) = log\left(\frac{p_{tCi}}{1 - p_{tCi}}\right) \\
= \beta_0 + \beta_1\ (length_i) + \beta_2\ (category) + \beta_3\ (time) + \beta_4\ (length_i)^2 + \\
\beta_5\ (length_i)(category) + \beta_6\ (length_i)(time) + \beta_7\ (category)(time) + \\
\beta_8\ (category)(length_i)^2 + \beta_9\ (time)(length_i)^2 + \\
\beta_{10}\ (length_i)(category)(time) + \beta_{11}\ (category)(time)(length_i)^2
\end{aligned}
$$

Motivation to use this complicated capture formula with quadric *length* can be explained by considering the size selectivity of the gill nets used to capture walleyes (Figure A.15 in Appendix A). Very large and very small walleyes are difficult to capture. The *length* frequency of captured walleyes displays a unimodal distribution suggestive of a quadratic relationship of catchability versus *length*.

Estimates of the parameters were obtained by maximizing the conditional log likelihood function. Table 2.3 gives the estimates for the parameters and their standard errors for sub-sample proportions, category proportions and population abundance using the best fitted covariate model $\{p(length * category * time + length^2 * category * time), \theta(t), \lambda(c)\}$ with the individual covariate *length*. Estimates and the standard errors for β_0, β_1, ... , β_{11} are given in Appendix A.4.3. The estimate of population abundance N is 279,230 ($SE = 57,034$). Variance estimates of population abundance N and category totals N_M and N_F under the individual covariate model are higher compared to the methods discussed in previous Chapters 2.3 and 2.4. Higher estimates are a result of residual individual heterogeneity having been modeled. Also the individual covariate model is highly parameterized compared to the models used in the previous sections. Estimates of category proportions under the individual covariate model are $\lambda_M = 0.293$ ($SE = 0.068$) and $\lambda_F = 0.707$ ($SE = 0.068$). These estimates are similar to the estimates found without the individual covariate in Chapters 2.3 and 2.4 using MLE and Bayesian methods, respectively.

Figure 2.3 shows that estimated capture probabilities for male and female walleyes against length at sample occasions 1 and 2. According to this figure, male walleyes have a much higher capture probability at sample occasion 1 than female walleyes. At the second occasion, females have a higher capture probability compared to males. Moreover the
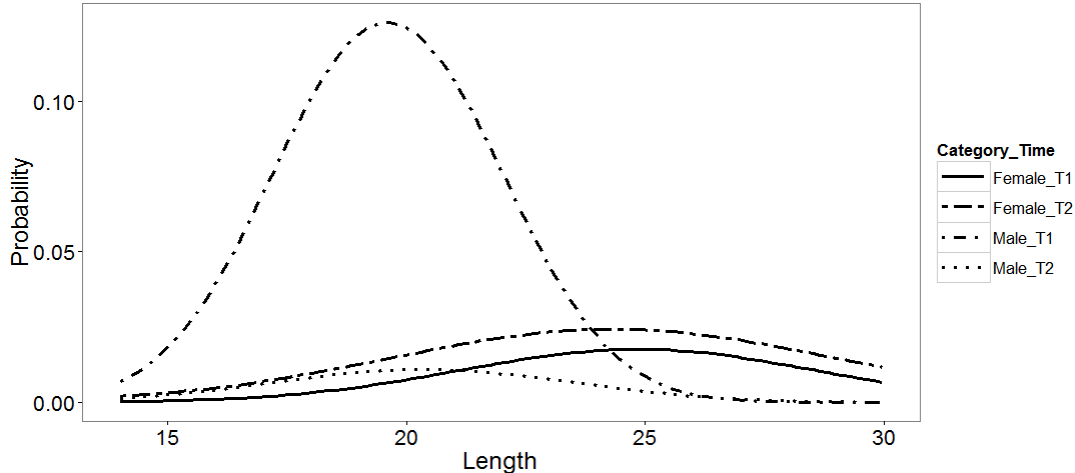
Figure 2.3: Estimated capture probabilities versus the individual covariate length (inches) of males and females at capture time 1 and 2 using the model $\{p(length*category*time + length^2*category*time), \; \theta(t), \; \lambda(c)\}$.

catchability of males between 17 inches and 21 inches in length was very high at the first occasion. Virtually all walleyes longer than 27 inches were female.

The estimated capture probabilities in Figure 2.3 can be explained by using the summary distribution of length of walleyes in Figure A.15 in Appendix A. Therefore we can expect that the fitted model using the individual covariate *length* fits the walleye data well.

2.7 Discussion

Capture heterogeneity can cause bias in estimates of abundance in two-sample capture-recapture experiments for closed populations. In fishery experiments this heterogeneity is often related to characteristics such as sex or size of the fish.

If there is heterogeneity in capture probabilities in each category, the simplest way to address the heterogeneity is to stratify it into different categories and use the stratum-specific estimates. Then the sum of these stratum-specific estimates gives the estimate for the overall abundance. But complete stratification is not always possible in experiments. In such cases we can do a partial stratification where a sub-sample of the captured animals are selected at each sampling occasion and assigned to categories.

The optimal allocation procedures helps us to find sampling effort for a given cost among the various costs of the study to obtain the estimate for the population abundance with smallest variance. It also shows that many different solutions are possible at the optimal allocation.

The Bayesian method provides improved precision for the estimates of population abundance and category totals because it allows us to use expert prior knowledge on the parameters of the model. We observed that the Bayesian solutions are sensitive to the choice

of prior distributions. It is important to use informative prior distributions, especially on category proportions (sex ratios) in order to fit a better model. Having good knowledge of the sex ratio is important to obtain estimates of the population abundance with improved precision.

When additional information such as a continuous covariate *length* is available for each captured sample, the model development with individual covariates should be expected to produce better estimate for the population abundance compared to the methods developed without individual covariates. It is important to define an appropriate logistic regression model (e.g. quadratic relationship of catchability versus *length* for the walleye data) for capture probabilities to fit a good model for the given data with individual continuous covariates. However the precision of the population abundance produced by a highly parameterized model that uses continuous covariates can be worse compared to the precision given by models that were developed without individual covariates because there is always a compromise between accuracy and precision.

Bayesian models produced estimates with improved precision for population abundance and category totals over the MLE method for walleye data. Simulation studies show that performance under large population sizes and small population sizes are similar for both MLE and Bayesian model development methods. When the individual lengths are considered for the walleye data, the conditional likelihood method produced estimates for category proportions and sub-sample proportions that were quite similar to the MLE and Bayesian methods. However the estimates of population abundance under the conditional likelihood method produced somewhat different values with poor precision compared to the previous two methods because the best fitted covariate model was highly parameterized.

We need to consider the issue of non-identifiability in model fitting. All the parameters can be estimated in two-sample capture-recapture studies similar to Lincoln Peterson (Williams et al., 2002) model fitting. However we would not be able to estimate some of the parameters, for example, if no females were observed. There is no non-identifiable issue on model fitting with walleye data because both males and females were observed. However there can be a non-identifiability issue with the population abundance parameter when modeling with individual heterogeneity as described in Link (2003), because reasonable alternative models might predict identical observations from population of different sizes.

Chapter 3

Study of k-Sample Capture-Recapture Experiments under Partial Stratification on Closed Population

3.1   Introduction

Capture-Recapture methods used to estimate abundance have been developed considering two types of populations classified as *open* and *closed*. Open populations allow additions due to birth or immigration or losses due to death or emigration during the period of study (Pollock et al., 1990). Closed populations do not allow additions or losses over the period of study. However known removals or losses on capture or known additions on capture (Otis et al., 1978) are also allowed in closed populations. Development of methods for estimating animal population abundance considering both open and closed populations are discussed in Schwarz and Seber (1999), Seber (1992), and Seber (1986). While using these methods in ecological experiments, new methods for capture-recapture experiments are developing rapidly over time.

In a simple capture-recapture experiment with two sample times, the simple Lincoln-Petersen (Williams et al., 2002) method can be used to estimate the abundance of a closed population. The Lincoln-Petersen estimate for abundance is $\widehat{N}_{LP} = n_1 n_2 / m$ where n_1 is the total number of individuals captured, marked and released in the first sample time, n_2 is the total number of individuals captured in the second sample time and m is the number of marked individuals captured in the second sample time. When there are more than two sample times, the Schnabel method (Schnabel, 1938) can be used. The Schnabel method is an extension of the Lincoln-Petersen method where the individuals are captured, examined for previous marks, marked and then released at each of k sample times. The estimate for the abundance using Schnabel method is $\widehat{N}_S = \sum_{t=1}^{k} C_t M_t / \sum_{t=1}^{k} R_t$. Here C_t is the total number of individuals caught in the current sample time t, M_t is the number of marked

individuals in the population just before the current sample time (i.e. $(t-1)^{th}$ sample time) and R_t is the number of marked individuals caught in sample time t. Both the Lincoln-Petersen and Schnabel methods assume that the all individuals in the population have the same capture probability in each sample time. But this assumption might not be satisfied in most of the ecological experiments. We can expect heterogeneity in capture probabilities.

Estimate of animal abundance for a closed population can be biased when there is heterogeneity in capture probabilities. For example if we stratify a particular animal population as males and females, capture probabilities might vary between these two categories as well as the subsequent sample times. However if we can stratify all the captured animals at each sample time, then finding an unbiased estimate for abundance is straightforward. We can simply use the Lincoln-Petersen method or Schnabel method and find stratum specific estimates. Then the estimate for the entire population abundance is computed by adding these stratum specific estimates. However stratification might not be possible for each sampled animal due to various reasons such as time/resources constraints or because morphological differences are slight. In such cases partial stratification can be done where a sub-sample is selected at each sample time and the stratum is determined. Methods for partial stratification in two-sample capture recapture experiments to estimates the populations abundance are developed by Premarathna, Schwarz and Jones (2018).

In this chapter we present new methods for partial stratification in k-sample ($k > 2$) closed capture-recapture experiments. We developed these new methods using maximum likelihood method and a Bayesian method. When $k = 2$, we developed methods for partial stratification in two-sample capture-recapture experiments (Premarathna, Schwarz and Jones, 2018) and applied those methods to Mille Lacs Lake walleye data, MN, USA. In k-sample case we did not have a real life data. Therefore we used these methods to a simulated data with three sample times and with two categories available in the population and allowing loss on capture. Analysis of this simulated data was carried out using R programing language (R Development Core Team, 2016).

3.2   Design Protocol

The protocol for the partial stratification in k-sample capture-recapture experiments can be explain as follows. An animal population of interest can be divided into non-overlapping categories. The experiment is carried out k sample times. At the first sample time a random sample of size n_1 animals is captured from the population. Then a sub-sample is selected randomly from the sample n_1. All animals in the sub-sample are stratified. All animal are marked with a unique tag number. All the animals captured are marked including the ones considered as loss on capture. All the marked animals are released to the population except the ones lost on capture. At each of the successive sample time t ($t = 2, 3, ..., k$), a random sample of size n_t animals is selected from the population. Sample n_t contains animals already

captured and marked during previous sample times (some of them are stratified and some of them are not stratified) and also animals not captured in previous sample times. A sub-sample of animals is selected randomly from those animals not captured during previous sample times. Again the animals in the sub-sample are stratified and marked with a unique tag. All the newly captured animals not selected to the sub-sample are also marked. Marked animals are released to the populations except the animals considered as loss on capture. All the captured animals are marked such that the sample times are identifiable from the marks. One of the requirements in this experiment is that some of the stratified sub-sample at previous sample times is recaptured at the current sample time.

Assumptions about the experiment are similar to standard capture-recapture experiments and some additional assumptions are also made.

- Known losses on capture might be occurred at each sample time.

- The population is considered as closed.

- The population can be divided into non-overlapping categories.

- Mark status is correctly identified at each sample time.

- Marks are not lost between sample times.

- Capture and marking does not affect subsequent catchability of an animal.

- The sub-sample at each sample time is a random sample of animals that are not marked at least once during previous sample times.

- The category of each animal in the sub-samples is successfully identified.

- Animal captures are independent.

3.3   Notations

Classical capture-recapture experiments use 1's or 0's to represent the capture history vector where '1' represents the individual was captured and '0' represents the individual was not captured in each sample time. In this experiment we use the following notation to represent the status of the all animals in the population at each sample time similar to Premarathna, Schwarz and Jones (2018). Some notations are defined similar to the notations defined by Cowen and Schwarz (2006).

	0	-	animal is not captured
	U	-	animal is captured but not stratified
	C	-	animal is captured and identified as belonging to the category C, where

$C = \{Category_1, Category_2 ..., Category_d\}$

In practice we use an unique letter to represent each category in the population. For example, if we stratify a population as male and female, then $C = \{M, F\}$.

Loss on capture is allowed in the experiment. Capture histories with negative number for the frequency indicate loss on capture. For example consider few possible capture histories and corresponding number of animals captured for a 3-sample capture-recapture study with $C = \{M, F\}$ in Table 3.1.

Table 3.1: Example data for 3-sample capture recapture data with loss on capture

Capture History	Number of animals
$U00$	1234
$U00$	-23
$MM0$	45
$MM0$	-2
$\vdots$	$\vdots$

If the number of animals related to the capture history $U00$ is positive (1234), it represents 1234 animals caught but not stratified at the first sample time and not caught them in the second or third sample times. Capture history $U00$ with negative number (-23) represents that 23 animals lost on capture but not stratified at the first sample time and then removed from the population. Capture history $MM0$ with a positive number represents animals caught at the first sample time and stratified and identified the category as 'male' and caught at the second sample time and not caught at the third sample time.

3.3.1 Statistics and Indicator Variables

k = number of sample times, $k \geq 2$

t = index for sample time, where $t = 1, 2, ..., k$

m = number of uniquely observed capture histories. This does not include the capture history ω_0 which represents individuals never caught in any sample time. A particular observed capture history can be paired with a positive number as well as a negative number where the loss on capture is indicated by the negative sign. In that case there are two unique capture history status for that particular capture history.

i = index for number of uniquely observed capture history status, where $i = 0, 1, 2, ..., m$; $i = 0$ is used to refer the history ω_0. ω_0 is unobserved.

d = number of categories (strata) in the population

r = index for number of categories, where $r = 1, 2, ..., d$

ω_i = uniquely observed capture history. where $\omega_i = (\omega_{i1} \, \omega_{i2} \, ... \, \omega_{ik})$ and

n_{ω_i} = absolute value of the total individuals captured with history ω_i.

n = total number of individuals captured in the study, $\quad n = \sum\limits_{i=1}^{m} n_{\omega_i}$

$$
\omega_{it} = \begin{cases} U & : \text{individual } i \text{ captured at the sample time } t \text{ was captured prior to the sample} \\ & \quad \text{time } t \text{ and marked as } U \text{ or individual } i \text{ is captured for the first time at the} \\ & \quad \text{sample time } t \text{ but not stratified} \\ C & : \text{individual } i \text{ captured at the sample time } t \text{ was captured prior to the sample} \\ & \quad \text{time } t \text{ and identified as belonging to the category } C \text{ or individual } i \text{ is} \\ & \quad \text{captured for the first time at the sample time } t \text{ and identified as belonging} \\ & \quad \text{to the category } C \\ 0 & : \text{individual } i \text{ is not captured at the sample time } t \end{cases}
$$

h_{it} - capture indicator for history at sample time t. i.e. ω_{it}

$$
h_{it} = \begin{cases} 1 & : \text{individual } i \text{ is captured at sample time } t \\ 0 & : \text{individual } i \text{ is not captured at sample time } t \end{cases}
$$

z_{it} - indicator to identify the availability to capture for ω_{it}

$$
z_{it} = \begin{cases} 1 & : \text{individual } i \text{ is available in the population at sample time } t \\ 0 & : \text{individual } i \text{ is not available in the population at sample time } t \end{cases}
$$

s_{it} - indicator to identify whether the stratification done at sample time t for ω_{it}.

$$s_{it} = \begin{cases} 1 & : \text{individual } i \text{ is stratified at sample time } t \\ 0 & : \text{individual } i \text{ is not stratified at sample time } t \end{cases}$$

f_{it} - indicator to identify sample time that the individual with the capture history ω_{it} is captured for the first time.

$$f_{it} = \begin{cases} 1 & : \text{individual } i \text{ is captured for the first time at sample time } t \\ 0 & : \text{individual } i \text{ is captured before the sample time } t \end{cases}$$

κ_{it} - loss on capture indicator for the capture history ω_{it}.

$$\kappa_{it} = \begin{cases} 1 & : \text{not lost at sample time } t \\ 0 & : \text{lost at sample time } t \end{cases}$$

u_{ir} - indicator to identify whether the individuals with capture history ω_i identified as belonging to a particular category C, where $C = \{category_1, category_2, ..., category_d\}$

$$u_{ir} = \begin{cases} 1 & : \text{individuals with capture history } \omega_i \text{ identified as belonging to } category_r \text{ or} \\ & \quad \text{capture history } \omega_i \text{ contains at least one } U \\ 0 & : \text{individuals with capture history } \omega_i \text{ identified as belonging to one of the} \\ & \quad \text{categories but do not belong to } category_r \end{cases}$$

Partial stratification in k-sample capture-recapture experiment with d number of categories in the population has $m = 2(d + 1)(2^k - 1)$ uniquely observable capture histories allowing for loss on capture. However many of the possible observable unique capture histories may not be observed in an experiment. Note that the capture history ω_0 (e.g. for a 3-sample capture-recapture study ω_0 is 000) is unobservable in an experiment.

3.3.2 Model Parameters

$$
\begin{array}{rcl}
p_{tC} & = & \text{capture probability of animals belong to category } C \text{ at sample time } t \\
\lambda_C & = & \text{proportion of category } C \text{ animals in the population,} \quad \sum_C \lambda_C = 1 \\
\theta_t & = & \text{sub-sample proportion at sample time } t \\
\nu_t & = & \text{loss on capture probability at sample time } t \\
N & = & \text{population abundance} \\
N_C & = & \text{population abundance of category } C \; ; \; N_C = N \times \lambda_C
\end{array}
$$

3.4 MLE Model Development

3.4.1 Probability Statements of Capture History

The probability statement for each of the uniquely observed capture history ω_i can be given explicitly as follows using the parameters p_{tC}, λ_C, θ_t, and ν_t.

$$P_{\omega_i} = \sum_C \lambda_C * u_{iC} \left\{ \prod_t^k p_{tC}^{h_{it}z_{it}} \left(1 - p_{tC}\right)^{(1-h_{it})z_{it}} \left(1 - \nu_t\right)^{h_{it}\kappa_{it}} \nu_t^{h_{it}(1-\kappa_{it})} \theta_t^{s_{it}} \left(1 - \theta_t\right)^{(1-s_{it})f_{it}} \right\}$$

Even though the capture history ω_0 is unobservable in an experiment, the probability statement can be given as follows.

$$P_{\omega_0} = \sum_C \lambda_C \left\{ \prod_t^k (1 - p_{tC}) \right\}$$

For example, the probability expressions for the following capture histories for a 3-sample capture-recapture study with $C = \{M, F\}$ can be given as follows.

Capture History	Number of animals	Probability statement
U00	1234	$\sum_C \lambda_C p_{1C}(1 - \theta_1)(1 - \nu_1)(1 - p_{2C})(1 - \nu_2)(1 - p_{3C})(1 - \nu_3)$
U00	-23	$\sum_C \lambda_C p_{1C}(1 - \theta_1)\nu_1$
MM0	45	$\lambda_M p_{1M}\theta_1(1 - \nu_1)p_{2M}(1 - \nu_2)(1 - p_{3M})(1 - \nu_3)$
MM0	-2	$\lambda_M p_{1M}\theta_1(1 - \nu_1)p_{2M}\nu_2$

3.4.2 Likelihood

We can model the number of animals related to each unique capture history ω_i using the multinomial distribution with unknown index (i.e. $n_{\omega_0} = N - n$). The likelihood is

$$L = \frac{N!}{n_{\omega_1}! \ \ n_{\omega_2}! \ \ ... \ \ n_{\omega_m}! \ \ (N - n)!} \prod_{i=1}^m (P_{\omega_i})^{n_{\omega_i}} \times (P_{\omega_0})^{(N-n)} \tag{3.1}$$

This can be written as $L = L_1 \times L_2$ (Sanathanan, 1972) where

$$L_1 = \frac{N!}{n! \ (N - n)!} \left(1 - P_{\omega_0}\right)^n \left(P_{\omega_0}\right)^{(N-n)}$$

$$L_2 = \frac{n!}{n_{\omega_1}! \ n_{\omega_2}! \ ... \ n_{\omega_m}!} \prod_{i=1}^m \left(\frac{P_{\omega_i}}{1 - P_{\omega_0}}\right)^{n_{\omega_i}} \tag{3.2}$$

Estimator for N based on Equation 3.1 is the maximum likelihood estimator and estimator based on the L_2 is the conditional maximum likelihood estimator where it is conditioned on the observed total n. The conditional maximum likelihood estimator for N is asymptotically equivalent to the maximum likelihood estimator (Sanathanan, 1972).

3.4.3 Parameter Estimation and Model Constraints

Estimates of the parameters p_{tC}, λ_C, θ_t, ν_t and N were computed using standard numerical methods. We used logit-link functions for the parameters p_{tC}, λ_C, θ_t and ν_t because it constrains probabilities between 0 and 1. We used log-link function for the parameter N because N is a positive number and log-link function constrains the value between 0 and infinity. First we computed the estimates and the variance-covariance matrix in the *logit* and *log* scales. Then we applied the delta-method to obtain the variance-covariance matrix in back-transformed scale.

Additional constraints on parameters can be placed through design matrices and offset vectors (offset value is used to fix a parameter at a certain value). We modeled the parameters p_{tC}, λ_C, θ_t and ν_t using logistic regression as described in White and Burnham (1999).

For example, the vector of parameters for capture probabilities $\{p_{tC}\}$ can be constrained by using the appropriate design matrix $\mathbf{X}$, offset vector and using beta parameter vector β.

$$logit(p_{tC}) = \mathbf{X}\beta + offset$$

The number of parameters to estimate is depend on the specified model. For example, consider a k-sample study with d number of categories in a population with the model where no constraints on the parameters. Then there are kd number of p_{tC} parameters, k number of θ_t parameters, k number of ν_t parameters, $d-1$ number of λ_C parameters (because of the constraint $\sum_C \lambda_C = 1$) and the parameter N to be estimated corresponding to the unconstrained model.

3.4.4 Model Specfication and Selection

Standard model identification notations were considered for naming the models as used in the computer program MARK (White and Burnham, 1999).

$$
\begin{aligned}
c * t \quad &= \quad \text{parameter varies by category and time} \\
t \quad &= \quad \text{parameter varies by time but not by category} \\
c \quad &= \quad \text{parameter varies by category but not by time} \\
. \quad &= \quad \text{parameter does not vary by time or by category}
\end{aligned}
$$

For example, the unconstrained model can be denoted as $\{p(c*t)\,\theta(t)\,\nu(t)\,\lambda(c)\}$. In this model $p(c*t)$ represents capture probabilities that vary by category and time; $\theta(t)$ represents

sub-sample proportions that vary by time; $\nu(t)$ represents loss on capture proportions that vary by time; and $\lambda(c)$ represents category proportions that vary by category. If there is no variation of capture probabilities by category and time then it is represented as $p(.)$. The model denoted by $\{p(c * t)\ \theta(t)\ \nu(t)\ \lambda(0.3)\}$ is the same as the unconstrained model except the category proportions are fixed. Here the category 1 proportion is fixed at 0.3 and category 2 proportion is fixed at 0.7.

Model selection was done using the Akaike's Information Criterion (AICc) and related methods (Burnham and Anderson, 2004).

3.4.5 Goodness of fit

Goodness of fit of the model to the data was assessed by two different methods. First method we applied was the residual plot using the standardized residuals (Dupuis and Schwarz, 2007) and the second method was the parametric bootstrap goodness fit test using the deviance statistic and the Tukey statistic (Brooks, Catchpole and Morgan, 2000).

Residual plots were created taking the standardized residuals for all unique capture histories. Standardized residual for the capture history ω_i is $(O_{\omega_i} - E_{\omega_i})/\sigma_{\omega_i}$, where O_{ω_i} and E_{ω_i} are the observed and expected counts for the capture history ω_i and and σ_{ω_i} is its standard deviation where $\sigma_{\omega_i} \approx \sqrt{E_{\omega_i}}$. Many of the possible capture histories relating to this experiment may not be observed during the experiment. Expected value of these observable but unobserved histories is small. We grouped all these counts into one history and denoted as ω_{OTHER}. Then the expected value of the capture history ω_{OTHER} was calculated and it is $E_{\omega_{OTHER}} = n - \sum_i^m E_{\omega_i}$. Because $O_{\omega_{OTHER}} = 0$, standardized residual for ω_{OTHER} was calculated as $(0 - E_{\omega_{OTHER}})/\sigma_{\omega_{OTHER}}$.

The parametric bootstrap goodness of fit tests involve the conditional likelihood where it is conditioned on the observed total n. Here we compared the fitted model to the saturated model. The saturated model is a multinomial model with probability for each capture history ω_i is n_{ω_i}/n. We calculated the deviance statistic and the Tukey statistic of the observed data and compared those statistics with bootstrap samples. Then we calculated the bootstrap p-value related to each method by calculating the number of deviance (Tukey) statistics calculated from the bootstrap samples greater than the deviance (Tukey) statistic calculated from the observed data and dividing by number of bootstrap samples. Larger goodness of fit p-value suggest that the fitted model is a good fit to the observed data.

3.5 Example : MLE Approach

3.5.1 Example with 3-sample study with two categories in the population

Simulated data set with 3-sample capture-recapture study under partial stratification with two categories in the population allowing loss on capture was considered to apply this new methods. The two categories in the population were denoted as 'M' and 'F' to represent

males and females in the population. We simulated the data such that there is heterogeneity in catchability. Data was simulated using R programing language and the true values of the parameters used for simulation are given in Table 3.5. Capture histories of one simulated data set are provided in Table 3.2.

Table 3.2: Simulated data for 3-sample capture-recapture study. M and F represent the two categories males and females in the population. If the number of animals captured is a negative values, it represents loss on capture. Following true parameter values were considered to simulate data.

$p_{1M} = 0.015$, $p_{1F} = 0.005$, $p_{2M} = 0.009$, $p_{2F} = 0.010$, $p_{3M} = 0.005$, $p_{3F} = 0.007$
$\lambda_M = 0.7$, $\lambda_F = 0.3$
$\theta_1 = 0.8$, $\theta_2 = 0.3$, $\theta_3 = 0.4$
$\nu_1 = 0.005$, $\nu_2 = 0.001$, $\nu_3 = 0.004$
$N = 300,000$

Capture History	Number of animals	Capture History	Number of animals
$00F$	-2	$0MM$	1
$00M$	-1	$0U0$	1960
$00U$	-3	$0UU$	6
$0M0$	-2	$F00$	333
$0U0$	-3	$F0F$	3
$F00$	-2	$FF0$	5
$M00$	-13	$M00$	2485
$U00$	-5	$M0M$	10
$00F$	246	$MM0$	18
$00M$	431	$U00$	700
$00U$	1024	$U0U$	4
$0F0$	275	$UU0$	6
$0M0$	540		

Six different models were fit to the data in Table 3.2 and the summary of model fitting is given in the Table 3.3. According to the AICc values and the related information, the best model fit to the data is the model $\{p(c * t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$ where the capture probabilities vary by category and time, sub-sample proportions vary by time, category proportions vary by category and loss on capture proportions vary by time.

Table 3.3: Model comparison table for simulated data in Table 3.2. *np* is the number of parameters to be estimated in the model.

