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AN EXTENSION OF THE JOLLY-SEBER MODEL COMBINING TWO SOURCES OF CAPTURE-RECAPTURE DATA

by

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Abstract

I propose a modification of the Jolly-Seber model, the two-source Jolly-Seber (TSJS) model, to estimate population size by combining two sources of capture-recapture data of the same population where there might be an unknown overlap between two independent datasets. This is the case with recent surveys of whales and dolphins where researchers use individual identification records from both photo-identification and DNA profiling of skin biopsy samples. This sampling configuration results in two datasets that might contain the same individuals. This new approach enables the estimation of the overlap and the calculation the population size using capture-recapture information arising from both sampling methods. Monte Carlo simulations are used to assess the properties of the present estimator. When all the assumptions are met, the estimator seems to be unbiased as long as the occasion-specific simultaneous sampling probability is above 0.2. Simulation analyses also indicate that the proposed method performs better than existing closed-population estimators when there is little heterogeneity among individuals in capture probabilities and when the average capture probability is high. Alternatives have been explored and a two-source version of model M_0 has also been developed and compared to the TSJS estimator. Traditional closed-population estimators have been compared to the new approaches (TSJS and two-source M_0 models) when the population is open and the assumption of homogeneous capture probability is violated. Both procedures are finally applied to real data on the humpback whale *Megaptera novaeangliae*, on the wintering grounds of New Caledonia (South Pacific), where individuals have been sampled independently by skin sampling biopsy and photo-identification or simultaneously by both methods on a same capture occasion. The proposed methods hold great promise in monitoring by providing researchers and managers with a method allowing a diversity of sampling protocols. It could be more efficient in estimating population size, in terms of both precision and bias, than models based only on one type of data. And as it is important to control variation in a sampling design, this methodology could also provide a useful way to reduce variation by increasing the sample size and, hence, to enhance the estimator precision.

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INTRODUCTION

Animal population size is typically a variable of importance in decision analysis to develop optimal management strategies for wildlife populations under uncertainty. Reliable estimates are essential for conservation purposes, especially to adequately monitor endangered populations and prevent extinction. The necessary and difficult challenge of sustainable harvest management also requires good estimates in the fishery and sport hunting industries where the management of commercially-interesting species is vital for the targeted species, the whole ecosystem balance and also for the industry itself. Investigating population size can also provide a measure of success in pest control management programs and it ultimately leads to a better understanding of ecology in general.

Historical background

The methodology behind modern population size estimation goes back to Graunt in England in 1662 with his work on ratios on the mortality due to the Black Plague, Süssmilch in the first part of the 17th century with his work on the probability of mortality and later Laplace in the second part of the 17th century and his work on the French population census (Hald, 1990; Horváth, 1991; Laplace, 1783). The impossibility for census to give a correct count, the cost of such surveys and a rather undeveloped administration at that time, led to the replacement of exhaustive knowledge by an extrapolation based on surveys of parts of the population. The goal was to find a multiplier that would give an estimated total size for the population, once applied to a count based only on a part of the population. Laplace in his mémoires “Sur les naissances, les mariages et les morts” (1783) gives the prelude of the importance and use of population size investigation in modern ecological studies:

> [1]*“Il est donc intéressant, à tous égards, de connaître la population de France, d’en suivre les progrès et d’avoir la loi suivant laquelle les hommes sont répandus sur la surface de ce grand royaume.”*

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[1] *“It is therefore interesting in every regard to know the population of France, to follow the progress of it, & to have a law according to which the population has spread over this large realm.”*

Overview of abundance estimation

In studying population dynamics in ecology it is indeed desirable to have an estimate of the population size to start with. Different methodologies have thus been developed to estimate such a parameter. There are three main approaches: census methods i.e. the complete count of the population, surveys based on samples i.e. sampling space, and methods based on the capture or removal of animals from the population i.e. sampling animals. The first one being limited to confined populations, a great majority of ecological studies deal with sample surveys or mark-recapture methods when trying to estimate abundance.

The main distinction between sample survey and capture methods is the framework of the survey protocol: while population size can be directly obtained from one survey occasion with sample surveys, capture methods typically require several occasions to produce an estimate.

Methods based on the capture or removal of animals from the population are mostly used for elusive organisms for which counts on one occasion would not provide reliable abundance estimates. Because of habitat characteristics, behavior, size or other aspects of the biology, for some species, animals are not easily observable in the wild and abundance estimation can only be accomplished by capturing individuals (e.g. by traps). Capture methods fall into two categories:

(1) removal methods in which the captured individuals are not returned to the population,

(2) capture-recapture methods in which individuals are released back into the population after capture.

In the latter, captured animals are usually marked and returned to the population hence the name: capture-mark-recapture (CMR) experiments. Repeated sampling occasions provide capture histories for the individuals, a consequence of which is the possibility to use probabilistic models to estimate population size. Those models can be divided in two categories (1) closed-population CMR models; and (2) open-population models.

Closed population models

In ecology an animal population that can be considered not subject to any death, birth, immigration or emigration processes over the study period is said to be closed. The closure assumption for those models thus implies no gain or loss of individuals (i.e. no turnover) during the entire duration of the experiment. Consequently, closed-population models rely on the following assumptions:

1. animals do not die or leave the population by permanent emigration during the sampling period,

2. animals do not enter the population by birth or permanent immigration during the sampling period.

Each model may in addition require other assumptions that will be specified as appropriate.

Two sampling occasions

Derived from the method used by Laplace (1783), the Lincoln-Peterson estimator is based on a two-sampling occasion capture-recapture experiment and is at the basis of the understanding of all CMR models (Begon, 1979; Pollock et al., 1990; Schwarz and Seber, 1999; Seber, 2002; Williams et al., 2002). In addition to the closure assumption, equal capture probability and no loss of mark are assumed. As a result of the assumption of equal capture probability, the proportion of marked animals recaptured in the second sample should be the same on average as the proportion of animals captured at the first occasion in the population. The Petersen estimate is therefore:

$\hat{N} = \frac{n_1 n_2}{m_2}$ where $\hat{N}$ is the estimated population size, n_1 the number of individuals captured on the first sampling occasion, n_2 the number of individuals captured on the second occasion and m_2 the number of marked individuals on the first occasion that are recaptured on the second.

However, a modification of this estimator, the Chapman's modification of the Lincoln-Petersen is known to perform better, with less bias and a finite variance estimate (Begon, 1979; Pollock et al., 1990; Seber, 2002):

$$\hat{N}_c = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$$

Multiple sampling occasions

If there are more than two sampling occasions, animals are captured, marked, released back and potentially recaptured on subsequent occasions. On each occasion the number of marked and unmarked animals captured in the sample is recorded. The type of marking used helps to distinguish between features of two methods to estimate abundance:(1) with only one type of marking there is no way of distinguishing between marked individuals; and (2) with a specific mark for each individual captured, all marked animals are uniquely recognizable.

The first marking option leads to a direct extension of the Lincoln-Petersen estimator: the Schnabel method (Seber, 2002). The probability of what was seen is written as a function of the number of captured individuals at the *t*th time (n_t) and the unknown parameter (N). This can be expressed as the product of the probability of obtaining m_t marked animals out of n_t and the conditional probability of the number of marked animals seen at the *t*th time given m_t, which depends only on the total (M_t) of marked animals in the population just before the *t*th sample is taken:

$$L(N, M_t) = P\{m_t | n_t; N\} P\{f_1, f_2 ... | m_t; M_t\}$$

As the probability of sighting a marked animal is M_t/N at each sighting, the probability of having m_t marked animals among n_t sightings (given the assumption that animals are sighted independently and with equal and constant probability) is given by the binomial distribution:

$$P\{m_t | n_t; N\} \propto \left(\frac{M_t}{N}\right)^{m_t} \left(1 - \frac{M_t}{N}\right)^{n_t - m_t}$$

As M_t is known, the likelihood of *N* given n_t and *M* is just $P\{m_t | n_t; N\}$ and m_t is sufficient for *N*. In this case the maximum likelihood for *N* is defined by the equation also known as the Schnabel census estimator:

$$\hat{N} = \frac{\sum_{t=1}^{T} M_t n_t}{\left(\sum_{t=1}^{T} m_t\right) + 1}$$

The marking option where all captured individuals are uniquely marked is used in multinomial models that are likelihood-based. Additional assumptions include:

1. Animals do not lose their mark/tag,

2. Tags/marks are correctly recognized (no misreading) and reported.

The simplest model, denoted M_0 (no variation in capture probability), also assumes that the capture probability *p* is constant over the capture occasions and equal among individuals (Amstrup et al., 2005; Borchers et al., 2002; Chao, 2001; Otis et al., 1978; Schwarz and Seber, 1999; Seber, 2002; Williams et al., 2002):

$$L(N, p) = \frac{N!}{(N - M_{T+1})! \prod_h a_h!} p^n (1 - p)^{TN - n}$$

where *T* denotes the number of capture occasions, *p* the capture probability, a_h the frequency for observable capture history *h*, $n = n_1 + n_2 + ... + n_T$ the total number of captures, M_{T+1} the number of unmarked animals caught during the study.

In this model there are only two parameters, *N* and *p*, and the statistics that are necessary to obtain them are M_{T+1} and *n*. The maximum likelihood estimator of *N* and *p* are then obtained using numerical methods that maximize the previous equation.

However, this simple model M_0 is often inappropriate when applied to real, heterogeneous populations (i.e. individuals vary in their availability for capture), and other models have been developed to relax the assumption of equal probability. They allow capture probabilities to vary with time, and/or among animals. Some of these models are described below (Amstrup et al., 2005; Borchers et al., 2002; Chao, 2001; Otis et al., 1978; Schwarz and Seber, 1999; Seber, 2002; Williams et al., 2002):

M_t: capture probabilities can vary from one occasion to the next

M_h: capture probabilities can vary among animals but are constant across time for each individual

M_{th}: capture probabilities can vary among animals and across time

M_b: a behavioral response to being captured affects the capture probability on subsequent occasions.

As closed population models might have very little relevance for some populations where significant turnover can be expected, for example over long monitoring periods and many biological cycles, open-population models are used to better represent the population and thus get more reliable estimates.

Open population models

When the population closure assumption is relaxed, models including potential gains, by birth and immigration, and losses, by deaths and emigration, for populations can be used to study the changing nature of those open populations. Open-population models allow estimation of a wide variety of biological parameters, including birth rate and survival rate (Lebreton et al., 1992; Lebreton and Pradel, unpublished; Lindberg et al., 2001; Nichols et al., 2004; Schwarz, 2001; Schwarz and Arnason, 1996; Seber, 1986).

At present, the only open-population model that estimates the population size is the Jolly-Seber (JS) model. This model relies on the following assumptions (Schwarz, 2001; Schwarz and Seber, 1999; Seber, 1986):

1. all animals present (marked or unmarked) in the population at the time of the t-th sample ($t = 1, 2, \ldots, T$) have an equal probability of being caught,

2. all marked animals present in the population immediately after the tth sample have an equal survival probability (ϕ_t) until the (t+1)th sampling time ($t = 1, 2, \ldots, T-1$),

3. animals do not lose their marks or tags,

4. immigration and emigration cannot be separated from birth and death without additional information,

5. all emigration from the sampling population is permanent.

The major criticism leveled at the JS model for the estimation of abundance and the probable reason why closed population models might sometimes be preferred is the fact that heterogeneity is not permitted in capture probability in the partial likelihood used in the JS model to estimate population size. Methods to overcome this issue and reduce the bias in the JS estimates have been developed but have seen little application (Hwang and Chao, 1995; Pledger and Efford, 1998).

The Cormack-Jolly-Seber (CJS) model is a widely used open-population model and is a partial likelihood of the JS model disregarding the terms for captures of unmarked animals and losses on capture. It relies on the following assumptions usually referred as the “iii (triple-I) assumptions” (Lebreton et al., 1992):

Identity of individuals (matching system is reliable, tags are not ambiguous and not lost),

Independence of individuals,

Independence of successive capture events.

However, it does not directly give an estimate of the population size as *N* does not appear in the likelihood. Therefore, McDonald and Amstrup (2001) have developed a Horvitz-Thompson estimator of population size that uses the capture probabilities obtained with the CJS model and relies on the assumption that marked and unmarked individuals have the same capture probability, an assumption not required in the CJS model.

Consequences of violating model assumptions

All abundance estimation methods are based on a set of assumptions under which the method is hopefully robust and reliable. However, it often arises that one or more assumptions cannot be met, even with the estimation method that seems the most appropriate. Studies based on simulations have been carried out to evaluate the characteristics of bias (expected range and direction) that occurs in the case of assumption violations (Chao, 1989; Devineau et al., 2006; McDonald et al., 2003; Wittes, 1972). It has been especially shown that estimators assuming equal catchability are usually negatively biased by heterogeneity in capture probabilities and that some estimators like the closed-population jackknife estimators for model M_h generally underestimate population size when the data are sparse while others, like Darroch’s model (Darroch, 1958), produce overestimations in such case (Carothers, 1973; Chao, 1987, 1989; Chao et al., 2000; Gilbert, 1973; Otis et al., 1978).

Marking methodology

Investigating abundance estimation of wild animal population using CMR experiments has been of growing interest in ecology and a large number of marking methods have been developed. For mammals, the most common are tagging and photo-identification when the individuals can be distinguished by some natural and stable-over-time body patterns such as pigmentation and shape (Adams and Hutchings, 2003; Blackwell et al., 2004; Calambokidis and Barlow, 2004; Derocher and Stirling, 1995; Forcada and Robinson, 2006; Karanth and Nichols, 1998).

The recent development of molecular ecology has led to the emergence of innovative techniques of genetic tagging or DNA fingerprinting that could be used as traditional marking methods in CMR models to estimate population size (Jones and Ardren, 2003; Manel et al., 2005; Palsbøll, 1999; Palsbøll et al., 1997). The use of non-invasive genetic methods by genotyping hair, feather, faeces, or sloughed skin represents an alternative to traditional marking methods and is becoming increasingly popular in conjunction with mark-recapture methods to estimate population size (Bellemain et al., 2005; Boulanger and Hamilton, unpublished; Boulanger et al., 2004a; Boulanger et al., 2004b; Creel et al., 2003; Eggert et al., 2003; Keller et al., 2005; Lukacs and Burnham, 2005; Mowat and Paetkau, 2002; Prugh et al., 2005; Wilson et al., 2003). Cost and intensity of sampling can be reduced and trap-response does not often arise as can be the case in traditional marking techniques (Brown et al., 1994; Clapham and Mattila, 1993; McKelvey and Schwartz, 2004; Mills et al., 2000; Taberlet et al., 1999; Weinrich et al., 1992; Weinrich et al., 1991). However, even if the advances in this field offer great promise, noninvasive genetic sampling still requires improvement in the methodology to be used reliably in CMR studies (Lukacs and Burnham, 2005; McKelvey and Schwartz, 2004; Mills et al., 2000; Palsbøll, 1999; Roon et al., 2005; Schwartz et al., 1999; Taberlet et al., 1999; Waits et al., 2001). And, despite ethical issues and because DNA is usually collected in greater quantities and of better quality, invasive sampling methodology could be more easily and reliably used with CMR models for some species when non-invasive sampling might be impossible (Garrigue et al., 2004; Keller et al., 2005; Palsbøll et al., 1997; Valsecchi et al., 1998).

Objectives

With the development of molecular ecology, multiple sources of data can be obtained for some species and combining them to obtain population size estimates would provide more information about abundance than each survey could provide alone. A good example is the humpback whale population in the South Pacific where improvement of whale population size estimates is required for conservation purposes and to address recent political issues. In the Southern hemisphere, humpbacks migrate from their feeding ground in Antarctica to warmer waters to breed in winter. New Caledonia is one of the breeding grounds for this species and whales are usually present from July to September. During this period, two sources of information are opportunistically collected during systematic boat surveys: photo-identification and genetic identity from skin biopsy. Individual whales are frequently photographed and genotyped on the same capture occasion. However, on a capture occasion, some whales may not fluke so cannot be photographed and some others cannot be approached closely enough to be genotyped. Researchers, thus, typically end up with two datasets that are analyzed separately for abundance purposes. Therefore, the problem of using both datasets together extends to a two-list approach with an unknown overlap between the lists that requires a formulation for this “matching dilemma”. The problem of estimating the size of a population by using multiple sources is often referred to as the multiple-recapture estimation problem (Darroch, 1958). Several approaches have been developed to model multiple-list census data for estimating the size of a closed population: Rasch-type models (Bartolucci and Forcina, 2001; Lindsay et al., 1991), log-linear models (Darroch et al., 1993; Fienberg, 1972a, b), Bayesian methods (Fienberg et al., 1999; Madigan and York, 1997; Smith, 1988). El-Khorazaty et al. (1977) reviewed the early literature on methods for multiple-system estimation.

My interest here was motivated by the situation often faced with marine mammal surveys for which researchers usually end up with two overlapping datasets. If both sets of data indeed lead to valid estimates, using the two datasets separately or using a mean of the estimates is unefficient since that implies missing some recapture information, i.e. when the animals are captured by one method and then recaptured by the other. The objective was thus to create an analytical framework that would allow a worker to combine two sources of data available in an open-population model to increase the sample size and provide a more robust monitoring estimator.

My first objective is the creation of an analytical framework that will allow the combination of two sources of data available in an open-population model. Therefore, I will present an ad hoc re-formulation of the JS model. I will investigate the ability of this extension of the JS method (Amstrup et al., 2005; Jolly, 1965; Seber, 1965, 2002) to use two sources of data by estimating the possible overlap of these data. However, I will also stress alternative models and approaches to this two-list latent variable problem in an effort to consider a wider range of sampling situations.

My second objective is to develop simulations to check the performance and robustness of the model when all assumptions are met, and when one or more fail. I especially focus on the violation of the assumption of homogeneous capture probability among individuals of the population. In the final stage, the simulations will aim at reproducing as closely as possible a long-lived open population, such as a humpback whale population, and the sampling protocol used to survey such a population, in order to check the error in the abundance estimate in this situation. Existing models currently used in this field for population assessment with only one list will be compared to this new approach.

As this new open-population model was motivated by the need to estimate the size of humpback whale populations, I will investigate the population size of this species in the South Pacific and the new estimation methods will be applied to data from New Caledonia and compared to estimates resulting from other abundance estimation methods already available.

1. Chapter One

An extension of Jolly-Seber model: the two-source Jolly-Seber model

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1.1. Abstract

The Jolly-Seber (JS) model has been used in open population abundance estimation for many years, for organisms ranging from whales to bears, squirrels to alligators. In particular, it has been used for humpback whale populations on a number of occasions where there sometimes are two datasets resulting from two different sampling methods. I propose a modification of the Jolly-Seber model, the two-source Jolly-Seber (TSJS) model, to estimate population size by combining two sources of capture-recapture data where there might be an unknown overlap between the two datasets. This is the case with recent surveys of whales and dolphins where researchers use individual identification records from both photo-identification and DNA profiling of skin biopsy samples. This sampling configuration results in two datasets that might contain the same individuals. For those individuals captured by both sampling methods, some have been captured by both methods on the same capture occasion and it is consequently possible to merge the records for those individuals, the two capture histories in each dataset, into one in the combined dataset. However, an unknown overlap sometimes occurs, in the combined dataset, when individuals have been captured by both sampling methods separately but never simultaneously by both, a consequence of which is the risk of over-estimating the population size if the data are inappropriately combined. Using the simultaneous double capture in the data, it is possible to estimate the "non-double identity" rate of each individual, namely the probability of having one and only one capture history in the combined dataset. This new approach enables researchers to avoid the over-estimation of the population size when using the combined dataset by estimating the probability of non-double identity which is then used in the Jolly-Seber framework to estimate the population size. I also investigate other approaches to answer the general issue of two overlapping datasets for the estimation of abundance in an effort to consider a wider range of sampling designs with closed-form likelihoods: an extension of model M_0 with two

overlapping sources of data referred to as the two-source M_0 model and latent multinomial models based on models M_0 and M_t, using a latent capture history approach. I finally discuss the limitation of an extension of these likelihood-based closed-population methodologies to open populations.