Model	np	$\hat{N}$ '000s	$s.e.(\hat{N})$ '000s	AICc	$\Delta AICc$	AICc Weights
$\{\, p(c*t)\, \theta(t)\, \nu(t)\, \lambda(c)\}$	14	382	52	165.9	0.0	0.84
$\{\, p(c*t)\, \theta(t)\, \nu(t)\, \lambda(0.5)\}$	13	476	65	169.2	3.3	0.16
$\{\, p(t)\quad \theta(t)\, \nu(t)\, \lambda(c)\}$	11	397	54	473.4	307.5	0.00
$\{\, p(t)\quad \theta(t)\, \nu(t)\, \lambda(0.7)\}$	10	397	54	704.2	538.3	0.00
$\{\, p(.)\quad \theta(t)\, \nu(t)\, \lambda(c)\}$	9	412	56	1139.6	973.6	0.00
$\{\, p(c)\quad \theta(t)\, \nu(t)\, \lambda(c)\}$	10	413	56	1141.5	975.6	0.00

Goodness of fit plots provide us whether the model selected according to the AICc criteria is a good fit to the simulated data. Standardized residual plots for the best four models according to the AICc criteria are given in Table 3.1. Parametric bootstrap goodness of fit plots for these four models using the deviance statistic and Tukey statistic are given in Figure B.1 and Figure B.2 in Appendix B. 1,000 bootstrap samples were considered for both parametric bootstrap methods using the deviance statistic and the Tukey statistic. Parametric bootstrap p-values and the standardized residual plots provide that the model $\{p(c*t)\, \theta(t)\, \nu(t)\, \lambda(c)\}$ is a good fit to the simulated data in Table 3.2.
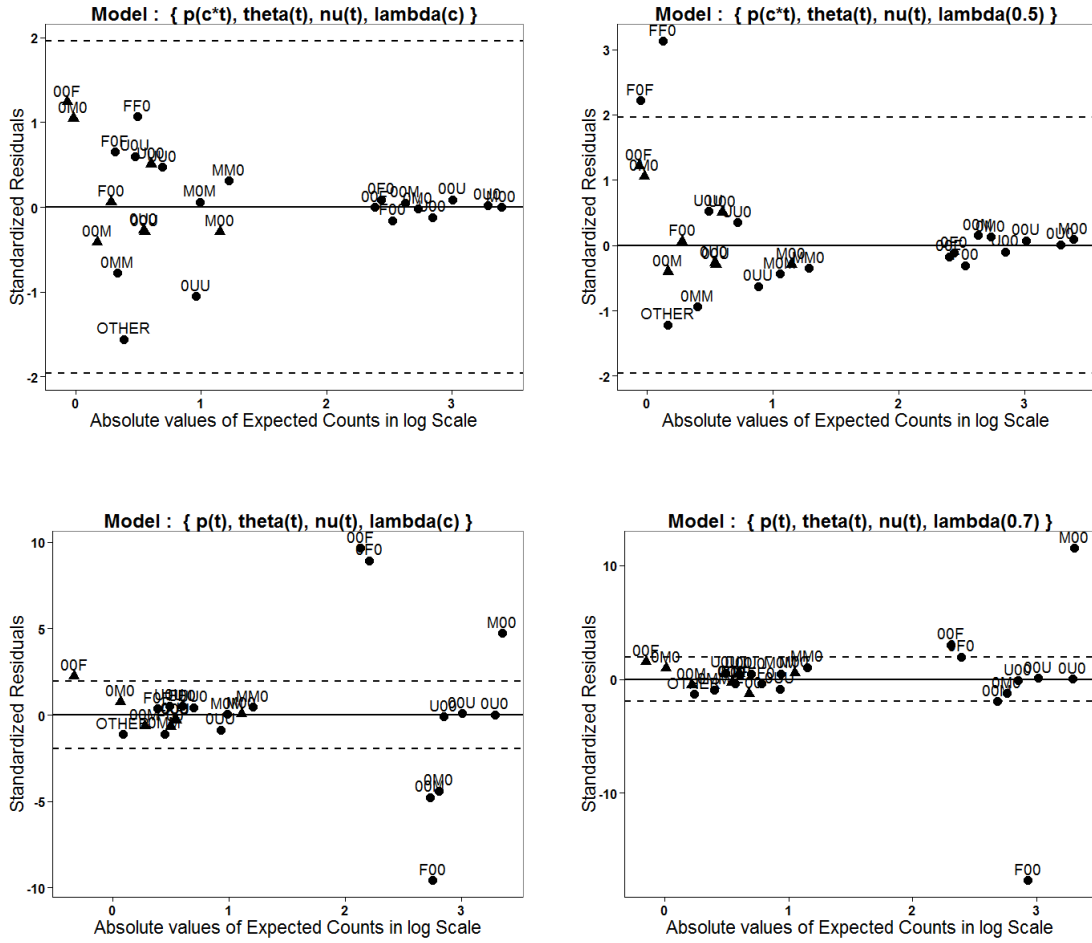
Figure 3.1: Standardized residual plots for the best four models according to AICc values. Note that the x-axis represents absolute values of the expected counts for unique capture histories. Solid triangles represent the loss of capture histories. Dashed horizontal lines are drawn at ± 1.96 to represent the region where most 95% of residuals should lie if model assumptions were met completely. A good fit occurs only in top left model.

Parameter estimates and their standard errors are given in Table 3.4 for the data in Table 3.2 using the MLE model fitting with the best fitted model $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$. According to this model fitting, estimated population abundance is $N = 381,808\ (SE = 52,232)$, estimated abundances for category M is $N_M = 279,327\ (SE = 45,638)$ and category F is $N_F = 102,481\ (SE = 33,593)$.

Table 3.4: Parameter estimation under MLE model fitting and Bayesian model fitting. Model under MLE method is $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$ and the model under Bayesian method is $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\ \lambda(c)(30,10)\}$.

Parameter	MLE model fitting		Bayesian model fitting	
	Estimate	SE	Posterior Mean	SD
p_{1M}	0.011	0.001	0.012	0.001
p_{1F}	0.004	0.001	0.005	0.001
p_{2M}	0.006	0.001	0.007	0.001
p_{2F}	0.009	0.003	0.011	0.002
p_{3M}	0.003	0.001	0.004	0.001
p_{3F}	0.006	0.002	0.007	0.002
λ_M	0.732	0.076	0.751	0.045
λ_F	0.268	0.076	0.249	0.045
θ_1	0.800	0.006	0.800	0.006
θ_2	0.293	0.008	0.294	0.008
θ_3	0.398	0.011	0.398	0.011
ν_1	0.005	0.001	0.006	0.001
ν_2	0.001	0.001	0.002	0.001
ν_3	0.003	0.001	0.004	0.001
N	381,808	52,232	352,892	42,638
N_M	279,327	45,638	264,927	35,821
N_F	102,481	33,593	87,965	19,590

3.6 Bayesian Model Development

3.6.1 Motivation for Bayesian Analysis

It is important to investigate how well the precision of the estimates can be improved when we have prior information available. We considered the best fitted model $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$ under the MLE method and the model $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(MLE)\}$ where the prior information is available for the category proportions and they are fixed at the MLE estimates produced by the best fitted model under the MLE method to compare the improvement of precision of population abundance estimates. Estimates for the parameters p_{tC}, λ_C, θ_t, ν_t and N are identical when we applied both $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$ model and $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(MLE)\}$ model, yet the second model produced improved precision of the estimates compared to first model. First model produced standard errors of 52,232, 45,638 and 33,593 respectively for the estimates of population abundance (N), abundance

of category M (N_M) and abundance of category F (N_F). Model $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(MLE)\}$ produced standard errors of 51,962, 38,011, 13,951 for the estimates of the parameters N, N_M and N_F. The improvement of the precision of the estimate of N is small for the second model. But there are around 16% and 55% improvement of the precision of the estimate of N_M and N_F.

Comparison of the standard errors using these two models shows that we can expect improved precision for the estimates of the population abundance and category abundance when we have prior information about category proportions. This was motivated to apply Bayesian methods to k-sample capture recapture experiments under partial stratification allowing loss on capture at each sample time with appropriate prior distributions for all the parameters in a model.

3.6.2 Prior Distributions

Prior distributions for the parameters were defined similar way as in Premarathna, Schwarz and Jones (2018). Because parameters p_{tC}, θ_t and ν_t takes values between 0 and 1, Beta prior distributions are appropriate for them. However we used normal prior distributions on the logit-scale for these parameters because we applied logit-link function in optimization of the likelihood. Prior distribution for λ_C was considered as Dirichlet prior because $\sum_C \lambda_C = 1$. Population abundance (N) is an unknown large value. Hence we used a Normal flat prior (Gelman et al., 2004) on the log-scale because we applied log-link function to re-parameterize N when optimizing the likelihood.

The prior specification are:

$$\text{logit}(p_{tC}) \ \sim \ N(\mu_{p_{tC}},\ \sigma^2_{p_{tC}})$$

$$\text{logit}(\theta_t) \quad \sim \ N(\mu_{\theta_t},\ \sigma^2_{\theta_t})$$

$$\text{logit}(\nu_t) \quad \sim \ N(\mu_{\nu_t},\ \sigma^2_{\nu_t})$$

$$\lambda_C \ \sim \ \text{Dirichlet}(m, n), \text{ where } m, n > 0$$

$$\log(N) \quad \sim \ N(\mu_N, \sigma^2_N)$$

Informative priors can be used based on previous data or expert opinion. Usually for an experiment with a large population, the capture probabilities and the loss on capture probabilities are small. These probabilities can be considered in the interval (0,0.1). A Beta(2,50) may be a good prior distributions to represent this information. Beta(2,50) distribution can be closely represented by the N(-4,1) distribution on the logit-scale (using trial and error method). In this situation we can use N(-4,1) distributions on the logit-scale as prior distributions for capture probabilities and loss on capture probabilities. When informative priors are not available, Beta(1,1) distribution can be used as prior distributions. Because we use priors on the logit-scale, $N(0, 1.78)$ distribution is considered as the prior distribution because it closely represents Beta(1,1) on the logit-scale.

3.6.3 Model Specification

Models specification was done similar to the models defined in Bayesian analysis section by Premarathna, Schwarz and Jones (2018). For example, consider the model denoted by $\{p(c*t)(0,0.1)\,\theta(t)(0,1)\,\nu(t)(0,0.1)\,\lambda(c)(30,10)\}$ in Table B.1 in Appendix B. Prior information is given within the parenthesis in front of each of the parameters in this model. $p(c*t)(0,0.1)$ represents capture probabilities vary by category and time and the prior belief for all the capture probabilities are withing the interval (0,0.1). In this situation Beta(2,50) is a good prior distribution for capture probabilities. Because we use Normal prior distribution on the logit-scale, $N(-4,1)$ is suitable distribution as descried in Section 3.6.2. In the model, $\theta(t)(0,1)$ represents sub-sample proportions vary by time and prior belief for all the sub-sample proportions are withing the interval (0,1). In this situation a suitable prior distribution is Beta(1,1) and we use $N(0,1.78)$ on the logit-scale as the prior distribution because it closely represents Beta(1,1). $\nu(t)(0,0.1)$ represents loss on capture proportions vary by time and prior distributions for loss on capture proportioare are similar to those are defined for capture probabilities in this model. $\lambda(c)(30,10)$ represents category proportions vary by category and prior distribution of category proportions is Dirichlet(30,10).

3.6.4 Model Selection and Goodness of Fit

We used the deviance information criterion (DIC) for Bayesian model selection procedure using posterior distributions. Posterior distribution of a given model was obtained by MCMC simulations using the Metropolis-Hasting method. The model with the smallest DIC value is considered as the best model for the data out of the given models. we considered two methods for the DIC calculation; the method using pD (Spiegelhalter et al., 2002) and the method using pv (Gelman et al., 2004).

Goodness of the fit of the selected model can be assessed by using Bayesian p-values (Brook, Catchpole and Morgan, 2000). Bayesian p-value is also called posterior predictive p-value and it is calculated using some discrepancy measure $\boldsymbol{D}$ using u number of posterior samples as follows.

$$p - value = \frac{1}{u}\sum_{j}^{u}\mathbf{1}[\boldsymbol{D}(\boldsymbol{X_j},\boldsymbol{\theta_j}) > \boldsymbol{D}(\boldsymbol{X},\boldsymbol{\theta_j})]$$

where $\boldsymbol{X}$ is the data, $\boldsymbol{\theta_j}$ is the jth posterior sample and $\boldsymbol{X_j}$ is the jth data set simulated from $\boldsymbol{\theta_j}$ using the model.

If there is no significant difference between the observed data discrepancies and simulated data discrepancies relating to the selected model, then the bayesin p-value should be close to 0.5 and it indicates that the selected model can describe the observed data well.

We considered two discrepancy statistics; deviance statistic and the Freman Tukey statistic to calculate p-values. Discrepancy calculated using Freeman-Tukey statistics (Freeman

and Tukey, 1950) has the form $\sum_i(\sqrt{O_i} - \sqrt{E_i})^2$ where O_i and E_i are observed count and expected count for capture history i for each posterior sample.

3.6.5 Example Baysian Analysis

MCMC Metropolis-Hasting method was applied for the data in Table 3.2 with 3 chains and each chain using 60,000 iterations for burn and 100,000 iterations for post-burn. MCMC output was thinned by a factor of 50. This produced a sample of 6,000 (3 chains each with 2,000 iterations) from the posterior distribution.

According to the DIC information, using two methods given in Table B.1 in Appendix B, the model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(30,10)\}$ where informative priors are considered for capture probabilities and for loss on capture probabilities is the best model as it has the minimum DIC value.

Bayesian p-value goodness of fit plots are given in Figure 3.2. The Bayesian p-values for the model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(30,10)\}$ is close to 0.5. It shows that this model fits the data well in Table 3.2.
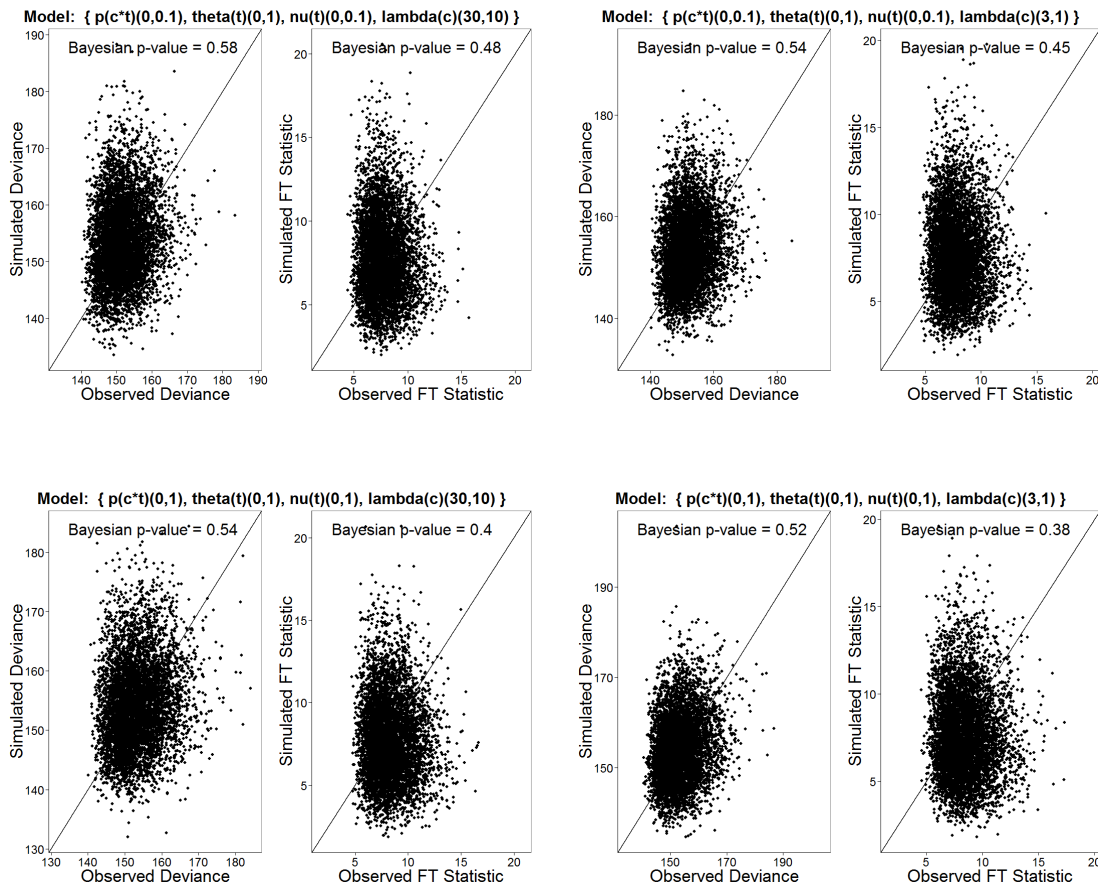
Figure 3.2: Bayesian p-value scatter plots for the first four models according to DIC criteria as in Table B.1 in Appendix B. Deviance Statistic and Freeman Tukey Statistic (FT) were considered as discrepancy functions to calculate p-values. For each of the model, 6000 samples from the posterior (3 chains each with 2000) were considered.

Convergence of the posterior distributions for all the parameters under best fitted model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(30,10)\}$ were assessed through trace plots, autocorrelation plots, and potential scale reduction plots ($\hat{R}$ plots). These plots indicate that chains mixed well. Figure B.4 in Appendix B shows the trace plots of all the beta parameters of the model. $\hat{R}$ (Rhat) values and the effective sample sizes (n.eff) for estimating the mean of the parameters are given in Table B.2 in Appendix B. Effective sample sizes are smaller for some of the parameters compared to the size of posterior samples 6000. It indicates that even though the chains mixed well, there is some autocorrelation between posterior samples even after thinning by 50.

Table B.2 in Appendix B shows the posterior distributions produced by the best fitted model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(30,10)\}$. Posterior means and standard deviations produced from this best fitted model are given in the Table 3.4. According to the Table 3.4, there is little difference between the estimates produced by Bayesian model fitting and
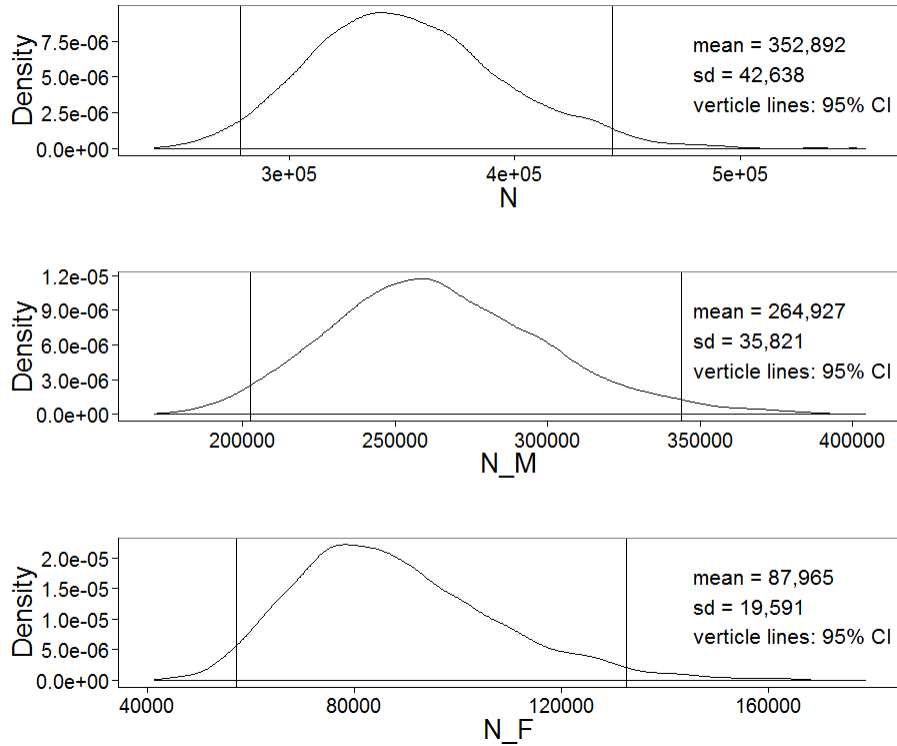
Figure 3.3: Posterior distributions for population abundance (N) and for each category total for category M (N_M) and category F (N_F) using samples of 6000 (3 chains each with 2000) from the posterior under the best model $\{p(c * t)(0, 0.1) \; \theta(t)(0, 1) \; \nu(0, 0.1)\lambda(c)(30, 10)\}$. Vertical lines are the 95% credible intervals.

MLE model fitting. But precision of the estimates of the parameters are improved under the Bayesian model fitting compared to the MLE model fitting and approximately 20%, 25% and 40% improvement of the precision of estimates of population abundance N, population category totals N_M and N_F respectively.

3.7   Simulation Studies for MLE and Bayesian Methods

Bayesian methods produced population estimates with improved precision compared to the MLE method when the simulated data in Table 3.2 were used. Because we used a simulated data for the analysis using MLE method and Bayesian method, we conducted a simulation study to test the validity and the precision of the estimates provided by this new methods. We simulated 1,000 samples (total sample size was around 8,000) for 3-sample capture-recapture study with two categories in the population (M, F). We applied the method of partial stratification and allowed loss on capture at each sample time. True parameter values used to simulate data in Table 3.2 were used to simulate the 1,000 samples. Mean parameter estimates and the standard errors for all the parameters p_{tC}, λ_C, θ_t, ν_t and N using both

the MLE best fitted model $\{p(c*t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$, and the Bayesian best fitted model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\ \lambda(c)(30,10)\}$ are given in Table 3.5. Histogram of the estimates of the parameters p_{tC}, λ_C, θ_t, ν_t and N for 1,000 simulated samples are given in Figure B.3 in Appendix B.

Table 3.5 shows that the mean estimates calculated from 1,000 simulated samples under both MLE and Bayesian methods are close to the true parameter values. That is a good indication that our methods produce unbiased estimators for all the parameters with reasonable precision. Further it shows that the Bayesian method produced improved precision for the population estimate because the standard deviation for population estimate is smaller compared to the MLE method.

Table 3.5: Simulation study considering a large population where 1,000 samples were simulated from the population. The model $\{\ p(c*t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$ was fitted to samples under the MLE method and the model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\ \lambda(c)(30,10)\}$ fitted to samples under the Bayesian method. Under both the MLE and Bayesian methods, the SE matches the actual mean SD of estimates over the simulated samples.

Parameter	True value	MLE Method		Bayesian Method	
		Mean	SE	Mean	SD
p_{1M}	0.015	0.0150	0.0020	0.0153	0.0018
p_{1F}	0.005	0.0050	0.0015	0.0063	0.0009
p_{2M}	0.009	0.0090	0.0012	0.0092	0.0011
p_{2F}	0.010	0.0101	0.0031	0.0125	0.0018
p_{3M}	0.005	0.0050	0.0007	0.0051	0.0006
p_{3F}	0.007	0.0071	0.0022	0.0088	0.0013
λ_M	0.7	0.6882	0.0828	0.7350	0.0294
λ_F	0.3	0.3117	0.0828	0.2650	0.0294
θ_1	0.8	0.8000	0.0067	0.7996	0.0068
θ_2	0.3	0.3001	0.0087	0.3000	0.0088
θ_3	0.4	0.4002	0.0115	0.3999	0.0117
ν_1	0.005	0.0049	0.0011	0.0053	0.0011
ν_2	0.001	0.0010	0.0005	0.0018	0.0005
ν_3	0.004	0.0040	0.0015	0.0049	0.0013
N	300,000	312,797	49,533	288,466	29,920

3.8 Discussion

Capture heterogeneity can lead to biased population estimates in k-sample capture-recapture experiments. When capture heterogeneity exists in experiments, we can stratify the population into different categories and then can calculate stratum specific estimates. When

complete stratification is not possible in experiments, then we can use partial stratification method in each sample time.

In this chapter we developed methods for estimating the abundance using partial stratification in k-sample capture-recapture experiments with known losses on capture allowed at each sample time. Both the MLE method and Bayesian method produced similar results for the estimates. However the Bayesian method produced estimates for population abundance with improved precision compared to MLE method, because Bayesian methods incorporate prior knowledge about the parameters in the model. We also could observe that more informative prior distributions lead to estimates with improved precision in Bayesian model fitting. Therefore prior distributions should be defined for each parameter sensibly, specially for category proportions.

Simulation studies show that our methods produce unbiased estimators for all the parameters with reasonable precision under the both MLE and Bayesian model development. Further it shows that the Bayesian method produced improved precision for the population estimate

Chapter 4

Integrated Population Modeling of Chinook Salmon with Capture-Recapture, Snorkel, Dead Recovery and Radio Telemetry Surveys

4.1 Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) are one of five Pacific salmon species broadly distributed in North American waters from California to Alaska. Chinook salmon also known as "spring" salmon because they return to some rivers earlier than other Pacific salmon species. Chinook salmon originating from the West Coast of Vancouver Island (WCVI) are a large portion of the Chinook population in North America. According to the report by Fisheries and Oceans Canada (DFO), "Chinook (*Oncorhynchus tshawytscha*) from the west coast of Vancouver Island (WCVI) are one of British Columbia's most important natural resources. These stocks have long been major contributors to First Nations, commercial troll, and sports catches, from Alaska to southern Vancouver Island" (DFO, 2012). This report also states that WCVI Chinook salmon inhabit over 100 rivers, with 60 rivers supporting population exceeding 100 spawners and spawning population sizes can range from less than 100 to more than 100,000 Chinook in rivers with major hatcheries. As reported by the DFO, 2012 science advisory report, these hatcheries contribute an average of about 90% of the annual WCVI Chinook production.

Current WCVI Chinook salmon are a population of concern. Wild WCVI Chinook salmon population has been declining over the last 15 years (DFO, 2012). Even with management actions such as hatchery supplementation, restrictions on harvest, and restriction on recreational fisheries etc., WCVI Chinook population status remains poor and stable at

low levels. However the factors affecting to the low level abundance are uncertain (DFO, 2012).

Pacific salmon migrate from ocean to their streams of origin where they spawn on gravel beds and die after spawning. Chinook salmon spend their early life in streams and swim to the ocean. Then they return to the upstream freshwater of origin to spawn when they have matured. Salmon escapement is the number of fish returning to the fresh water spawning habitat. Estimates of Pacific salmon escapement helps to enumerate spawn salmon population and used for conservation decisions such as determining fishing quotas.

Chinook salmon on the West Coast of Vancouver Island return to their spawning habitat in the fall. Peak spawning for Chinook salmon on the West Coast of Vancouver Island is usually from late September to mid-October (DFO, 2012). Depending on the rate of returning to the stream and water condition, timing of the peak can differs by a week or two across years. Burman River is one of the rivers in WCVI which has naturally spawned Chinook salmon. Chinook salmon escapements in Burman River are monitored under the 2009 Pacific Salmon Treaty between Canada-US for managing Pacific salmon. Burman River Chinook spend some time in stopover site (a pool in the lower stream near the upper limit of tidal influence) when returning to stream from the ocean, that is from saltwater to freshwater. This is because osmoregulatory transformation is needed to maintain homeostasis in freshwater. Also Chinook are waiting in stopover site until they have adequate water condition in the river to mover upstream. Stopover behaviours of Chinook in other nearby rivers in WCVI such as Gold River are similar to the Burman River. Upstream movements and spawning in these rivers are largely affected by the first significant freshet (Dunlop, 2015). Generally upstream movement from the stopover site is completed by mid-October and spawning is completed around end of October.

Figure 4.1 (Dunlop, 2015) shows the stopover site of the Burman River on the West Coast of Vancouver Island and the spawning area (Km 0 to 7.5 km).

In many salmon management and conservation decisions, the estimates of escapement are based on "area-under-the-curve" (AUC) method (Hilborn et al., 1999; Parken et al., 2003). DFO also use AUC method to estimate escapement in WCVI using snorkel surveys (count number of observable salmon in stream periodically). Under the AUC method, escapement can be estimated by dividing the area under the curve (snorkel counts are plotted over time with observer efficiency and the resulting area bounded by the curve is the area under the curve) by the residence time (length of time spent by a fish in the survey area) and multiplied by a correction factor for observer efficiency (fish visibility). This method requires counts of fish over time, survey life and observer efficiency (Hilborn et al., 1999). DOF escapement estimate in WCVI using AUC method was not reliable because mean residence time and observer efficiency are chosen subjectively (DFO 2014).