1.2. Introduction

Population size estimates are important for managing species for conservation purposes, sustainable development aims, pest control objectives and in many other situations. Investigating abundance estimation of wild animal population has been of growing interest in ecology and a large number of methods have been developed (Amstrup et al., 2005; Williams et al., 2002). The use of capture-mark-recapture (CMR) methods, such as photo-identification and genetic sampling, to estimate animal population size is especially increasing (Bellemain et al., 2005; Boulanger et al., 2004a; Calambokidis and Barlow, 2004; Calambokidis et al., 1990; Derocher and Stirling, 1995; Durban et al., 2005; Forcada and Robinson, 2006; Garrigue et al., 2004; Katona and Beard, 1990; Keller et al., 2005; Kohn et al., 1999; Larsen and Hammond, 2004; Lindeman, 1990; Lukacs and Burnham, 2005; Mowat and Paetkau, 2002; Palsbøll, 1999; Palsbøll et al., 1997; Parra et al., 2005; Pearse et al., 2001; Smith et al., 1999; Urbán et al., 1999). Photo-identification and genetic fingerprinting from skin sampling are widely used to survey marine mammals, as it enables researchers to sample more individuals and gives more information about the population. Doing so, researchers typically end up with two datasets that are usually analyzed separately for abundance purposes. The objective here is to develop a model for abundance estimation that uses the combined dataset arising from the binding of those two datasets and hence to use all the data available. At present most models used to get population size estimates are closed-population based (Amstrup et al., 2005; Borchers et al., 2002; Seber, 1986), even when the population is open (Garrigue et al., 2004; Larsen and Hammond, 2004; Urbán et al., 1999). Open-population models have been developed to overcome the violation of assumptions when using closed-population models for data collected over an extended period (Amstrup et al., 2005; Seber, 1986). In terms of population size estimation, they can also provide useful information on abundance trend. Nevertheless, open-population models, like the Cormack-Jolly-Seber (CJS) model, are mostly used to estimate parameters such as survival rate and capture probability

(Cormack, 1964). Even though one possibility to estimate abundance with the CJS model is to use a Horvitz-Thompson-like estimator after estimating the capture probabilities, currently only the Jolly-Seber (JS) model leads to a direct estimate of population size (Amstrup et al., 2005; Jolly, 1965; Lebreton et al., 1992; McDonald and Amstrup, 2001; Seber, 1965; Seber, 1986). The JS model has been used for organisms ranging from whales to bears, squirrels to alligators (for examples see (Amstrup et al., 2005; Calambokidis and Barlow, 2004; Derocher and Stirling, 1995; Pollock et al., 1990; Williams et al., 2002)). Joint modeling of several sources of recapture data (mark-recapture, tag-resighting, tag-recovery) has been previously investigated by Burnham (1993), Barker (1997), Barker and White (2001) and Barker et al. (2004): likelihoods and a framework to make full use of these sources of reobservation data were developed, leading to parameter estimators equivalent to Jolly’s (1965) under random emigration, i.e. non permanent emigration. However, those sources of recapture data contribute to observations of marked individuals and there is no unknown overlap between the different types of data. Moreover, it is not possible to estimate population size under random (short-term relative to the monitoring period) migration without restrictive assumptions about the movement of recruits or without additional information (Barker, 1997). So here I propose an extension of the formulation developed by Jolly (1965) and Seber (1965) to obtain population size estimates by combining two different sources of live capture-mark-recapture data where there might be an unknown overlap between the datasets. The focus here is on aspects of study design that are especially relevant to open populations. However, I also consider closed form likelihoods and discuss a possible extension to open populations in order to extend the methodology to a broader range of sampling situations.

This chapter first describes the original JS model and related existing models before presenting the two-source Jolly-Seber (TSJS) model which uses two independent sources of mark-recapture information. This method enables researchers to have bigger sample size for the purpose of population size estimation, in the case where all individuals of a population are not necessarily available by a single sampling method. A likelihood based approach is introduced using latent multinomial models, based on model M_0 and a latent multinomial capture history approach (Link and Barker, 2010), based on models M_0 and M_t. Finally, extension of these likelihood approaches to open populations is discussed as a future direction for research when the computing power (or a suitable algorithm) becomes available to make it feasible.

1.3. The classic Jolly-Seber model

The JS model (Jolly, 1965; Seber, 1965, 2002) is, at present, the most popular capture-recapture open-population model used to estimate population size. The data required to use such a model are similar to the data for capture-recapture closed-population models: animals are captured, marked and released to be recaptured at subsequent discrete sampling periods. At each capture occasion, marked and unmarked animals have to be recorded, leading to capture histories being available for each caught individual. From those capture histories, population size can be calculated at most sampling times as well as survival, recruitment rate and capture probability.

1.3.1. Model components

Originally Jolly (1965) and Seber (1965) developed different likelihood approaches which led to the same estimator for the parameters. I detail here the approach of Brownie et al. (1986) based on Jolly's (1982) work. This likelihood for a *T*-sampling-occasion study can be decomposed into 3 components:

1. The component L_1 models the captures of unmarked individuals in terms of conditionally independent binomial terms. Each binomial probability gives the likelihood of capturing u_t unmarked individuals on occasion *t* given there are U_t unmarked animals in the population each of whom has a probability p_t of being captured on that occasion:

$$P_1\left(\{u_t\}|\{U_t\},\{p_t\}\right)=\prod_{t=1}^{T}\left[\frac{U_t}{u_t!(U_t-u_t)!}p_t^{u_t}(1-p_t)^{U_t-u_t}\right]$$

where u_t is the number of unmarked individuals captured at occasion *t*, with *t*=1, 2,…, *T*, U_t the available population of unmarked individuals and p_t the capture probability.

2. The component L$_2$, concerning loss on capture, i.e. captured animals not released back into the population:

$$P_2\left(\{d_t, d_t^{'}\} \middle| \{m_t, u_t\}, \{\eta_t, \eta_t^{'}\}\right) = \prod_{t=1}^{T}\left[\frac{u_t!}{d_t^{'}!(u_t - d_t^{'})!}(\eta_t^{'})^{u_t - d_t^{'}}(1-\eta_t^{'})^{d_t^{'}}\right]$$

$$\times\prod_{t=2}^{T}\left[\frac{m_t!}{d_t!(m_t - d_t)!}(\eta_t)^{m_t - d_t}(1-\eta_t)^{d_t}\right]$$

where m_t is the number of marked animals captured at time *t*, with *t*=1, 2,…, *T*, $d_t, d_t^{'}$ the number of m_t and u_t respectively not released back into the population and $\eta_t, \eta_t^{'}$ the probability of release into the population for marked and unmarked animals m_t and u_t.

The component L$_2$ is a product, in two parts, of binomial likelihoods. The first part is a product of likelihoods dealing with the unmarked individuals: each gives the probability on occasion *t* of releasing into the population $u_t - d_t^{'}$ individuals, i.e. the number of the unmarked animals u_t that were captured on occasion *t* and did not die on capture, each of whom has a probability $\eta_t^{'}$ of being released into the population on that occasion. The second part of component L$_2$ is a product of likelihoods dealing with the marked individuals: each binomial probability gives the probability on occasion *t* of releasing into the population $m_t - d_t$ individuals, i.e. the number of the marked animals m_t that were captured on occasion *t* and did not die on capture, each of whom has a probability η_t of being released into the population on that occasion.

3. The component L$_3$, originally derived by Cormack (1964) and usually referred to as the Cormack-Jolly-Seber (CJS) model, containing the recapture data m_{tj} (number of animals seen at time *t* and seen again at time *j*) conditional on the numbers of newly and previously marked animals released at each occasion:

$$P_3\left(\{m_{tj}\} \;\middle|\; \{R_t\},\{\phi_t\},\{p_t\}\right) = \prod_{t=1}^{T-1}\frac{R_t}{(m_{t,t+1})!(m_{t,t+2})!\ldots(m_{t,T})!(R_t - r_t)!}(\phi_t p_{t+1})^{m_{t,t+1}}$$

$$\times\{\,[\phi_t(1-p_{t+1})\phi_{t+1}p_{t+2}]^{m_{t,t+2}}\times\ldots\times[\phi_t(1-p_{t+1})\ldots\times\phi_{T-1}p_T]^{m_{t,T}}\,\chi_t^{R_t - r_t}\,\}$$

where R_t denote the number of releases at time *t*, r_t the number of R_t captured again later, ϕ_t the apparent survival at time *t* and χ_t the probability that an animal alive and in the study population at time *t* is not caught or observed again at any time after capture occasion *t*.

The component L_3 of the JS model is a product of *T*-1 conditionally independent multinomial distributions that specify a probability for each possible capture history given the number of animals exhibiting each capture history. Under the CJS model, all parameters are based on the time index only and there are 2*T*-3 identifiable parameters: $\phi_1, \ldots, \phi_{t-2}$ and $p_2,..$, p_{t-1}. The initial capture probability p_1 cannot be estimated and the final survival and capture probability cannot be estimated separately but only as a product $\phi_{t-1}p_t$. It is also important to note that the parameter ϕ_t is a product of two biologically interpretable parameters: $\phi_t = S_tF_t$. S_t is the probability of surviving between capture occasion *t* and *t*+1, also referred as “true survival” (as opposite to “apparent survival”) and F_t is the probability of an animal being in the study area at that time, given it is alive at occasion *t*+1, also referred as “fidelity”.

1.3.2. Abundance estimation

In the JS model, population size does not appear directly in the likelihood but can be derived from component L_1 with the estimation of the size of the unmarked population being: $\hat{U}_t = \frac{u_t}{\hat{p}_t}$. It follows that the population size is similar to the Petersen-Lincoln estimator: $\hat{N}_t = \hat{U}_t + \hat{M}_t = \frac{n_t}{\hat{p}_t} = \frac{\hat{M}_t n_t}{m_t}$ where $\hat{p}_t = \frac{m_t}{\hat{M}_t}$ and $\hat{M}_t$ is the estimated number of marked animals.

However, the difficulty here lies in the estimation of M_t, the total number of marked individuals in the population immediately before time *t*, as it is an open-population model and thus death and emigration can happen. This is done by estimating the size of two different groups of animals in the population:

1. the group $(M_t - m_t)$ of marked animals not seen at time *t*,

2. the group R_t of animals seen at time *t*, marked and released for subsequent recaptures.

Taking z_t and r_t as members of, respectively $(M_t - m_t)$ and R_t, which are seen at least once again after time *t*, this leads, under the assumption of equal catchability, to the ratios of $\frac{z_t}{M_t - m_t}$ and $\frac{r_t}{R_t}$ being approximately equal: $\frac{z_t}{M_t - m_t} \approx \frac{r_t}{R_t}$

Consequently an estimator of M_t is given by: $\hat{M}_t = m_t + \frac{R_t z_t}{r_t}$

This estimator is defined for *t*= 1,…, *T*-1 with $M_1 = 0$, as animals are required to have been seen before and after each time *t*. Moreover if no loss happens on capture, R_t is equivalent to n_t, the total of animals captured at occasion *t*. However, the estimators $\hat{N}_t$ and $\hat{M}_t$ are biased and Seber (2002) recommended that m_t and r_t be greater than 10 for the following approximately unbiased estimators:

$$\hat{N}_t = \frac{(n_t + 1)\hat{M}_t}{m_t + 1}$$

$$\hat{M}_t = \frac{z_t(R_t + 1)}{r_t + 1} + m_t$$

$\hat{\phi}_t = \frac{\hat{M}_{t+1}}{\hat{M}_t - m_t + n_t}$ where $\hat{\phi}_t$ is the natural survival rate at time *t*

$\hat{B}_t = \hat{N}_{t+1} - \hat{\phi}_t \hat{N}_t$ where $\hat{B}_t$ is the estimator of the recruitment between time *t* and *t*+1

$$\hat{p}_t = \frac{m_t}{\hat{M}_t}$$

The asymptotic variance for $\hat{N}_t$ is given by:

$Var(\hat{N}_t | N_t) = N_t[N_t - E(n_t)] \times \left\{ \frac{M_t - E(m_t) + R_t}{M_t} \times \left[\frac{1}{E(r_t)} - \frac{1}{R_t} \right] + \frac{N_t - M_t}{N_t \times E(m_t)} \right\}$ (Pollock et al., 1990)

This variance needs to be distinguished from the variance used by Seber (2002) which includes both sampling variability and non-sampling variability associated with the stochasticity of the birth and death processes. This above formulation for the asymptotic variance was chosen over Seber's formulation because researchers are usually interested in the variance associated with their estimation, i.e. $Var(\hat{N}_t | N_t)$, and because the other term present in Seber's formulation, $Var(\hat{N}_t)$, which represents an approximation for:

$Var(\hat{N}_t) = E(N_t) - \sum_{h=0}^{t-1} \frac{E[N_t(h)]^2}{B_h}$ where $t > h$, $N_{h+1}(h) = B_h$ and the expectations are conditioned on the $\{B_t\}$ (the number of animals that enter the population between occasion *t* and *t*+1) is usually much smaller than $Var(\hat{N}_t | N_t)$ and can therefore be ignored in most cases (except maybe when p_t is large) (Jolly, 1965; Seber, 2002).

The variances of $\hat{M}_t$, $\hat{\phi}_t$, $\hat{B}_t$ and $\hat{p}_t$ are given in Appendix 1.

1.3.3. Assumptions

The standard JS model relies on the following assumptions:

i. Within each capture method, the capture probabilities can vary over time but not among individuals,
ii. All animals have the same probability of survival between occasion *t* and occasion *t*+1 for all values of *t*,
iii. Marked animals do not lose their marks and marks are not overlooked,
iv. Sampling periods are short enough to avoid death during a sampling period,
v. Emigration is permanent,
vi. Capture events are independent of each other.

1.3.4. Derived models

From the original JS model described above, other models have been developed to target specific biological considerations that the original JS model did not permit (Schwarz, 2001). However, under those models, total population size estimation is not always possible.

Partially open models

These models involve a sampling situation that varies from the original JS model in a way that restricts partially the openness of the population. In the death-only model developed by Darroch (1959), the population is not subject to immigration and to recruitment over the course of the study period. Thus, under this model, true survival can be estimated along with capture probability and population size with the following estimator:

$$\hat{N}_t = n_t + \frac{R_t z_t^{'}}{r_t}$$

where $z_t^{'}$ is the number of animals not caught at time *t* known to be alive because seen alive later.

Birth only models have also been considered by Darroch (1959) for situations where there is no death or emigration but where recruitment can happen in the population. Under this model, the estimator for the population size is identical to the one of the JS model:

$$\hat{N}_t = \frac{\hat{M}_t n_t}{m_t}$$

However, here, the estimation of the marked population is straightforward as there is no death or emigration.

The Cormack-Jolly-Seber model

The CJS model is based on the component L_3 of the likelihood of the JS model and provides a flexible framework for conditional open-population modeling. This model permits the modeling of apparent survival and capture probability and the multistate models, especially the Conditional-Arnason-Schwarz (CAS) and Jolly Movement (JMV) models, derived from it allow the modeling and estimation of capture probability, apparent or true survival, and probability of transition between states (Arnason, 1972, 1973; Brownie et al., 1993; Hestbeck et al., 1991; Lebreton et al., 1992; Schwarz et al., 1993). Estimation of capture probability and of probability of transition between states is illustrated in an application on real data in chapter five.

To estimate population size, a Horvitz-Thompson estimator of population size has been proposed by McDonald and Amstrup (2001) for use with open models such as the CJS model and where individual covariates of capture are available:

$$\hat{N}_t = \sum_{i=1}^{N_t} \frac{I_{it}}{\hat{p}_{it}} = \sum_{i=1}^{N_t} \frac{1}{\hat{p}_{it}}$$

where $\hat{N}_t$ is the estimated size of the population at time *t*,

n_t is the number of animals captured at time *t*,

I_{it} is an indicator variable that takes the value 1 if animal *i* is captured at time *t* and 0 if not,

$\hat{p}_{it}$ is the estimated capture probability for animal *i* at time *t*.

However, this appears to be an inefficient estimator (R. Barker, pers. Comm.) so I do not consider it any further in the present thesis.

Age-dependent models

In the JS model, all individuals belong to a single-age group. However, in many animal populations, survival and capture probability may depend on the age of the individuals. Thus, Pollock (1981) developed a model derived from the JS model allowing age specificity: age-specific capture probability $p_t^{(\upsilon)}$ are estimated for periods t=2,…,T-1 and ages υ=1,…,ℓ. The likelihood for this model can be written as a product-multinomial likelihood that specifies a probability for each capture history and maximum likelihood allows the estimation of the capture probability $p_t^{(\upsilon)}$ and the survival rate $\phi_t^{(\upsilon)}$ for each age-class. The sampling design for such a model requires that timing of sampling and age transition coincide and that every captured animal is correctly assigned to an age-class. Then it is possible to estimate age-specific abundance:

$$\hat{N}_t^{(\upsilon)} = \frac{n_t^{(\upsilon)}}{\hat{p}_t^{(\upsilon)}}$$

Total abundance for all ages can be obtained by summing the abundance of all age classes. However, the age-specific capture probabilities are based on marked individuals and in order to estimate total population size using the previous equation, these capture probabilities need to be applicable to unmarked animals.

The assumptions are similar to those of the JS model with the additional requirements that capture probability and survival are equal within an age-class. Moreover, under this sampling design, any new unmarked individual is assumed to be correctly assigned to an age-class. In many situations, it is only possible to distinguish young individuals from adults and another approach is available where the age of an animal is only known if it has been captured at age 0 (Amstrup et al., 2005). In such models, it is possible to estimate the number of marked animals alive in each class using the actual number of caught individuals at the corresponding sampling occasion and their capture probability and survival. However, abundance estimation is usually not possible because unmarked individuals caught cannot be assigned to a specific age unless they were caught at age 0. Thus, the unmarked individuals caught at time *t* are a mixture of animals from different age classes and only the information provided by the known-age animals can be regarded but do not lead to an estimate of the total population size (Williams et al., 2002).

Another alternative to the general age-dependent model is the age-specific breeding model, related to the CJS model (Clobert et al., 1994), that permits the abundance estimation of the breeding part of the population. In this model, caught animals are either young (age 0) or adults breeders (age *k*+), all adults assumed to be breeders. Capture probabilities are assumed to be the same for marked and unmarked breeders leading to the following abundance for breeders:

$$\hat{N}_t^{(k+)} = \frac{n_t^{(k+)}}{\hat{p}_t^{(k+)}}$$

where $n_t^{(k+)}$ is the number of breeding-age animals caught at time *t* and equal to the sum of the marked and unmarked breeders $n_t^{(k+)} = m_t^{(k+)} + u_t^{(k+)}$.

However, under this model, neither the abundance of the animals of age 0 nor that of the non-breeders of age υ>0 can be estimated.

Reduced-parameter models

In these models survival and/or capture probability are assumed constant over time and the approach to calculate the abundance differs from the one used in the JS model. Jolly (1982) and Brownie et al. (1986) proposed the following population estimation method for reduced-parameter models:

as in the JS model: $\hat{N}_t = \hat{U}_t + \hat{M}_t$

and to estimate $\hat{M}_t$ and $\hat{U}_t$, they used:

$E(m_t + z_t | M_t) = M_t(1 - q_t\chi_t)$ and $E(u_t | U_t) = U_t p$

leading to: $\hat{M}_t = \dfrac{m_t + z_t}{(1 - \hat{q}\hat{\chi})}$ and $\hat{U}_t = \dfrac{u_t}{\hat{p}}$

where $\hat{q}$ =1- $\hat{p}$ and χ_t is the probability that an animal alive and in the population at sampling time *t* is not caught or observed again at any sampling time after time *t*.

Another difference from the JS model is that, with reduced-parameter models, it is possible to estimate the population size at time 1 and *T* as the capture probability is assumed to be constant over time.

1.4. The two-source Jolly-Seber model

The standard sampling experiment for the TSJS model is that of a JS experiment with two sampling methods and no loss on capture. In the following, individuals of a population can be sampled, on any capture occasion, by a method “1” or by a method “2” or by both simultaneously on the same occasion, designated as “3”. As usual in Jolly-Seber models, “birth” refers to any mechanism by which new individuals enter the population: reproduction or immigration. Similarly “death” refers to any mechanism by which individuals leave the population: death or emigration.

1.4.1. Assumptions

Assumptions are similar to those of the JS model, with three additional assumptions which are specific to the TSJS model:

vii. There is no loss on capture, i.e. animals are returned to the population following a capture,

viii. Having a capture by one method in the capture history does not depend on whether there has, or has not, been a capture by the other method,

ix. The same individual cannot be caught by the two separate sampling methods on an occasion without knowing it is the same individual, i.e. no unknown overlap occurs on each capture occasion, i.e. being caught by method 1, by method 2 or by both simultaneously are mutually exclusive events on each capture occasion.

The consequences of the violation of those assumptions will be discussed in chapters three and four.

1.4.2. Notation

$p_{t,k}$ = probability of capture at time t by method k (“1”, “2” or “3”)

ϕ_t = probability that an animal survives between time t and time t+1 given it was alive at time t, t=1, …, T-1

B_t = net birth, number of animals that enter and remain in the population between occasion t and t+1,

t=1, …, T-1. B_0 represents the number of animals alive just prior the first sampling occasion

n_t= total number of animals, marked and unmarked, captured at occasion t

$R^*_{t,k}$ = number of unmarked animals captured for the first time at occasion t by method k

u_t = total number of unmarked animals captured at occasion t

$r_{t,1}$= number of marked animals recaptured at occasion t by method 1 given that they were never captured simultaneously

$r_{t,2}$= number of marked animals recaptured at occasion t by method 2 given that they were never captured simultaneously

$r_{t,3}$= number of marked animals recaptured at occasion t by method k given that they have at least one simultaneous “3” capture in their record

$r'_{t,1}$= number of animals captured at occasion t by method 1, given they were never captured simultaneously, that are captured again by method 1

$r'_{t,2}$= number of animals captured at occasion t by method 2, given they were never captured simultaneously, that are captured again by method 2

$r'_{t,3}$= number of animals captured at occasion t by method k given that they have at least one simultaneous “3” capture in their record, that are captured again by method k

M_t^* = total number of marked animals captured by either method before occasion t

m'_t= total number of marked animals captured at time t

z_t= number of animals captured before t, not captured at t and captured again later

$z'_{t,1}$= number of animals captured by method 1 before t, not captured at t and captured by method 1 again later

$z'_{t,2}$= number of animals captured by method 2 before t, not captured at t and captured by method 2 again later

$z'_{t,3}$=number of animals captured before t, not captured at t and captured again later, that have at least one simultaneous “3” capture in their record

I_{id}= probability of an individual having a single entry in the combined data set, i.e. it either only appears in the dataset for one capture method, or, if it does appear in both, it has, at least once, been captured by both on the same occasion.

1.4.3. Data structure

The two sampling methods are used opportunistically and can also be used simultaneously on any capture occasion (which can be considered a third sampling method). At the end of the study, there is a capture-recapture dataset for method 1 (dataset 1) and a capture-recapture dataset for method 2 (dataset 2). A dataset is defined as a set of capture histories. The purpose of the model is to use the combined dataset arising from the binding of those two datasets. The starting point is a two-dataset approach with some unknown overlap between the datasets and this requires the use of the information resulting from simultaneous captures (when an animal is simultaneously sampled by method 1 and method 2 on the same occasion). Simultaneous captures enable the model to make the link between dataset 1 and dataset 2. Therefore, individuals with at least one simultaneous capture on one occasion and separate captures by method 1 and by method 2 on at least two other occasions, thus belonging to dataset 1 and dataset 2, will be identified as one individual and will have only one capture history in the final dataset when dataset 1 and dataset 2 are compiled together. This will therefore increase the number of effective recaptures and consequently the precision of the estimation. The problem comes from the individuals that have never been sampled simultaneously by method 1 and 2 but have been captured separately by method 1 and 2 on different occasions. Those individuals will have a capture history (also called entry) in dataset 1 and another in dataset 2. However, when the two datasets are compiled together, those individuals will appear twice in this combined dataset as it will not be possible to make the link between the capture history with method 1 and the one with method 2, in other words to know that they are the same individuals.

In this sampling situation, the observed data can be arranged in a 2x2 contingency table:

		In the method 2 dataset	
		Present	Absent
In the method 1 dataset	Present	n_{12}	$n_{1.}$
	Absent	$n_{.2}$	–

where n_{12} is the observed number of individuals in both dataset 1 and dataset 2, $n_{1.}$ is the observed number of individuals in dataset 1 only and $n_{.2}$ is the number of individuals in dataset 2 only. However, given the misclassification issue, the assignment to the correct dataset for each individual is unknown. Hence, the true numbers underlying n_{12}, $n_{1.}$ and $n_{.2}$ are unknown, biased by the number n_u (the number of animals in datasets 1 and 2 but never caught simultaneously by both 1 and 2 at the same time). Thus, $n_{1.}$ and $n_{.2}$ are too large by n_u, while n_{12} is too small by the same amount.

The approach here aims at estimating the probability that an individual has a single entry (or capture history) in the combined dataset in order to extend the the Jolly-Seber model to an ad hoc two-overlapping-list model to estimate abundance. The first step is to estimate this probability I_{id}.

1.4.4. Estimation of the probability of single identity I_{id}

The possible histories of captured animals can be seen more clearly in Fig. 1-1, the set of all possible histories of captured animals for a *T*=6 study. Thus, the number of animals actually caught by method 1 is the number of animals in $B \cup G \cup E \cup F$, by method 2 the number of animals in $C \cup D \cup E \cup F$, and by both simultaneously, method 3, the number of animals in $A \cup B \cup C \cup E$. However, when lists 1 and 2 are combined, the resulting list will be loo large by the number in $E \cup F$. Those animals in E will be easily identified and corrected thanks to the information provided by the simultaneous capture, but those in F will not.

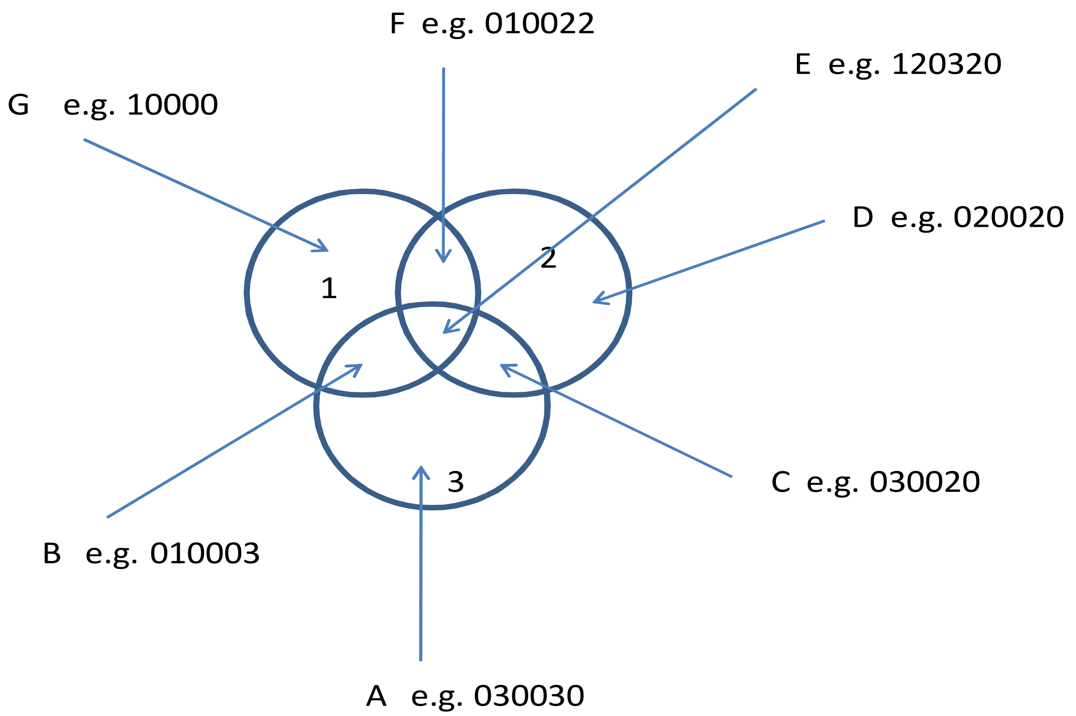


Fig. 1-1- A Venn diagram showing the possible types of capture histories (with examples) for captured animals for a *T*=6 study.

N.B.: in what follows, “Pr” means “probability”.

I define the following events:

$\ell_1 = \{$animal *i* belongs to list 1$\} = B \cup G \cup E \cup F$

$\ell_2 = \{$animal *i* belongs to list 2$\} = C \cup D \cup E \cup F$

$\ell_3 = \{$animal *i* belongs to list 3$\} = A \cup B \cup C \cup E$

It is assumed that:

1. membership of the lists is independent: the probability of an individual being included in the first list does not depend on whether it was included in the other lists,
2. there is homogeneity in the probability of inclusion on a list that does not vary from individual to individual.

The first assumption is only justified asymptotically as the number of periods goes to infinity, since the incidence of a capture by one method reduces the number of trials available for another method (in the present sampling protocol, there is only one capture type possible at each capture occasion). But, provided that an animal is captured (or not) by any of the methods on occasion *t* is independent of that on *t*+1, the simulation (Appendix 2) shows that the approximation is good, though always an underestimate, even at low number of occasions (*T*=5), provided the proportion of capture histories that include one or more simultaneous captures (list 3) does not get too large. As expected, the approximation improves as the number of sampling occasions increases (see Appendix 3 for details).

The second assumption is equivalent to assuming that the probabilities of capture by the three methods does not vary among individuals also assumed by the original JS method.

In all that follows, I reason conditionally on detection with $P_1 = \Pr(\ell_1)$, $P_2 = \Pr(\ell_2)$ and $P_3 = \Pr(\ell_3)$.

Given events ℓ_1 and ℓ_2 are independent, events ℓ_1 and ℓ_2, i.e. ($\ell_1 \cap \ell_2$) is equivalent to $(\mathrm{E} \cup \mathrm{F})$ in Fig. 1-1 and: $\Pr(\ell_1 \cap \ell_2) = P_1 P_2$.

The probability of belonging to list 1 and list 2 given the animal was sampled on some occasions can be written as the sum of two probabilities:

1) the probability of belonging to list 1 and list 2 separately and being acknowledged to belong to both list 1 and list 2, P(E),

2) and the probability of belonging to list 1 and list 2 separately and not being acknowledged as belonging to both list 1 and list 2, P(F),

such that: $\Pr(\ell_1 \cap \ell_2) = \Pr((\ell_1 \cap \ell_2) \cap \ell_3) + \Pr((\ell_1 \cap \ell_2) \cap \overline{\ell}_3)$

Therefore: $\Pr(\ell_1 \cap \ell_2) = P_1 P_2 P_3 + P_1 P_2 (1 - P_3)$

And the probability of the unknown overlap between list 1 and list 2, i.e. the probability that an individual has an entry in list 1 and an entry in list 2 but is not acknowledged as being in both lists, i.e. P(F), is $\Pr((\ell_1 \cap \ell_2) \cap \overline{\ell}_3) = P_1 P_2 (1 - P_3)$.

It follows that the probability that an individual has a single entry in the combined list is $I_{id} = 1 - \Pr((\ell_1 \cap \ell_2) \cap \overline{\ell}_3) = 1 - P_1 P_2 (1 - P_3)$.

In a real dataset, the probabilities P_1, P_2, P_3 can be estimated as being:

$$\hat{P}_1 = \frac{\text{number of individuals with a capture by method 1 on at least one occasion}}{\text{total number of individuals in the combined dataset}} = \hat{\Pr}(\ell_1)$$

$$\hat{P}_2 = \frac{\text{number of individuals with a capture by method 2 on at least one occasion}}{\text{total number of individuals in the combined dataset}} = \hat{\Pr}(\ell_2)$$

$$\hat{P}_3 = \frac{\text{number of individuals with a capture by both methods on at least one occasion}}{\text{total number of individuals in the combined dataset}} = \hat{\Pr}(\ell_3)$$

The overlap rate as estimated above might be biased by the way probabilities P_1, P_2, P_3 are estimated. Indeed the total number of individuals used to estimate those probabilities is likely to be overestimated due to the unknown number of individuals appearing twice in the combined dataset. As the total number of individuals includes some individuals twice (n_w, the number in set F), the estimates of probabilities P_1, P_2, P_3 using the total number of individuals as a denominator will be negatively biased.

Two somewhat ad hoc approaches have been investigated to try to solve this probable source of bias in the approximation of the probability of single identity, hence in the population size estimation. I first tried an iterative approach to get an unbiased estimate of I_{id}.

An iterative approach

The idea was to use an iterative method to correct the value of I_{id} with the previous value calculated. At the start of the iteration, no correction is made to the $\hat{I}_{id}$ parameter and the formula is the following:

$$\hat{I}_{id} = 1 - \hat{P}_1\hat{P}_2(1-\hat{P}_3)$$

However, as mentioned earlier, the estimates of P_1, P_2, P_3 and of parameter I_{id}, respectively $\hat{P}_1$, $\hat{P}_2$, $\hat{P}_3$ and $\hat{I}_{id}$ might be biased by the total number of individuals used as the denominator in the estimation of P_1, P_2, P_3. The total number of individuals is likely to be overestimated due to the presence of individuals appearing in list 1 and in list 2 but not acknowledged as the same individuals (those that have been captured by method 1 and 2 separately but never simultaneously, i.e. the number of individuals in F (Fig. 1-1)).

The primary purpose of using I_{id} is to correct the population size estimate for duplicated, "phantom", individuals when using two datasets, so it seems legitimate to use it as well to correct the total number of individuals. To correct for the potential overestimation of the total number of individuals, the total number of individuals in the calculation of $\hat{P}_1$, $\hat{P}_2$, $\hat{P}_3$ is multiplied by the previous value of the parameter. In the second step of the iteration, the $\hat{I}_{id}$ parameter becomes then:

$$\hat{I}'_{id} = 1 - \left(\frac{1}{\hat{I}^2_{id}} \hat{P}_1\hat{P}_2 - \frac{1}{\hat{I}^3_{id}} \hat{P}_1\hat{P}_2\hat{P}_3 \right)$$

The iteration should continue substituting the previous value of $\hat{I}_{id}$ calculated to get the next one until convergence. However, the present iteration method results in unstable estimates where the iteration does not converge as shown in Fig.1-2:

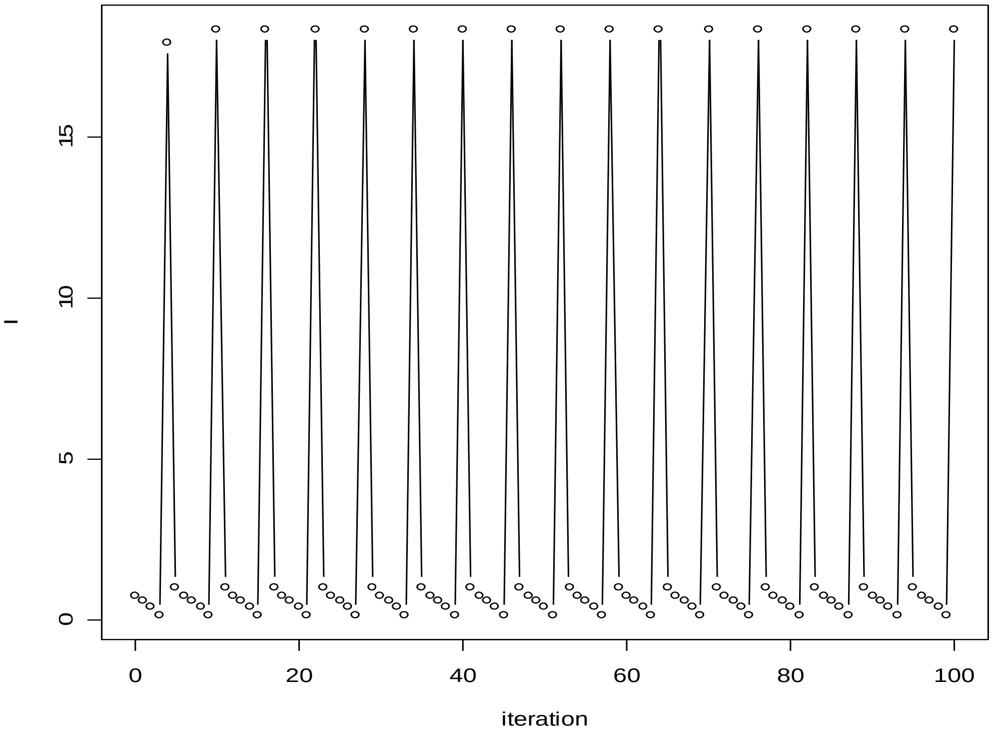


Fig.1-2- Value of the parameter $\hat{I}_{id}$ over 100 steps of the iteration.

The reason for non-convergence is that if the $\hat{I}_{id}$ estimate overshoots the true value and goes too small then because of the reciprocal of high powers of $\hat{I}_{id}$, the estimate gets massively inflated and the process starts again.

Then I tried to modify the influence of the previous values, and to reduce the degree of "overshoot" by using the mean of the two previous values:

$$\hat{I}_{id}^{'} = 1 - \left(\frac{1}{\left[\hat{I}_{id(i-1)} + \hat{I}_{id(i-2)}\right]^2} \hat{P}_1 \hat{P}_2 - \frac{1}{\left[\hat{I}_{id(i-1)} + \hat{I}_{id(i-2)}\right]^3} \hat{P}_1 \hat{P}_2 \hat{P}_{12} \right) \text{ for } i \in [3, +\infty)$$

Unfortunately this did not work.

Similarly, weighted means (with a variety of weighting schemes) have also been tried to fix the instability and produce convergence, but with no success.

Thus, an alternative approach was developed.

The function approach

Following the work on the iteration, an algebraic function of I_{id} can be written (Ross Ihaka, pers. Comm.):

$$f(\hat{I}_{id}) = 1 - \left(\frac{1}{\hat{I}_{id}^2} a - \frac{1}{\hat{I}_{id}^3} ab \right)$$

where $a = \hat{P}_1 \hat{P}_2$ and $b = \hat{P}_{12}$

The idea here is to find the root(s) of $f(\hat{I}_{id})$. The root(s) I of a function of $\hat{I}_{id}$ can be found at $f(\hat{I}_{id}) = I$, which is equivalent to $f(\hat{I}_{id}) - I = 0$ for a continuous monotonic function.

The parameter I_{id} belongs to [0,1] and $f(\hat{I}_{id})$ is not necessarily monotonic on [0,1]: the behavior of $f(\hat{I}_{id})$ on [0,1] depends on the values of the probabilities a and b. It appears that there are 4 possible scenarios denoted as A, B, C, D for the behavior of $f(\hat{I}_{id})$ on [0,1] that result in $f(\hat{I}_{id})$ having either a single root (scenarios B, C, D and some cases of A) or three roots (in some cases of scenario A). The different scenarios A, B, C and D are illustrated in Fig.1-3.