Funding was provided annually for surveys from 2009 to 2014 to improve estimates of Chinook salmon escapement in Burman River in WCVI due to the lack of certainty
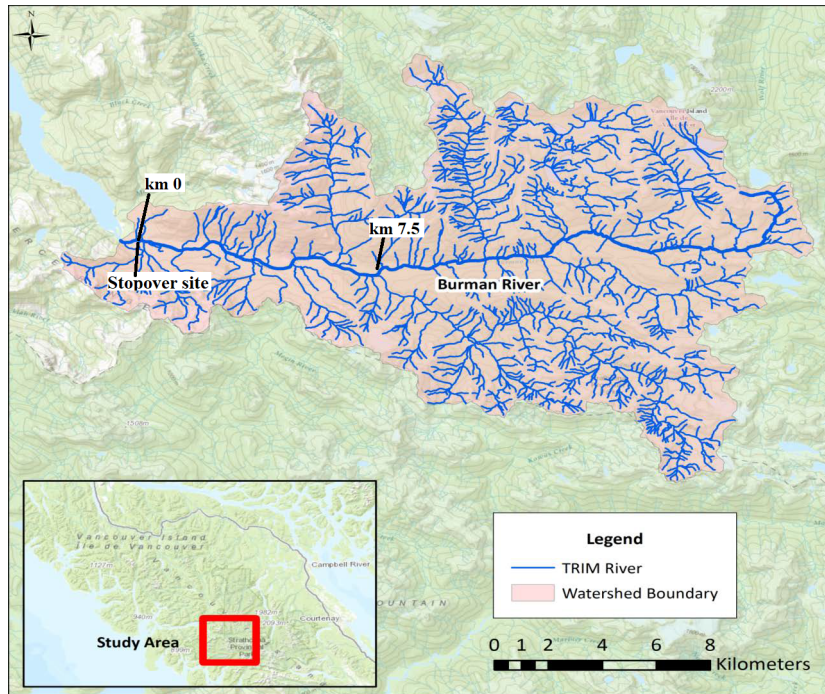
Figure 4.1: Study area and overview of Burman River on the West Coast of Vancouver Island, BC, Canada.

of estimates obtained with AUC approach (DFO 2015). Sentinel Stocks Program (SSP) under the 2009 Pacific Salmon Treaty provided funding from 2009-2013 and PSC Southern Endowment Fund supported for 2014 data. While capture-recapture survey, snorkel surveys and dead recovery (carcass) surveys were conducted every year in Burman River from 2009 to 2014, radio telemetry surveys were conducted only in 2012.

An integrated population model was developed using data from capture-recapture survey, snorkel survey and carcass survey and applied to the Burman River data collected in 2012 (Beliveau, 2016) to estimate escapement and other related parameters. A variant of Jolly-Seber method (Jolly 1965; Seber 1965) was also applied to 2012 data to estimate escapement and transition probability from the stopover pool to the spawning area and capture probabilities using capture-recapture data. The integrated population model developed for Burman River data has the advantage over the Jolly-Seber method because it provides insight on mean stopover time, mean residence time and snorkel observer efficiency (Beliveau, 2016).

In this chapter we further develop and apply the integrated population model under Bayesian approach which was developed (Beliveau, 2016) with data from capture-recapture, snorkel and carcass surveys by additionally incorporating data from radio telemetry surveys in the Burman River in 2012. This chapter mainly focuses on how the radio telemetry data provides insight on escapement, stopover times, survey life, and snorkel observer efficiency.

We present notation in Section 4.3, methods in Section 4.4 and we apply it to the Burman River data in Section 4.5.

4.2   Sampling Protocol

The study area of Burman River is located on the West Coast of the Vancouver Island, British Columbia, Canada (Figure 4.1). The Burman River watershed is 244.16 km^2 and drains into Matchlee Inlet in Nootka Sound. The main river channel is 31.3 km in length. Salmon spawning occurs in the river upto 7.5km along the river from the ocean because downstream gravels and cobbles and the channel gradient are suitable for spawning (Dunlop, 2015). In 2012, Burman River Chinook salmon surveys were conducted in September to early November. Capture-recapture surveys, snorkel surveys, dead recovery (carcass) surveys and radio telemetry surveys were conducted in 2012. Sampling protocols for these surveys are described (Dunlop, 2015) as follows (Figure 4.2).
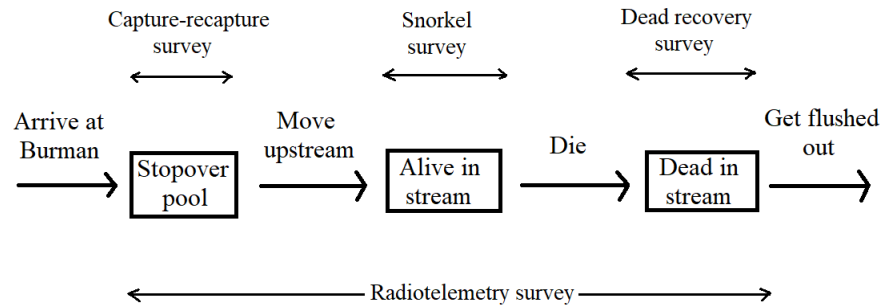
Figure 4.2: States and transitions of integrated population model and survey protocols.

Capture-Recapture Surveys

Capture-recapture surveys took place in lower river stopover pool (Figure 4.1) located near the upper limits of tidal influence. Chinook salmon started to arrive to the stopover pool from the ocean in September. Capture-recapture surveys took place two to three days per week. Fish were captured with a beach seine. Three beach-seine sets per day were used for sampling over the sampling period in an effort to keep the sampling effort roughly constant each week. Capture-recapture surveys continued until no catch in three consecutive survey days. This suggests that most fish had moved to the spawning area from the stopover pool. Chinook captured for the first time were visually examined and assigned sex, tagged and measured post-orbital hypural (POH) length to nearest 5 mm. Fish with POH length less than 500 mm were classified as 'jacks' and fish identified as jacks during the capture-recapture survey are not considered for this study. Dorsally visible 80 lb monofilament-cored

individually numbered tags were used for tagging fish. These tags were secured with a size 'J' aluminum sleeves. Further, secondary permanent marks were applied to asses tag loss.

Snorkel Surveys

As Chinook salmon moved upstream (Spawning area) from the stopover pool, snorkel surveys continued until live fish were no longer present. Snorkel surveys were carried out periodically in the Burnam River over the 0-7.5 km (Figure 4.1 and Figure 4.2). Two snorkelers recorded observations of fish as marked or unmarked and the tag colour of marked fish in each 500 m snorkel section. It is difficult to record the the tag number of marked fish because it is usually not clear enough in snorkel surveys. The visibility of the stream during the snorkel survey is also recorded. Snorkel surveys also depends on flood conditions because of visibility and safety reasons. Joint observations from two snorkelers from each 500m section of the river are available from the snorkel surveys.

Carcass Surveys

Carcass surveys are conducted in the Burman River over the 7.5 km reach until carcasses were no longer present. On the days selected for carcass surveys, crew recovered dead fish along a selected route down the stream with foot-based visual counts. Tag id, tag color, sex and POH length were recorded for recovered carcasses those were marked. We avoid double sampling of carcasses by sectioning the head of the sampled carcasses and removing the otoliths from carcasses. All carcasses present in the river in a given carcass survey day were not sampled because of inaccessibility. Some of them could have been stuck in unreachable places in the river and some of them may have been flushed out. Carcasses identified as jacks during the carcasses survey are not considered for this study.

Radio Telemetry Surveys

Some of the Chinook salmon in the Burman River were fitted with external radio tags (Lotek MCFT2-3L), 2.5 cm white visual spaghetti tags (80 lb monofilament-cored secured with a size 'J' aluminum sleeve) and also had a mutilation mark. Radio tags were fitted to adult Chinook salmon at the downstream (stopover pool) of the river. Each radio tags contained a motion sensor that transmits an identification code. Chinook movements into the spawning area were monitored with fixed radio telemetry receiver stations and by mobile surveys (surveys on foot, or occasionally by raft) using radio telemetry receivers with an antenna to identify the signals from radio-tagged fish. Radio tags were intended to emit signals differently to identify dead individuals after 12 hour period of inactivity. Fixed telemetry sites were established at the lower level and upper level of the spawning area.

Hatchery Removals

Natural production is augmented by a hatchery program at the Burman River in 2012. Unrelated to the sampling protocol, hatchery removal samples were collected in the stopover pool during the survey period and number of fish removed from the pool was recorded.

4.3 Notations

In this study, we use same notations used in integrated population model developed by Beliveau (2016) using capture-recapture, snorkel and carcass surveys. Data summary tables for that model development used an m-array (Williams et al., 2002) form where applicable. We use notation for the integrated modeling with additionally incorporating radio telemetry data as consistent with the notations used in the model developed by Beliveau (2016).

Snorkel survey data and radio telemetry data outside the combined range of dates from capture-recapture surveys and carcass surveys are discarded form this study. We denote the survey dates as follows.

$$
\begin{aligned}
K^{\text{capt}} &= \text{last day with non-zero catch occurred during the capture-recapture survey} \\
K^{\text{pool}} &= \text{last day that we assume Chinook salmon are present in the stopover pool} \\
K^{\text{carc}} &= \text{last day of carcass survey}
\end{aligned}
$$

Day one of the study is considered to be the first day of the capture-recapture survey. The last day of the study is K^{carc}.

There are 3 types of individual fish in this study; marked (under the capture-recapture survey), unmarked, and radio tagged. Even though almost all the radio tagged fish are marked in these type of studies, there can be unmarked but radio tagged fish. Data collected from capture-recapture, snorkel, carcass and radio telemetry surveys and number of hatchery removal at the Burman River are represented using the notation in Table 4.1.

Parameters related to integrated population model are defined the same way as used in Beliveau (2016) and given in Table 4.2.

Table 4.1: Notations to describe the data collected in all surveys at the Burman River in 2012.

Survey	Variable	Definition
Capture-recapture	$C_{j,s}^m$	Number of fish of sex s captured, marked and released for the first time on day j
Capture-recapture	$M_{i,j,s}^m$	Number of fish of sex s marked and released on day i and recaptured next on day j
		Continued on next page

Table 4.1 – continued from previous page

Survey	Variable	Definition
Capture-recapture	$R_{j,s}^m$	Number of marked fish of sex s released on day j
		This can be computed from $\mathbf{C}$ and $\mathbf{M}$
		$R_{j,s}^m = C_{j,s}^m + \sum_{i=1}^{j-1} M_{i,j,s}^m$
Capture-recapture	$C_{j,s}^{nRm}$	Number of fish of sex s captured, marked and released
		without radio tags for the first time on day j
		$C_{j,s}^m = C_{j,s}^{nRm} + C_{j,s}^{Rm}$
Capture-recapture	$C_{j,s}^{Rm}$	Number of fish of sex s related to capture-recapture
& Radio telemetry		survey released for the first time on day j with a radio
		tag
Capture-recapture	$M_{j,s}^R$	Number of radio tagged fish of sex s recaptured on day j
& Radio telemetry		
Radio telemetry	$C_{j,s}^{Ru}$	Number of radio tagged fish of sex s not related to
		capture-recapture survey (unmarked), released for the first
		on day j
Radio telemetry	$C_{j,s}^R$	Number of radio tagged fish of sex s released for the
		first time on day j
		$C_{j,s}^R = C_{j,s}^{Ru} + C_{j,s}^{Rm}$
Radio telemetry	$N_{j,s}^R$	Number of radio tagged fish of sex s in the stopover pool
		at midday on day j
Radio telemetry	$T_{j,s}^R$	Number of radio tagged fish of sex s that transition from
		the stopover pool to the spawning area after midday on
		day j and before midday the next day
Radio telemetry	$A_{j,s}^R$	Number of radio tagged fish of sex s alive in spawning
		area before midday on day j
Radio telemetry	$D_{j,s}^R$	Number of radio tagged fish of sex s that died after
		midday on day j and before midday the next day
Radio telemetry	$X_{j,s}^R$	Number of dead radio tagged fish of sex s present in the
		river at midday on day j
Snorkel survey	Y_j^u	Snorkel count of unmarked fish on day j
Snorkel survey	Y_j^m	Snorkel count of marked fish on day j
Snorkel survey	Y_j^R	Snorkel count of radio tagged fish on day j
Snorkel survey	ν_j	Fish visibility on day j. Visibility can be low, medium,
		high or unknown
Carcass survey	$Z_{j,s}^u$	Number of unmarked fish of sex s whose carcass recovered
		on day j

Table 4.1 – continued from previous page

Survey	Variable	Definition
Carcass survey	$Z_{i,j,s}^{m}$	Number of marked fish of sex s whose carcass recovered on day j and that were released previously on day j and not recaptured since
Carcass survey & Radio telemetry	$Z_{j,s}^{R}$	Number of radio tagged fish of sex s whose carcass recovered on day j
Hatchery removals	$H_{j,s}^{u}$	Number of unmarked fish of sex s removed by the hatchery on day j

Table 4.2: Notations for parameters related to integrated population model. Superscripts u, m, and R represents unmarked, marked and radio tagged fish respectively. Subscript s represents either males (m) or females (f).

Parameter	Definition
$B_{j,s}$	Number of fish of sex s that arrive (from the ocean) to the stopover pool after midday on day j and before midday the next day. $B_{0,s}$ is the number of individuals of sex s in the pool right before midday on day 1.
$N_{j,s}^{u}$	Number of unmarked fish of sex s in the stopover pool at midday on day j.
$N_{i,j,s}^{m}$	Number of marked fish of sex s in the stopover pool at midday on day j and were released previously on day i and not recaptured prior to day j.
$T_{j,s}^{u}$	Number of unmarked fish of sex s that transition from the stopover pool to the spawning area after midday on day j and before midday the next day.
$T_{i,j,s}^{m}$	Number of marked fish of sex s that transition from the stopover pool to the spawning area between midday on day j and midday on next day and were released previously on day i and not recaptured since.
$A_{j,s}^{u}$	Number of unmarked fish of sex s alive in spawning area before midday on day j.
$A_{i,j,s}^{m}$	Number of marked fish of sex s alive in the spawning area before midday on day j and were released previously on day i and not recaptured since.
$D_{j,s}^{u}$	Number of unmarked fish of sex s that died after midday on day j and before midday the next day.
$D_{i,j,s}^{m}$	Number of marked fish of sex s died between midday on day j and midday the next day and were released previously on day i and not recaptured since.

Table 4.2 – continued from previous page

Parameter	Definition
$X_{j,s}^u$	Number of dead unmarked fish of sex s present in the river at midday on day j.
$X_{i,j,s}^m$	Number of marked fish of sex s died and are present in the river at midday on day j and were released previously on day i and not recaptured since.
$F_{j,s}^u$	Number of dead unmarked fish of sex s got flushed out between midday on day j and midday the next day.
$F_{i,j,s}^m$	Number of dead marked fish of sex s got flushed out between midday on day j and midday the next day and were released previously on day i and not recaptured since.
$F_{j,s}^R$	Number of dead radio tagging fish of sex s that got flushed out between midday on day j and midday the next day.
$p_{j,s}^{\text{capt}}$	Capture probability of fish of sex s in the stopover pool at midday on day j
$p_{j,s}^{\text{move}}$	Probability ofr fish of sex s in the stopover pool at midday on day j to move to the spawning area before midday the next day.
$\phi_{j,s}$	Probability of fish of sex s alive in the spawning area at midday on day j to survive until midday the next day.
p_j^{flush}	Probability of dead fish in the river at midday on day j to get flushed out before midday the next day.
p^{recov}	Recovery probability of carcasses present in the river at midday on a given carcass survey day.
p_j^{snor}	Probability of fish alive in the river at midday on day j to be counted in the snorkel survey.
$\mu_{\text{low}}^{\text{snor}}$	Intercept, on the non-logit scale, used to model $\text{logit}\left(p_j^{\text{snor}}\right)$
α_v	Linear effect of fish visibility v, on the logit scale, used to model $\text{logit}\left(p_j^{\text{snor}}\right)$. α_{low} is set equal to 0.
σ_v	Standard deviation used to model logit $\left(p_j^{\text{snor}}\right)$ for a given visibility v.
Δ_j	Number of marked fish miscounted as unmarked in the snorkel survey on day j.
p^Δ	Probability of marked fish to be miscounted as unmarked in a given snorkel survey.

4.4 Integrated Population Model

4.4.1 Model Development

We present a integrated population model, specifically to estimate escapement (number of salmon migrate from the ocean to their freshwater spawning habitat in the river) of the Burman River Chinook salmon in the West Coast of Vancouver Island (WCVI) and other related parameters using data from capture-recapture survey, snorkel survey, carcass survey and radio telemetry survey. In this study we modify the integrated model developed in Beliveau (2016) with additional source of radio telemetry data. Figure 4.2 and Figure 4.3 shows the states (fish in the stopover pool, alive in the stream and dead in the stream) and transitions (arrive to the river from the ocean, move upstream, die and get flushed out) related to migration of Chinook salmon at the Burman River in WCVI. Table 4.3 gives variables, parameters and data related to the integrated population model.

Some assumptions are required to develop the integrated population model (Beliveau, 2016). We assume that adult Chinook salmon are in the ocean near to the Burman River and studies start at the time Chinook start to migrate to the river. At the first capture-recapture survey day, we assume that there are male and female ($B_{0,m}$ and $B_{0,f}$) Chinook salmon has already present in the stopover pool. We consider that $B_{j,m}$ and $B_{j,f}$ Chinook salmon newly arrive to the stopover pool from the ocean each day between midday of day $j = 1, \ldots, K^{\text{capt}} - 1$ and midday of the next day. Also we assume that Chinook arrive to the stopover pool on a particular day do not leave to the spawning area until the midday of the next day. The probability of moving from stopover pool to the spawning area and number of transitions for unmarked, marked and radio tagged fish are as defined in Table 4.2. Even though the last day of the capture-recapture studies is on K^{capt}, the last day that we assume Chinook salmon are present in the stopover pool is a arbitrary day K^{pool}. That is we allow new arrivals to the stopover pool from the ocean to move from the stopover pool to the spawning area up to the day $j = K^{\text{pool}} - 1$ but no further movement after that. We assume that all remaining Chinook in the stopover pool move to the spawning area by midday of $j = K^{\text{pool}}$. Therefore we set $B_{j,s} = 0$ for $j = K^{\text{pool}}, \ldots, K^{\text{carc}} - 1$ and $p_{K^{\text{pool}}}^{\text{move}} = 1$. The number of fish (either marked or unmarked) transition from stopover pool to the spawning area also set to zero for $j = K^{\text{pool}} + 1, \ldots, K^{\text{carc}} - 1$. Another assumption is number of fish alive in the spawning area in the day 1 of the study is equal to the number of fish alive at day 2 of the study. The probability that a fish dies before midday of the next day that is alive in day $j = 1, \ldots, K^{\text{carc}} - 1$ is $1 - \phi_{j,s}$. We assume that there are no carcasses in the midday of day 1 of the study period. We set the capture probabilities equal for each sex for the first two captures occasions as in the integrated model developed by Beliveau (2016) to avoid identifiability issues. We consider the same equality assumption for the last two capture occasions. The probability that a dead fish in the river at midday on day j gets flushed out before midday the next day for $j = 2, \ldots, K^{\text{carc}} - 1$ is p_j^{flush}. On a snorkel

Table 4.3: Latent variables and data related to states and transitions, transition probabilities, parameters relate to latent variables through data in the integrated population model

Transition	State	Latent Variable	Transition probabilities	Data	Parameters relate to latent variables through data
Arrive at Burman River		$\mathbf{B}$			
	In the stopover pool	$\mathbf{N^u}$, $\mathbf{N^m}$		$\mathbf{C^m}$, $\mathbf{M^m}$, $\mathbf{R^m}$, $\mathbf{C^R}$, $\mathbf{M^R}$, $\mathbf{N^R}$	$p^{\mathbf{capt}}$
Move upstream		$\mathbf{T^u}$, $\mathbf{T^m}$	$p^{\mathbf{move}}$	$\mathbf{T^R}$	
	Alive in the stream	$\mathbf{A^u}$, $\mathbf{A^m}$		$\mathbf{Y^u}$, $\mathbf{Y^m}$, $\mathbf{A^R}$, $\mathbf{v}$	$p^{\mathbf{snor}}$, $\mu_{\mathrm{low}}^{\mathrm{snor}}$, α, σ, Δ, p^{Δ}
Die		$\mathbf{D^u}$, $\mathbf{D^m}$	ϕ	$\mathbf{D^R}$	
	Dead in the stream	$\mathbf{X^u}$, $\mathbf{X^m}$		$\mathbf{Z^u}$, $\mathbf{Z^m}$, $\mathbf{Z^R}$, $\mathbf{X^R}$	$p^{\mathbf{recov}}$
Flushed out		$\mathbf{F^u}$, $\mathbf{F^m}$	$p^{\mathbf{flush}}$	$\mathbf{F^R}$	

survey day, alive fish are counted with probability p_j^{snor} and these counts are dependent on visibility level of the stream. Carcasses are recovered in the stream with probability p^{recov} on a carcass survey day j.

Integrated population model under Bayesian framework allows to estimate parameters for each day (including the days that a survey was not conducted) within the survey days according to the above assumptions. Once the posterior sample is obtained, we can calculate escapement and other parameters interested such as mean stopover time by arrival day to the stopover pool and mean residence time by arrival day to the spawning area for males and females, population size in the stopover pool over the time and median snorkel observer efficiency.
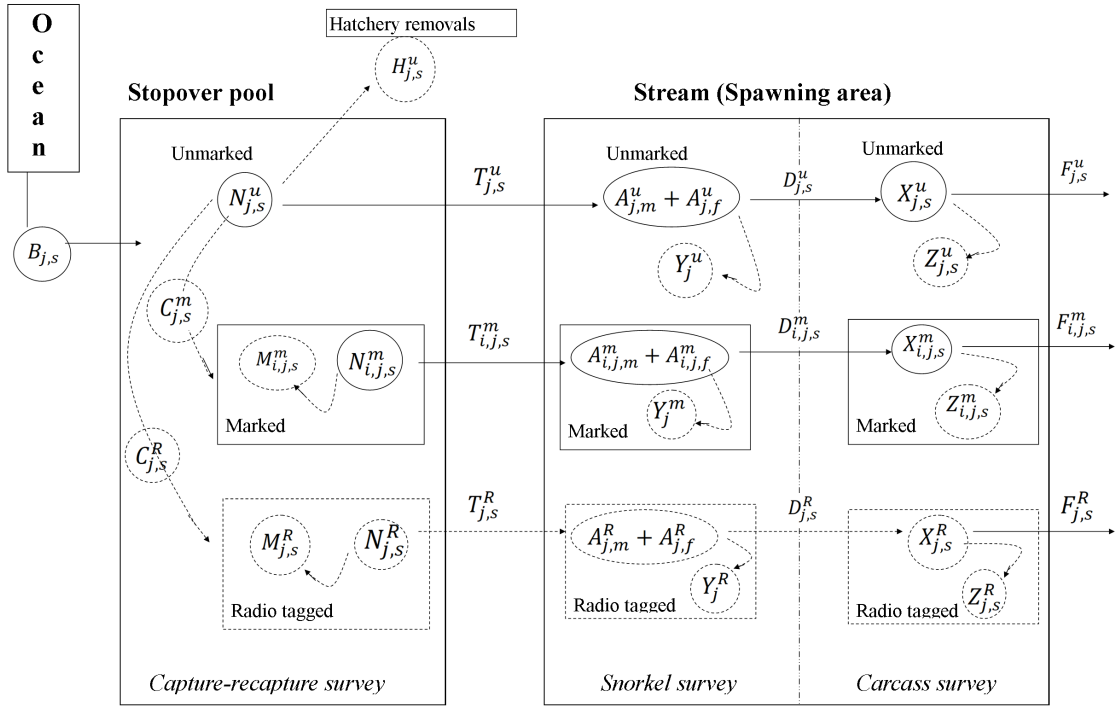
Figure 4.3: Schematic representation to link together all state equations and data. Horizontal arrows represent state transitions. Dashed lines represent observed data.

State equations for size of populations of sex s in the stopover pool for unmarked, marked and radio tagged fish at midday on day j are given by following equations. Subscript s represents either males (m) or females (f). Schematic representation to link together all of states equations and data is given in Figure 4.3.

Number of unmarked fish of sex s in the stopover pool at midday on day j

$$N_{j,s}^u = N_{j-1,s}^u + B_{j-1,s} - C_{j-1,s}^m - T_{j-1,s}^u - C_{j,s}^{Ru} - H_{j-1,s}^u \qquad ; j = 2, \ldots, k^{\text{pool}} \qquad (4.1)$$

where

$$N_{1,s}^u = B_{0,s}$$

$$C_{j,s}^m = C_{j,s}^{nRm} + C_{j,s}^{Rm}$$

$$C_{j,s}^R = C_{j,s}^{Ru} + C_{j,s}^{Rm}$$

Number of marked fish of sex s in the stopover pool at midday on day j and were released previously on day i and not recaptured prior to the day j

$$N_{i,i+1,s}^m = R_{i,s}^m - T_{i,i,s}^m \tag{4.2}$$

and

$$N_{i,j,s}^m = N_{i,j-1,s}^m - M_{i,j-1,s}^m - T_{i,j-1,s}^m \qquad ; j = i+2, \ldots, K^{\text{pool}} \tag{4.3}$$

Number of radio tagged fish in the stopover pool at midday on day j

$$N_{j,s}^R = N_{j-1,s}^R + C_{j-1,s}^R - T_{j-1,s}^R \qquad ; j = 2, \ldots, K^{\text{pool}} \tag{4.4}$$

Capture-recapture data are modeled as

- $C_{j,s}^m \sim \text{Binomial}\left(N_{j,s}^u, p_{j,s}^{\text{capt}}\right)$, for capture survey days $j \in \{1, \ldots, K^{\text{capt}}\}$

- $M_{i,j,s}^m \sim \text{Binomial}\left(N_{i,j,s}^m, p_{j,s}^{\text{capt}}\right)$, for capture survey days $j \in \{i+1, \ldots, K^{\text{capt}}\}$

Radio tagged recapture data are modeled as

- $M_{j,s}^R \sim \text{Binomial}\left(N_{j,s}^R, p_{j,s}^{\text{capt}}\right)$, for capture survey days $j \in \{2, \ldots, K^{\text{capt}}\}$

Radio tagged transition data are modeled as

- $T_{j,s}^R \sim \text{Binomial}\left(N_{j,s}^R + C_{j,s}^R, p_{j,s}^{\text{move}}\right)$, for $j = 1, \ldots, K^{\text{pool}}$

Unobservable transitions are modeled as

- $T_{j,s}^u \sim \text{Binomial}\left(N_{j,s}^u - C_{j,s}^m, p_{j,s}^{\text{move}}\right)$, for $j = 1, \ldots, K^{\text{pool}}$

- $T_{i,i,s}^m \sim \text{Binomial}\left(R_{i,s}^m, p_{i,s}^{\text{move}}\right)$

  $T_{i,j,s}^m \sim \text{Binomial}\left(N_{i,j,s}^m - M_{i,j,s}^m, p_{j,s}^{\text{move}}\right)$, for $j = i+1, \ldots, K^{\text{pool}}$

State equations for number of alive fish of sex s in the stream for unmarked, marked and radio tagged fish in the in the river at midday on day j are given my following equations. Subscript s represents either males (m) or females (f).

Number of unmarked fish alive in the stream at midday on day j

$$A^u_{j,s} = A^u_{j-1,s} + T^u_{j-1,s} - D^u_{j-1,s} \qquad ; j = 2, \ldots, K^{\text{carc}} \text{ and with } A^u_{1,s} = A^u_{2,s}$$

Number of marked fish alive in the stream at midday on day j

$$A^m_{i,j,s} = A^m_{i,j-1,s} + T^m_{i,j-1,s} - D^m_{i,j-1,s} \qquad ; j = i+1, \ldots, K^{\text{carc}}$$

Number of radio tagged fish alive in the stream at midday on day j

$$A^R_{j,s} = A^R_{j-1,s} + T^R_{j-1,s} - D^R_{j-1,s} \qquad ; j = 2, \ldots, K^{\text{carc}} \text{ and } A^R_{1,s} = 0$$

The number of fish of sex s that died after midday on day j and before midday the next day are modeled as

- $D^u_{j,s} \sim \text{Binomial}\left(A^u_{j,s} + T^u_{j,s}, (1 - \phi_{j,s})\right)$, for $j = 1, \ldots, K^{\text{carc}} - 1$

- $D^m_{i,j,s} \sim \text{Binomial}\left(A^m_{i,j,s} + T^m_{i,j,s}, (1 - \phi_{j,s})\right)$, for $j = i, \ldots, K^{\text{carc}} - 1$

- $D^R_{j,s} \sim \text{Binomial}\left(A^R_{j,s} + T^R_{j,s}, (1 - \phi_{j,s})\right)$, for $j = 1, \ldots, K^{\text{carc}} - 1$

The snorkel count of sex s on snorkel survey days on day j are modeled as

- $Y^u_j \sim \text{Binomial}\left(\left(A^u_{j,m} + A^u_{j,f} + \Delta_j\right), p^{\text{snor}}_j\right)$, for snorkel survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

- $Y^m_j \sim \text{Binomial}\left(\left(\sum_{\text{all possible } i}\left[A^m_{i,j,m} + A^m_{i,j,f}\right] - \Delta_j\right), p^{\text{snor}}_j\right)$, for snorkel survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

- $Y^R_j \sim \text{Binomial}\left(\left(A^R_{j,m} + A^R_{j,f}\right), p^{\text{snor}}\right)$, for snorkel survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

- $\text{logit}\left(p^{\text{snor}}_j\right) \sim \text{Normal}\left(\text{logit}\left(\mu^{\text{snor}}_{\text{low}}\right) + \alpha_{v_j}, \sigma^2_{v_j}\right)$, for snorkel survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

- $\Delta_j \sim \text{Binomial}\left(\sum_{\text{all possible } i}\left[N^m_{i,j,m} + N^m_{i,j,f}\right], p^{\Delta}\right)$, for snorkel survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

State equations for number of dead fish (carcasses) of sex s in the stream for unmarked, marked and radio tagged fish in the in the river at midday on day j are given my following equations. Subscript s represents either males (m) or females (f).