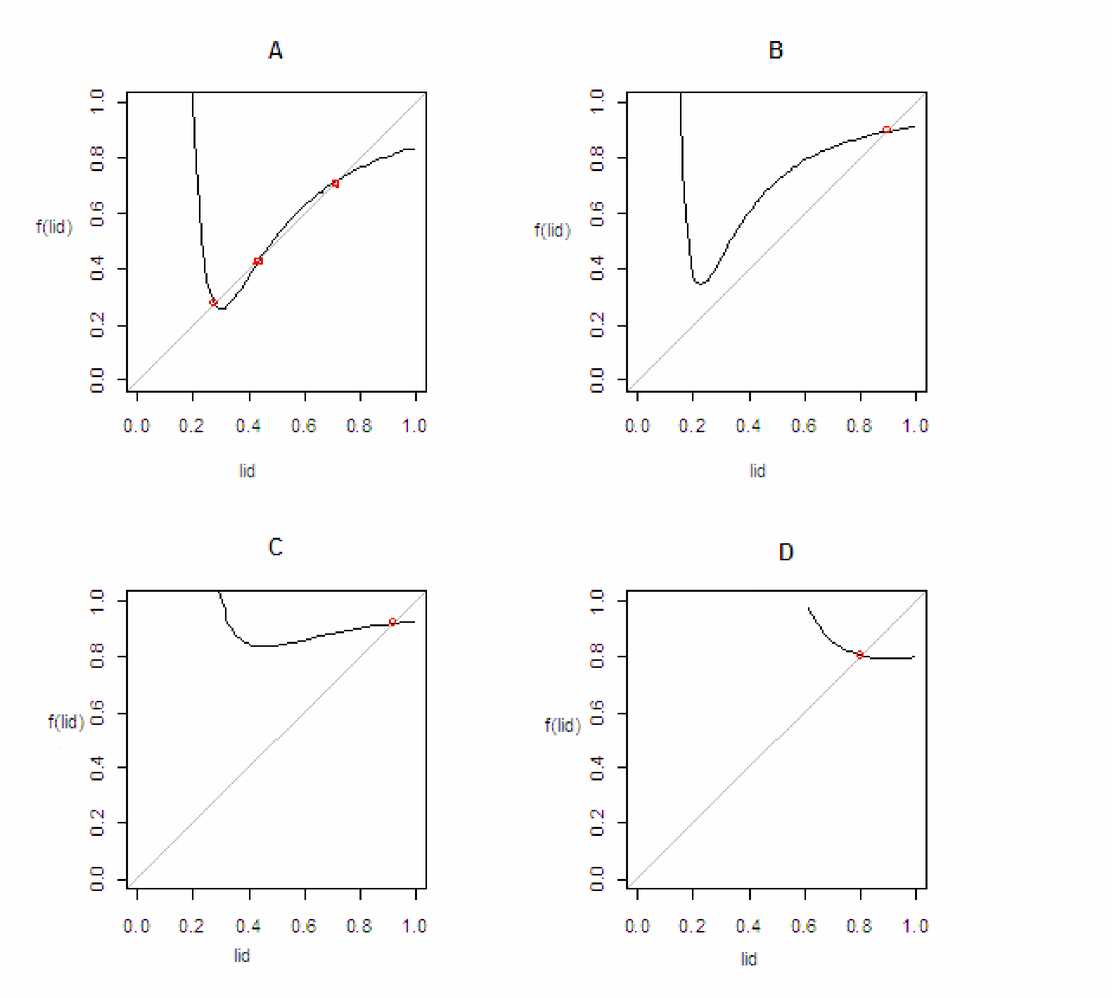


Fig.1-3- Root of the function $f(\hat{I}_{id})$ in scenario A, B, C and D.

For scenarios B, C, D and some cases of scenario A, the corrected value of $\hat{I}_{id}$ corresponds to the root of $f(\hat{I}_{id})$ in [0, 1]. For scenario B and C, the first and second derivatives are used to obtain the root of $f(\hat{I}_{id})$. Here the first derivative $f(\hat{I}_{id})$ is:

$$f'(\hat{I}_{id}) = \frac{2a}{\hat{I}_{id}^3} - \frac{3ab}{\hat{I}_{id}^4}$$

and the second derivative of $f(\hat{I}_{id})$ corresponds to:

$$f'(\hat{I}_{id}) = \frac{-6a}{\hat{I}_{id}^4} + \frac{12ab}{\hat{I}_{id}^5}$$

If $f(\hat{I}_{id})$ is monotonic on [0, 1] (scenario D), then the corrected value for $\hat{I}_{id}$ corresponds to the root of $f(\hat{I}_{id})$ in [0, 1].

If $f(\hat{I}_{id})$ has an inflection point in [0, 1] and does not display any optimum in [0, root of the second derivative] (scenario C), then the corrected value for $\hat{I}_{id}$ corresponds to the root of $f'(\hat{I}_{id})$ in [0, 1].

If $f(\hat{I}_{id})$ has an inflection point in [0, 1], has a local minimum in [0, 1] and $\left(f(\hat{I}_{id}) - I\right)$ is strictly positive (scenario B and in some cases of scenario A), then the corrected value for $\hat{I}_{id}$ corresponds to the root of $f'(\hat{I}_{id})$ in [0, 1].

If $f(\hat{I}_{id})$ has an inflection point in [0, 1], has a local maximum and a local minimum in [0,1] and $\left(f(\hat{I}_{id}) - I\right)$ is strictly negative (scenario A), then there are three possible roots. The largest root seems to be the most appropriate as the estimator produces a smaller bias than with the other two roots.

Using the estimation of the probability of single identity, it is then possible to correct the Jolly-Seber estimator to obtain an estimation of population size, survival and recruitment based on two overlapping datasets.

1.4.5. Estimating population size

The traditional mark-recapture formula $\frac{m'_t}{n_t} = \frac{M_t^*}{\hat{N}_t}$ is used which leads to: $\hat{N}_t = \frac{n_t M_t^*}{m'_t}$

where $m'_t = r_{t,3} + r_{t,1}\hat{I}_{id} + r_{t,2}\hat{I}_{id}$

$$n_t = m'_t + u_t$$

$$u_t = R^*_{t,3} + R^*_{t,1}\hat{I}_{id} + R^*_{t,2}\hat{I}_{id}$$

The estimator for the probability of single identity $\hat{I}_{id}$ has to be used for m'_t and u_t to avoid counting twice individuals present in list 1 and list 2 but not acknowledged to be the same individuals.

As in the JS model, an estimator for M_t^* is then needed because the total number of marked animals in the population is not known as this is an open model. Following the method in JS model to estimate $\hat{M}_t$:

$$\frac{z_t}{\hat{M}_t^* - m'_t} \approx \frac{r'_t}{n_t} \approx \frac{r'_{t,3} + r'_{t,1}\hat{I}_{id} + r'_{t,2}\hat{I}_{id}}{n_t}$$

with $z_t = z'_{t,3} + z'_{t,1}\hat{I}_{id} + z'_{t,2}\hat{I}_{id}$

This leads to the following estimator for M_t^*:

$$\hat{M}_t^* = \frac{z_t n_t}{r'_t} + m'_t$$

However, the estimators $\hat{N}_t$ and $\hat{M}_t^*$ are biased and Seber (2002) recommended the following approximately unbiased estimators:

$$\hat{N}_t = \frac{(n_t + 1)\hat{M}_t^*}{m'_t + 1}$$

$$\hat{M}_t^* = \frac{z_t(n_t + 1)}{r'_t + 1} + m'_t$$

The variance for $\hat{N}_t$ is of the form of the formula of Pollock et al. (1990):

$$Var(\hat{N}_t | N_t) = N_t[N_t - E(n_t)] \times \left\{ \frac{M_t^* - E(m'_t) + n_t}{M_t^*} \times \left[\frac{1}{E(r'_t)} - \frac{1}{n_t} \right] + \frac{N_t - M_t^*}{N_t \times E(m'_t)} \right\}$$

Confidence intervals for $\hat{N}_t$ displayed in the results are classical approximate 95% confidence intervals of the form: $\hat{N}_t \pm 1.96 \times se$. As confidence intervals constructed by assuming that $\hat{N}_t$ is lognormally distributed sometimes perform better than those constructed by assuming than $\hat{N}_t$ is normally distributed, a log-transformation approximation is also used in comparison to get improved 95% confidence intervals such that $(\hat{N}_t / C; \hat{N}_t \times C)$ where $C = \exp\left\{ 2\sqrt{\log(1 + \frac{Var(\hat{N}_t)}{\hat{N}_t^{\ 2}})} \right\}$ (Buckland et al., 1993).

Note that corrected estimates for survival $\hat{\phi}_t$ and recruitment $\hat{B}_t$ and their variances at time *t* of the form of the formula of Pollock et al. (1990) can also be obtained with the TSJS model:

$$\hat{\phi}_t = \frac{\hat{M}^*_{t+1}}{\hat{M}^*_t - m'_t + n_t}$$

$$\operatorname{var}(\hat{\phi}_t | \phi_t) = \phi_t^2 \left\{ \frac{\left[M^*_{t+1} - E(m'_{t+1})\right] \times \left[M^*_{t+1} - E(m'_{t+1}) + n_{t+1}\right]}{M^{*2}_{t+1}} \times \left[\frac{1}{E(r'_{t+1})} - \frac{1}{n_{t+1}}\right] \right.$$
$$\left. + \frac{\left[M^*_t - E(m'_t)\right]}{\left[M^*_t - E(m'_t) + n_t\right]} \times \left[\frac{1}{E(r'_t)} - \frac{1}{n_t}\right] \right\}$$

and

$$\hat{B}_t = \hat{N}_{t+1} - \hat{\phi}_t \hat{N}_t$$

$$\operatorname{var}(\hat{B}_t | B_t) = \left\{ \frac{B_t^2 \left[M^*_{t+1} - E(m'_{t+1})\right] \times \left[M^*_{t+1} - E(m'_{t+1}) + n_{t+1}\right]}{M^{*2}_{t+1}} \right\} \times \left[\frac{1}{E(r'_{t+1})} - \frac{1}{n_{t+1}}\right]$$
$$+ \frac{\left[M^*_t - E(m'_t)\right]}{\left[M^*_t - E(m'_t) + n_t\right]} \times \frac{\left[\phi_t n_t \left(N_t - M^*_t\right)\right]^2}{M^{*2}_t} \times \left[\frac{1}{E(r'_t)} - \frac{1}{n_t}\right]$$
$$+ \frac{\left[N_t - E(n_t)\right] \times (N_{t+1} - B_t) \times (N_t - M^*_t) \times (1 - \phi_t)}{N_t \times \left[M^*_t - E(m'_t) + n_t\right]}$$
$$+ \frac{N_{t+1}\left[N_{t+1} - E(n_{t+1})\right] \times (N_{t+1} - M^*_{t+1})}{N_{t+1} \times E(m'_{t+1})}$$
$$+ \frac{\phi_t^2 N_t \left[N_t - E(n_t)\right] \times (N_t - M^*_t)}{N_t E(m'_t)}$$

1.5. Alternative models

In the present thesis, other modeling approaches are considered as alternatives to the above extension of the JS estimator (the TSJS model), in order to estimate population size with two overlapping datasets.

1.5.1. The variance-weighted mean of the JS estimators

The first obvious approach to answer the issue of two overlapping datasets would be to obtain an average of the estimates given by each dataset separately. If both sampling methods lead to a valid estimate for the population size and if these sampling methods are independent, then one simple solution would be a weighted mean between the values x_i of the Jolly-Seber estimator provided by each source of data. The variances σ_i^2 of the estimates x_i can be used as weight such that: $w_i = \frac{1}{\sigma_i^2}$ (Seber, 2002). In other words, the smaller the variance is, the bigger the weight is and the more influential the value x_i is in the weighted mean.

The weighted mean $\bar{x}$ is in this case: $\bar{x} = \frac{\sum_{i=1}^{n} \frac{x_i}{\sigma_i^2}}{\sum_{i=1}^{n} \frac{1}{\sigma_i^2}}$

and the variance of the weighted mean is given by:

$$\sigma_{\bar{x}}^2 = \frac{1}{\sum_{i=1}^{n} \frac{1}{\sigma_i^2}}$$

The assumptions are those of the JS model for each separate estimate and for the variance-weighted mean to hold, as mentioned earlier, both sampling methods need to be independent and to sample the same population. However, such a solution is unlikely to be as efficient as the TJSJ as the total number of captures will be smaller and the number of recorded recaptures, which is an important contributor to the precision of the final estimate, will usually be less in this method as an animal caught first by method 1 and subsequently by method 2 will not have this recapture used by the estimator. This solution will be compared to the TSJS estimator in various simulation experiments in chapter four and on real data in chapter five.

1.5.2. A closed form likelihood approach

The closed population approaches developed here involve some number $T > 1$ of discrete sampling occasions at which any animal i, i=1, 2, …, N, belonging to a closed population of N individuals, can be caught by one of two sampling methods or by both simultaneously. As for the TSJS model, on each sampling occasion t, t=1, 2, …, T, unmarked animals that are caught are given unique codes and released back into the population, while identification codes are recorded for previously marked animals which are also released back into the population.

Two-source M$_0$ model

A closed form likelihood using both overlapping sources of data was contributed by Dr Rachel Fewster. It is included here as it represents an important stepping stone to the more flexible approach presented in section 1.4. This likelihood is a two-source version of model M$_0$ for closed populations and will therefore be referred to as the two-source M$_0$ model. It is presented here as its performance and results are later compared with the TSJS model in chapters four and five.

Capture events are defined as following:

$$\mathrm{P}_{it} = \{\text{animal } i \text{ is sampled by method 1 on capture occasion } t\}$$

$$\mathrm{G}_{it} = \{\text{animal } i \text{ is sampled by method 2 on capture occasion } t\}$$

with:

1) $\Pr(\mathrm{P}_{it}) = p$ for all i=1, 2, …, N and t=1, 2, …, T

2) $\Pr(\mathrm{G}_{it}) = g$ for all i=1, 2, …, N and t=1,2, …, T

3) $\Pr(\mathrm{P}_{it} \cap \mathrm{G}_{it}) = \alpha p$ for all i=1, 2, …, N and t=1, 2, …, T

or alternatively $\Pr(\mathrm{G}_{it} \mid \mathrm{P}_{it}) = \alpha$

Therefore, events P_{it} and G_{it} are not assumed independent.

From 1), 2) and 3), it follows that:

$\Pr(\mathrm{P}_{it} \cap \mathrm{G}_{it}) = \alpha p$ is the probability that animal *i* is sampled at occasion *t* by method 1 and method 2,

$\Pr(\mathrm{P}_{it} \cap \overline{\mathrm{G}}_{it}) = (1-\alpha)p$ is the probability that animal *i* is sampled at occasion *t* by method 1 but not by method 2,

$\Pr(\overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it}) = g - \alpha p$ is the probability that animal *i* is sampled at occasion *t* by method 2 but not by method 1,

and $\Pr(\overline{\mathrm{P}}_{it} \cap \overline{\mathrm{G}}_{it}) = 1 - p - g + \alpha p$ is the probability that animal *i* is not sampled at occasion *t* by method 1 nor by method 2.

Repeated sampling then results in capture histories that can be organized into three separate data frames:

1) D_{B}: all histories in which there was at least one simultaneous capture, i.e. $\mathrm{P}_{it} \cap \mathrm{G}_{it}$ for some occasion *t* (“B” for “Both”), such that, for example:

$$\begin{array}{cc} & T\text{ capture occasions} \qquad (T\text{=7 here}) \\ h_B \text{ histories} & \begin{pmatrix} 0 & 1 & 0 & 3 & 2 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 3 & 0 \\ 2 & 0 & 3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 3 & 0 & 0 & 0 \\ \ldots & & & & & & \end{pmatrix} \end{array}$$

where, on any capture occasion *t*, a “3” means a simultaneous capture by both method 1 and method 2, i.e. $\mathrm{P}_{it} \cap \mathrm{G}_{it}$, a “2” means a capture by method 2 only, i.e. $\overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it}$, a “1” means a capture by method 1 only, i.e. $\mathrm{P}_{it} \cap \overline{\mathrm{G}}_{it}$ and a “0” means no capture, i.e. $\overline{\mathrm{P}}_{it} \cap \overline{\mathrm{G}}_{it}$.

2) D_1: all histories consisting of captures by method 1 only, such that:

$$\begin{array}{cc} & T\text{ capture occasions} \\ h_1\text{ histories} & \begin{pmatrix} 0 & 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 1 \\ \ldots & & & & & & \end{pmatrix} \end{array}$$

where, on any capture occasion *t*, a “1” means a capture by method 1 only i.e. $\mathrm{P}_{it} \cap \overline{\mathrm{G}}_{it}$ and a “0” means no capture by method 1, i.e. $\overline{\mathrm{P}}_{it}$. Therefore, every row has at least a “1” but it is not possible to have a “2” or “3”, otherwise history would be in data frame D_B, not D_1. However, it is not known if the same individuals have been also caught by method 2 and the same individuals might also appear in D_2.

3) D_2: all histories consisting of captures by method 2 only, such that:

$$\begin{array}{cc} & T\text{ capture occasions} \\ h_2\text{ histories} & \begin{pmatrix} 0 & 0 & 2 & 2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 2 & 0 \\ 0 & 2 & 0 & 2 & 0 & 2 & 0 \\ 2 & 0 & 0 & 0 & 0 & 0 & 0 \\ \ldots & & & & & & \end{pmatrix} \end{array}$$

where, on any capture occasion *t*, a “2” means a capture by method 2 only, i.e. $\overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it}$ and a “0” means no capture by method 1, i.e. $\overline{\mathrm{G}}_{it}$. Therefore, every row has at least a “2” but it is not possible to have a “1” or “3”, otherwise history would be in data frame D_B, not D_2. However, as mentioned for D_1, it is not known if the same individuals have been also caught by method 1 and therefore the same individuals might also appear in D_1.

Model assumptions

1) The population is closed, i.e. there is no death/emigration, and no recruitment (birth or immigration) during the study period,
2) Capture probabilities are assumed to be the same for all individuals on all occasions,

3) There is no loss on capture,
4) Marks are correctly recorded,
5) Animals do not lose their marks,
6) If event $\mathrm{P}_{it} \cap \mathrm{G}_{it}$ happens, then it is known that it happens, i.e. it is not possible to catch the same individual by the two different methods on the same occasion without knowing it is the same individual, i.e. being caught by method 1, by method 2 or by both simultaneously are mutually exclusive events on each capture occasion. This assumption is the same as assumption ix of the TSJS model.

Estimating the population size N

The key problem is the same as for the TSJS model: it is not known how many individuals are in both D_1 and D_2, i.e. captured separately by the two different methods but never simultaneously.

The approach here aims at first describing the numbers of histories in datasets D_B, D_1 and D_2, in terms of the model parameters *p*, *g* and α, then conditioning them on membership of each dataset, in order to find the probability of the individual history records.

Data summary statistics:

h_B = number of histories in D_B (= number of individuals in D_B)
h_1 = number of histories in D_1
h_2 = number of histories in D_2

N.B.: each history in D_1 and D_2 describes an individual but there is an unknown overlap between D_1 and D_2 resulting in some individuals having an history in both D_1 and D_2.

$n_{\mathrm{B}0}$, $n_{\mathrm{B}1}$, $n_{\mathrm{B}2}$, $n_{\mathrm{B}3}$: respectively number of captures in D_B that are “0”, “1”, “2”, “3”
n_{10}, n_{11}: respectively number of captures in D_1 that are “0” and “1”
n_{20}, n_{22}: respectively number of captures in D_2 that are “0” and “2”

Likelihood components:

The probability distribution of the observed data given the parameters can be split into four components:

i) $L_{\mathrm{H}}(h_{\mathrm{B}},h_1,h_2\ ;\ N,p,g,\alpha) = \Pr(\text{numbers of histories in each dataset } \mathrm{D_B}, \mathrm{D_1}, \mathrm{D_2})$,

ii) $L_{\mathrm{B}}(n_{\mathrm{B0}},n_{\mathrm{B1}},n_{\mathrm{B2}},n_{\mathrm{B3}} \mid h_{\mathrm{B}}\ ;\ N,p,g,\alpha)$: probability of the $\mathrm{D_B}$-captures “0”, “1”, “2”, “3”, conditional on membership of dataset $\mathrm{D_B}$,

iii) $L_1(n_{10},n_{11} \mid h_1\ ;\ N,p,g,\alpha)$: probability of the $\mathrm{D_1}$-captures “0” and “1”, conditional on membership of dataset $\mathrm{D_1}$,

iv) $L_2(n_{20},n_{22} \mid h_2\ ;\ N,p,g,\alpha)$: probability of the $\mathrm{D_2}$-captures “0” and “2”, conditional on membership of dataset $\mathrm{D_2}$.

The overall likelihood is, therefore, given by: $L(\text{data}\,;\text{parameters}) = L_{\mathrm{H}}L_{\mathrm{B}}L_1L_2$ or $\log L = \log L_{\mathrm{H}} + \log L_{\mathrm{B}} + \log L_1 + \log L_2$ with:

1) *Component* L_{B}

$$L_{\mathrm{B}} \propto p_{\mathrm{B0}}^{n_{\mathrm{B0}}} \times p_{\mathrm{B1}}^{n_{\mathrm{B1}}} \times p_{\mathrm{B2}}^{n_{\mathrm{B2}}} \times p_{\mathrm{B3}}^{n_{\mathrm{B3}}}$$

where $p_{\mathrm{B}c} = \Pr(\text{ capture} = \mathrm{c} \mid \text{capture is in dataset } \mathrm{D_B}) = \Pr(\mathrm{c} \mid \mathrm{D_B}) \qquad \mathrm{c} = 0, 1, 2, 3$

and $L_{\mathrm{B}} \propto \ldots$ with a constant of proportionality that does not depend on the parameters.

The probability $\Pr(\mathrm{D_{B\mathit{i}}})$ that a capture history is in data set $\mathrm{D_B}$ is given by:

$$\Pr(\mathrm{D_{B\mathit{i}}}) = \Pr(\text{ history is in dataset } \mathrm{D_B}) = 1 - \Pr(\text{ animal } i \text{ never caught simultaneously out of all } T \text{ occasions})$$

Then $\Pr(\mathrm{D_{B\mathit{i}}}) = 1 - (1 - \alpha p)^T$

And: $p_{\mathrm{B3}} = \Pr(\mathrm{P}_{it} \cap \mathrm{G}_{it} \mid \mathrm{D_{B\mathit{i}}}) = \dfrac{\Pr(\mathrm{D_{B\mathit{i}}} \mid \mathrm{P}_{it} \cap \mathrm{G}_{it}) \times \Pr(\mathrm{P}_{it} \cap \mathrm{G}_{it})}{\Pr(\mathrm{D_{B\mathit{i}}})}$ so $p_{\mathrm{B3}} = \dfrac{1 \times \alpha p}{1 - (1 - \alpha p)^T}$

$$p_{\mathrm{B2}} = \Pr(\overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it} \mid \mathrm{D_{B\mathit{i}}}) = \frac{\Pr(\mathrm{D_{B\mathit{i}}} \mid \overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it})\Pr(\overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it})}{\Pr(\mathrm{D_{B\mathit{i}}})} \quad \text{so} \quad p_{\mathrm{B2}} = \frac{\left[1 - (1 - \alpha p)^{T-1}\right](g - \alpha p)}{1 - (1 - \alpha p)^T}$$

with: $\Pr(\mathrm{D}_{\mathrm{B}i} \mid \overline{\mathrm{P}}_{it} \cap \mathrm{G}_{it}) = 1-(1-\alpha p)^{T-1}$ because it is known that there was no simultaneous capture for individual *i* on occasion *t*, i.e. $\overline{\mathrm{P}}_{it} \cap \mathrm{G}$, so that leaves *T*-1 other occasions, at least one of which must be a simultaneous capture in order for event $\mathrm{D}_{\mathrm{B}i}$ to happen.

Similarly:

$$p_{\mathrm{B1}} = \Pr(\mathrm{P}_{it} \cap \overline{\mathrm{G}}_{it} \mid \mathrm{D}_{\mathrm{B}i}) = \frac{\Pr(\mathrm{D}_{\mathrm{B}i} \mid \mathrm{P}_{it} \cap \overline{\mathrm{G}}_{it})\Pr(\mathrm{P}_{it} \cap \overline{\mathrm{G}}_{it})}{\Pr(\mathrm{D}_{\mathrm{B}i})} \quad \text{so} \quad p_{\mathrm{B1}} = \frac{\left[1-(1-\alpha p)^{T\text{-}1}\right](1-\alpha)p}{1\text{-}(1\text{-}\alpha p)^{T}}$$

and $p_{\mathrm{B0}} = \Pr(\overline{\mathrm{P}}_{it} \cap \overline{\mathrm{G}}_{it} \mid \mathrm{D}_{\mathrm{B}i}) = \dfrac{\left[1-(1-\alpha p)^{T\text{-}1}\right](1-p-g+\alpha p)}{1\text{-}(1\text{-}\alpha p)^{T}}$

Consequently:

$\log L_{\mathrm{B}} = n_{\mathrm{B0}} \log p_{\mathrm{B0}} + n_{\mathrm{B1}} \log p_{\mathrm{B1}} + n_{\mathrm{B2}} \log p_{\mathrm{B2}} + n_{\mathrm{B3}} \log p_{\mathrm{B3}}$ (up to an additive constant that can be ignored)

2) *Component* L_1

The probability $\Pr(\mathrm{D}_{1i})$ that a capture history *i* is in dataset D_1, i.e.

$\Pr(\mathrm{D}_{1i}) = \Pr(\text{ individual } i \text{ is never caught simultaneously, but is caught by method 1 at least once})$

is given by: $\Pr(\mathrm{D}_{1i}) = \left(\Pr(\overline{\mathrm{P}_{it} \cap \mathrm{G}_{it}})\right)^{T} - \left(\Pr(\overline{\mathrm{P}}_{it})\right)^{T}$

so $\Pr(\mathrm{D}_{1i}) = (1-\alpha p)^{T} - (1-p)^{T}$

Given: $p_{10} = \Pr(\text{ capture} = 0 \mid \text{capture is in dataset } \mathrm{D}_1)$

and $p_{11} = \Pr(\text{ capture} = 1 \mid \text{capture is in dataset } \mathrm{D}_1)$

$$p_{10} = \Pr(\overline{\mathrm{P}}_{it} \mid \mathrm{D}_{1i}) = \frac{\Pr(\mathrm{D}_{1i} \mid \overline{\mathrm{P}}_{it}) \times \Pr(\overline{\mathrm{P}}_{it})}{\Pr(\mathrm{D}_{1i})} \quad \text{so} \quad p_{10} = \frac{\left[(1\text{-}\alpha \mathrm{p})^{T\text{-}1} - (1-p)^{T-1}\right] \times (1-p)}{(1-\alpha p)^{T} - (1-p)^{T}}$$

with: $\Pr(\mathrm{D}_{1i} \mid \overline{\mathrm{P}}_{it}) = (1-\alpha p)^{T-1} - (1-p)^{T-1}$ because it is known that there was no capture by method 1 on occasion *t*, i.e. $(\overline{\mathrm{P}}_{it})$, so that leaves *T*-1 occasions on which no simultaneous capture should occur and ≥1 capture(s) by method 1 need(s) to happen.

Further: $p_{11} = 1 - p_{10}$

Consequently:

$\log L_1 = n_{10} \log\ p_{10} + n_{11} \log\ p_{11}$ (up to an additive constant that can be ignored)

3) *Component* L_2

The probability $\Pr(\mathrm{D}_{2i})$ that a capture history *i* is in dataset D_2, i.e.

$\Pr(\mathrm{D}_{2i}) = \mathrm{P}($ individual *i* is never caught simultaneously, but is caught by method 2 at least once)

is given by: $\Pr(\mathrm{D}_{2i}) = \left(\Pr(\overline{\mathrm{P}_{it} \cap \mathrm{G}_{it}})\right)^T - \left(\Pr(\overline{\mathrm{G}}_{it})\right)^T$

so $\Pr(\mathrm{D}_{2i}) = (1-\alpha p)^T - (1-g)^T$

Given $p_{20} = \Pr(\text{ capture} = 0 \mid \text{capture is in dataset } \mathrm{D}_2)$ and

$p_{22} = \Pr(\text{ capture} = 2 \mid \text{capture is in dataset } \mathrm{D}_2)$

$$p_{20} = \Pr(\,\overline{\mathrm{G}}_{it} \mid \mathrm{D}_{1i}) = \frac{\Pr(\mathrm{D}_{1i} \mid \overline{\mathrm{G}}_{it}) \times \Pr(\overline{\mathrm{G}}_{it})}{\Pr(\mathrm{D}_{1i})} \quad \text{so} \quad p_{20} = \frac{\left[(1\text{-}\alpha p)^{T\text{-}1} - (1-g)^{T-1}\right] \times (1-g)}{(1-\alpha p)^T - (1-g)^T}$$

with: $\Pr(\mathrm{D}_{1i} \mid \overline{\mathrm{G}}_{it}) = (1-\alpha p)^{T-1} - (1-g)^{T-1}$ because it is known that there was no capture by method 2 on occasion *t*, i.e. $(\overline{\mathrm{G}}_{it})$, so that leaves *T*-1 occasions on which there needs to be no simultaneous captures and ≥ 1 capture(s) by method 2.

Further: $p_{22} = 1 - p_{20}$

Consequently:

$\log L_2 = n_{20} \log\ p_{20} + n_{22} \log\ p_{22}$ (up to an additive constant that can be ignored)

4) *Component* L_{H}

Consider a latent multinomial formulation where each individual can be:

1. In no dataset (never observed)
2. In D_{B}
3. In D_1 only
4. In D_2 only
5. In both D_1 and D_2

This is a partition, i.e. every individual is in exactly one of those 5 outcomes, and all probabilities need to be linked to each outcome.

Let $\underset{\sim}{X}$ be the associated multinomial random variable:

Outcome	Probability	Number of animals with this outcome
Never observed	$\vartheta_0 = (1-p-g+\alpha p)^T$	X_0
In D_B	$\vartheta_\mathrm{B} = 1-(1-\alpha p)^T$	X_B
In D_1 only	$\vartheta_1 = (1-g)^T - (1-p-g+\alpha \mathrm{p})^T$	X_1
In D_2 only	$\vartheta_2 = (1-p)^T - (1-p-g+\alpha p)^T$	X_2
In both D_1 and D_2	$\vartheta_{12} = (1-\alpha p)^T \text{ - } (1-p)^T - (1-g)^T + (1-p-g+\alpha p)^T$	X_{12}

Then $(X_0, X_B, X_1, X_2, X_{12}) = \underset{\sim}{X} \sim \text{Multinomial}\,(N; \vartheta_0, \vartheta_\mathrm{B}, \vartheta_1, \vartheta_2, \vartheta_{12})$

But $\underset{\sim}{X}$ is not observed completely and what is observed is:

X_B = number of histories in $\mathrm{D}_\mathrm{B} = h_\mathrm{B}$

$X_1 + X_{12}$ = number of histories in $\mathrm{D}_1 = h_1$

$X_2 + X_{12}$ = number of histories in $\mathrm{D}_2 = h_2$

It is necessary to know X_{12} in order to use the multinomial formula. One solution is to partition over all possible values of X_{12} such that:

$$L_\mathrm{H}((h_\mathrm{B}, h_1, h_2) \mid N, \underset{\sim}{\vartheta}) = \sum_{\text{all possible values of } X_{12}} \Pr((h_\mathrm{B}, h_1, h_2) \cap X_{12} \mid N, \underset{\sim}{\vartheta})$$

$$L_\mathrm{H}((h_\mathrm{B}, h_1, h_2) \mid N, \underset{\sim}{\vartheta}) = \sum_{x_{12}} \Pr\left(\underset{\sim}{\mathrm{X}} = \begin{pmatrix} N - h_\mathrm{B} - h_1 - h_2 - x_{12} \\ h_\mathrm{B} \\ h_1 - x_{12} \\ h_2 - x_{12} \\ x_{12} \end{pmatrix} \,\middle|\, N, \underset{\sim}{\vartheta}\right)$$

Consequently $L_\mathrm{H}((h_\mathrm{B}, h_1, h_2) \mid N, \underset{\sim}{\vartheta})$ is gained by summing the multinomial distribution over all possible values of X_{12}.

For the variance of the maximum likelihood estimator (MLE) $\hat{N}$, we assume that the MLE is unbiased and therefore we use the Cramer-Rao lower bound: $\operatorname{var}(\hat{N}) = \frac{1}{\mathrm{I}(N)}$ where $\hat{N}$ is any unbiased estimator of N that attains the Cramer-Rao lower bound and $\mathrm{I}(N)$ is the Fisher information.

Though clearly this method offers an elegant approach to the problem, at present it is limited to the simplest (and least useful) of the closed population models. Any development of the model to the other closed population forms, M_t, M_h, and M_{th}, let alone the open populations will have to be left to others.

Multinomial models based on a latent capture history approach

An alternative, less mathematically demanding, approach is based on latent multinomials outlined in chapter 10 in Link and Barker (2010). The purpose in this section is to construct, using the raw encounter histories, a closed-population likelihood based on a complete data likelihood expressed in terms of true histories which are then corrupted into observed capture histories.

On each sampling occasion t of a T-occasion experiment, there are four possible events for each individual:

1) Not being caught, denoted “0” in a capture history

2) Being caught by method 1 only, denoted “1” in a capture history

3) Being caught by method 2 only, denoted “2” in a capture history

4) Being caught by both methods simultaneously, denoted “3” in the capture history.

There are therefore 4^T possible latent histories $(\omega_1, \omega_2, ..., \omega_T)$, uniquely identified by indices $i = 1 + \sum_{t=1}^{T} \omega_t 4^{t-1}$. However, since any latent history containing a “1” and “2” but no “3” cannot be observed, there are less types of observable records than there are latent ones.

For instance, an individual with latent histories “12021” is recorded as two separate individuals: one individual with record “10001” and the other with record “01010”. The exact number of possible types of observable histories is 4^T-Y-1where Y=3^T-2^{T+1}+1 is the number of sequences of size T that contain both “1”s and “2”s but no “3” (i.e. that can never be observed). One is subtracted as the T zero-vector is also not observable. A recorded frequency vector (vector of observations) of the form $\boldsymbol{f}^+ = (f_2, f_3, ..., f_{4^T-Y-1})$ can then be assumed to be an affine transformation of latent history frequencies $\boldsymbol{X} = (x_1, x_2, ..., x_{4^T})$ with $\boldsymbol{f}^+ = \boldsymbol{A}'\boldsymbol{X}$, where $\boldsymbol{A}$ is a $4^T(4^T-Y-1)$ matrix: $\boldsymbol{A}_{i,j-1}$= 1 if latent history i gives rise to recorded history j. In the case of T=3 illustrated in Table 1-1, $\boldsymbol{A}$ is created by replacing each dot in the contributed record matrix with a zero and every number by a 1. The null space of matrix $\boldsymbol{A}'$ (Link and Barker, 2010) is required in order to map the latent histories to the observed histories. This could be achieved by using the R function Null() (library(MASS) ****).

i	Latent history	Contributed records	*j*	Recorded history
1	000	…….52 dots	1	000
2	100	2……	2	100
3	200	.3……	3	200
4	300	..4……	4	300
5	010	...5…..	5	010
6	110	....6….	6	110
7	210	.3.5...	7	310
8	310	…..7	8	020
9	020	8	9	030
10	030	9	10	130
11	120	2.....8......	fill to 52	
12	130	10		
fill to 64				

Table 1-1- Latent histories *i* and recorded histories *j* for a *T*=3-occasion experiment.

General model assumptions include:

1) The population is closed, i.e. there is no death/emigration, and no recruitment (birth or immigration) during the study period,
2) Capture probabilities are assumed to be the same for all individuals,
3) There is no loss on capture,
4) Marks are correctly recorded,
5) Animals do not lose their marks,
6) It is not possible to catch the same individual by the two seperate methods on the same occasion without knowing it is the same individual, i.e. being caught by

method 1, by method 2 or by both simultaneously are mutually exclusive events on each capture occasion. This assumption is the same as assumption (ix) of the TSJS model and assumption 6 of the two-source M_0 model.

The latent capture histories can then be modeled by making assumptions corresponding to the model of interest: model M_0 and M_t.

Under model M_0

Under model M_0, the capture probability is assumed to be the same for all individuals and does not vary over time. Therefore, the latent capture histories can be modeled, for all *i* with *i* in (1, …, *N*), by making the following assumptions and based on the approach used above in Rachel Fewster's two-source M_0 model:

1) the probability of being caught by method 1 at time *t*, *t*=1, …, *T* is $\Pr(p_{it}^{(1)}) = p^{(1)}$

2) the probability of being caught by method 2 at time *t*, *t*=1, …, *T* is $\Pr(p_{it}^{(2)}) = p^{(2)}$

3) the probability of being caught by both method 1 and method 2 at time *t*, *t*=1, …, *T* is $\Pr(p_{it}^{(1)} \cap p_{it}^{(2)}) = \alpha p^{(1)}$ for all *i*=1, 2, …, *N* and *t*=1, 2, …, *T*

or alternatively $\Pr(p_{it}^{(2)} \middle| p_{it}^{(1)}) = \alpha$. Therefore, events $p_{it}^{(1)}$ and $p_{it}^{(2)}$ are not assumed independent,

4) *N* is the unknown number of animals in a closed population.

From these assumptions, the following probabilities can be derived:

$$\Pr(\overline{p}_{it}^{(1)} \cap \overline{p}_{it}^{(2)}) = 1 - p^{(1)} - p^{(2)} + \alpha p^{(1)}$$

$$\Pr(p_{it}^{(1)} \cap \overline{p}_{it}^{(2)}) = (1-\alpha) p^{(1)}$$

$$\Pr(\overline{p}_{it}^{(1)} \cap p_{it}^{(2)}) = p^{(2)} - \alpha p^{(1)}$$

Thus, the likelihood that an individual has latent history w_{it} can be formulated as:

$\pi_i = \prod_{t=1}^{T} \left[1 - p^{(1)} - p^{(2)} + \alpha p^{(1)}\right]^{I(w_{it}=0)} \left[(1-\alpha) p^{(1)}\right]^{I(w_{it}=1)} \left[p^{(2)} - \alpha p^{(1)}\right]^{I(w_{i,t}=2)} \left[\alpha p^{(1)}\right]^{I(w_{i,t}=3)}$ for i=1,2,…, 4^T

Conditioning on being N individuals ever in the population, the probability of a vector $x = (x_1, x_2, ..., x_{4^T})'$ of latent frequencies is given by:

$$\left[x \middle| N, p^{(1)}, p^{(2)}, \alpha\right] = \left\{ \frac{N!}{\prod_{i=1}^{4^T} x_i!} \prod_{i=1}^{4^T} \pi_i^{x_i} \right\} I\left(\sum_{i=1}^{4^T} x_i = N\right)$$

The probability of the recorded data $\boldsymbol{f}^+$, conditional on the latent frequencies, is:

$$[\boldsymbol{f}^+ | x, N, p^{(1)}, p^{(2)}, \alpha\ \mathbf{]} = I\ (\ \boldsymbol{f}^+ = \boldsymbol{A}'\boldsymbol{X})$$

Extension to model M_t

Under model M_t, the capture probability is assumed to be the same for all individuals but varies over time. Therefore, the latent capture histories can be modeled, for all i with i in (1, …, N), by making the following assumptions:

1) the probability of being caught by method 1 at time t, t=1, …, T is $\Pr(p_{it}^{(1)}) = p_t^{(1)}$

2) the probability of being caught by method 2 at time t, t=1, …, T is $\Pr(p_{it}^{(2)}) = p_t^{(2)}$

3) the probability of being caught by both method 1 and method 2 at time t, t=1, …, T is $\Pr(p_{it}^{(1)} \cap p_{it}^{(2)}) = \alpha p_t^{(1)}$ for all i=1, 2, …, N

or alternatively $\Pr(p_{it}^{(2)} | \, p_{it}^{(1)}) = \alpha$

Therefore, events $p_{it}^{(1)}$ and $p_{it}^{(2)}$ are not assumed independent.