Number of unmarked dead fish of sex S present in the stream at midday on day j

$$X^u_{j,s} = X^u_{j-1,s} + D^u_{j-1,s} - F^u_{j-1,s} - Z^u_{j-1,s} \qquad ; j = 2, \ldots, K^{\text{carc}}$$

Number of marked dead fish of sex S present in the stream at midday on day j

$$X^m_{i,j,s} = X^m_{i,j-1,s} + D^m_{i,j-1,s} - F^m_{i,j-1,s} - Z^m_{i,j-1,s} \qquad ; j = 2, \ldots, K^{\text{carc}}$$

Number of radio tagged dead fish of sex S present in the stream at midday on day j

$$X^R_{j,s} = X^R_{j-1,s} + D^R_{j-1,s} - F^R_{j-1,s} - Z^R_{j-1,s} \qquad ; j = 2, \ldots, K^{\text{carc}}$$

The number of fish of sex s that got flushed out between midday on day j and midday the next day are modeled as

- $F^u_{j,s} \sim \text{Binomial}\left(X^u_{j,s}, p^{\text{flush}}_j\right) \qquad ; j = 2, \ldots, K^{\text{carc}} - 1$

- $F^m_{i,j,s} \sim \text{Binomial}\left(X^m_{i,j,s}, p^{\text{flush}}_j\right) \qquad ; j = 2, \ldots, K^{\text{carc}} - 1$

- $F^R_{j,s} \sim \text{Binomial}\left(X^R_{j,s}, p^{\text{flush}}_j\right) \qquad ; j = 2, \ldots, K^{\text{carc}} - 1$

The number of fish of sex s whose carcass recovered on day j are modeled as

- $Z^u_{j,s} \sim \text{Binomial}\left(X^u_{j,s}, p^{\text{recov}}\right)$, for carcasses survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

- $Z^m_{i,j,s} \sim \text{Binomial}\left(X^m_{i,j,s}, p^{\text{recov}}\right)$, for carcasses survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

- $Z^R_{j,s} \sim \text{Binomial}\left(X^R_{j,s}, p^{\text{recov}}\right)$, for carcasses survey days $j \in \{1, \ldots, K^{\text{carc}}\}$

4.4.2 Model Specification and Parameter Estimation

Data from multiple surveys are used to jointly analyze a population of interest in integrated population modeling. Under the Bayesian framework many integrated population models are possible for the data from Burman River surveys in 2012. We consider the models given in Table 4.4 to study the impact of the radio telemetry survey data on estimates on population parameters and other related quantities. Table 4.5 gives the formulas used to calculate interested quantities for each model defined in Table 4.4.

Table 4.4: Model specification with integrated population modeling for analysis of the data collected at Burman River in 2012.

Model	Description
B	Integrated population model developed by Beliveau (2016) considering data from capture-recapture, snorkel and dead recovery surveys. No radio telemetry data were considered in this model.
BC	Radio telemetry data collected in capture-recapture survey and data used in model B are considered in this model. The data used in model B is augmented with information on the number of radio tagged fish in the stopover pool and capture prior to moving upstream in model BC.
BCT	Radio telemetry data collected in transitions and data used in model BC are considered for this model. The data used in model BC is augmented with number of radio tagged fish moving from stopover pool to upstream (spawning area) in model BCT.
BCTS	Radio telemetry data collected in snorkel survey and data used in model BCT are considered in this model. The data used in model BCT is augmented with number of radio tagged fish alive in the stream and counted in snorkel survey in model BCTS.
BCTSD	Radio telemetry data collected in carcass survey and data used in model BCTS are considered in this model. The data used in model BCTS is augmented with number of radio tagged carcasses present and recovered in the stream in model BCTSD.

Table 4.5: Formulas used to estimate quantities of interest for integrated population model. Number of individuals in the stopover pool and the spawning area at day j represents 'midday' on day j. Stopover time and residence time on day j represent individuals arriving between "midday on day j" and "midday of next day". Time unit is in days. Under the assumption that movement of fish is distributed uniformly within a day, we use (d-0.5) in the mean stopover time and mean residence time.

Estimates of interest	Formula
Escapement for sex s	$\sum_{j=0}^{K^{\text{pool}}-1} B_{j,s}$
Total Escapement	$\sum_{j=0}^{K^{\text{pool}}-1} (B_{j,m} + B_{j,f})$
Total number of individuals of sex s in the stopover pool at day j	$N_{j,s}^u + \sum_{i=1}^{j} N_{i,j,s}^m + N_{j,s}^{Rum}$
Mean stopover time for individual of sex s arriving at the stopover pool on day j	$0.5 p_{j,s}^{\text{move}} + \sum_{d=2}^{K^{\text{pool}}-j} (d-0.5) \, p_{j+d-1,s}^{\text{move}} \prod_{l=j}^{j+d-2} \left(1 - p_{l,s}^{\text{move}}\right)$
Mean residence time for individual of sex s arriving at the spawning area on day j	$0.5 \left(1 - \phi_{j,s}\right) + \sum_{d=2}^{K^{\text{carc}}-j} (d-0.5) \left(1 - \phi_{j+d-1,s}\right) \prod_{l=j}^{j+d-2} \phi_{l,s}$
Total number of individuals of sex s alive in the spawning area at day j	$A_{j,s}^u + \sum_{i=1}^{j} A_{i,j,s}^m + A_{j,s}^{Rum}$
Snorkel survey observer efficiency at visibility level ν	$\text{logit}^{-1}\left(\text{logit}\left(\mu_{\text{low}}^{\text{snor}}\right) + \alpha_\nu\right)$

4.5 Analysis of Burman River 2012 Data

Burman River Chinook salmon surveys were conducted using four methods; Capture-recapture, snorkel surveys, dead recovery (carcass) and radio telemetry surveys in September to early November in 2012. Data also available for hatchery removals during this period. The time line of data collection in the Burman River is given in Figure 4.4. We did not consider data for other surveys outside of the combined range of dates from capture-recapture surveys and carcass surveys for this analysis. We considered the survey period from September 10,

2012 to October 27, 2012 corresponding to the first day of the capture-recapture survey and the last day of the carcass survey.

Figure 4.4: Time line of Chinook salmon surveys at Burman River in WCVI. Snorkel survey data and radio telemetry data outside the combined range of dates from capture-recapture surveys and carcass surveys are discarded form the analysis. Mobile radio telemetry surveys occurred every other day during survey period. Only the tagged dates and dead dates for radio tagged fish are presented in this survey time line.

A total of 1179 adult Chinook salmon (407 males and 772 females) were marked during 19 capture-recapture survey days and 348 marked fish were recaptured. Most of the recaptured fish were recaptured only once. Twenty-five snorkel surveys were conducted from September 10 and November 10, 2012. During the snorkel survey days, the minimum snorkel count reported was 7 (November 10, 2012) and the maximum snorkel count was 725 (October17, 2012). No marked Chinook salmon were observed (before September 10 or after October 27) during the snorkel survey outside the study period that was considered for the data analysis. A total of 299 adult carcasses (199 males and 115 females) were recovered during dead recovery surveys and 65 of them were marked (44 males and 21 females) during capture-recapture surveys. Out of recovered carcasses approximately 40% were unmarked males, 38% were unmarked females, 15% were marked males and 7% were marked females. Radio telemetry surveys were carried out with 108 (66 males and 42 females) radio tagged adult Chinook salmon. Fixed radio telemetry station placed in both lower and upper stream detected signals from radio tagged fish through out the survey period and mobile telemetry surveys occurred every other day during survey period. Adult Chinook salmon were removed for the hatchery on September 21 and 22, 2012. Unmarked fish were considered for hatchery

and 55 males and 25 females were removed on September 21, 2012 and 47 males and 67 females were removed on September 22, 2012.

Summary of the radio tagged data is given in Figure 4.5. Summaries of the data for capture-recapture surveys, snorkel surveys, carcass survey, and radio telemetry survey are given in Appendix C.
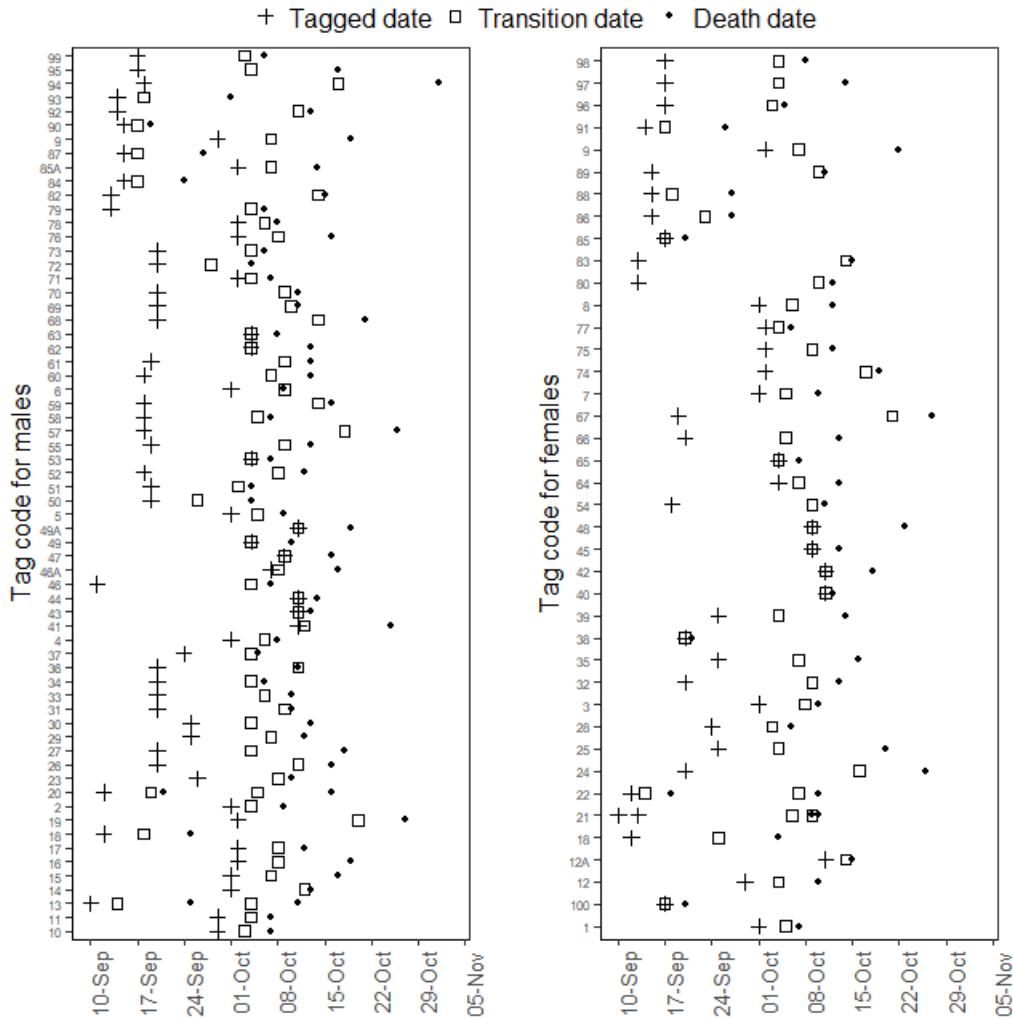

Figure 4.5: Summary of radio tagged Chinook salmon fish data at Burman River in 2012 survey.

Chinook salmon transition from the stopover pool to the stream in the Burman River is related to water discharge. However water discharge data in Burman River is not available. Mean daily discharge $(\text{m}^3\text{s}^{-1})$ at the Gold River in 2012 during the Chinook salmon migration period is given in Figure 4.6 and is believed to have similar water discharge pattern to the nearby Burman River. The first big freshet was observed on October 14, 2012. However the last day of positive capture in capture-recapture surveys was October 11, 2012.

Therefore we believe that there were Chinook salmon in the stopover pool after October 11. We assume all remaining fish were moved to upstream from stopover pool by October 15 because the big freshet was on October 14. We consider K^{pool} is October 15 in integrated population model development and set $p_{j,s}^{\text{move}} = 1$ (Beliveau, 2016) on this day.
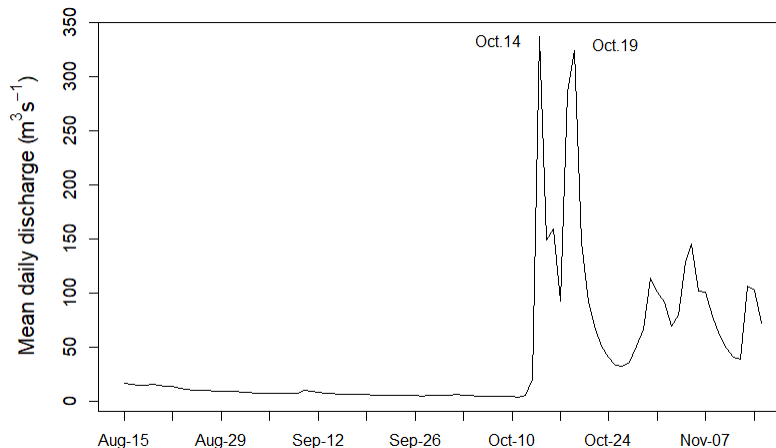

Figure 4.6: Mean daily discharge $(\text{m}^3\text{s}^{-1})$ at the Gold River in 2012 during the Chinook salmon migration period. Water discharge data is not available for Burman River. Although Gold River discharge records have not been correlated with Burman River flows, the date of the first major freshet is identical. The first big freshet was on October 14, 2012.

We fit integrated population models as defined in Table 4.4 with Bayesian approach using the JAGS software and used 2 chains each with 2 million iterations for post-burn in samples. We ran 250,000 iterations for adaptation and burn-in phase. We thinned post-burn in samples by a factor of 1000. This produced a samples of 4,000 from the posterior distribution. Results from these posterior samples were summarized with posterior mean estimates and corresponding highest probability density (HPD) credible intervals. Trace plots, potential reduction scale values (Rhat), and effective sample sizes showed that the convergence of posterior distributions are good and dependence between posterior samples among (thinned) samples were very small.

We consider sensible prior distributions for parameters (Beliveau, 2016). Uniform(0,400) prior distributions are used for $B_{j,s}$. Because $B_{j,s}$ is the number of fish of sex s that arrive to the stopover pool from the ocean after midday on day j and before midday the next day, values from the prior distributions are rounded to the nearest integer. We use Beta(1,1) distributions (i.e. Uniform(0,1) distributions) as prior distributions for various probability parameters $p_{j,s}^{\text{capt}}$, $p_{j,s}^{\text{move}}$, $\phi_{j,s}$, p_j^{flush}, p^{recov}, p_j^{snor}, $\mu_{\text{low}}^{\text{snor}}$ and p^Δ. Visibility levels considered during snorkel surveys were low, medium, high and unknown. We considered Gamma(shape=0.5, rate=0.005) as the prior distribution for visibility effect α_{medium}. This ensure that observer efficiency for medium visibility is higher than low visibility because we

set $\alpha_{\text{low}} = 1$. Moreover observer efficiency for high visibility should be higher than medium visibility. Therefore we add Gamma(shape=0.5, rate=0.005) effect to the prior on α_{medium} as the prior for α_{high}. Gamma(shape=0.5, rate=0.005) prior distribution is considered for α_{unknown}. We use Uniform(0,4) distributions for σ_ν as priors.

Table 4.6 shows escapement estimates for five models defined in Table 4.4. Model B is the integrated model developed (Beliveau, 2016) using data from capture-recapture, snorkel, and carcass surveys. The remaining models in Table 4.6 consider data from radio telemetry surveys and the data used in model B. Even though credible intervals overlap for escapement estimates for males, females and total for all five models, the credible intervals become narrower with the addition of radio telemetry data to the model B in different states of the study. Model BCTSD which use radio telemetry data collected during capture-recapture surveys, transitions, snorkel surveys and dead recovery surveys has the narrowest credible intervals for escapements of males, females and total. Table 4.6 shows the biggest change in the credible intervals (narrower) particularly in female escapement and the total escapement for the models those were integrated with radio telemetry data. It is a good indication that the radio telemetry data can produce estimates for escapement with improved precision in integrated population modeling.

Estimates of male and female Chinook salmon in the stopover pool at midday using five integrated models are given in Figure 4.7 with highest posterior density (HPD) credible intervals. In model development we assumed all Chinook salmon moved to the spawning area by October 15, 2012. Therefore number number of Chinook at the stopover pool on October 16 is zero. Models BCT, BCTS, and BCTSD have similar estimates throughout the stopover pool days and we can see some deviation from the remaining models starting around October 4 to the last day at the pool. Three models BCT, BCTS, and BCTSD use radio telemetry data for transition from stopover pool to the spawning area and Figure C.5 shows that most of the radio tagged fish moved to the spawning area after October 3. Also the number of alive fish in the spawning area given in Figure 4.10 explains the behaviour of the models in Figure 4.7 starting around October 4 to the last day at the stopover pool.

Estimates for transition probabilities for males and female Chinook salmon are given in Figure 4.8 and transition probabilities are similar for all five integrated models. As we assumed in model development that all fish moved to the spawning area by October 15, the probability of transition is 1. Credible intervals for the last three days before October 15 are wide because there is no capture-recapture data for those dates (last date of the capture-recapture survey was October 11) are available and only few radio tagged fish remain in the stopover pool and no transitions were observed for those days.

Figure 4.9 shows estimated mean stopover time for male and female Chinook salmon by arrival day to the stopover pool for five models as defined in 4.4. The model BCTSD produced narrowest credible intervals for the estimates compared to other models. Stopover time estimates are similar for all five integrated models for males. However, the estimates

Table 4.6: Escapement estimates for integrated population models defined in Table 4.4. Model 'B' does not consider data from radio telemetry survey. Model 'BCTSD' consider data from all sources including radio telemetry surveys. Formulas used to calculate escapement are given in Table 4.5. CI denotes HPD credible interval.

Model	Male Escapement			Female Escapement			Total Escapement		
	Estimate	95% CI	Width of CI	Estimate	95% CI	Width of CI	Estimate	95% CI	Width of CI
B	2454	2208-2778	570	3110	2490-4073	1583	5564	4924-6600	1676
BC	2460	2175-2713	538	2967	2386-3481	1095	5427	4857-6047	1190
BCT	2344	2129-2594	465	2882	2457-3348	891	5226	4818-5815	997
BCTS	2541	2279-2820	541	3014	2530-3538	1008	5555	5060-6098	1038
BCTSD	2499	2224-2782	558	2713	2284-3134	850	5212	4757-5689	932

from the models vary considerable at the start of the survey period (roughly between September 10, 2012 to September 19, 2012) for females. This is explained by the transition probabilities for females given in Figure 4.8. Transition probabilities are also different for females at start because only few female radio tagged fish were available around the first week and hence almost no transitions during that time.

The number of alive Chinook salmon in the the stream estimated by five models are given in Figure 4.10. This figure shows all five models give similar estimates in most of the days during the study period except around October 4 to October 16. Deviations during this period are given by models BCTS and BCTSD because most of radio tagged fish moved to spawning area from the stopover pool during this period.

Mean residence times are given in Figure 4.11 for five integrated models by arrival day to the spawning area. Both models BCTS and BCTSD have different estimates compared to the other models because these two models use radio telemetry data in transitions and snorkel survey. The model BCTSD has different estimates for mean residence time specially for females. Probability of fish alive in the spawning area is used to calculated the mean residence time. Since the model BCTSD uses information on number of radio tagged fish alive and die in each survey day in the stream, probability of fish alive at each day can be estimates with improved precision compared to the remaining models. Therefore the model BCTSD can produce different estimates for mean residence time compared to other models. Residence time is one of the important components used in AUC method in DFO analysis.

Observer efficiency estimates in the snorkel surveys and recovery probability in carcass surveys for all models are given with HPD credible intervals in Table 4.7. Observer efficiency estimates produced by models B, BC, and BCT are almost similar. While the two models BCTS and BCTSD produced similar estimates observer efficiency, these is big change (estimates and credible intervals are considerably smaller than the other three models) compared to the remaining three models. The reason to have this big difference is that the number of alive fish and snorkel counts for radio tagged fish are considered in both models BCTS and BCTSD.

Estimates for carcasses recover probabilities are given in the last row of Table 4.7. These estimates are very much the same for all integrated population models.

Table 4.7: Observer effecency estimates in the snorkels survey and recovery probabilities in carcass survey for integrated population models defined in Table 4.4. CI denotes HPD credible interval.

Observer Efficiency

Visibility level	Model B		Model BC		Model BCT		Model BCTS		Model BCTSD	
	Est	95% CI	Est	95% CI	Est	95% CI	Est	95% CI	Est	95% CI
Low	0.33	0.01-0.73	0.31	0.01-0.68	0.33	0.02-0.72	0.24	0.02-0.48	0.24	0.03-0.45
Medium	0.65	0.26-0.98	0.58	0.21-0.87	0.64	0.28-0.95	0.38	0.20-0.55	0.38	0.21-0.53
High	0.83	0.64-0.99	0.70	0.52-0.92	0.76	0.59-0.98	0.43	0.28-0.59	0.43	0.28-0.58
Unknown	0.86	0.46-1.00	0.92	0.66-1.00	0.91	0.57-1.00	0.61	0.26-0.97	0.59	0.23-0.94