4) N is the unknown number of animals in a closed population.

From these assumptions, the following probabilities can be derived:

$$P(\overline{p}_{it}^{(1)} \cap \overline{p}_{it}^{(2)}) = 1 - p_t^{(1)} - p_t^{(2)} + \alpha p_t^{(1)}$$

$$\mathrm{P}(p_{it}^{(1)} \cap \overline{p}_{it}^{(2)}) = (1-\alpha)\, p_t^{(1)}$$

$$\mathrm{P}(\overline{p}_{it}^{(1)} \cap p_{it}^{(2)}) = p_t^{(2)} - \alpha p_t^{(1)}$$

Thus, the likelihood that an individual has latent history w_{it} can be formulated as:

$$\pi_i = \prod_{t=1}^{T} \left[1 - p_t^{(1)} - p_t^{(2)} + \alpha p_t^{(1)}\right]^{I(w_{it}=0)} \left[(1-\alpha)\, p_t^{(1)}\right]^{I(w_{it}=1)} \left[p_t^{(2)} - \alpha p_t^{(1)}\right]^{I(w_{i,t}=2)} \left[\alpha p_t^{(1)}\right]^{I(w_{i,t}=3)}$$

for i =1,2,…, 4^T

Conditioning on there being N individuals ever in the population, the probability of a vector $x = (x_1, x_2, ..., x_{4^T})'$ of latent frequencies is given by:

$$\left[x \middle| N, p_1^{(1)}, ..., p_T^{(1)}, p_1^{(2)}, ..., p_T^{(2)}, \alpha\right] = \left\{ \frac{N!}{\prod_{i=1}^{4^T} x_i!} \prod_{i=1}^{4^T} \pi_i^{x_i} \right\} I\left(\sum_{i=1}^{4^T} x_i = N\right)$$

The probability of the recorded data f^+, conditional on the latent frequencies, is:

$$[\boldsymbol{f}^+ | x, N, p_1^{(1)}, ..., p_T^{(1)}, p_1^{(2)}, ..., p_T^{(2)}, \alpha\,] = I\,(\,\boldsymbol{f}^+ = \boldsymbol{A}'\boldsymbol{X})$$

Under model M$_t$, α is set, here, to be constant. However, α could potentially vary over time, i.e. α_t with t=1, …, T: in such case, at every capture occasion, $p_t^{(1)}$ and $p_t^{(2)}$ would need to be estimated. This implies a heavy parameterisation and potentially a loss in precision for the other parameters. So, depending on the application, α can be set to be constant or to vary over time, both options having drawbacks that researchers need to take into account.

These models could be formulated as a Bayesian problem and evaluated using Monte Carlo Markov chains as outlined by Link and Barker (2010). However, for real problems where the number of sampling occasions becomes large enough to be useful for field ecologists doing monitoring work (say 10 sampling periods or more), the size and complexity of the problem make this approach unattractive to ecologists.

1.6. Discussion

While double sampling may be an efficient approach to minimize study costs, increase sample size and enhance the power of capture-recapture analysis (Salewski et al., 2007), minimize possible sampling bias and permit a deeper insight into the ecology of the population of interest (Laiolo et al., 2007; Salewski et al., 2007), there are a number of issues when data provided by the two sampling methods can only be partially linked. This sampling situation particularly leads to difficulties in estimating population size when the two partially-overlapping datasets are combined: some individuals may appear twice in the combined dataset, resulting in an overestimation of the abundance and large standard errors. In the present thesis, an extension of the Jolly-Seber model, the two-source Jolly-Seber (TSJS) model, is proposed as a solution to this issue and discussed along with alternative approaches. The objective is the development of an analytical framework allowing the combination of two sources of data available in an open-population model to increase the sample size and provide a useful monitoring estimator, i.e. robust to departure from the underlying assumptions. However, researchers should keep in mind that differences in estimates provided by two sampling methods should not necessarily be taken as a problem but this difference could be a source of information about the population of interest and ways to use this information should be considered (Laiolo et al., 2007; Vögeli et al., 2008).

The first important aspect is that care should be taken when comparing results from two sources of data. Researchers especially need to make sure that the two sampling methods indeed sample the same population. Recent studies (Salewski et al., 2007; Vögeli et al., 2008) have highlighted differences in estimates of survival between different sampling methods suggesting the existence of subsets of individuals differentially sampled within the population. Depending on which sampling method results are drawn upon, conclusions might differ drastically, potentially affecting predictions on the population dynamics and resulting in inappropriate conservation plans. In such a case, the two methods should be considered as complementary rather than alternative and should be combined: the unique information for one sampling method could correct the estimation provided by the other sampling method, providing a better insight into the population characteristics and dynamics. The other solution would be to acknowledge that the two subsets of the population are different and to study them separately.

There are several solutions to the estimation of abundance with two overlapping datasets: three new frameworks, all based on the fundamental assumption that the sampling methods sample the same population, were presented in this chapter. Two of those approaches, the TSJS and the two-source M_0 models are applicable. The former is an extension of the JS model and therefore shares the basic properties and assumptions of the classic JS model. The TSJS model is an open population model leading to the estimation of population size, capture probability and less straightforwardly survival rate and recruitment. Population size is the parameter of interest in many ecological studies and is investigated in the present thesis. I however, show how survival and recruitment can be estimated under the TSJS framework. They are important population parameters that are not necessarily biased by the same assumption violations as the population size estimates can be. Survival estimates are especially relatively robust to heterogeneity in capture probabilities (Carothers, 1973, 1979; Hwang and Chao, 1995), a major issue investigated for population size estimates in the present thesis. Consequently, survival and recruitment parameters would deserve a full investigation with a different approach.

A restrictive assumption of the TSJS model (and also of the JS model) is the assumption of homogeneity in capture probability among individuals because heterogeneity of capture probabilities among individuals is an ubiquitous feature in animal population (Boulanger et al., 2004c; Crespin et al., 2008; Hammond, 1990) leading to substantial bias in population size estimation with the standard JS model (Carothers, 1973, 1979; Hwang and Chao, 1995). Therefore, I explore, in chapter three, the robustness of the TSJS estimator from the departure of this underlying assumption to see its limitation at handling this common source of bias in population size estimates.

The TSJS model also relies on the assumption that having a capture by one method in the capture history does not depend on whether the animals also have (or not) captures by the other methods (assumption viii). This assumption can only be justified asymptotically as the number of capture occasions increases since, on each occasion, captures by each sampling method are mutually exclusive. This assumption could be especially at risk in studies where the animals become trap-shy or trap-happy by a sampling method affecting the probability of the other sampling methods. This assumption is also at risk if some animals are more available than others due to the sampling protocol or due to the behaviour of the animals: if the same kind of animals is favoured by both sampling methods, then a lack of independence between the types of captures will be induced.

All the new models presented in this chapter (the TSJS model, the two-source M_0 model and the Bayesian latent-capture-history M_0 and M_t approaches) rely on the assumption that the same individual cannot be caught by the two separate sampling methods on the same occasion without knowing it is the same individual, i.e. no unknown overlap occurs within a capture occasion, captures by each sampling method are mutually exclusive events on each capture occasion (assumption ix of the TSJS model). Therefore, a point of interest concerns the sampling occasion and how the definition of sampling occasion differs from one species or one field study to another. The length of the sampling occasion in particular differs depending on the species. For some animal population, the sampling occasion lasts a day but for some other animal populations (such as humpback whales) a sampling occasion could last over a few months. When sampling occasions are spread over a long period of time, secondary sampling occasions usually occur within these primary sampling occasions, like in a robust design experiment (Pollock, 1982). The longer the primary sampling occasion is, the better the chance of capturing the same individuals at least twice. Therefore, in some cases, multiple captures of the same individuals can occur during the secondary sampling occasion but only one capture appears on the primary sampling occasion scale in the capture histories of the individuals and the multiple aspect of the capture on the secondary sampling scale is ignored. However, if a simultaneous capture is lacking in the capture histories and if the multiple captures during secondary sampling occasions are of the form of captures by the single methods alone, the multiple aspect of the capture will be recorded at the primary sampling occasion, to the capture history of two different individuals that are actually one. If some individuals are captured by both sampling methods separately but not simultaneously during such a long primary sampling occasion, overlap will occur resulting in a further inflation of the population size.

Lengthy sampling occasions might also jeopardise assumption iv of the TSJS model (same assumption exists in the JS model): sampling periods are short enough to avoid death during a sampling period. For long-lived species with a high survival rate, the assumption will hold. However, an animal seen late in the sampling period is more likely to be seen again in the next sampling occasion. Moreover, for species with high survival rate, therefore very small chance of dying during the sampling occasion, long sampling occasions could be used in a stopover duration analysis, i.e. study of duration of time spent on stopover sites for refuelling (typically in migratory birds) (Pledger et al., 2009; Schaub et al., 2001), the results of which could then be used to better redesign the sampling protocol. Indeed when study cost is a major issue, this type of analysis might especially permit the optimization of the sampling experiment because a stopover duration analysis could help identifying the best time period to sample the largest number of individuals by estimating residence time. Researchers using long sampling occasions should also consider, when appropriate, a robust-design type of experiment, i.e. an experimental design with primary sampling periods spaced apart and secondary sampling periods within each primary sampling period, during which the population is assumed closed (Pollock, 1982).

Advantages of the TSJS framework include the possibility of reducing the proportion of totally uncatchable animals with the double-sampling experiment, which results in negatively biased abundance estimates (Aebischer, 1986). However, the sampling methods used in the double-sampling experiment need to sample the same population, otherwise the estimate would describe a population that does not exist or at least not the population of interest, misleading researchers and potentially leading to inappropriate management decisions. Moreover, for a more parsimonious parameterization and hence a better precision in the population size estimate, the use of covariates in modeling the capture probabilities (Pollock, 2002) could be especially useful. Modeling capture probabilities with auxiliary variables, such as individual covariates, could help to better explain heterogeneity in capture probabilities, which is a major cause of negatively-biased abundance estimates in many ecological studies. However, the TSJS model as presently formulated has the potential disadvantage of not allowing the use of covariates.

Alternative modeling approaches have been considered to answer the issue of two overlapping datasets in the estimation of population size. These alternative models, also presented in chapter one, are rooted in different conceptual frameworks (e.g. closed population, likelihood-based, Bayesian) with different interpretation and involve different mathematical arguments compared to the TSJS approach. The first intuitive alternative solution of the TSJS model would simply be an average population size estimate of the estimates provided separately by the two sampling methods. The question is then how to combine them. Later on (chapter four), I explore a variance-weighted mean of the Jolly-Seber estimates based on each sampling method.

The likelihood based-approach of the two-source M_0 model enables us to highlight the difficulties of an extension of such likelihood to an open-population framework. With the two-source M_0 model, identities of individuals are treated as latent variables and, in order to estimate the population size, it is necessary to sum over all possibilities. In an open-population approach, the extension of this closed-population based likelihood would require taking survival and dispersal into account. Therefore, in an open population, when there is for instance a “0” in the capture history, the possibilities for the latent variable are extended to being alive but missed on this occasion and to being dead on this occasion (against simply being missed in the closed-population approach). Individuals will not simply fall into the five categories any more (as they do in the table on p.43). The five categories can no longer be expressed in terms of the detection probabilities and the model needs to allow for every possible combination of “arriving” (e.g. birth, immigration) and “leaving” (death, emigration) events within the survey. Then summing over all possibilities would become tremendous implementation-wise and require a powerful computer. Similarly, it would theoretically be possible to extend the multinomial models based on the latent history approach of Link and Barker (2010). The approach, though even more intractable with current technology and software, would consist in defining two more “events” that can occur at a sampling occasion (though associated with that occasion). They would be a “5” if the animal was as yet “unborn” and a “6” if it was “dead”. Thus, a history such as “5501366” would represent an animal that appeared in the population between sampling occasions 2 and 3, but disappeared after a mere three occasions in the population during which time it was caught once by method 1 and once by method 3. Enumerating the complete list of possible latent histories for any but the shortest of studies would be best left to a computer, and ensuring the MCMC process adequately sampled the full space would probably be a considerable logistical problem.

2. Chapter Two

Results of simulation studies on the two-source Jolly-Seber model

2.1. Abstract

Simulations are used here to test the performance of the two-source Jolly-Seber (TSJS) estimator when all assumptions are met and when survival and birth rates are constant in time. The mean relative error (MRE) and the root mean square relative error (RMSRE) are chosen to provide information on the suitability of the estimator given different situations. The simulations enable researchers to measure the dependence of the estimator on factors such as capture probability, sample size, and length of the experiment. The results show that the TSJS estimator is generally unbiased for capture probabilities equal or greater than 0.2 and for a simultaneous sampling probability greater than 0.2 per occasion. Increasing the population size results in a substantial reduction of the error and permits a greater inequality between the two single sampling probabilities (i.e. when the probability of sampling by one method is greater than the probability of sampling by the other single method on each capture occasion) that the model can handle.

2.2. Introduction

The TSJS model is an open-population model, so the assumption of demographic closure of the population is relaxed and the one of geographic closure partially relaxed (the animals can enter or leave the study area only once during the monitoring period, i.e. temporary, short to medium term immigration or emigration is not allowed). Being an extension of the Jolly-Seber (JS) model, it relies on assumptions that are similar to those of the JS model (Jolly, 1965; Seber, 1965):

i. all animals present (marked or unmarked) in the population at the time of the t-th sampling occasion ($t = 1, 2, \ldots, T$) have an equal probability of being caught,

ii. all marked animals present in the population immediately after the t-th sampling occasion have an equal survival probability until the (t+1)th sampling time ($t = 1, 2, \ldots, T-1$),

iii. animals do not lose their marks or tags,

iv. immigration cannot be separated from birth without additional information,

v. all emigration from the sampling population is permanent.

Given the mathematical formulation of the TSJS model, it seems essential to explore thoroughly the performance of the estimator. The first logical step is to measure the error on the estimator when all assumptions are met. Then later (chapter three), the error will be measured when the underlying assumptions are violated. In this chapter, the effect of the population size, the number of capture occasions, the effect of the capture probability and the effect of the sampling probabilities are tested and the results are expressed in terms of mean relative error, root mean square relative error and confidence interval coverage rates. A simulation program was written in the statistical programming language R to generate capture histories for open populations sampled opportunistically by two methods and create the same data structure as described in chapter one (section 1.4.2).

In the TSJS model, the I_{id} parameter (also referred to as probability of single identity, see chapter one) is used as a way of estimating the unidentified overlap in experimental designs where two sampling methods are used but lack systematic simultaneous capture by both methods. It is therefore expected that the I_{id} parameter will be of greater importance as the number of individuals in the class F (Fig.1-1) increases in the combined dataset (see chapter one, section 1.4.3). It is also expected that the relative error will decrease as capture probability, population size and number of capture occasions increase, as in the standard JS model (Gilbert, 1973).

2.3. Methods

2.3.1. Simulation Description

The simulation is an attempt to model an animal population in order to evaluate the performance of the new extension of the JS estimation described in chapter one. For the purpose of chapter two, the simulations have a basic form representing a general animal population and the base parameter settings are for a large long lived animal with recruitment as single young litters.

Demographic process

At the start of the simulation, a population of *n* living, unmarked individuals is created. A sex ratio can be used to determine the number of males and females in the population. Then an age is randomly given to each individual. Through each occasion of the simulations, individuals first die at a determined death rate. Uniform random numbers between 0 and 1 are used to determine the fate of each individual (die/live) on every occasion: if the random number associated with the individual is smaller than the death rate then this individual dies.

Then age is updated by adding 1 before the reproduction process. A reproductive rate is assigned to mature females. Uniform (0, 1) random numbers are again used to create the birth history matrix (Fig.2-1) to keep track of the reproductive history of each mature female: if the random number associated with the female is smaller than the reproductive rate, then the female has an offspring on this occasion.

$$\begin{array}{cc} & \text{Occasion} \\ \text{Individual} & \begin{pmatrix} 101001 \\ 011000 \\ ..... \\ . \\ . \\ 000000 \\ 000000 \end{pmatrix} \end{array}$$

Fig.2-1- Structure of the birth matrix produced by the program.

Each row of the birth history matrix represents the birth history of each individual whale: it is filled with “0” for males, immature females and those who never gave birth. For example, in Fig.2-1 individual 1 (first row) was a female which had an offspring in time 1, 3 and 6, individual 2 was a female which had an offspring on two consecutive occasions (occasions 2 and 3). The last animals did not reproduce as they are new born, so immature and possibly male.

Sex is then assigned to each new born randomly with a user-defined sex ratio and those new born are added to the population matrix recording the history of each individual. This matrix is filled by “0” when the individuals were not born in the corresponding occasion or died on this occasion or in a previous occasion, and by “1” when it was alive in the corresponding occasion.

$$\begin{array}{cc} & \text{Occasion} \\ \text{Individual} & \begin{pmatrix} 111111 \\ 111000 \\ ..... \\ . \\ . \\ 001110 \\ 000011 \end{pmatrix} \end{array}$$

Fig.2-2- Structure of the history matrix produced by the program.

Each row represents, in Fig.2-2, the history of an individual. In this example, individual 1 was alive for the 6 occasions of the simulation while individual 2 died on the fourth occasion, the last individual was born on occasion 5 and still alive on occasion 6. As new born are added as the program runs, the first *n* lines are the population of origin that was created at the beginning of the simulations and the lines after line *n* are the new born individuals. So the last line corresponds to the last individual born.

Once the population is created, the next step is to sample from it.

Sampling process

From the history matrix, a matrix of availability for sampling of each individual is created. At each time period, if the individual is alive, it is available for capture and sampling with probabilities defined as follows and illustrated in Fig.2-3:

Let $S = \{s_1, s_2, s_3\}$ be a discrete sample space with:

$s_1 = \{\text{sampled by method 1}\}$

$s_2 = \{\text{sampled by method 2}\}$

$s_3 = \{\text{sampled simultaneously by both methods}\}$

The s_k events are mutually exclusive and together cover everything in S , i.e. form a partition of S , so $\Pr(S) = \Pr(s_1 \cup s_2 \cup s_3) = \Pr(s_1) + \Pr(s_2) + \Pr(s_3) = 1$

Now let the event $c = \{\text{captured}\}$ such that $c \subseteq S$. From the partition theorem, it follows that:

$\Pr(c) = \Pr(c \cap s_1) + \Pr(c \cap s_2) + \Pr(c \cap s_3)$

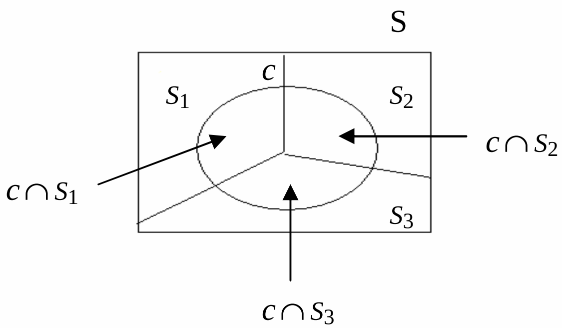


Fig.2-3- Venn Diagram illustrating the structure of the sampling process in the simulation.

Generating random numbers, the fate of the individual is set on every occasion: if the random number generated on the considered occasion is smaller than the set capture probability $\Pr(c)$ then the individual is recorded as being captured.

Then each captured individual, on the considered occasion, is set to be sampled by either method 1 with probability $\Pr(s_1)$ or method 2 with probability $\Pr(s_2)$ or by both simultaneously with probability $\Pr(s_3)$, such that $\Pr(s_1)+\Pr(s_2)+\Pr(s_3)=1$ as illustrated in Fig.2-3. For example, individuals can have an occasion-specific sampling probability defined as following: $\Pr(s_1)=0.1$, $\Pr(s_2)=0.1$ and $\Pr(s_3)=0.8$. Probabilities $\Pr(s_1)$, $\Pr(s_2)$, $\Pr(s_3)$ will later on be expressed as percentages and referred to as single sampling probabilities for $\Pr(s_1)$ and $\Pr(s_2)$, and simultaneous sampling probability for $\Pr(s_3)$. For the previous example, the individuals are set up to be, on all capture occasions, available for sampling with an 80% chance by both methods simultaneously , with an 10% chance by method 1 only and with an 10% chance by method 2 only (under the assumption of temporal homogeneity of $\Pr(s_1)$, $\Pr(s_2)$, $\Pr(s_3)$). They may, of course not be captured, but the captures will be in those proportions.

Thus, using uniform random numbers, the type of sampling method (method 1, method 2 or both simultaneously) is defined as follows: if the random number is smaller than the value of $\Pr(s_3)$ then the individual is available by both methods simultaneously; if it is between the values of $\Pr(s_3)$ and $\Pr(s_3)+\Pr(s_1)$ then the individuals is available by method 1 and if it is between the values $\Pr(s_3)+\Pr(s_1)$ and 1 then it is a method-2-capture type.

Note that the probabilities $\Pr(s_1)$, $\Pr(s_2)$, $\Pr(s_3)$ and $\Pr(c)$ can be seen as resulting from the breakdown in two parts of a third kind of probabilities: the occasion-specific probabilities of being recorded in the dataset by methods 1, 2 and 3 which would be defined as the probabilities of being detected and available for sampling by method 1, 2 or 3, so respectively as:

$$\Pr(r_1)=\Pr(c\cap s_1)=\Pr(c)\times\Pr(s_1)$$

$$\Pr(r_2)=\Pr(c\cap s_2)=\Pr(c)\times\Pr(s_2)$$

$$\Pr(r_3)=\Pr(c\cap s_3)=\Pr(c)\times\Pr(s_3)$$

This simulation structure for the sampling process was developed in order to be able to vary independently the detection and the sampling availability by each method for different classes of individuals in the population: in chapters three and four, the population will be split into four demographic classes g (calves, adult males, non-breeding females, breeding females). Therefore, given this simulation structure, it will be possible to assign to each class of individuals specific detection and availability probabilities denoted $\Pr(c)_g$, $\Pr(s_1)_g$, $\Pr(s_2)_g$, $\Pr(s_3)_g$ and measure the performance of the TSJS estimator with various forms of heterogeneity (e.g. heterogeneity in sampling availability and/or heterogeneity in capture among the classes).

Creation of the capture history

Capture data for each individual can be summarized using the following encounter history codes:

Code	*Definition*
0	Not captured
1	First capture by method 1 and no simultaneous capture in the record
2	First capture by method 2 and no simultaneous capture in the record
4	Recapture by method 1 and never simultaneously captured
5	Recapture by method 2 and never simultaneously captured
10	First capture in the record, by method 1 with a later simultaneous recapture
11	First capture in the record, by method 2 with a later simultaneous recapture
9	First capture in the record and a simultaneous one
6	First recapture by method 1 when the first capture was a simultaneous one
7	First recapture by method 2 when the first capture was a simultaneous one
8	Simultaneous recapture after a “9”
14	First simultaneous recapture after a “10” or “11”
15	First recapture by method 1 after a “11” in the record
16	First recapture by method 2 after a “10” in the record
12	Recapture by method 1 after a “10” or a “15”
13	Recapture by method 2 after a “11” or a “16”
17	Recapture by method 2 after a “7” in the record
18	Recapture by method 1 after a “6” in the record
19	Simultaneous recapture after a “14” in the record

Creating the overlap

It is necessary to recreate the situation that researchers face in their datasets when individuals have been captured by both single methods but have not been captured by both methods simultaneously.

So far the simulation produces one line of capture history for each individual. However, it is essential to create in addition the two capture histories for individuals that would have been captured by method 1 and method 2 but never captured simultaneously. So the overlapping situation is generated by splitting in two capture histories any capture history that contains captures by both single methods in the absence of a simultaneous capture.

For example, before the creation of the overlap, the simulation can produce a capture history such as “0102045”: the individual is captured by method 1 on the second occasion, recaptured by method 2 on the fourth occasion, then recaptured by method 1 on the sixth occasion and recaptured by method 2 on the last occasion. In the field, in the absence of a simultaneous capture, such a record would actually not exist and what would appear in the final dataset is two “observed” capture histories. So it is necessary to split such simulated records into two capture histories in the simulation to mimic reality. Therefore, a capture history such as “0102045” will become two capture histories, “0100040” and “0002005”, in the simulation. The resulting matrix will be used to estimate the population size (except in the case of tag loss, see later) and will be referred to as the CMR (Capture-Mark-Recapture) matrix.

Assumptions

The general assumptions of the simulations in this chapter are:

i. capture probability $\Pr(c)$ is constant over time,

ii. sampling probabilities $\Pr(s_1)$, $\Pr(s_2)$, $\Pr(s_3)$ are constant over time,

iii. there is no loss of mark: once an individual is marked (captured) it cannot lose its mark and will be necessarily recognised the next time it is captured ,

iv. permanent emigration cannot be dissociated from death,

v. as all entering individuals are new-born, there is no immigration *per se*,

vi. all individuals have the same survival rate.

2.3.2. Relative error and measure of difference

The relative error can be described by measures of difference, especially by measures of the mean error. These measures aim at quantifying the estimate of the difference between values predicted by a model and actual values from the population (which may or may not be observable in real life). The performance of the model estimates at a given sampling period is discussed in terms of relative error (RE) calculated as following:

$$RE = \frac{\hat{N} - N}{N}$$

where $\hat{N}$ is the estimated population size and N the true population size.

Averaging the relative error over all simulation runs for a given set of parameters gives the mean relative error MRE per occasion *t*:

$$MRE_t = \frac{\sum_{j=1}^{\alpha} \frac{\hat{N}_{tj} - N_{tj}}{N_{tj}}}{\alpha} = \frac{1}{\alpha} \sum_{j=1}^{\alpha} \frac{\hat{N}_{tj}}{N_{tj}} - 1$$

the expected value of the estimate as a proportion of the true value, minus 1. It is therefore a measure of bias,

where $\hat{N}_{tj}$ is the predicted population size given by the model at occasion *t*, for simulation run *j*,

N_{tj} is the observed, true population size at occasion *t*, for simulation run *j*,

α is the number of "successful" simulation runs ("successful" because N_{tj} can be inestimable due to the values of the simulated data).

I also chose to measure the performance, the overall error, of the TSJS estimator in terms of root mean squared relative error (RMSRE):

$$RMSRE_t = \sqrt{\frac{\sum_{j=1}^{\alpha} \frac{\left(\hat{N}_{tj} - N_{tj}\right)^2}{N_{tj}^2}}{\alpha}}$$

Here I discuss the choice of the mean relative error (MRE) and the root mean square relative error (RMSRE) rather than the mean absolute error (MAE), the mean square error (MSE) and other classic indices, to measure the error of the TSJS model.

These other indices take the form:

$$MSE_t = \frac{\sum_{j=1}^{\alpha}\left(\hat{N}_{tj} - N_{tj}\right)^2}{\alpha}$$

$$RMSE_t = \sqrt{\frac{\sum_{j=1}^{\alpha}\left(\hat{N}_{tj} - N_{tj}\right)^2}{\alpha}}$$

$$MAE_t = \frac{\sum_{j=1}^{\alpha}\left|\hat{N}_{tj} - N_{tj}\right|}{\alpha}$$

$$MARE_t = \frac{\sum_{j=1}^{\alpha}\frac{\left|\hat{N}_{tj} - N_{tj}\right|}{N_{tj}}}{\alpha}$$

The MAE and RMSE are reported to be among the best overall measures of model performance by Willmott (1982) and are similar measures. Although the MAE is less sensitive to extreme values than the RMSE, Willmott reports the MSE as being more commonly used by statisticians because it is amenable to a greater degree of complexity in statistical analysis. Nonetheless, in the present case, it might not be the best way to answer the biological question of interest:

"How close to the true values are the estimates given by the model relative to the population size?"

On the other hand, the measure MARE (mean absolute relative error) and RMSRE give an estimate of the relative average error, in other words both measures calculate the average of the error taken as a relative proportion of the true value. Moreover the information provided by the MARE is similar to the one given by the RMSRE. The important difference between the two indices, MRE and RMSRE, is that the MRE provides information on the average error (i.e. the bias of the proportion), while the RMSRE measures the bias and the random variation around the expected value. The RMSRE can be seen as a measure of overall utility of the method and could be large even in the absence of bias.

Therefore, estimates of both the MRE and the RMSRE across simulations will be reported to study the error produced by the TSJS model:

1) the MRE will simply provide a measure of the relative error,

2) the RMSRE will give the average deviation of estimates from the true value (i.e. bias+error).

Finally, confidence intervals are one of the most effective ways to measure the accuracy of a method. So it is also important to evaluate how well the confidence interval works to see how useful the model is. Here, the coverage rate of the confidence intervals (CI coverage rate) will be calculated as the ratio of the number of times that the true value falls between the bounds of the estimated normal and log-normal 95% confidence interval over the total number of simulation runs.

2.3.3. Number of simulation runs

Preliminary simulations were done in order to decide the appropriate number of replicates necessary to obtain reliable and representative estimates of error and variation. A replicate corresponds to the generation of one population going through the cycle “Aging-Surviving-Reproducing-Sampling” over T occasions. The output of each replicate is a matrix of capture histories leading to the estimation of the size of this population by the TSJS model. It will also include the estimation of the size of this population by the standard JS model (one for each sampling method), the variance-weighted mean of the two standard JS models (each based on one of the two datasets provided by the two sampling methods), the two-source M_0 model and the closed population model M_t by Darroch, M_h by Chao and M_{th} (based only on one of the two datasets) for the purposes of chapter four.

Running 1000 replicates of the simulation for all the experiments in the thesis would have been impractical in terms of computer time. So it was necessary to see if the same results could be achieved by running a smaller number of runs. The case with homogeneity in capture probability, over 10 occasions, with a starting population of 500 individuals and sampling availability scenario “20-40-40”, i.e. $\Pr(s_3) = 0.2$ and $\Pr(s_1) = \Pr(s_2) = 0.4$, was used to decide how many runs of the simulation would give representative results in a reasonable computer time. This case includes a medium size sample size and a medium number of capture occasions to avoid confounding trends in the MRE and RMSRE that would result from small sample size or short study period. It will also be seen later that this case represents the minimum probability of double-tagging ($\Pr(s_3) = 0.2$) per occasion needed for the estimator to produce reasonable unbiased results and was thus thought to be the most suitable case for showing the number of replicates necessary to achieve representative results.

Investigating the MRE

It is necessary to see if running 100, 200 or 1000 replicates can give equivalent results in terms of MRE. Here, as the estimation of the population size with the TSJS estimator is not possible on the very first and very last occasions, the MRE is only available for 8 occasions.

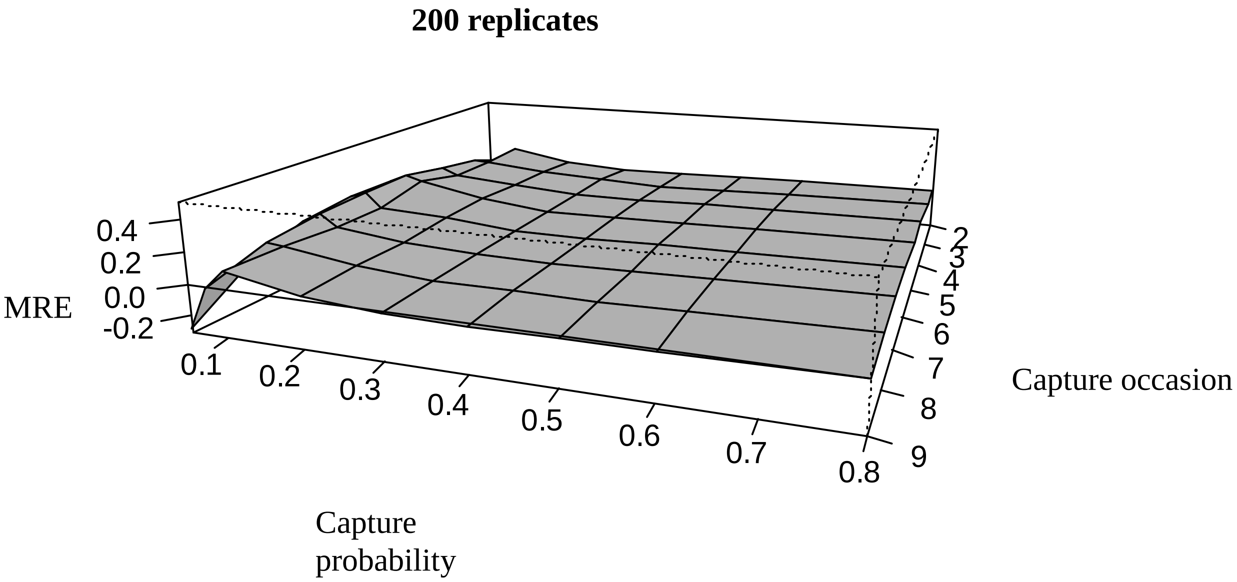
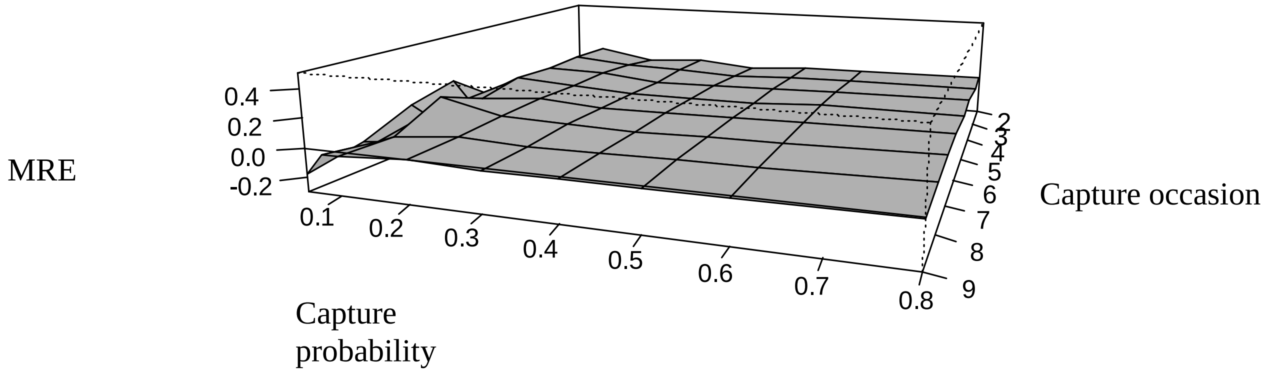


Fig.2-4- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 500 individuals for 200 replicates**.**

Looking at the consequences on the MRE of increasing the number of replicates, Fig.2-4 and Fig.2-5 (see also Appendix 4) show that it only influences the results for small capture probabilities (<0.1) by flattening the graph. Running 200 replicates appears to be slightly better in term of variability of the MRE for small probabilities and just double the running time compared to running a 100 replicates which would still be reasonable. However, compared to the results with 200 replicates, running 1000 replicates does not seem to be worth multiplying the computer time by 5.

100 replicates



1000 replicates

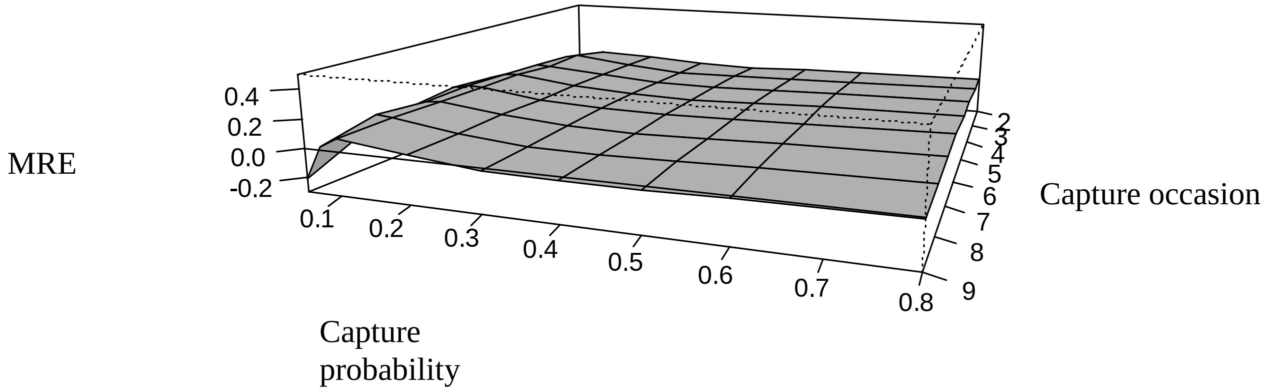


Fig.2-5- MRE for 200 replicates as a function of the capture probability and capture occasion over 10 years, with a starting population of 500 individuals for 100 and 1000 replicates.

The objective here was to reduce the computer time (approximately 6 hours for 100 replicates, 12 hours for 200 replicates and 60 hours for 1000 replicates) while roughly keeping the precision and dispersion of the bias achieved with a high number of loops. In the light of the present results, using 200 replicates for the simulation seems appropriate and will thus be applied for all simulation experiments in the thesis.

2.3.4. Analysis steps

In the following, I investigate the effect of the population size *N*, of the number of capture occasions *T*, and of the capture probability $\Pr(c)$ on the performance of the TSJS estimator. I also investigate the performance of the estimator with various simultaneous sampling probabilities $\Pr(s_3)$ and single sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$.

It is worth noting that when 100% of caught individuals have been simultaneously double-tagged at least once, the situation is that of the standard JS model with no unknown overlapping between the datasets of the two sampling methods. Doing a full factorial design with all the possible combinations of these factors would be impractical in computer time and representative scenarios were chosen to illustrate and detect potential impacts.

2.4. Effect of the simultaneous sampling probability

The objective here is to investigate the performance of the model for various simultaneous sampling probabilities $\Pr(s_3)$: it is of particular interest to see if the model responds equally well for high and low probabilities of double-marking. It appears also important to investigate the performance of the estimator when the single sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ are not equal as this situation will occur in most ecological studies and which will introduce a form of heterogeneity that could be expected to bias the TSJS estimates.

A starting population of *N*=500 individuals over *T*=10 capture occasions is used for the simulations in this part of chapter two. It was chosen to use a medium size population and a medium length of study to avoid confounding possible problems inherent to small sample size and short study period and to avoid masking the error with large sample size and long experimental duration.

2.4.1. With equal single sampling probabilities

In this section the single sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ are set equal. Several simultaneous sampling probabilities $\Pr(s_3)$ are used to test the TSJS estimator for relative error: when individuals have a 50%, 20% and 17% probability of being double tagged, i.e. $\Pr(s_3) = 0.5$, $\Pr(s_3) = 0.2$ and $\Pr(s_3) = 0.17$. The scenarios are expressed in terms percentages of sampling probabilities and are summarized as follows: value of the simultaneous sampling probability $\Pr(s_3)$, value of sampling probability by method 1 $\Pr(s_1)$, value of sampling probability by method 2 $\Pr(s_2)$.

So scenario 50-25-25 represents the situation where $\Pr(s_3) = 0.5$, $\Pr(s_1) = \Pr(s_2) = 0.25$.

Minimum simultaneous sampling probability for the two-source Jolly-Seber model

The first investigation of the behavior of the TSJS model aims at determining if there is a critical simultaneous sampling probability $\Pr(s_3)$. The MRE for the scenarios 50-25-25, 20-40-40, 17-41.5-41.5 and 10-45-45 are investigated and illustrated in Fig.2-6 and Fig.2-7 (see also Appendix 4). It is clear from Fig.2-7 that, if $\Pr(s_3)$ is below 0.2 on every capture occasion, the TSJS estimator is (sometimes extremely) negatively biased for capture probabilities $\Pr(c)$ smaller than 0.5.