|	Model B		Model BC		Model BCT		Model BCTS		Model BCTSD	
	Est	95% CI	Est	95% CI	Est	95% CI	Est	95% CI	Est	95% CI
Recovery probability	0.11	0.06-0.19	0.10	0.06-0.15	0.12	0.06-0.19		0.06-0.18	0.13	0.08-0.18
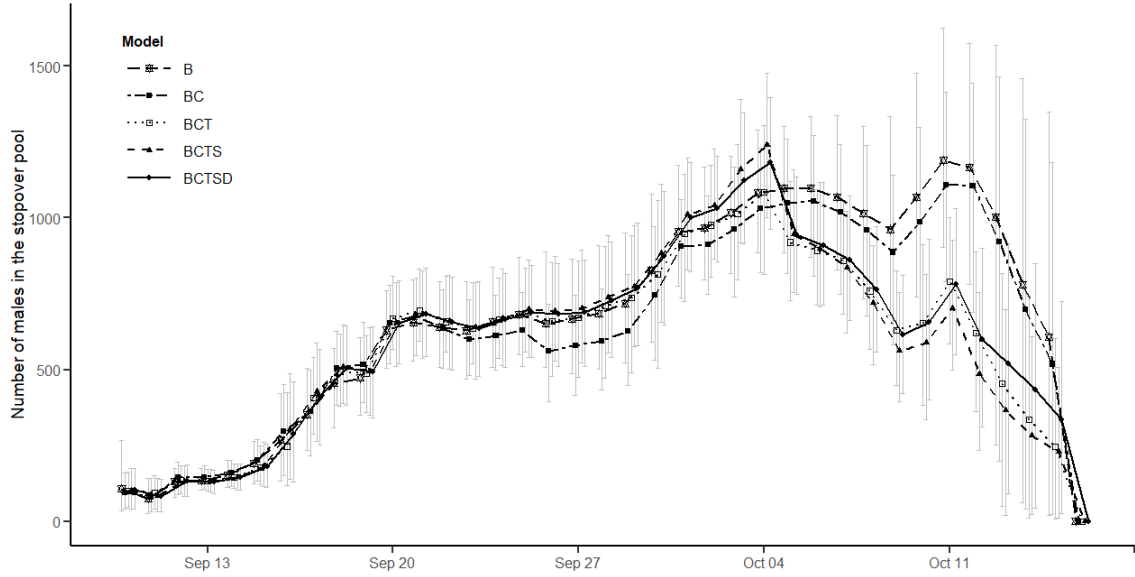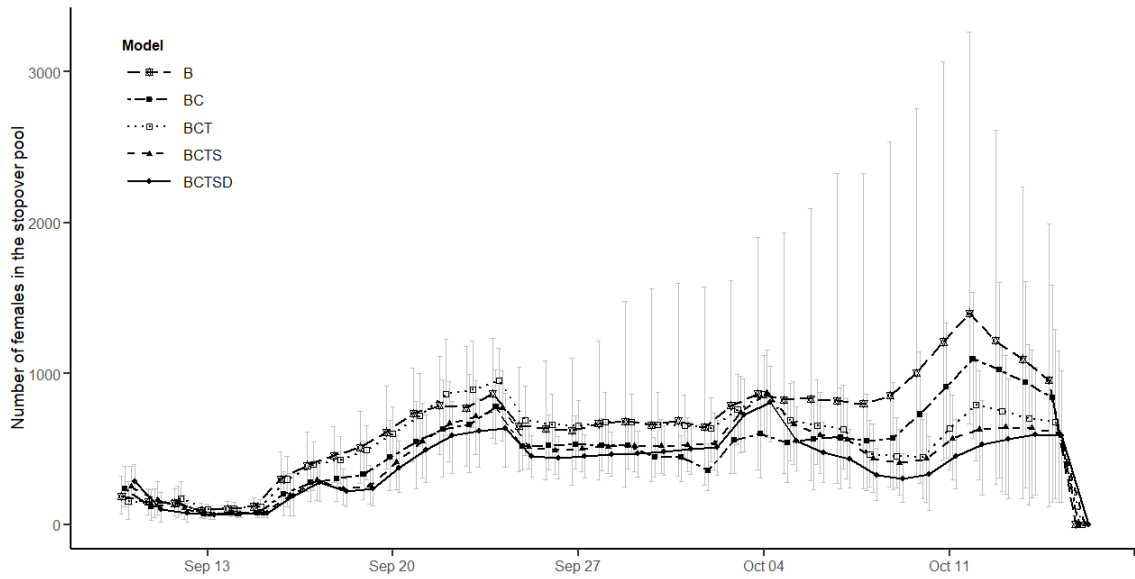
Figure 4.7: Estimates of the population size for males (graph a) and females (graph b) Chinook salmon in the stopover pool based on five models defined in Table 4.4 and formulas defined in Table 4.5. 95% HPD credible intervals are given for selected days for five models.
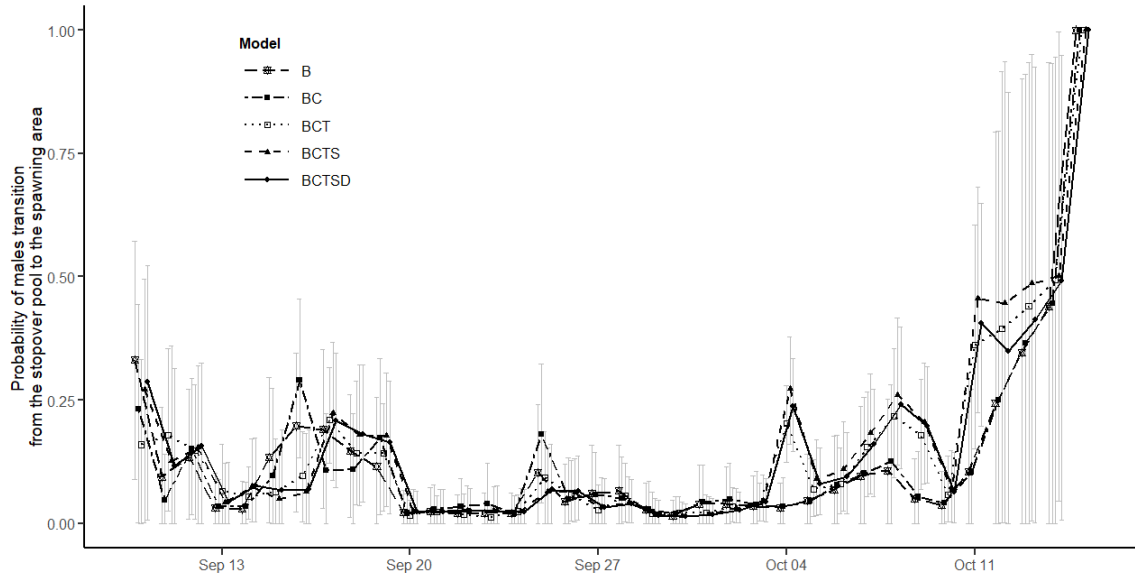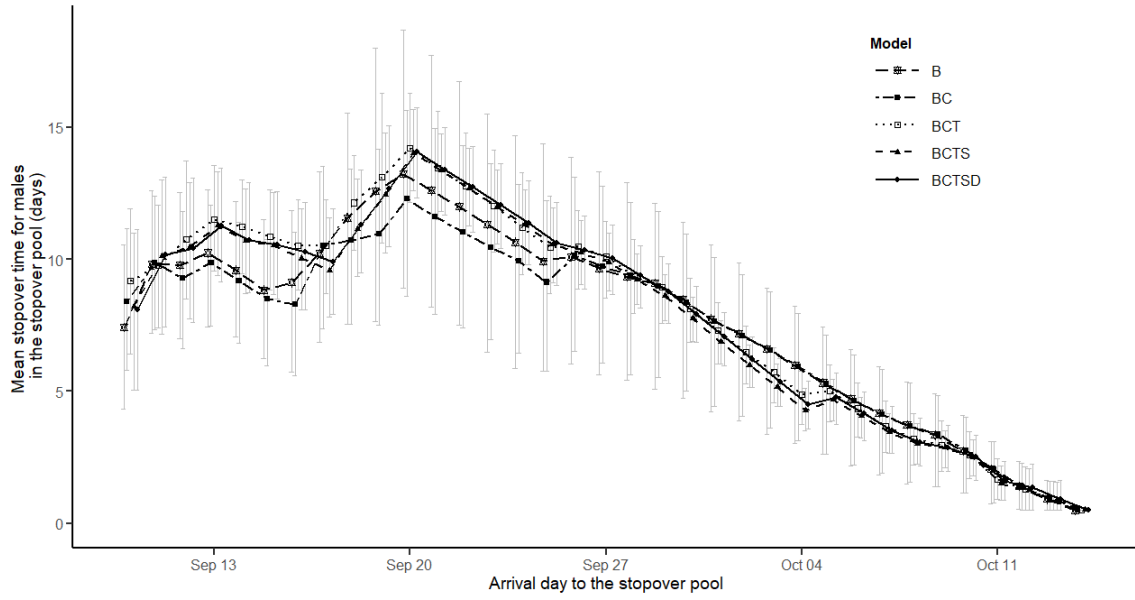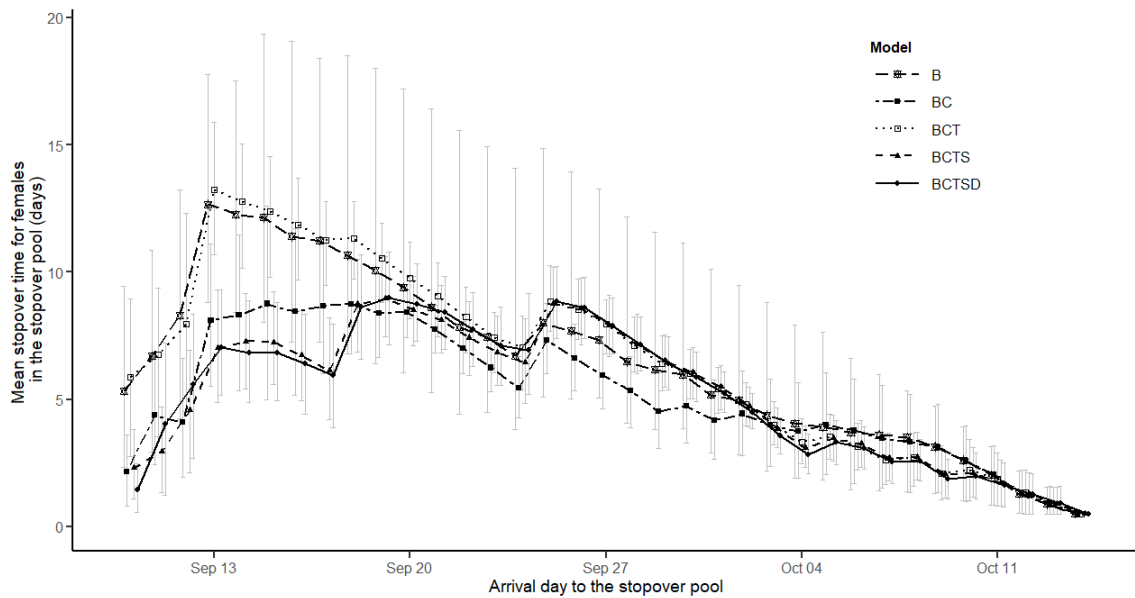
(a)
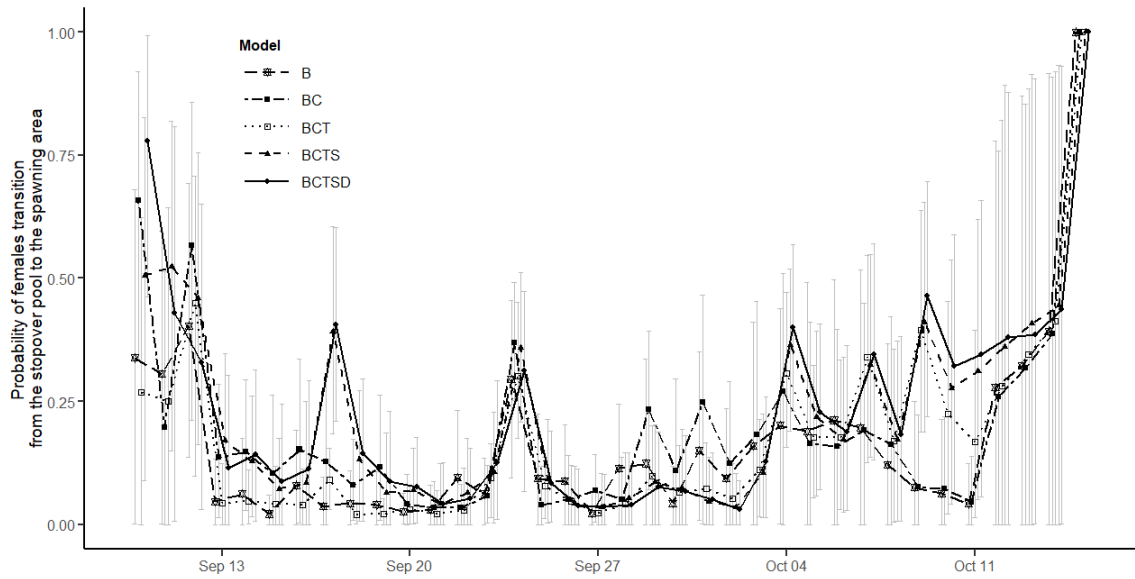
(b)

Figure 4.8: Estimates of transition probabilities from stopover pool to the spawning area for males (graph a) and females (graph b) Chinook salmon based on five models defined in Table 4.4. 95% HPD credible intervals are given for selected days for five models.
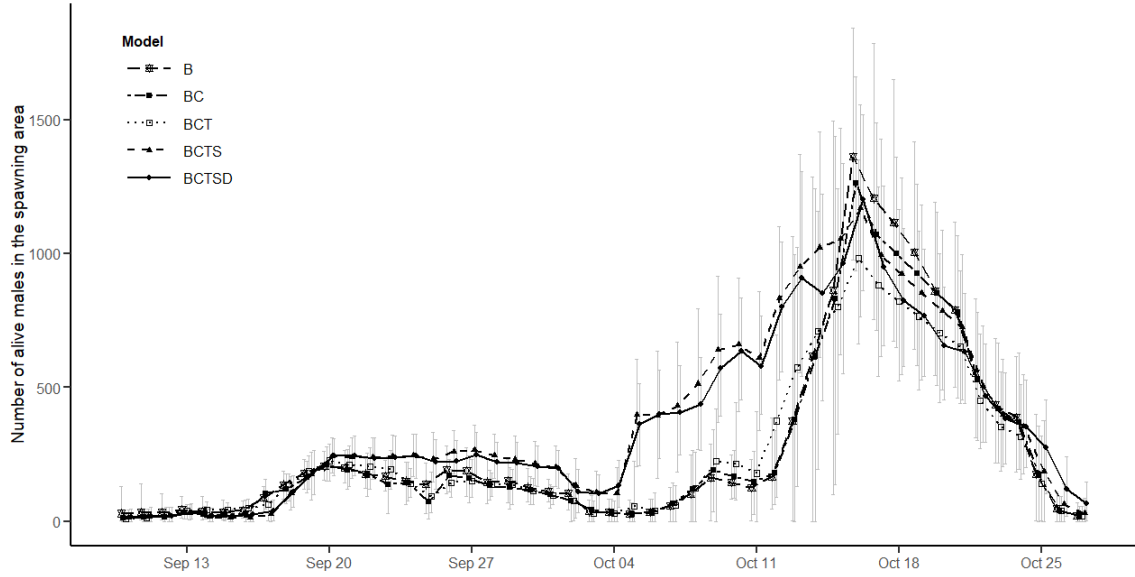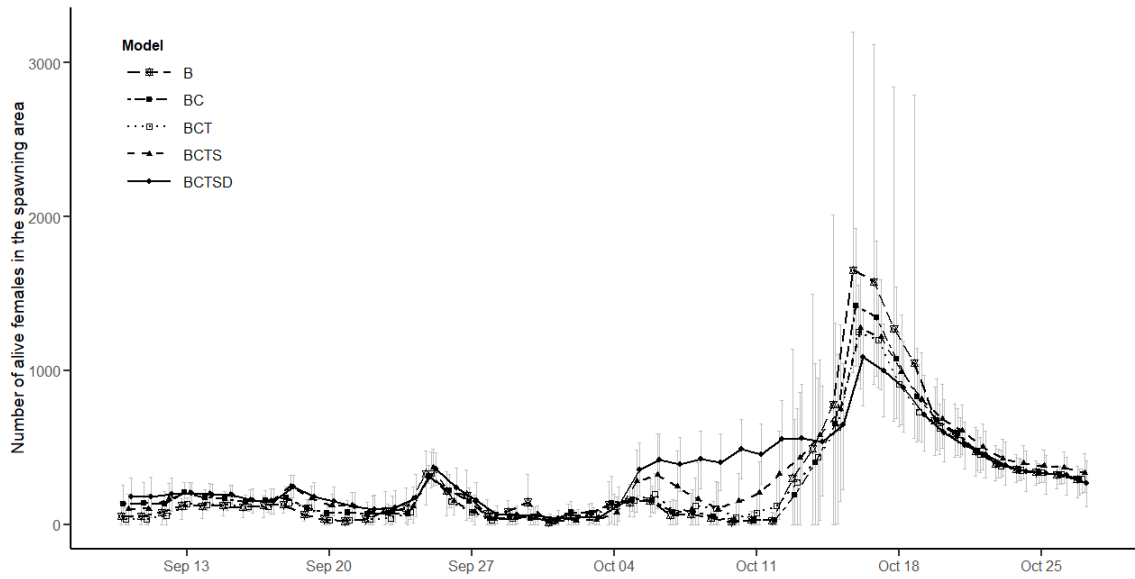
(a)

(b)

Figure 4.9: Estimates of stopover times for males (graph a) and females (graph b) Chinook salmon by arrival day to the stopover pool based on five models defined in Table 4.4 and formulas defined in Table 4.5. 95% HPD credible intervals are given for selected days for five models.
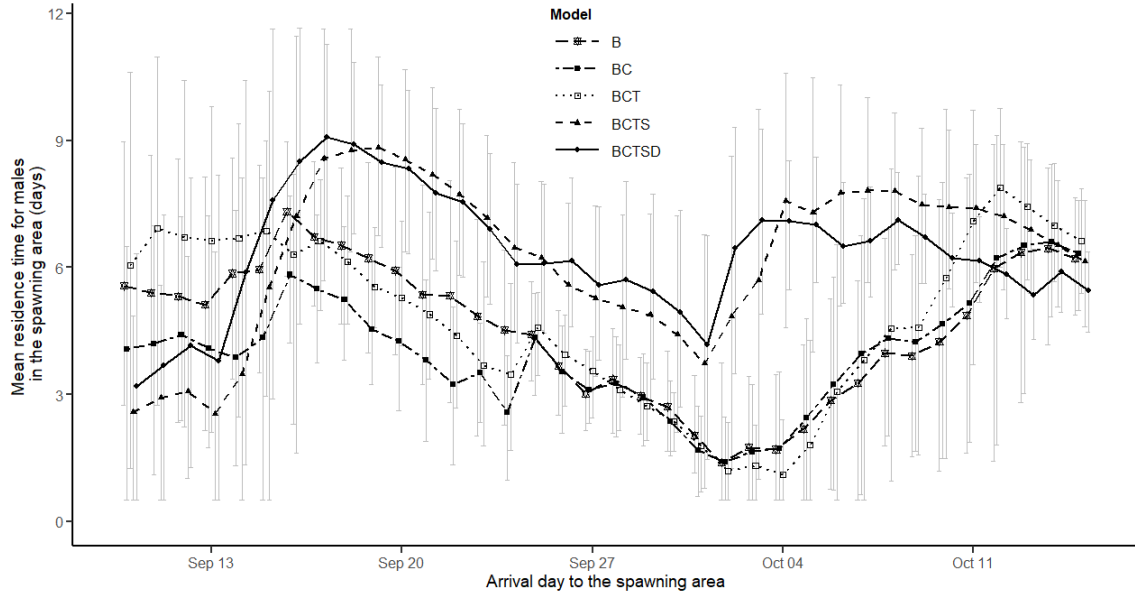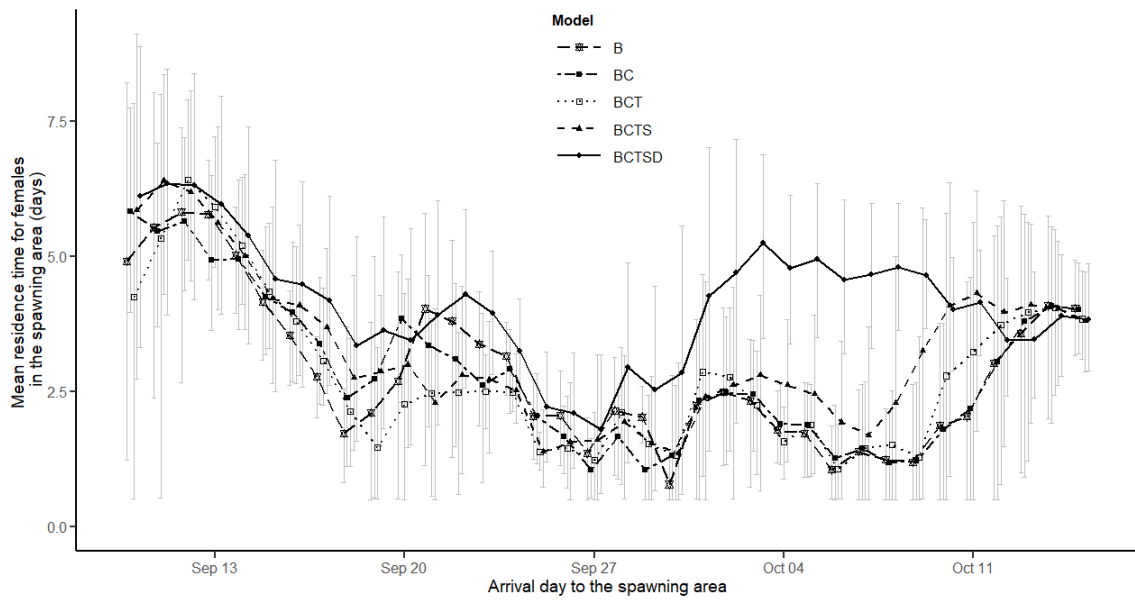
(a)

(b)

Figure 4.10: Estimates of the alive population size for males (graph a) and females (graph b) Chinook salmon in the spawning area based on five models defined in Table 4.4 and formulas defined in Table 4.5. 95% HPD credible intervals are given for selected days for five models.

(a)

(b)

Figure 4.11: Estimates of residence times for males (graph a) and females (graph b) Chinook salmon by arrival day to the spawning area based on five models defined in Table 4.4 and formulas defined in Table 4.5. 95% HPD credible intervals are given for selected days for five models.

Goodness of the fit of the integrated population model can be assessed by using Bayesian p-values (Brook, Catchpole and Morgan, 2000). A Bayesian p-value is calculated using some discrepancy measure $\boldsymbol{D}$ using n posterior samples as follows.

$$p - value = \frac{1}{n} \sum_{j}^{n} \mathbf{1}[\boldsymbol{D}(\boldsymbol{X_j}, \boldsymbol{\theta_j}) > \boldsymbol{D}(\boldsymbol{X}, \boldsymbol{\theta_j})]$$

where $\boldsymbol{X}$ is the data, $\boldsymbol{\theta_j}$ is the jth posterior sample and $\boldsymbol{X_j}$ is the jth data set simulated from $\boldsymbol{\theta_j}$ using the model.

We considered number of marked fish of sex s released in capture-recapture survey as the discrepancy measure using Freeman-Tukey statistics (Freeman and Tukey, 1950) which has the form $(\sqrt{O} - \sqrt{E})^2$ where O and E are observed count and expected count for each posterior sample. The discrepancy statistic in this case is

$$\boldsymbol{D}(\boldsymbol{X}, \boldsymbol{\theta_j}) = \left(\sqrt{R_{j,s}} - \sqrt{\left(N_{j,s}^u + \sum_{i=1}^{j} N.i, j, s^m + N_{j,s}^{Rum} \right) p_{j,s}^{\text{capt}}} \right)^2$$

for possible capture-recapture days i. We used $u = 4,000$ posterior samples to calculate p-values for each model. If there is no significant difference between the observed data discrepancies and simulated data discrepancies relating to the selected model, then the Bayesin p-value should be close to 0.5.
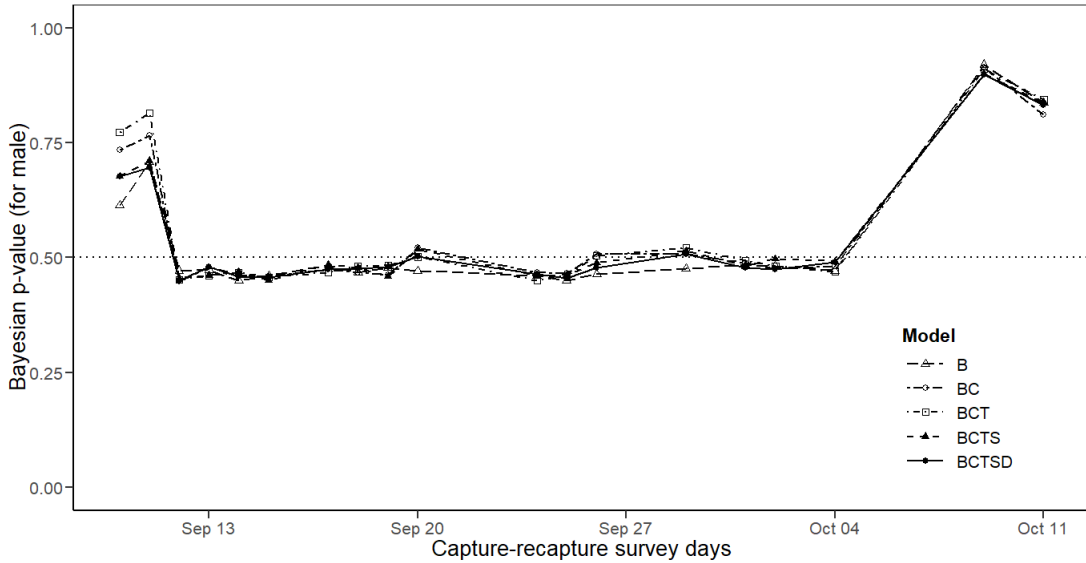

Figure 4.12: Bayesian p-values using Freeman Tukey statistics for the assessment of integrated population models defined in Table 4.4. Bayesian p-values are calculated at each capture-recapture survey day considering the number of male Chinook salmon.

Bayesian p-values for males and females for each capture-recapture day for all the models defined in Table 4.4 are given in Figure 4.12 and Figure 4.13. All p-values for all the models

are close to 0.5 except for first two survey days and the last two survey days of the capture-recapture survey. We assumed that the capture probabilities for the first two days are same and those are same for the last two days. However the larger p-values at these days suggest that those assumption might not be suitable in model development. However average p-value considering both males and females is close to 0.5 for each integrated population model. This suggest that each model fits well to the Burman River data.
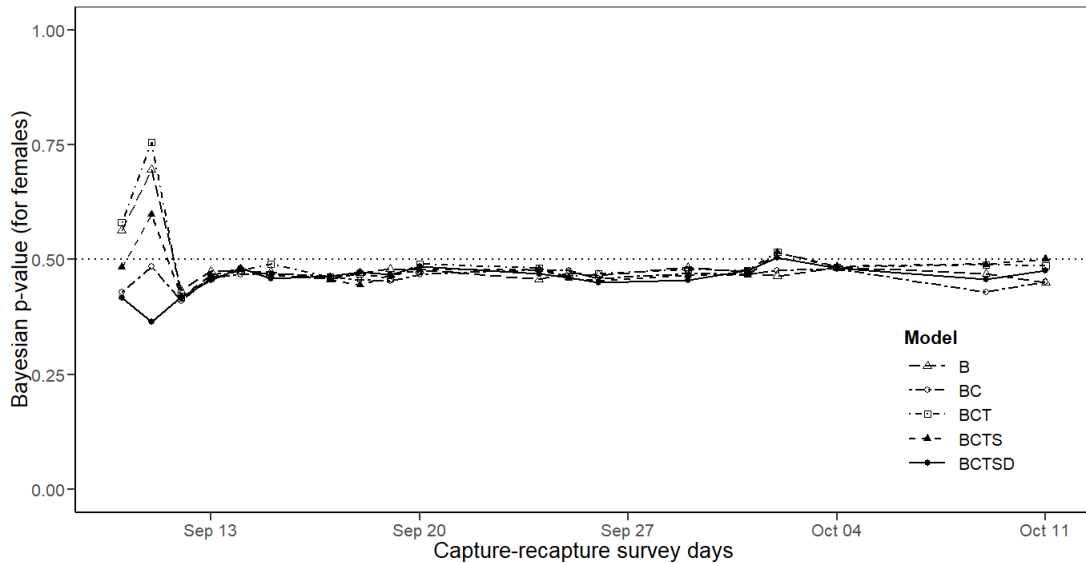

Figure 4.13: Bayesian p-values using Freeman Tukey statistics for the assessment of integrated population models defined in Table 4.4. Bayesian p-values are calculated at each capture-recapture survey day considering the number of female Chinook salmon.

4.6 Discussion

In this study, we developed and applied integrated population models using Bayesian approach using data from capture-recapture, snorkel, carcasses and radio telemetry surveys and hatchery removal data collected in the Burman River in the West Coast of Vancouver Island (WCVI) in 2012. A sequence of integrated models obtained by adding radio telemetry data sources to model one at a time showed we can obtain better estimates (with narrower credible intervals) for escapements, mean stopover times, mean residence time and number of alive Chinook population in the stream when radio telemetry data available for all surveys. This is because radio telemetry survey can provide very high detectability throughout the survey period. That is, once a fish is radio tagged at the stopover pool, its movement can be determined until die in the spawning area. Escapements estimates show that there is high impact of radio telemetry data in the stopover pool and transition from stopover pool to the spawning area because the model BCT provide estimates with narrower credible

intervals. Estimates on observer efficiency show that radio telemetry data on snorkel survey cause high impact on estimates. However there is not much impact of radio telemetry data in carcass survey because estimates for carcass recovery probabilities for all integrated models are almost the same. We can conclude that the integrated population model with radio telemetry data used in the stopover pool, transitions, and snorkel survey has a big impact on estimates. The reason for low impact of radio telemetry data in carcass survey is that the number of radio tagged carcasses recovered were fairly low. The number of radio tagged fish used for radio telemetry survey is small compared to other surveys. One can suggest that we can have estimates with improved precision if we can have a larger sample size in radio telemetry survey. However the fixed and operational cost for radio telemetry surveys are really high compared to other surveys and therefore larger sample sizes are not available in radio telemetry survey.

In this study we did not consider tag loss and loss on capture. Also in this study, we did not consider hatchery removals of marked fish because there were no marked fish in hatchery removals in 2012 in the Burman River data.

Chinook salmon surveys (capture-recapture, snorkel, carcass recovery) were conducted in Burman River from 2009 to 2014. Integrated population model incorporating radio telemetry surveys can only be used for 2012 because radio telemetry surveys were employed only in 2012. Chinook salmon surveys were conducted in 2014 in the Conuma River that is a nearby river to the Burman River in WCVI. Radio telemetry surveys also conducted in Conuma River (Dunlop, 2015). In future work, we can apply integrated population model incorporating radio telemetry data to Conuma River survey data in 2014.

Chapter 5

Summary

In this thesis we have considered three research projects and developed new methods for estimating abundance of fish population and other related parameters in the study. New methods developed for the first two projects are given in Chapter 2 and Chapter 3 in this thesis. These new methods are developed using capture-recapture surveys. New methods developed for the last project is given in Chapter 4 of this thesis. In that chapter we discuss development of new methods using integrated population modeling with a capture-recapture survey, a snorkel survey, a dead recovery survey and a radio telemetry survey.

In Chapter 2, we present new methods using partial stratification in two-sample capture-recapture experiments for closed populations (number of individuals in the population do not change throughout the study period). Capture heterogeneity (i.e. animals in different strata have different capture probabilities) can cause bias in estimates of abundance in two-sample capture-recapture experiments for closed populations. Capture heterogeneity is often related to observable fixed characteristics of the animals such as sex. If this information can be observed for each handled animal at both sample occasions, then it is straightforward to stratify (e.g. by sex) and obtain stratum-specific estimates. However in many experiments full stratification at each sample occasion might not be possible because it is difficult to stratify all captured animals. In that case, partial stratification at each sample occasion is considered in capture-recapture experiments. For these types of experiment, we developed new methods to estimate population abundance using maximum likelihood estimation, a Bayesian method and also using conditional likelihood when individual covariates are available. We apply these methods to estimate the abundance of walleye in Mille Lacs Lake, MN, USA. Both Bayesian and MLE methods produced similar estimates using walleye data. However Bayesian models produced estimates with improved precision for population abundance and category totals over the MLE method for walleye data. When the individual lengths are considered for the walleye data, the conditional likelihood method produced estimates for category proportions and sub-sample proportions that were quite similar to the MLE and Bayesian methods. However the estimates of population abundance under the conditional likelihood method were higher with worse precision compared to the

previous two methods because the best fitted covariate model was highly parameterized and there is individual capture heterogeneity at each sample time.

Further we developed optimal allocation of sampling effort for given cost. In a partial stratified two-sample capture-recapture study, there is a cost to capturing an animal at each sample occasion, a cost to identify the category of the captured animal in the sub-samples, and also a fixed cost regardless of the sample size. If there is a fixed amount of funds to be used in the study, then the objective is to find the optimal number of animals to capture at both sample occasions and the optimal sizes of the sub-samples to be categorized so that the variance of the estimated population abundance is minimized. Optimal allocation examples show that there are many optimal solutions are available.

We performed simulation studies with the models developed under the MLE and Bayesian methods. Simulation studies show that our models fit well to the data produced by partial stratification in two-sample capture-recapture experiments. Simulation studies also show that both MLE and Bayesian model development methods equally perform in estimating population abundance under large population sizes and small population sizes. Bayesian models produced estimates with improved precision for population abundance a when informative priors are used in model fitting.

Chapter 3 is an extension of the models developed in Chapter 2. Now we consider partial stratification of capture-recapture experiments in k-samples ($k \geq 2$) times. In Chapter 3, we developed new methods using partial stratification in k-sample capture-recapture experiments of a closed population with known losses on capture to estimate abundance. Loss on capture occurs when the captured animal is not available for successive sampling due to various reasons (e.g. animal may die when capturing or removed from the population for further investigation). In this study we allow the experiment to be carried out in successive sample times ($k \geq 2$). The population may consist of two or more non-overlapping categories and capture probabilities may vary between categories and also between sample times. We present the new methods using maximum likelihood method and using a Bayesian method for a large population. Simulated data was used to illustrate the new methods presented in this study. Simulation studies show that our model developments are good for data collected from partial stratification two-sample capture-recapture experiments and our methods produce unbiased estimators for all the parameters with reasonable precision under the both MLE and Bayesian model development. Further, it shows that the Bayesian method produced improved precision for the population estimate when informative priors are used.

In Chapter 4, we developed integrated population models under Bayesian approach using data from capture-recapture surveys, snorkel surveys, carcass surveys and radio telemetry surveys. We applied these models to the Burman River data collected in 2012 to estimate escapement (number of fish migrate from the ocean to the spawning ground in the upper levels of the river) of Chinook salmon and other related parameters. We also focused on

how the radio telemetry data provides insight on escapement, stopover times, survey life, and snorkel observer efficiency. A sequence of integrated models obtained by adding radio telemetry data sources to model one at a time showed we can obtain improved estimates (with narrower credible intervals) for escapements, mean stopover times, mean residence time and number of alive Chinook population in the stream when radio telemetry data available for all surveys. Escapements estimates show that radio telemetry data collected in the stopover pool and transition from stopover pool to the spawning area cause high impact on estimates because these radio tag data produced estimates with improved precision. Estimates on observer efficiency show that radio telemetry data on snorkel survey produce estimates with improved precision. We can conclude that the integrated population model with radio telemetry data used in the stopover pool, transitions, and snorkel survey produced estimates with improved precision. However adding radio tagged carcass survey data to integrated population model does not provide any improvement to the precision of the estimates. This is because radio tagged carcasses recovered were fairly low compared to the total number of dead radio tagged individuals available at a given day.

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Appendix A

Supplementary Materials for Chapter 2: Partial Stratification in Two-sample Capture-Recapture Experiments

A.1 Sampling Protocol

Consider an animal population that can be divided into non-overlapping categories where the stratification variable has been determined. At the first sample occasion a random sample of size n_1 is captured. Then a sub-sample of size n_1^* is selected from n_1 and the stratum is determined for all animals in the sub-sample. All captured animals are marked, usually with a unique tag number. All captured animals are released to the population after marking. Again some time later, another sample of animals of size n_2 is captured randomly from the population. The animals captured at the second sample occasion contains animals captured and marked at the first occasion (some of them might be stratified and some of them might not be stratified) as well as the animals not captured at the first occasion. From animals not previously captured, a sub-sample of size n_2^* is selected and the stratum determined. A pictorial view of the sampling protocol is given in Figure A.1.
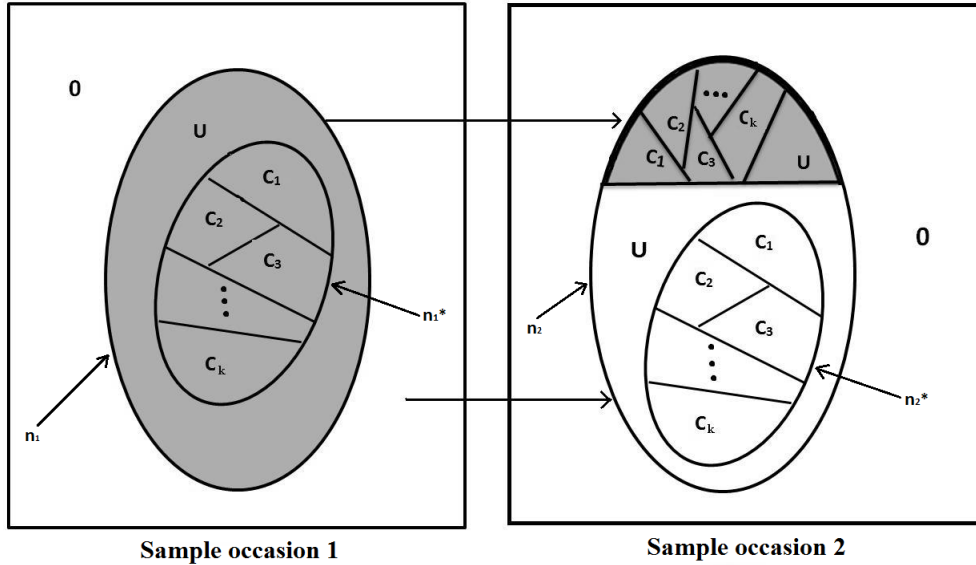
Figure A.1: Sampling protocol: Partial stratification in two-sample capture-recapture experiments. The shaded areas represent marked animals. some of the marked animals in the sample occasion 1 are stratified into strata $C_1, \ldots, C_k$; some are left unstratified (U). A similar representation is used at sample occasion 2.

A.2   MLE Approach

A.2.1   Identify Poor Model Fit and Violation of Assumptions Through Residual Plots

The assumptions of partial stratification in two-sample capture-recapture experiments might be violated in an experiment. In such cases it is important to know whether the model assessment procedures can identify model violations through standardized residual plots and goodness of fit plots. We considered the following four cases for identifying model violation of assumptions through standardized residual plots.

(a)   Heterogeneity in catchability among the animals within each category
(b)   Failure of non-death assumption
(c)   Entering of new animals to the sampled population between the first and second time period
(d)   Fit a model forcing the capture probabilities to be equal when actually they vary between categories and/or occasion

Each of these cases was tested using simulated data. The violation of assumptions given in the first three cases cannot be identified by residual plot or goodness of fit plots because the generated capture histories do not have any information attached regarding those failures of assumptions. However the residual plots revealed that the violation given by the last case can be well identified.

To test the last case given above, we simulated data where the capture probabilities varied between categories and sample occasions, and fitted a model where they are forced to be equal. We considered the following information in Table A.1 for data generation when there are two categories in the population, M and F.

Table A.1: Data generation information to test model fit

Parameter	Value
p_{1M}	0.07
p_{1F}	0.05
p_{2M}	0.08
p_{2F}	0.10
λ_M	0.60
λ_F	0.40
θ_1	0.60
θ_2	0.50
sample size $= n =$	4000

The model $\{\, p(.)\, \theta(t)\, \lambda(c)\}$ was fitted to the generated data assuming that capture probabilities do not vary by time and by category. The standardized residual plot for this model clearly shows that the fitted model does not fit the generated data because some residuals fall outside ± 1.96 (Figure A.2). In general, we can find poor model fitting of a given data set through residual plots.
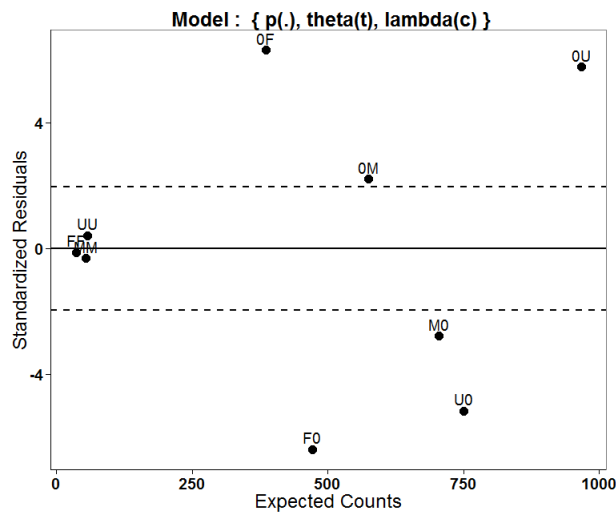

Figure A.2: Identify violation of assumptions for generated data using standardized residual plot. Data is generated from the model $\{p(c*t)\theta(t)\lambda(c)\}$. The fitted model is $\{p(.)\theta(t)\lambda(c)\}$. Dashed lines are drawn at ± 1.96 to represent the region where approximately 95% of residuals should lie if model assumptions were met completely.

A.2.2 Power Analysis

Power analysis is carried out with generated data with two categories (M and F) in the population to detect the changes of capture probabilities, category proportions and sample sizes. The method based on expected values (Devinue et al., 2006) is considered for power analysis and then we used simulation to verify the power. In each situation, we set $\alpha = 0.05$.

For power analysis to detect changes of capture probabilities, we generated data where the capture probabilities vary between categories and sample occasions and fit a model where capture probabilities vary only by sample occasions. We then calculated the power with the change (Δ_p) of the capture probabilities for category F. We considered the values for Δ_p from 0 to 0.1. Parameter values used for data generation are given in Table A.2.

Table A.2: Data generation information for power analysis with capture probabilities

Parameter	Value
p_{1M}	0.08
p_{1F}	$0.08 + \Delta_p$
p_{2M}	0.04
p_{2F}	$0.04 + \Delta_p$
λ_M	0.60
λ_F	0.40
θ_1	0.80
θ_2	0.50
sample size $= n =$	2000

We considered the null model H_0 and the alternative model H_a as follows

$$H_0 : \{\, p(t)\, \theta(t)\, \lambda(c)\,\}$$

$$H_a : \{\, p(c*t)\, \theta(t)\, \lambda(c)\,\}$$

Figure A.3 shows the power analysis using the method based on expected values (Devinue et al., 2006) and verifies the power using a simulation study for capture probability with $\alpha = 0.05$. According to Figure A.3, 80% power was achieved with $\Delta_p = 0.040$ for a sample size 2000.
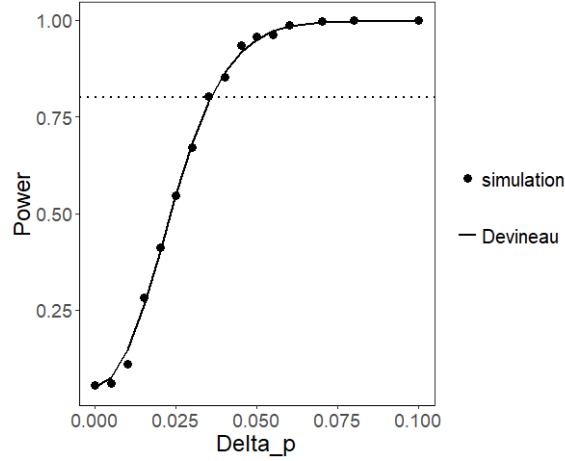
Figure A.3: Power analysis with capture probability using Devineau method and verified power using simulation study with sample size $= 2000$ at $\alpha = 0.05$. Δ_p (denoted in the graph as Delta_p) is the difference between the capture probability of two categories (F - M capture probabilities) at each sample occasion. Models under H_0 and H_a are H_0 : $\{ p(t) \, \theta(t) \, \lambda(c) \}$ and H_a : $\{ p(c*t) \, \theta(t) \, \lambda(c) \}$. Horizontal dotted line indicates 80% power.

The power analysis was repeated for sample sizes ranging from 1,000 to 4,000 (Figure A.4). Parameter values used for data generation are given in Table A.2. Larger samples allowed us to detect small differences between the capture probabilities of two categories at each occasion. For example, with a sample size of 4,000, 80% power was achieved when $\Delta_p = 0.025$.
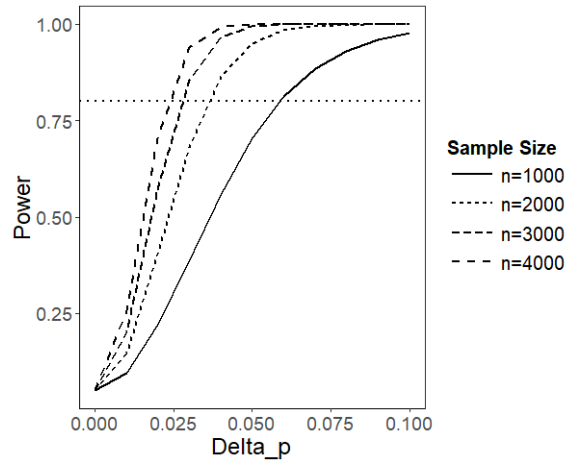

Figure A.4: Power analysis with different sample sizes at $\alpha = 0.05$. Delta_p is the difference between the capture probability of two categories (F - M capture probabilities) at each sample occasion. Models under H_0 and H_a are H_0 : $\{p(t)\theta(t)\lambda(c)\}$ and H_a : $\{p(c*t)\theta(t)\lambda(c)\}$. Horizontal dotted line indicates 80% power.

For the power analysis to detect changes of category proportions, we used generated data such that the capture probabilities varied between categories and sample occasions, and

category proportions were different. Then a model was fitted that forced fixed category proportions. Parameter values used for data generation are given in Table A.3.

Table A.3: Data generation information for power analysis with category proportions

Parameter	Value
p_{1M}	0.05
p_{1F}	0.08
p_{2M}	0.10
p_{2F}	0.12
λ_M	0.4
λ_F	0.6
θ_1	0.80
θ_2	0.50
sample size $= n =$	2000

We considered the the Null model H_0 and the alternative model H_a as follows.

$$H_0 : \{ \, p(c * t) \, \theta(t) \, \lambda(0.4 + \Delta_M) \}$$

$$H_a : \{ \, p(c * t) \, \theta(t) \, \lambda(c) \}$$

We considered different values for Δ_M as 0, 0.05, 0.1, 0.15, 0.2, 0.25, 0.3, 0.35, and 0.4. Then the corresponding values of λ_M under H_0 are 0.4, 0.45, 0.5, 0.55, 0.6, 0.65, 0.7, 0.75, and 0.8. We used these values for power analysis. Finally we verified the power using a simulation study.

Figure A.5 shows the power analysis for λ_M with $\alpha = 0.05$ with sample size 2,000. At $n = 2,000$ 80% power was achieved with $\Delta_M = 0.2$.
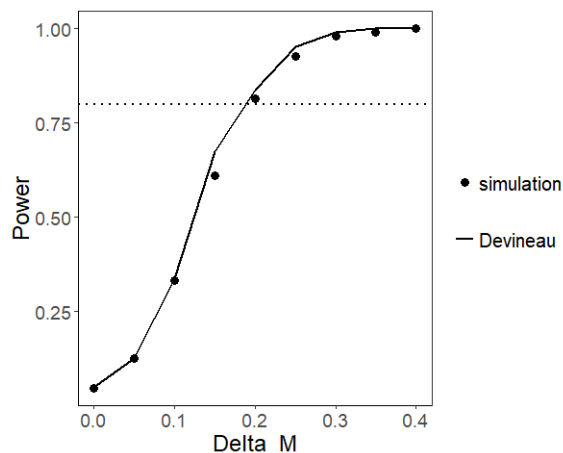

Figure A.5: Power analysis with category proportion (λ) using Devineau method and verifyied power using simulation study with sample size $= 2,000$ and $\alpha = 0.05$. Delta_M (Δ_M) is the increment of λ_M from 0.4. Models under H_0 and H_a are $H_0 : \{p(c*t)\theta(t)\lambda(0.4+\Delta_M)\}$ and $H_a : \{ \, p(c * t) \, \theta(t) \, \lambda(c) \}$. Horizontal dotted line indicates 80% power.

A.2.3 Model Assessment: Analysis of Mille Lacs Lake Walleye Data

Standardized Residual Plots

Standardized residual plots for the top four models in Table 2.2 in Chapter 2 are given in Figure A.6 .
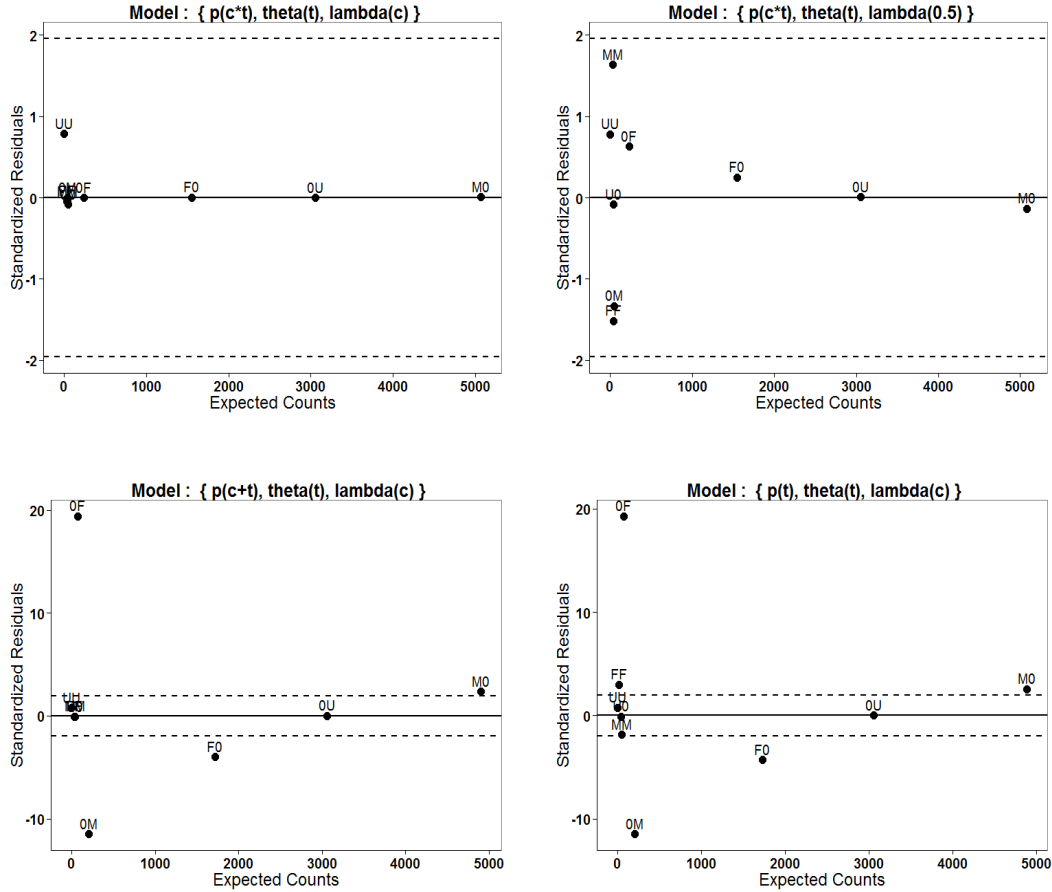

Figure A.6: Standardized residual plots for the best four models according to AICc values in Table 2.2. Dashed lines are drawn at ± 1.96 to represent the region where approximately 95% of residuals should lie if model assumptions were met completely. Good fit in top row; poor fit in bottom row.

Model Assessment using Parametric Bootstrap Method

Figure A.7 and A.8 show the parametric bootstrap goodness of fit plots for the best four models according to the AICc criteria using the two discrepancy statistics; the deviance statistic and the Tukey statistic for 1,000 bootstrap samples. Plot (a) in both of these figures refers to the model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ which has the smallest AICc value. The observed deviance and the observed Tukey statistic and the corresponding p-values suggest that the model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ fits to the walleye data.
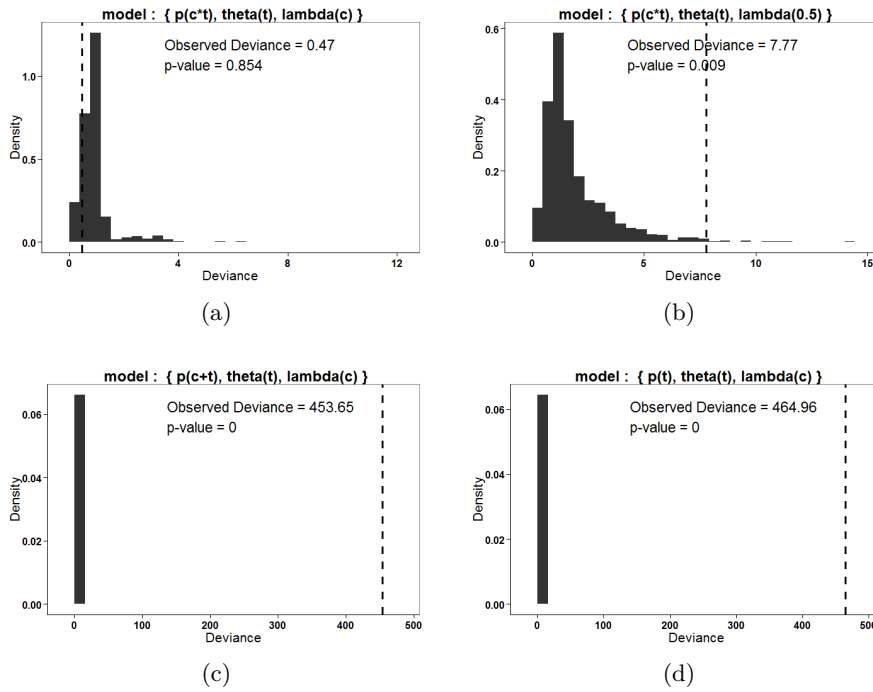
Figure A.7: Parametric bootstrap plots using deviance statistic for 1,000 bootstrap samples. The vertical dashed line indicates the deviance for the observed walleye data.
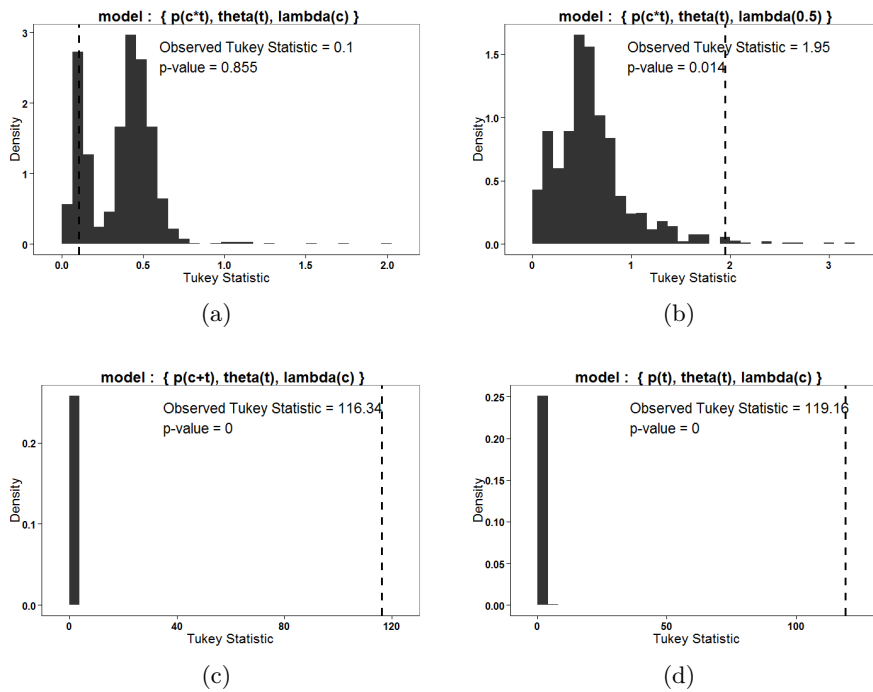

Figure A.8: Parametric bootstrap plots using the Tukey statistics for 1,000 bootstrap samples. The vertical dashed line indicates the Tukey statistic for the observed walleye data.

A.2.4 Approximate Closed Form Estimates

A closed form solution for the parameter estimates is derived with the use of a moment type estimation method (Davidson and Solomon, 1974). We consider two-sample capture-recapture experiments with two categories (M and F) in the population. The two capture histories UU and $U0$ are combined as U^*, and counts n_{UU} and n_{U0} for the combined histories are combined to n^*.

The moment type estimation method gives

$$n_i = E[n_i] = N \times P_i$$

where $n_i = n^*$, n_{M0}, n_{MM}, n_{F0}, n_{FF}, n_{0M}, n_{0F}, and n_{0U} and $P_i = P_{U^*}$, P_{M0}, P_{MM}, P_{F0}, P_{FF}, P_{0M}, P_{0F}, and P_{0U} respectively.

Then the resulting moment equations are

$$
\begin{aligned}
n^* &= N \left[\lambda_M \, p_{1M} \, (1 - \theta_1) + (1 - \lambda_M) \, p_{1F} \, (1 - \theta_1) \right] \\
n_{M0} &= N \, \lambda_M \, p_{1M} \, \theta_1 \, (1 - p_{2M}) \\
n_{MM} &= N \, \lambda_M \, p_{1M} \, \theta_1 \, p_{2M} \\
n_{F0} &= N \, (1 - \lambda_M) \, p_{1F} \, \theta_1 \, (1 - p_{2F}) \\
n_{FF} &= N \, (1 - \lambda_M) \, p_{1F} \, \theta_1 \, p_{2F} \\
n_{0M} &= N \, \lambda_M \, (1 - p_{1M}) \, p_{2M} \, \theta_2 \\
n_{0F} &= N \, (1 - \lambda_M) \, (1 - p_{1F}) \, p_{2F} \, \theta_2 \\
n_{0U} &= N \left[\lambda_M \, (1 - p_{1M}) \, p_{2M} \, (1 - \theta_2) + (1 - \lambda_M) \, (1 - p_{1F}) \, p_{2F} \, (1 - \theta_2) \right]
\end{aligned}
$$

Closed form solutions are obtained by solving these equations to give:

$$\theta_1 = \frac{1}{1 + \frac{n^*}{n_{0M} + n_{MM} + n_{0F} + n_{FF}}}$$

$$\theta_2 = \frac{1}{1 + \frac{n_{0U}}{n_{0M} + n_{0F}}}$$

$$p_{1M} = \frac{1}{1 + \frac{n_{0M}(n_{0M} + n_{MM} + n_{0F} + n_{FF})(n_{0M} + n_{0F} + n_{0U})}{n_{MM}(n_{0M} + n_{0F})(n^* + n_{0M} + n_{MM} + n_{0F} + n_{FF})}}$$

$$p_{1F} = \frac{1}{1 + \frac{n_{0F}(n_{0M} + n_{MM} + n_{0F} + n_{FF})(n_{0M} + n_{0F} + n_{0U})}{n_{FF}(n_{0M} + n_{0F})(n^* + n_{0M} + n_{MM} + n_{0F} + n_{FF})}}$$

$$p_{2M} = \frac{1}{1 + \frac{n_{M0}}{n_{MM}}}$$

$$p_{2F} = \frac{1}{1 + \frac{n_{F0}}{n_{FF}}}$$

$$\lambda_M = \frac{1}{1 + \frac{n_{F0} p_{1M} (1 - p_{2M})}{n_{M0} p_{1F} (1 - p_{2F})}}$$

$$\lambda_F = 1 - \lambda_M$$

$$N = \frac{n_{M0} + n_{MM}}{\lambda_M p_{1M} \theta_1}$$

The closed form solutions for the parameter estimates using the model $\{\, p(c*t)\,\theta(t)\,\lambda(c)\}$ for the walleye example are given in Table A.4. These estimates are very similar to the numerical MLEs in Table 2.3 in Chapter 2.

Table A.4: Closed form MLEs using the model $\{p(c*t)\,\theta(t)\,\lambda(c)\}$.

Parameter	Moment estimate
p_{1M}	0.074
p_{1F}	0.011
p_{2M}	0.008
p_{2F}	0.020
λ_M	0.323
λ_F	0.677
θ_1	0.994
θ_2	0.083
N	215,113
N_M	69,385
N_F	145,728

A.2.5 Optimal Allocation of Sampling Effort

Optimal allocation of the sample sizes for a given cost for partial stratification in two-sample capture-recapture experiments with two categories in the population is discussed in Chapter 2.3.3 using Mille Lacs walleye Data 2013.

Optimal allocation of sample sizes and sub-sample sizes produced by the numerical methods for the given costs are $n_1 = 8,929$, $n_1^* = 8,908$, $n_2 = 8,359$ and $n_2^* = 1,412$. At these optimal values $SE(\widehat{N})$ is 13,657

A conditional contour plot for standard error of $\widehat{N}$ is given in Figure A.9 when the n_1^* and n_2^* are fixed at the optimal values. Figure A.10 shows the conditional contour plot for standard error of $\widehat{N}$ when the n_1 and n_2 are fixed at the optimal values. These contour plots show that many solutions are possible for optimal allocation.

The following packages were used for numerical optimization in R programing language (R Development Core Team, 2016). General-purpose optimization with L-BSGS-B method (Byrd, Lu, Nocedal, & Zhu, 1995) was used for numerical optimization. Simulated annealing method with GenSA package (Xiang, Gubian, Suomela, & Hoeng, 2013) can also be used for optimization of the conditional likelihood. Rsolnp package (Ghalanos & Theussl, 2015) was used for general nonlinear optimization with constraints.
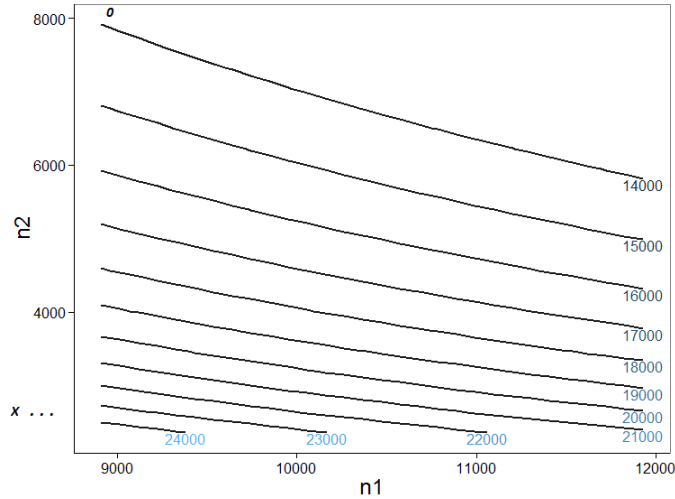
Figure A.9: Conditional contour plot for the standard error of $\widehat{N}$ when n_1^* and n_2^* are fixed at the optimal values. '×' represents the current allocation ($n_1 = 6,741$ and $n_2 = 3,409$) and 'o' represents the optimal allocation ($n_1 = 8,929$ and $n_2 = 8,908$). Note that the current allocation falls outside the graph on the left side.
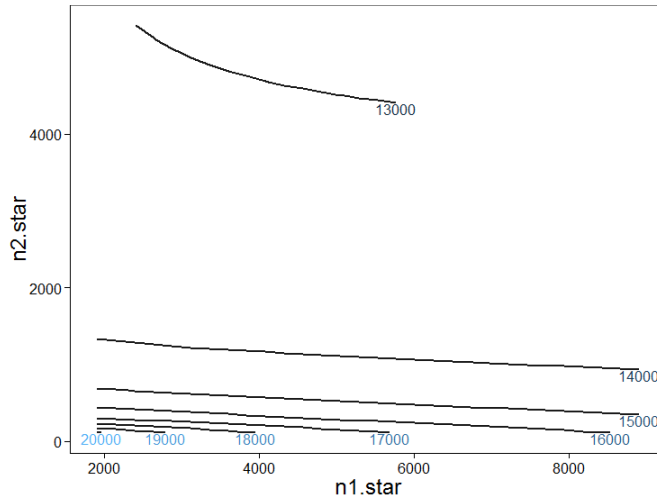

Figure A.10: Conditional contour plot for the standard error of $\widehat{N}$ when n_1 and n_2 are fixed at the optimal values.

A.2.6 Precision of the Estimates when Additional Information is Available

We compare the standard errors (Table A.5) of the estimates for the parameters under two models using the Mille Lacs Lake walleye data to see how well the precision of the estimate of population abundance can be improved in the presence of additional information. Let the first model be $\{p(c*t)\,\theta(t)\,\lambda(c)\}$ and the second model be $\{p(c*t)\,\theta(t)\,\lambda(MLE)\}$. The first

model is the best fitted model to the walleye data under the MLE method and the second model can be considered as the model where the sex ratio is known and fixed at the MLE values obtained from the first model. Therefore λ_M is fixed at 0.323 (i.e. λ_F is 0.677) for the second model.

Table A.5: Comparison of the precision of the estimates of two models; the first model is the best model $\{\, p(c*t)\, \theta(t)\, \lambda(c)\}$ and the second model $\{\, p(c*t)\, \theta(t)\, \lambda(MLE)\}$ where the sex ratios are fixed at the MLE values obtained from the best model

Parameter	SE - best model $\{\, p(c*t)\, \theta(t)\, \lambda(c)\}$	SE - second model $\{\, p(c*t)\, \theta(t)\, \lambda(MLE)\}$
p_{1M}	0.015	0.010
p_{1F}	0.002	0.001
p_{2M}	0.001	0.001
p_{2F}	0.004	0.003
λ_M	0.060	-
λ_F	0.060	-
θ_1	0.001	0.001
θ_2	0.005	0.005
N	27,032	26,103
N_M	13,335	8,431
N_F	24,771	17,672

A.3   Bayesian Analysis

A.3.1   Bayesian Analysis Model Comparison Table

Table A.6 shows the DIC values and related information for six different models using two methods as described in Chapter 2.4.1.

A.3.2   Bayesian p-value Scatter Plots

Bayesian p-value plots are given in Figure A.11 using discrepancy functions: deviance statistic and Freeman Tukey statistic.

Table A.6: Bayesian analysis model comparison table.

Model	np	Using pD				Using pv			
		pD	DIC	ΔDIC	DIC Weight	pv	DIC	ΔDIC	DIC Weight
$M1 \equiv \{p(c*t)(0,0.3)\ \theta(t)(0.7,1)(0,0.3)\ \lambda(c)(20,40)\}$	8	7.25	76.57	0.05	0.27	8.23	77.55	0.00	0.34
$M2 \equiv \{p(c*t)(0,0.3)\ \theta(t)(0.7,1)(0,0.3)\ \lambda(c)(3,4)\}$	8	7.01	76.52	0.00	0.27	8.93	78.44	0.89	0.22
$M3 \equiv \{p(c*t)(0,0.3)\ \theta(t)(0.7,1)(0,0.3)\ \lambda(c)(2,4)\}$	8	7.23	76.94	0.42	0.22	8.74	78.45	0.90	0.22
$M4 \equiv \{p(c*t)(0,1)\ \theta(t)(0,1)(0,1)\ \lambda(c)(7,3)\}$	8	7.25	76.87	0.35	0.23	8.98	78.60	1.05	0.20
$M5 \equiv \{p(c*t)(0,1)\ \theta(t)(0,1)(0,1)\ \lambda(0.5)\}$	7	6.91	82.63	6.11	0.01	7.69	83.40	5.85	0.02
$M6 \equiv \{p(c)(0,1)\ \theta(t)(0.7,1)(0,0.3)\ \lambda(c)(2,4)\}$	6	5.82	1,658	1,581	0.00	6.83	1,659	1,581	0.00

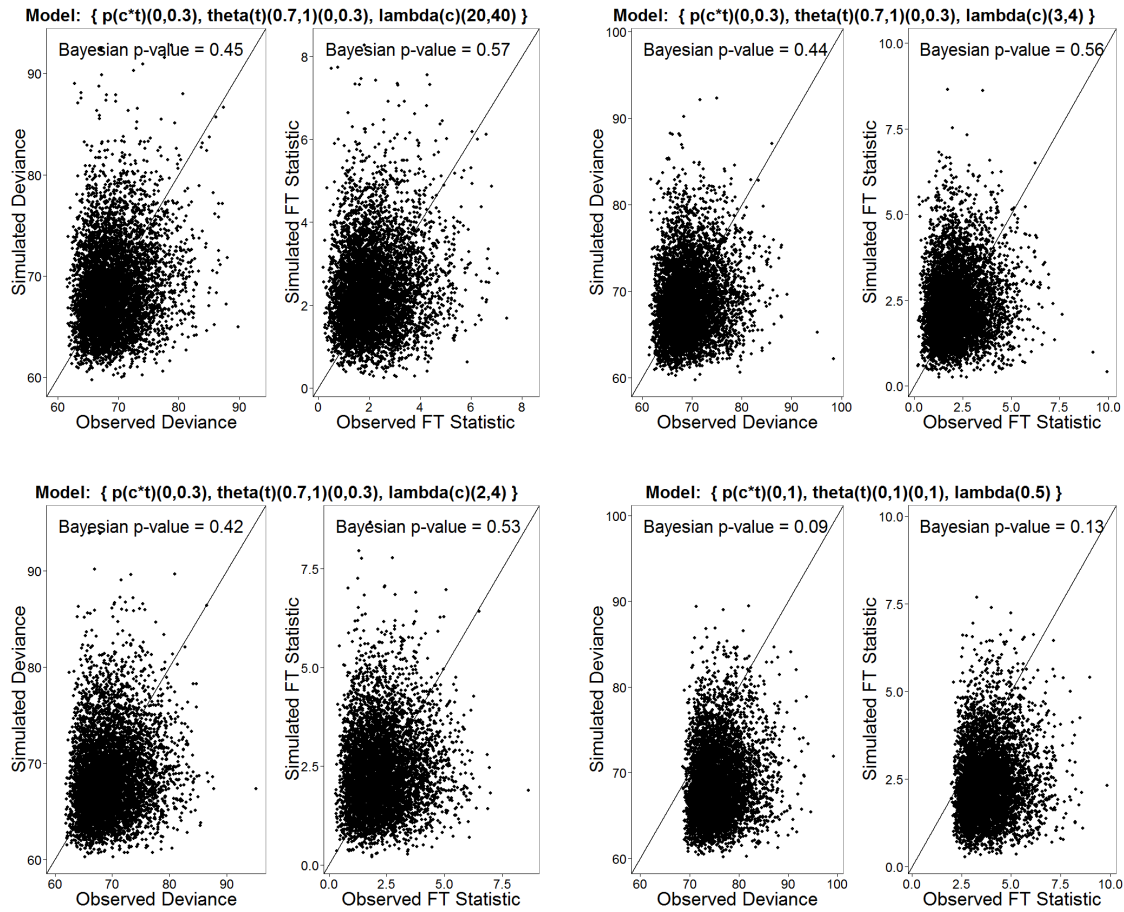np = number of parameters

95

Figure A.11: Bayesian p-value scatter plots for the first four models according to DIC criteria as in Table A.6 using the discrepancy functions (a) Deviance Statistic and (b) Freeman Tukey Statistic (FT). For each of the model, 6000 samples from the posterior (3 chains each with 2000) were considered.

A.3.3 Posterior Summary Values

Results produced by the MCMC Metropolis-Hasting simulations for the best fitted model $\{p(c*t)(0,0.3)\ \theta(t)(0.7,1)(0,0.3)\ \lambda(c)(20,40)\}$ are given in Table A.7.

Table A.7: Numerical output of the posterior summary values for the best fitted model $\{p(c * t)(0, 0.3)\ \theta(t)(0.7, 1)(0, 0.3)\ \lambda(c)(20, 40)\}$. n.eff is a rough measure of the effective sample size for each parameter. Rhat is the potential scale reduction factor.

Parameter	mean	sd	2.5%	97.5%	Rhat	n.eff
beta[1]	-2.428	0.169	-2.752	-2.077	1.0	170
beta[2]	-4.358	0.147	-4.650	-4.072	1.0	6000
beta[3]	-4.773	0.139	-5.047	-4.505	1.0	630
beta[4]	-3.761	0.150	-4.061	-3.467	1.0	2100
beta[5]	-0.688	0.188	-1.055	-0.326	1.0	350
beta[6]	4.988	0.148	4.709	5.286	1.0	6000
beta[7]	-2.396	0.063	-2.522	-2.274	1.0	6000
beta[8]	12.159	0.117	11.931	12.394	1.0	530
p_{1M}	0.082	0.013	0.059	0.111	1.0	170
p_{1F}	0.013	0.002	0.009	0.016	1.0	6000
p_{2M}	0.008	0.001	0.006	0.011	1.0	630
p_{2F}	0.023	0.003	0.017	0.030	1.0	2100
λ_M	0.336	0.042	0.258	0.419	1.0	340
λ_F	0.664	0.042	0.580	0.742	1.0	350
θ_1	0.993	0.001	0.991	0.995	1.0	6000
θ_2	0.083	0.005	0.074	0.093	1.0	6000
N	192,229	22,923	151,969	241,445	1.0	530
N_M	64,327	9,990	46,250	85,524	1.0	170
N_F	127,902	18,631	96,027	167,791	1.0	6000

Parameters beta[1] to beta[7] are in logit scale and beta[8] is in log scale. Parameters beta[1]to beta[4] correspond to capture probabilities (p_{1M}, p_{1F}, p_{2M} and p_{2F}), beta[5] corresponds to category proportion (λ_M), beta[6] and beta[7] correspond to θ_1 and θ_2, and beta[8] corresponds to population abundance (N).

A.3.4 Posterior Distributions for Capture Probabilities, Category Proportions and Sub-Sample Proportions

Figure A.12 gives the posterior distribution of the capture probabilities p_{1M}, p_{1F}, p_{2M} and p_{2F}. Figure A.13 and Figure A.14 give the posterior distributions of the category proportions and the sub-sample proportions.
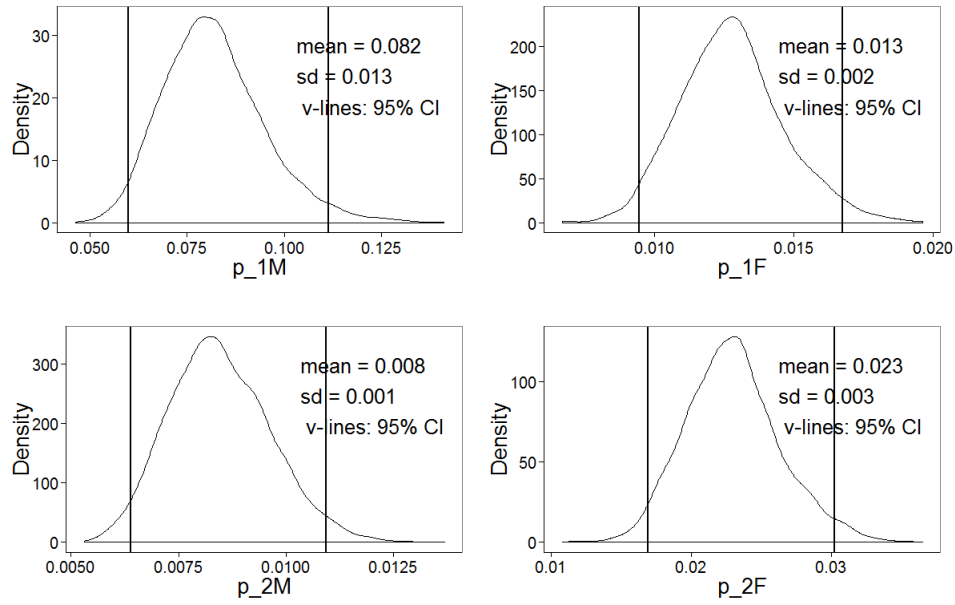
Figure A.12: Posterior distributions for capture probabilities using a sample of 6000 (3 chains each with 2000) from the posterior for the best model $\{p(c * t)(0, 0.3)\ \theta(t)(0.7, 1)(0, 0.3)\ \lambda(c)(20, 40)\}$. Vertical bars are the 95% credible intervals.
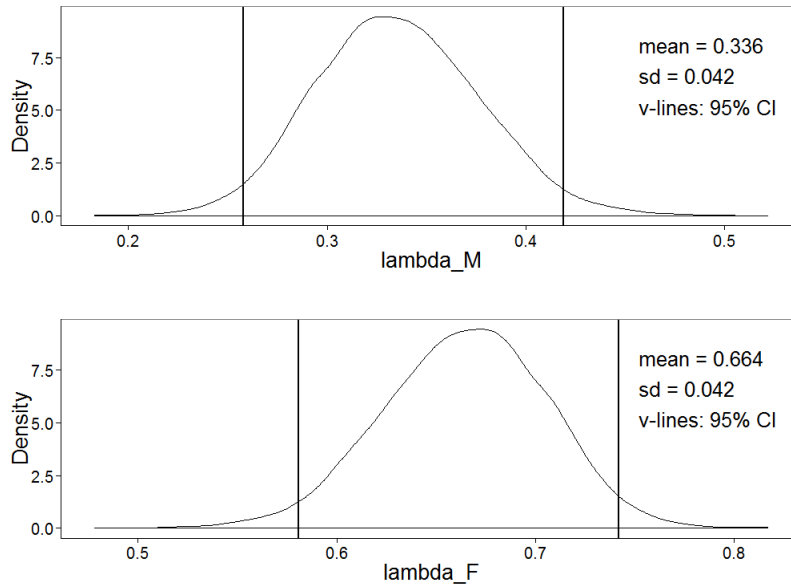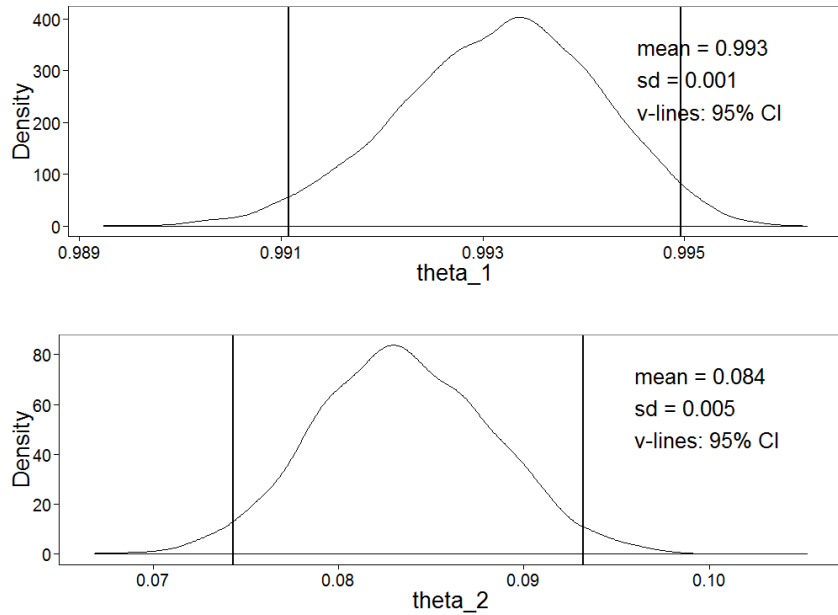

Figure A.13: Posterior distributions for category proportions (λ_M and λ_F) using a sample of 6000 (3 chains each with 2000) from the posterior for the best model $\{p(c * t)(0, 0.25)\ \theta(t)(0.7, 1)(0, 0.3)\ \lambda(c)(20, 40)\}$. Vertical bars are the 95% credible intervals.

Figure A.14: Posterior distributions for sub-sample proportions (θ_1 and θ_2) using a sample of 6000 (3 chains each with 2000) from the posterior for the best model $\{p(c * t)(0, 0.3)\ \theta(t)(0.7, 1)(0, 0.3)\ \lambda(c)(20, 40)\}$. Vertical bars are the 95% credible intervals.

A.4 Analysis with Individual Covariates

A.4.1 Summary of Distribution of Lengths of Walleyes

The summary distribution of length of Mille Lacs Lake walleyes captured in both sample occasions is given in Figure A.15. More males were captured than females at the first sample occasion and more females were captured than males at the second sample occasion. Sub-sample size was much larger at the first sample occasion compared to the second occasion. Females tended to be larger than males.
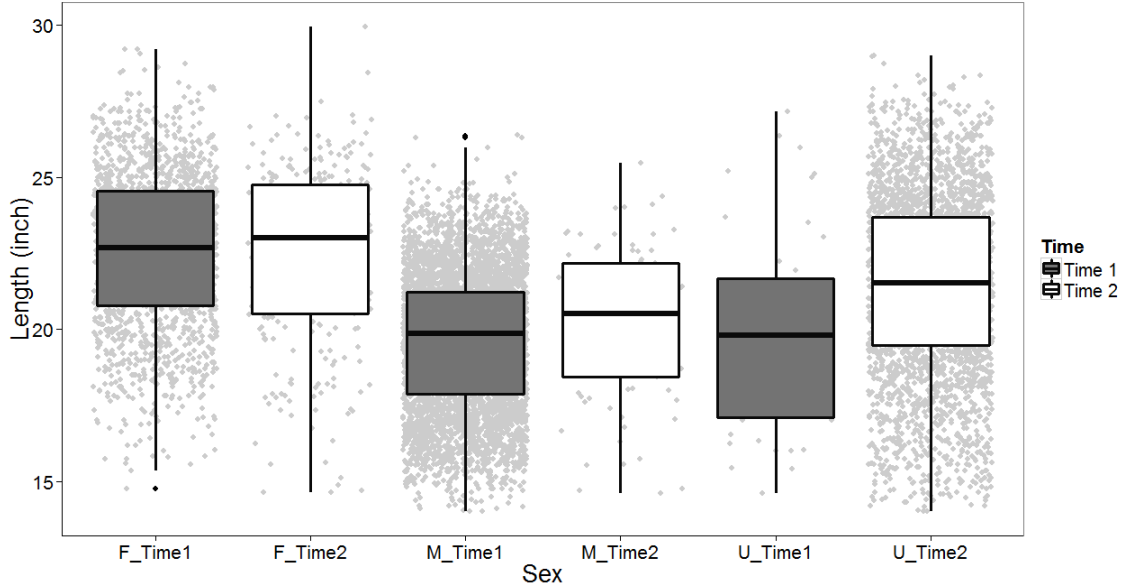
Figure A.15: Summary of distribution of lengths of walleyes in the sample. M, F and U in the x-axis denote male, female and not identify the sex along with they captured in time 1 (first sample occasion) or time 2 (second sample occasion). Dots spread though each box plot represent the actual data points.

A.4.2 Model Selection

Seven different models were fitted to walleye data (Table A.8). Note that the last two models do not have the individual covariate *length*. These two are the same models given in Table 2.2 in Chapter 2. According to the AICc criteria, the best model for the walleye data is the model $\{p(length * category * time + length^2 * category * time), \theta(t), \lambda(c)\}$.

Model specification with the individual covariate *length* is similar to models specified in the MLE method described in Chapter 2.2.1 except for the capture probabilities. Because we consider a logistic regression model for the capture probabilities that depends on a capture formula, we specify the capture formula in the model specification. Capture formula in the best fitted model was given as $p(length * category * time + length^2 * category * time)$. Then the capture probabilities for each individual i for each category C at time t can be found as follows.

$$
\begin{aligned}
logit(p_{tCi}) = log\left(\frac{p_{tCi}}{1 - p_{tCi}}\right) = {} & \beta_0 + \beta_1\,(length_i) + \beta_2\,(category) + \beta_3\,(time) + \beta_4\,(length_i)^2 + \\
& \beta_5\,(length_i)(category) + \beta_6\,(length_i)(time) + \beta_7\,(category)(time) + \\
& \beta_8\,(category)(length_i)^2 + \beta_9\,(time)(length_i)^2 + \\
& \beta_{10}\,(length_i)(category)(time) + \beta_{11}\,(category)(time)(length_i)^2
\end{aligned}
$$

$$(A.1)$$

Table A.8: Model comparison table for walleye example with individual covariate 'length'.

Model	np	$\hat{N}$ '000s	s.e.$(\hat{N})$ '000s	AICc	$\Delta AICc$	AICc Weights
{p(length * category * time + lengthsq * category * time), θ(t), λ(c)}	15	279.2	57	21230	0	1.0
{p(length * category * time + lengthsq * category), θ(t), λ(0.32)}	12	326.9	75	21251	21	0.0
{p(length * category * time + lengthsq), θ(t), λ(c)}	12	393.3	72	21474	244	0.0
{p(length * category * time), θ(t), λ(c)}	11	752.3	393	21501	271	0.0
{p(lengthsq * category * time), θ(t), λ(c)}	11	217.3	28	23261	2031	0.0
{p(category * time), θ(t), λ(c)}	7	209.1	27	23602	2372	0.0
{p(category + time), θ(t), λ(c)}	6	357.1	49	24053	2823	0.0

np = number of parameters

lengthsq represents the $length^2$ term in the models

We used standardized length to reduced the correlation between length and $length^2$

A.4.3 Parameter Estimation

The estimates for the parameters and their standard errors using the best model $\{p(length * category * time + length^2 * category * time), \theta(t), \lambda(c)\}$ for the walleye data are shown in Table A.9. Estimates for $\beta_0, \beta_1, ..., \beta_{11}$ are in logit scale. All the other estimates are in regular scale. We use Equation A.1 in Appendix A.4 to calculate the estimated capture probability for each individual.

We use the values 1 and 0 for category 'M' and 'F' (for males and females) and the values 0 and 1 for 'time 1' and 'time 2' respectively with the standardized $length$ to reduce the correlation between $length$ and $length^2$ in Equation A.1 in Appendix A.4 when calculating the estimated individual capture probabilities (Table A.9).

The last two models in Table A.9 do not have the individual covariate $length$. For these models, estimated capture probabilities for all the individuals for a certain category at a certain time are the same. These two models are the same models given in Table 2.2 in Chapter 2.3. The estimates for the parameters for these two models under the analysis with covariates gave the same results that we found in Chapter 2.3. However the methods used were different. Having similar results for the same models using different methods shows that the methods used in the analysis with individual covariates are reliable.

Table A.9: MLEs using the model $\{p(length * category * time + length^2 * category * time), \theta(t), \lambda(c)\}$.

Parameter	MLE	SE
$\beta_0 \equiv p : (Intercept)$	-4.660	0.2532
$\beta_1 \equiv p : length$	0.307	0.0564
$\beta_2 \equiv p : category\_M$	2.608	0.3510
$\beta_3 \equiv p : time\_T2$	0.659	0.0583
$\beta_4 \equiv p : length^2$	-0.037	0.0135
$\beta_5 \equiv p : length : category\_M$	-0.519	0.0160
$\beta_6 \equiv p : length : time\_T2$	-0.136	0.0174
$\beta_7 \equiv p : category\_M : time\_T2$	-3.118	0.2610
$\beta_8 \equiv p : category\_M : length^2$	-0.059	0.0046
$\beta_9 \equiv p : time\_T2 : length^2$	0.013	0.0039
$\beta_{10} \equiv p : length : category\_M : time\_T2$	0.310	0.0619
$\beta_{11} \equiv p : category\_M : time\_T2 : length^2$	0.031	0.0185
λ_M	0.293	0.068
λ_F	0.707	0.068
θ_1	0.993	0.001
θ_2	0.083	0.005
N_M	81,833	25,398
N_F	197,397	44,625
N	279,230	57,034

Values related to β's are in $logit$ scale and all the other values in regular scale

Appendix B

Supplementary Materials for Chapter 3: Study of k-Sample Capture-Recapture Experiments under Partial Stratification on Closed Population

B.1 Goodness of Fit using Parametric Bootstrap Method

One of the method to assess the fitted model is to use the parametric bootstrap goodness of fit plots in the study of k-Sample capture-recapture experiments under partial stratification with loss on capture allowed. We considered both deviance statistic and Tukey statistic with 1000 bootstrap sample to create goodness of fit plots. Bootstrap goodness of fit plots for the best four models using deviance statistics and Tukey statistic according to the AICc criteria in Table 3.3 in Chapter 3 are given in Figure B.1 and Figure B.2. The observed deviance statistic and the observed Tukey statistic for the data using the given models and the corresponding p-values show that the model $\{p(c * t)\ \theta(t)\ \nu(t)\ \lambda(c)\}$ which is the best model according to the AICc criteria, fit the data well .
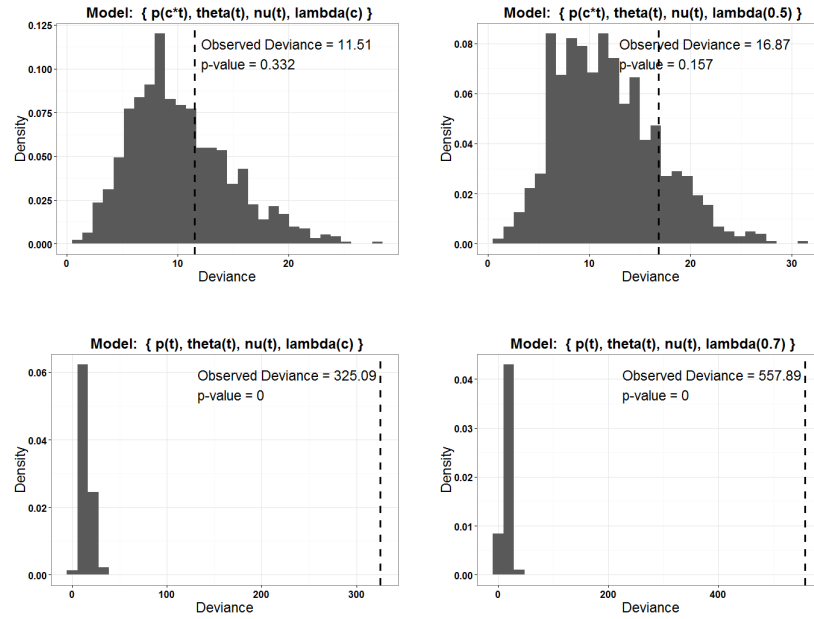
Figure B.1: Parametric bootstrap goodness of fit plots using deviance statistic with 1000 bootstrap samples. The vertical dashed lines indicates the observed deviance statistic using the given model for the data in Table 3.2 in Chapter 3.
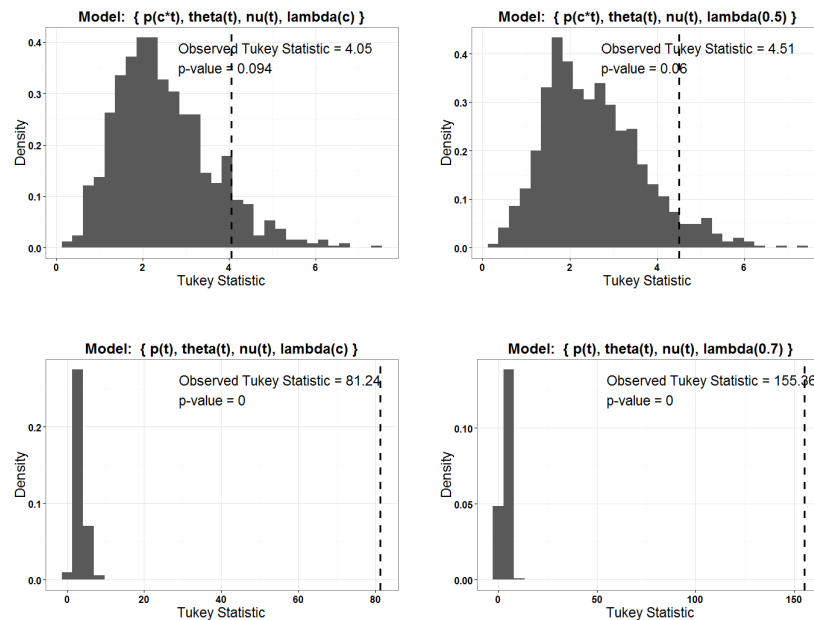

Figure B.2: Parametric bootstrap goodness of fit plots using Tukey statistic with 1000 bootstrap samples. The vertical dashed lines indicates the observed Tukey statistic using the given model for the data in Table 3.2 in Chapter 3.

B.2 Simulation Study

Simulation study was conducted to test the MLE and Bayesian methods discussed in Chapter 3. We simulated 1,000 samples for 3-sample capture-recapture study with two categories in the population (M, F) using partial stratification and allowing loss on capture at each sample time. Histogram of the estimates of the parameters for simulated samples under the MLE method using the best fitted model $\{p(c * t) \ \theta(t) \ \nu(t) \ \lambda(c)\}$ are given in Figure B.3. Estimates of the parameters using the particular data set given in Table 3.2 in Chapter 3 that was used for analysis, are marked in vertical dashed lines in these histograms.
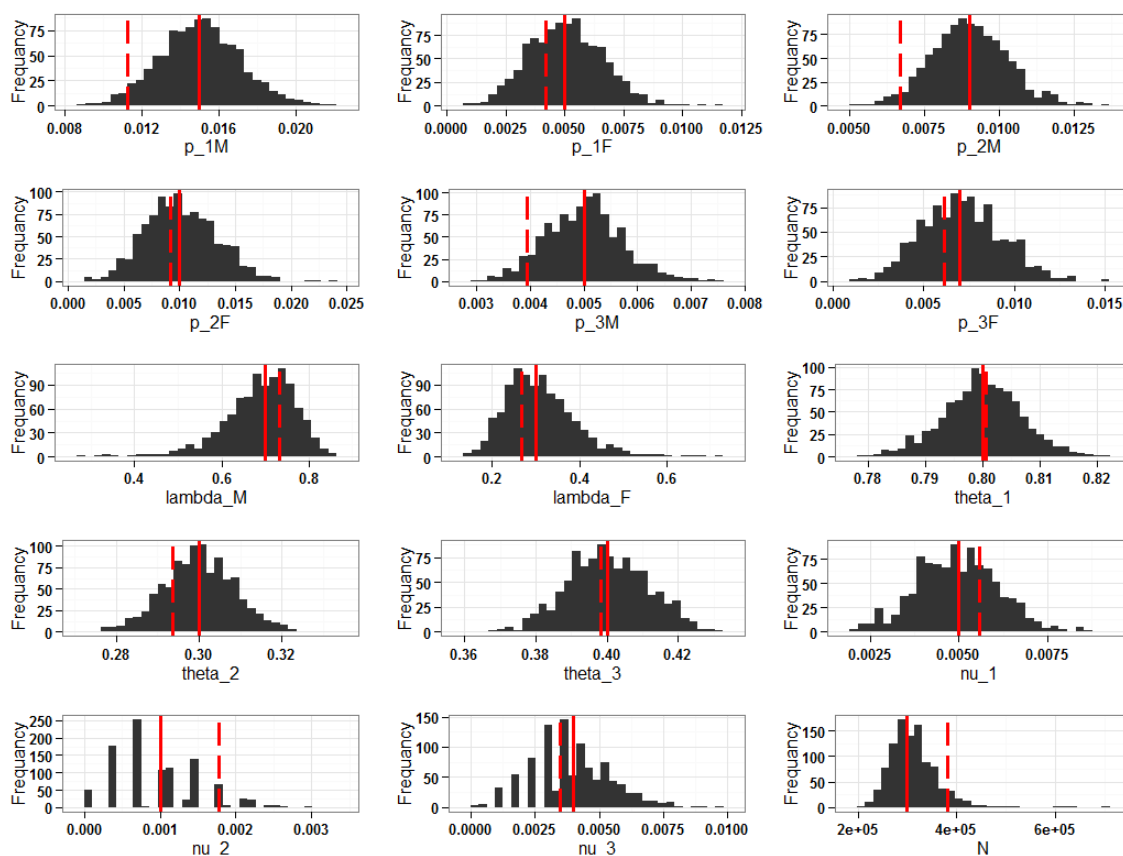

Figure B.3: Histogram of the estimates of the parameters p_{tC}, λ_C, θ_t, ν_t and N where $t = 1, 2, 3$ and $C = \{M, F\}$ for 1000 simulated data sets using the MLE best fitted model $\{p(c*t) \ \theta(t) \ \nu(t) \ \lambda(c)\}$. Vertical solid lines indicate the true parameter values given in Table 3.5 in Chapter 3. Vertical dashed lines indicate the estimates under MLE method in Table 3.4 in Chapter 3 calculated from simulated data in Table 3.2 in Chapter 3.

B.3 Bayesian Analysis

Table B.1 shows the the deviance information criterion (DIC) for Bayesian model selection procedure. Samples from the posterior distribution for each of the given model were obtained

by MCMC simulations using the Metropolis-Hasting method. We considered 6,000 samples (3 chains each with 2,000) from the posterior from post-burn sample after thinning by the factor of 50.

Trace plots of all the beta parameters for the best model cording to DIC criteria are given in Figure B.4.

Table B.2 shows the results produced by the MCMC Metropolis-Hasting simulations for the best fitted model $\{p(c*t)(0, 0.1)\ \theta(t)(0, 1)\ \nu(0, 0.1)\lambda(c)(30, 10)\}$.
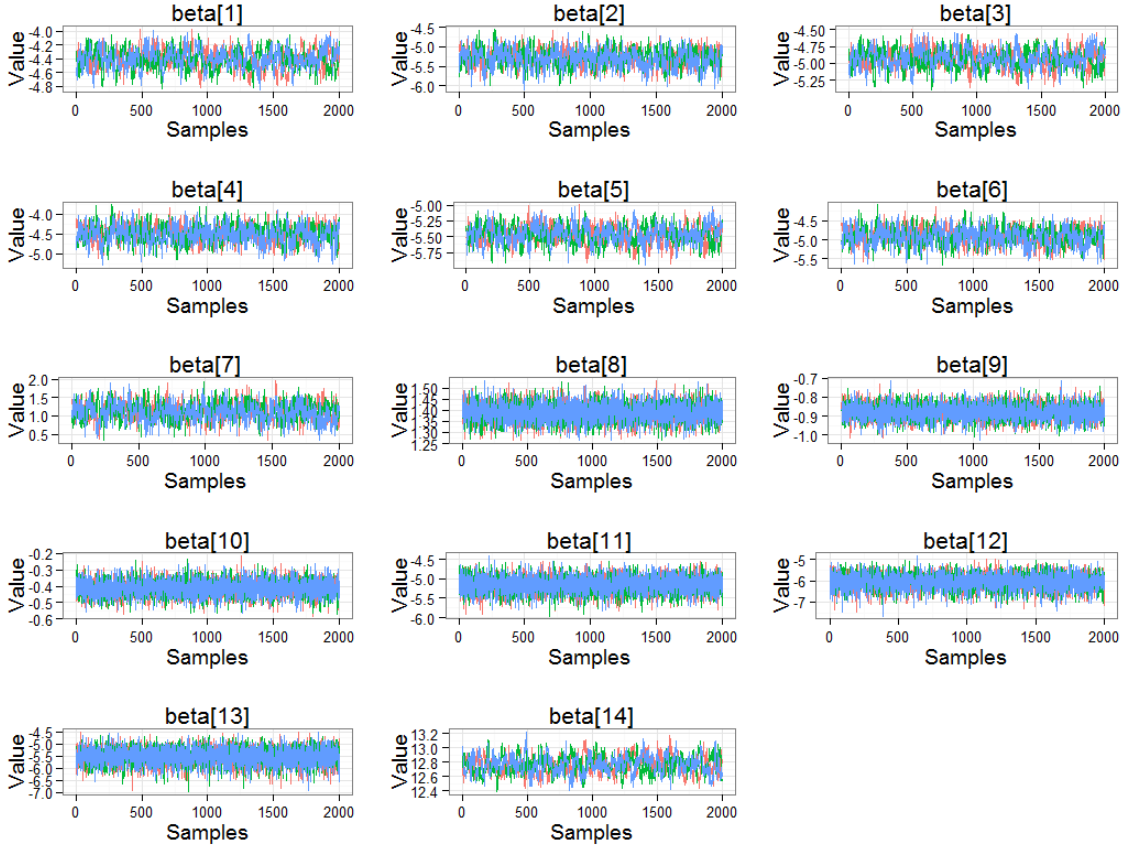

Figure B.4: Trace plots for all the beta parameters using a sample of 6000 (3 chains each with 2000) observations from the posterior distribution for the best fitted model $\{p(c*t)(0, 0.1)\ \theta(t)(0, 1)\ \nu(0, 0.1)\lambda(c)(30, 10)\}$. beta[1] to beta[6] corresponds to capture probabilities (p_{1M}, p_{1F}, p_{2M}, p_{2F} p_{3M} and p_{3F}). beta[7] corresponds to category proportion (λ_M). beta[8] to beta[10] corresponds to sub-sample proportions (θ_1, θ_2 and θ_3). beta[11] to beta[13] corresponds to loss on capture proportions (ν_1, ν_2 and ν_3). beta[14] corresponds to population abundance (N). Values in the y-axis are in logit form except for the beta[14] which is in log form.

Table B.1: Model comparison table for Bayesian analysis using DIC criteria. np is the number of parameters to be estimated in the model.

Model	np	Spiegelhalter Method			Gelman Method		
		DIC	ΔDIC	DIC Weight	DIC	ΔDIC	DIC Weight
$\{p(c*t)(0,0.1)\theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(30,10)\}$	14	164.5	0.00	0.40	165.6	0.00	0.57
$\{p(c*t)(0,0.1)\theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(3,1)\}$	14	165.1	0.56	0.30	166.7	1.16	0.32
$\{p(c*t)(0,1)\ \theta(t)(0,1)\ \nu(0,1)\ \lambda(c)(30,10)\}$	14	166.5	1.99	0.15	170.2	4.63	0.06
$\{p(c*t)(0,1)\ \theta(t)(0,1)\ \nu(0,1)\ \lambda(c)(3,1)\}$	14	166.7	2.15	0.14	170.8	5.24	0.04
$\{p(c*t)(0,1)\ \theta(t)(0,1)\ \nu(0,1)\ \lambda(0.5)\}$	13	170.9	6.38	0.02	175.3	9.71	0.00

Table B.2: Summary of the estimated posterior for the best fitted model $\{p(c*t)(0,0.1)\ \theta(t)(0,1)\ \nu(0,0.1)\lambda(c)(30,10)\}$. n.eff is a rough measure of effective sample size for each parameter. Rhat is the potential scale reduction factor. beta[1] to beta[6] corresponds to capture probabilities (p_{1M}, p_{1F}, p_{2M}, p_{2F} p_{3M} and p_{3F}). beta[7] corresponds to category proportion (λ_M). beta[8] to beta[10] corresponds to sub-sample proportions (θ_1, θ_2 and θ_3). beta[11] to beta[13] corresponds to loss on capture proportions (ν_1, ν_2 and ν_3). beta[14] corresponds to population abundance (N). All beta Values are in logit form except for the beta[14] which is in log form.

Parameter	Mean	SD	2.5%	97.5%	Rhat	n.eff	Parameter	Mean	SD	2.5%	97.5%
beta[1]	-4.409	0.137	-4.685	-4.142	1.003	680	p_{1M}	0.0122	0.0016	0.0091	0.0156
beta[2]	-5.292	0.223	-5.471	-4.870	1.007	330	p_{1F}	0.0051	0.0011	0.0031	0.0076
beta[3]	-4.935	0.137	-5.208	-4.668	1.003	750	p_{2M}	0.0071	0.0009	0.0054	0.0092
beta[4]	-4.501	0.221	-4.944	-4.082	1.008	280	p_{2F}	0.0112	0.0024	0.0070	0.0165
beta[5]	-5.467	0.140	-5.753	-5.198	1.003	690	p_{3M}	0.0042	0.0006	0.0031	0.0055
beta[6]	-4.912	0.222	-5.357	-4.500	1.007	290	p_{3F}	0.0074	0.0016	0.0047	0.0109
beta[7]	1.117	0.243	0.638	1.589	1.016	180	λ_M	0.7508	0.0452	0.6545	0.8306
							λ_F	0.2492	0.0452	0.1693	0.3454
beta[8]	1.388	0.041	1.307	1.471	1.001	4100	θ_1	0.8003	0.0066	0.7871	0.8132
beta[9]	-0.878	0.041	-0.959	-0.796	1.001	2200	θ_2	0.2936	0.0085	0.2768	0.3107
beta[10]	-0.412	0.049	-0.506	-0.314	1.001	6000	θ_3	0.3984	0.0117	0.3759	0.4219
beta[11]	-5.144	0.214	-5.579	-4.744	1.001	6000	ν_1	0.0059	0.0012	0.0037	0.0086
beta[12]	-6.050	0.370	-6.833	-5.372	1.001	6000	ν_2	0.0025	0.0009	0.0010	0.0046
beta[13]	-5.498	0.343	-6.219	-4.894	1.001	1700	ν_3	0.0043	0.0014	0.0098	0.0074
beta[14]	12.766	0.119	12.537	13.002	1.001	5800	N	352,892	42,638	278,538	443,446
							N_M	264,927	35,821	202,430	343,883
							N_F	87,965	19,590	57,034	132,450

Appendix C

Supplementary Materials for Chapter 4: Integrated Population Modeling of Chinook Salmon with Capture-Recapture, Snorkel, Dead Recovery and Radio Telemetry Surveys

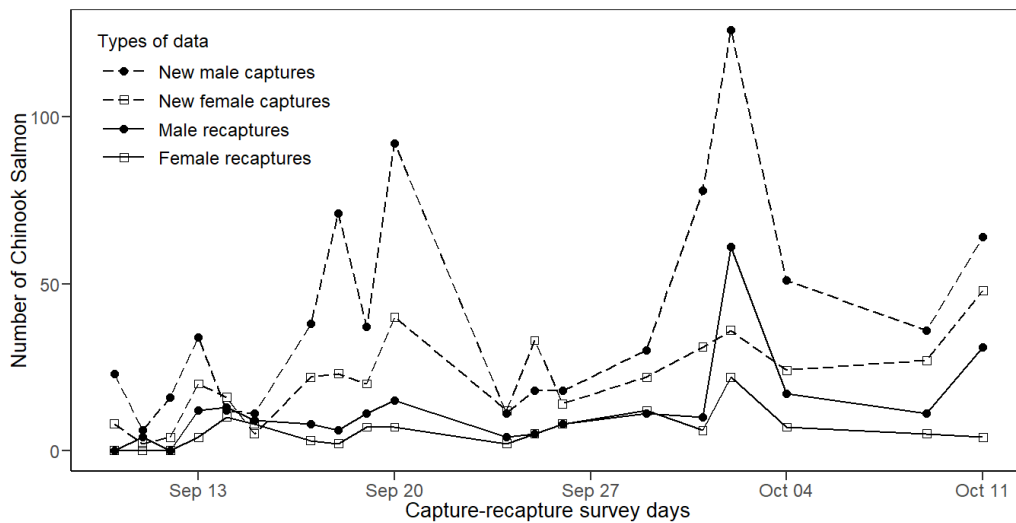## C.1   Burman River Chinook salmon data summaries in 2012

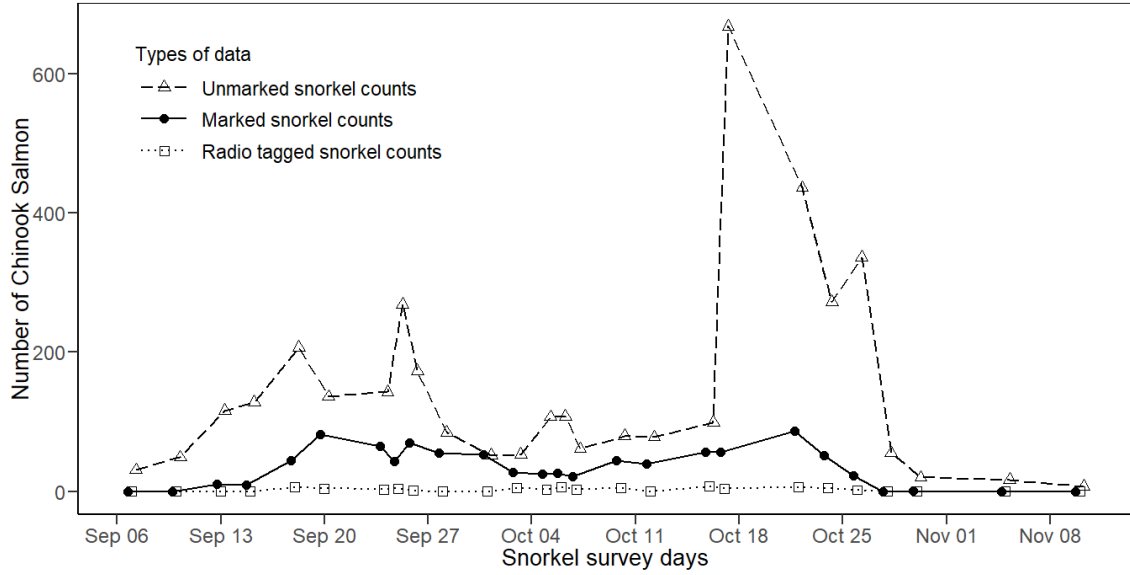Figure C.1: Capture-recapture data summaries for marked male and female Chinook at the stopover pool.

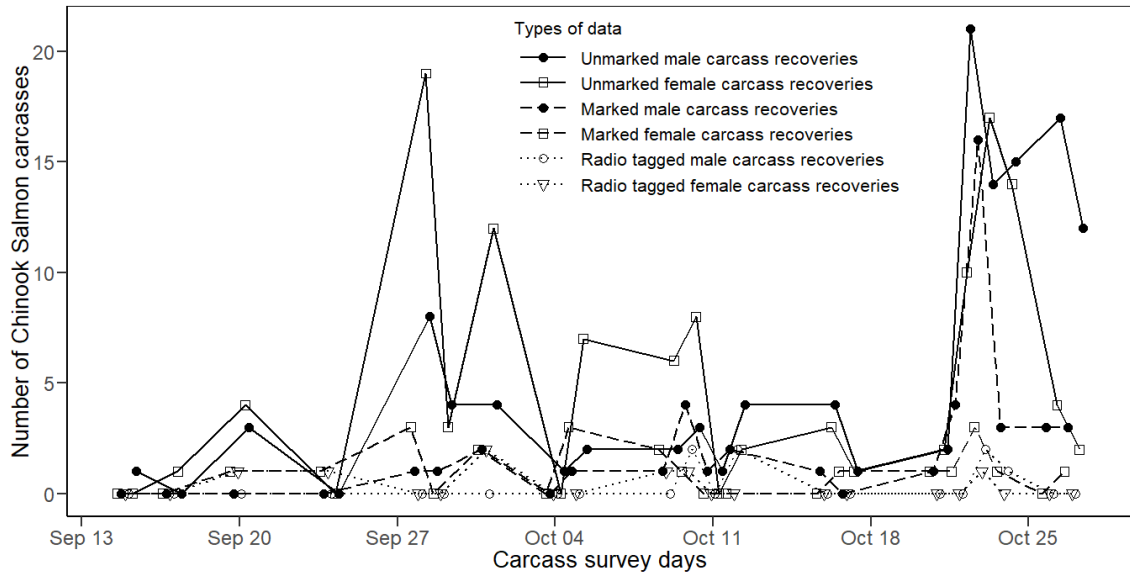Figure C.2: Snorkel survey data summaries for unmarked, marked, and radio tagged Chinook.

Figure C.3: Carcass survey data summaries for male and female unmarked, marked, and radio tagged Chinook.
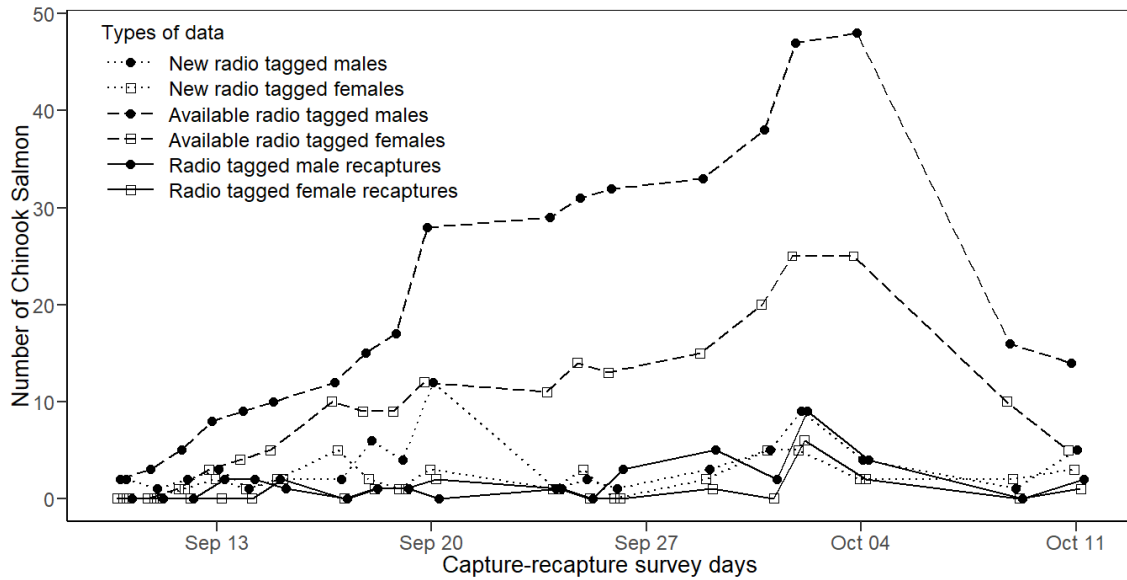
110

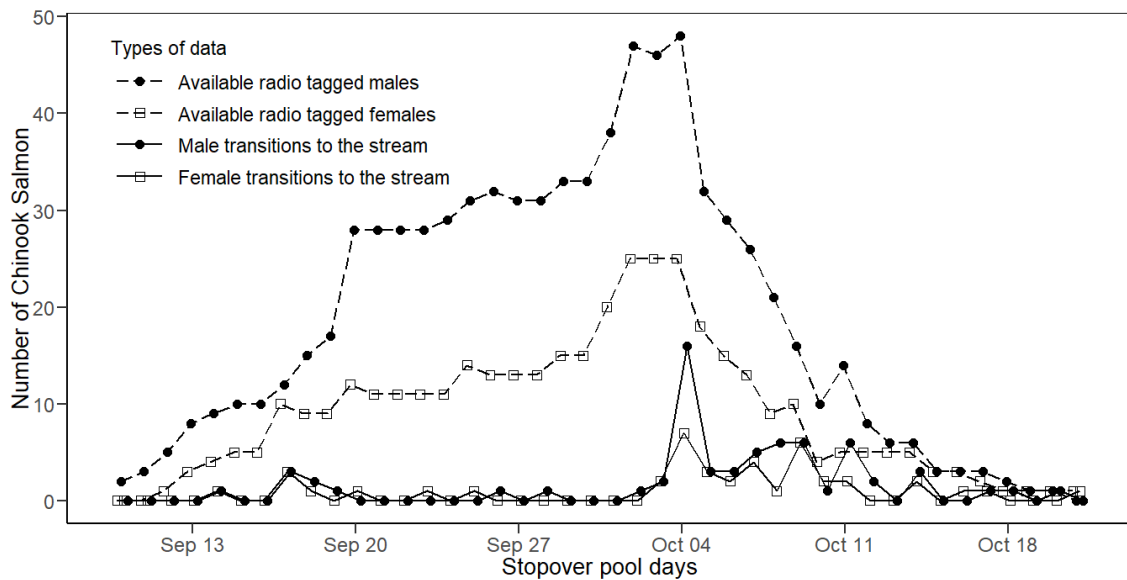Figure C.4: Capture-recapture data summaries for radio tagged male and female Chinook at the stopover pool.

Figure C.5: Radio tagged male and female Chinook transition from stopover pool to the spawning area and available at the stopover pool at each day.
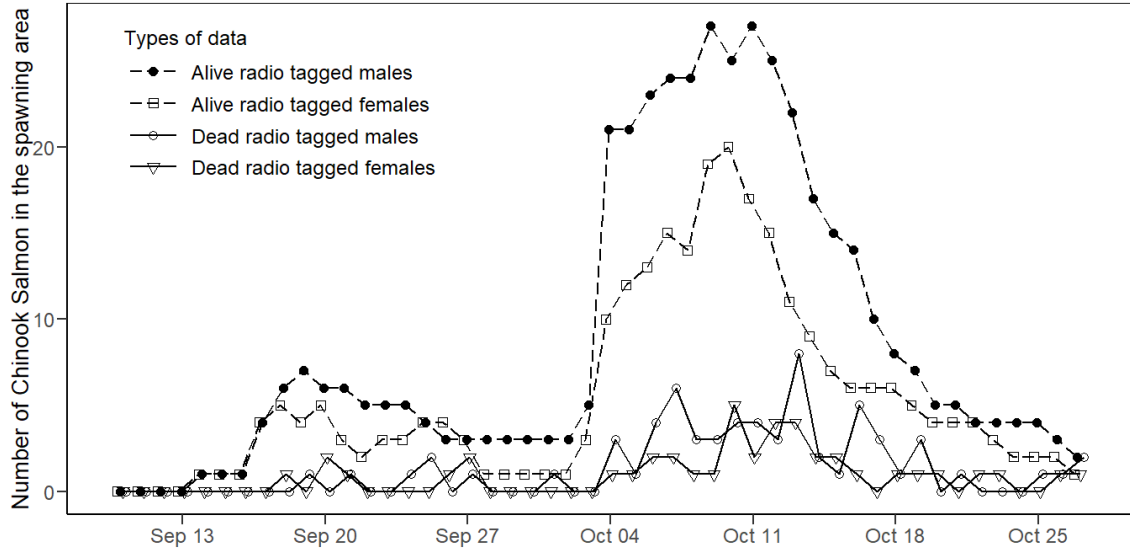
Figure C.6: Radio tagged male and female Chinook alive and die in the spawning area at each day.