The other effects of double tagging are discussed below. It is worth noting that the estimates for periods 2 and 9 (the first and last estimates available) are likely to be unreliable because the first estimates may lack sufficient number of first captures on the first capture occasion and the last estimates may lack sufficient number of recaptures on the last capture occasion.

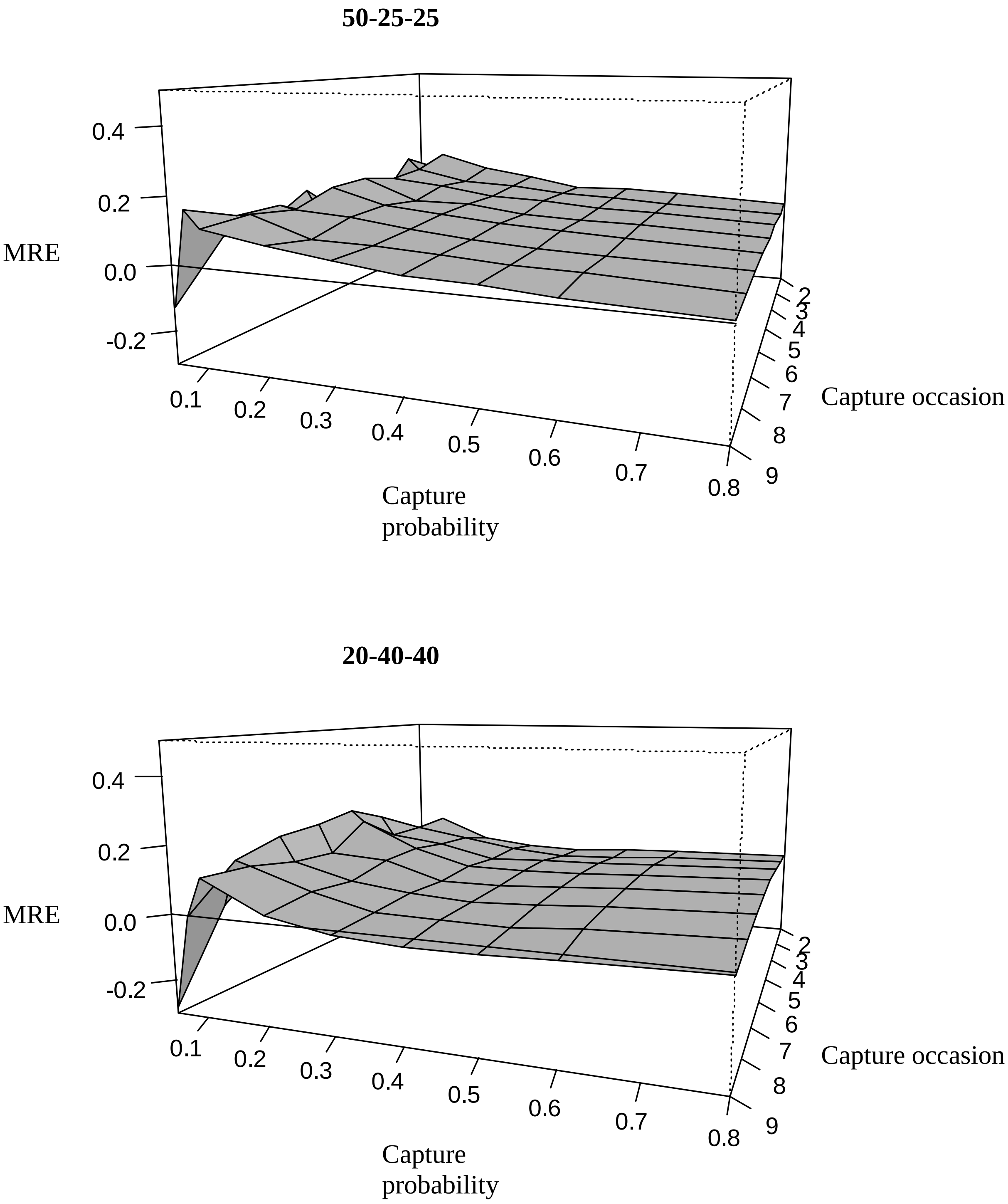


Fig.2-6- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 500 individuals for scenarios of sampling probabilities 50-25-25 and 20-40-40**.**

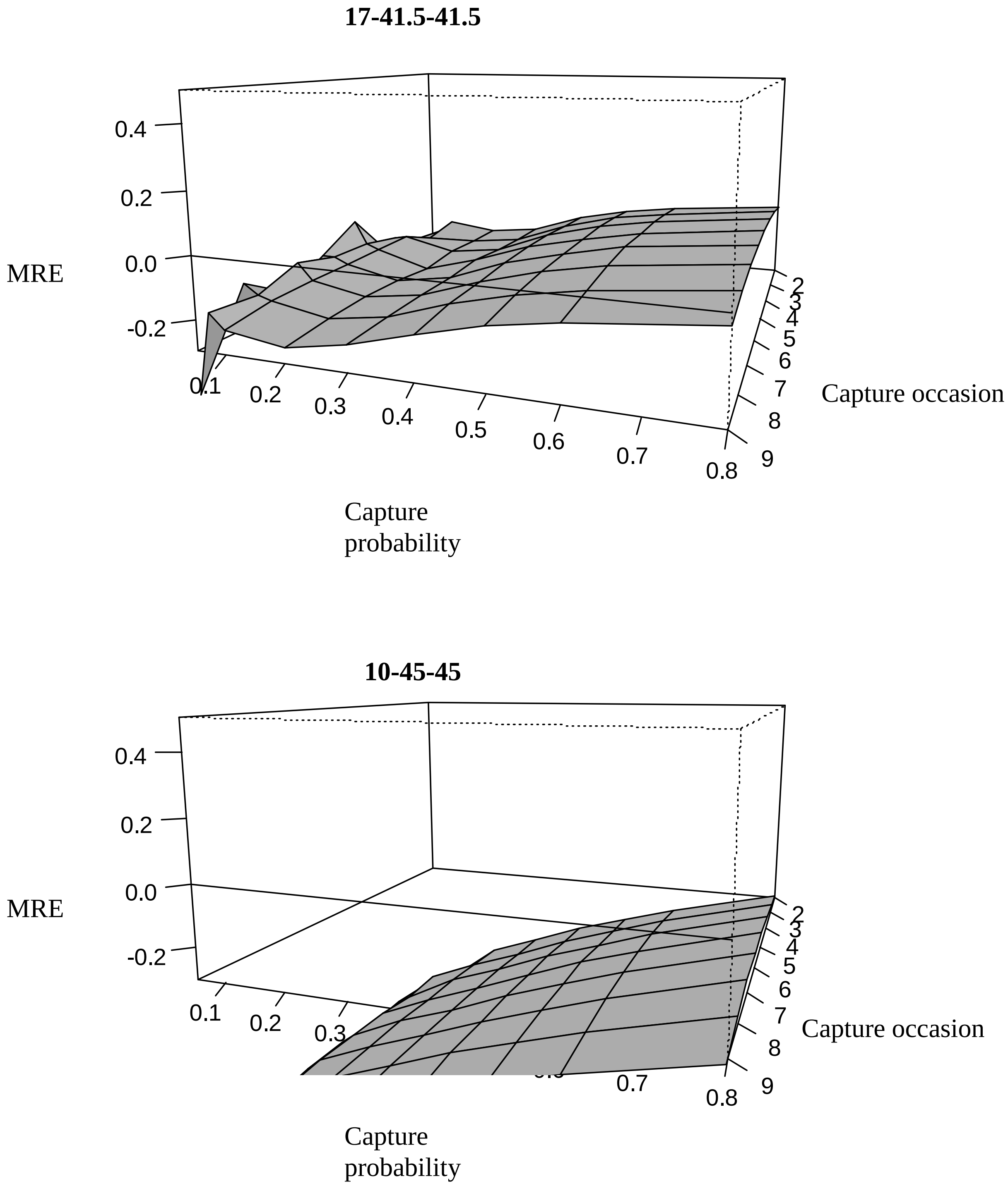


Fig.2-7- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 500 individuals for scenarios of sampling probabilities 10-45-45 and 17-41.5-41.5.

In the light of Fig.2-7, a simultaneous sampling probability of 0.2, i.e. $\Pr(s_3) = 0.2$, seems to be the critical value below which the model performs particularly poorly. Thus, for the following, I will investigate the relative error of the TSJS estimator for a minimum simultaneous sampling probability of 0.2.

Effect of an increase of the simultaneous sampling probability

The next step in the investigation of the model aims at studying the impact of the simultaneous sampling probability $\Pr(s_3)$ above the critical value of 0.2 to see whether the relative error is reduced when this value increases. As shown in Fig.2-6, increasing the simultaneous sampling probability $\Pr(s_3)$ leads to an average relative error being positive. This positive error induced with a simultaneous sampling probability $\Pr(s_3)$ of 0.5 is equivalent to the absolute value of the negative error present when the simultaneous sampling probability is 0.2.

Looking at Fig.2-8, where the MRE is averaged for each capture probability $\Pr(c)$ over the study period, the median is very close to zero, at equal capture probability, for both scenarios and, as expected, the MRE decreases with the increase of capture probability.

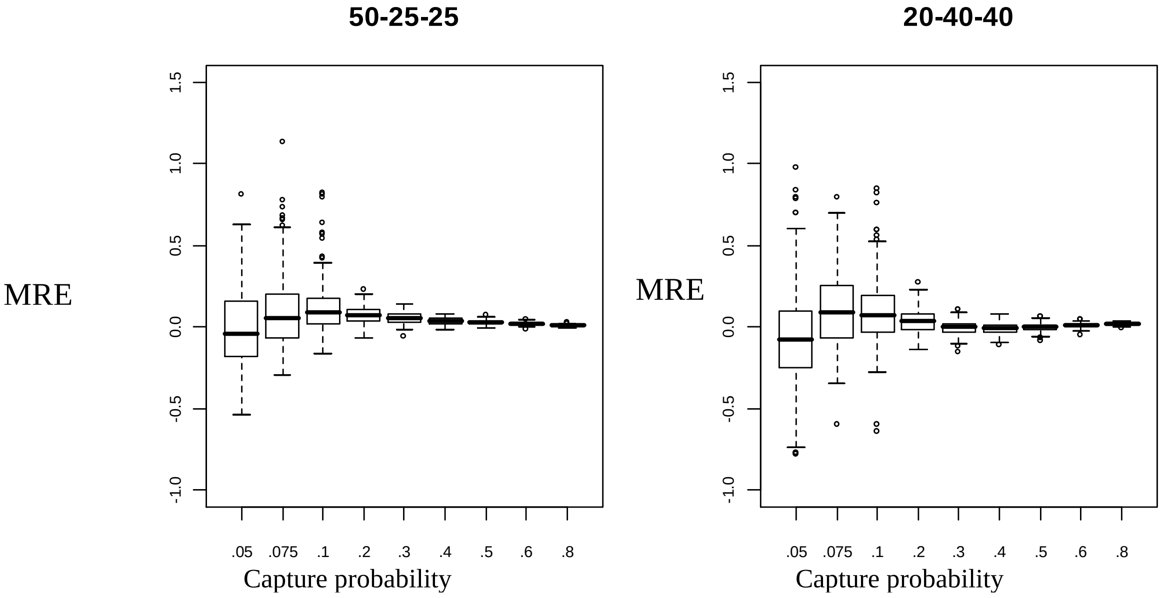


Fig.2-8- Box plots of MRE averaged over the study period per capture probability for an experiment of 10 years, with a starting population of 500 individuals and simultaneous sampling probability of 0.2 and 0.5.

Increasing $\Pr(s_3)$ only seems to affect the number of outliers for small capture probabilities ($\Pr(c) \leq 0.1$) which slightly increases for $\Pr(s_3) = 0.2$. The variability in the MRE also appears to be higher for $\Pr(s_3) = 0.2$, at small capture probabilities, especially at $\Pr(c) = 0.05$.

From the MRE perspective, it seems that, when all assumptions are met, the TSJS model produces almost no relative error for capture probabilities $\Pr(c)$ higher or equal to 0.2 when $\Pr(s_3)$ is above the critical value of 0.2 when the length of the experiment (*T*) is 10 and the population size (*N*) is greater than 500. However, this needs to be confirmed by the study of the RMSRE and CI coverage rates which will give a measure of the utility of the estimator.

Table 2-1 and Appendix 5 display, for a probability of simultaneous sampling $\Pr(s_3)$ of respectively 0.2 and 0.5, the average MRE and the RMSRE along with the mean estimated and true values on each capture occasion for capture probabilities $\Pr(c)$ varying between 0.05 and 0.8.

Both cases are equivalent showing that, as long as $\Pr(s_3)$ is equal to or above 0.2 when *T*=10 and *N*=>500, the performance of the TSJS estimator does not depend $\Pr(s_3)$ (except, as noted previously, occasional estimates for sample occasions 2 and 9).

Table 2-1- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-year study for different capture probabilities with scenario 20-40-40 and a starting population of 500 individuals.

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(*c*)=0.05							
$\hat{N}_2$	391	627	-0.38	259	0.56	62	81
$\hat{N}_3$	546	653	-0.16	323	0.62	73	84
$\hat{N}_4$	670	695	-0.04	372	0.89	75	86
$\hat{N}_5$	778	719	0.08	419	1.1	80	83
$\hat{N}_6$	873	748	0.17	466	1.3	84	87
$\hat{N}_7$	734	766	-0.04	396	0.61	75	88
$\hat{N}_8$	805	799	0.01	432	0.8	76	83
$\hat{N}_9$	653	834	-0.22	351	0.69	64	77

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(*c*)=0.075							
$\hat{N}_2$	614	626	-0.02	252	0.72	68	71
$\hat{N}_3$	699	654	0.07	257	0.64	78	83
$\hat{N}_4$	779	693	0.13	278	0.74	84	84
$\hat{N}_5$	836	719	0.16	292	0.75	85	89
$\hat{N}_6$	842	745	0.13	293	0.55	88	90
$\hat{N}_7$	823	764	0.08	282	0.49	90	88
$\hat{N}_8$	931	795	0.17	317	0.77	83	84
$\hat{N}_9$	787	831	-0.05	269	0.54	70	76
Pr(*c*)=0.1							
$\hat{N}_2$	643	627	0.03	194	0.63	74	74
$\hat{N}_3$	696	656	0.06	186	0.4	84	86
$\hat{N}_4$	785	694	0.13	203	0.46	90	87
$\hat{N}_5$	803	719	0.12	204	0.44	87	88
$\hat{N}_6$	817	745	0.1	205	0.39	88	88
$\hat{N}_7$	880	762	0.15	220	0.45	85	84
$\hat{N}_8$	834	794	0.05	209	0.42	86	86
$\hat{N}_9$	937	829	0.13	234	0.77	75	75
Pr(*c*)=0.2							
$\hat{N}_2$	648	626	0.04	78	0.28	67	67
$\hat{N}_3$	678	653	0.04	77	0.19	79	79
$\hat{N}_4$	713	692	0.03	80	0.17	86	86
$\hat{N}_5$	755	718	0.05	85	0.18	87	85
$\hat{N}_6$	769	743	0.03	87	0.17	85	84
$\hat{N}_7$	801	762	0.05	91	0.17	85	81
$\hat{N}_8$	820	793	0.03	94	0.16	89	87
$\hat{N}_9$	860	828	0.04	100	0.24	74	74
Pr(*c*)=0.3							
$\hat{N}_2$	633	627	0.01	40	0.14	61	61
$\hat{N}_3$	662	655	0.01	41	0.1	76	76
$\hat{N}_4$	697	694	0	45	0.09	85	87
$\hat{N}_5$	719	718	0	47	0.08	87	88
$\hat{N}_6$	746	745	0	50	0.08	90	90
$\hat{N}_7$	768	763	0.01	52	0.09	89	90

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_8$	795	796	0	55	0.09	88	87
$\hat{N}_9$	822	830	-0.01	58	0.12	81	82
Pr(*c*)=0.4							
$\hat{N}_2$	608	626	-0.03	22	0.1	50	50
$\hat{N}_3$	643	653	-0.02	25	0.07	71	71
$\hat{N}_4$	693	694	0	29	0.06	82	85
$\hat{N}_5$	717	719	0	31	0.05	88	89
$\hat{N}_6$	747	745	0	33	0.05	91	91
$\hat{N}_7$	764	764	0	35	0.06	87	88
$\hat{N}_8$	787	796	-0.01	37	0.07	82	84
$\hat{N}_9$	813	829	-0.02	40	0.08	73	76
Pr(*c*)=0.5							
$\hat{N}_2$	619	627	-0.01	14	0.07	54	54
$\hat{N}_3$	652	654	0	16	0.04	35	35
$\hat{N}_4$	698	694	0	20	0.04	60	60
$\hat{N}_5$	727	720	0.01	22	0.04	70	70
$\hat{N}_6$	750	744	0	24	0.04	79	79
$\hat{N}_7$	764	763	0	25	0.04	70	69
$\hat{N}_8$	793	795	0	27	0.04	71	73
$\hat{N}_9$	809	830	-0.02	29	0.06	55	56
Pr(*c*)=0.6							
$\hat{N}_2$	618	626	-0.01	9	0.05	41	42
$\hat{N}_3$	657	654	0	11	0.03	66	67
$\hat{N}_4$	706	693	0.02	14	0.03	79	79
$\hat{N}_5$	732	718	0.02	16	0.03	80	80
$\hat{N}_6$	760	744	0.02	18	0.03	82	82
$\hat{N}_7$	773	762	0.01	19	0.03	90	90
$\hat{N}_8$	795	793	0	20	0.03	90	91
$\hat{N}_9$	814	828	0.02	22	0.04	73	75
Pr(*c*)=0.8							
$\hat{N}_2$	623	625	0	2	0.02	27	27
$\hat{N}_3$	662	651	0.02	4	0.02	35	35
$\hat{N}_4$	711	693	0.03	7	0.03	31	31
$\hat{N}_5$	740	716	0.03	8	0.04	25	26

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_6$	768	743	0.03	10	0.04	30	30
$\hat{N}_7$	783	761	0.03	11	0.03	46	47
$\hat{N}_8$	808	792	0.02	12	0.03	74	75
$\hat{N}_9$	823	827	0	13	0.02	89	90

$\hat{N}_2$, …, $\hat{N}_9$ =population size estimate at time 2, …, 9.

N.B.: mean estimates, mean true values and mean estimated standard errors are rounded to the nearest integer in the above table and in all subsequent ones, as population size and associated variables are generally integers.

The TSJS estimator can be severely biased with values of the MRE reaching -0.38 on the second capture occasion for $\Pr(c)=0.05$ and $\Pr(s_3)=0.2$. However, the estimates can also be unbiased with values of the MRE as low as 0.01. So, from the MRE perspective, there is no clear trend for the relative error: it is not stable, with no specific direction and unpredictable for capture probabilities smaller than 0.1. However, for a capture probability $\Pr(c)$ equal to or higher than 0.1, the MRE quickly stabilizes and reaches values below 10% of the true population size. For the MRE, there is also no pattern concerning the evolution of the relative error during the study: though the first and last estimated values are more biased for a capture probability of 0.05, this is not the case for the other values of capture probabilities.

Concerning the magnitude of the overall relative variation represented by the RMSRE, it follows the evolution of the MRE: its values are irregular for both $\Pr(s_3)=0.2$ and $\Pr(s_3)=0.5$, varying between 0.4 and 1.3 for capture probabilities smaller than 0.1, and then stabilizes at small values (<0.2) above this capture probability.

As expected, the standard error decreases with an increase in the value of the capture probability $\Pr(c)$ and it increases with the capture occasion. For capture probabilities smaller than 0.1, the standard errors are large (in the order of 50% of the estimated population size) while, for large capture probabilities, the standard error is generally much smaller. Consequently, the CI coverage rate is better for small capture probabilities ($\Pr(c)$<0.1), generally above 80% with both the nominal and log-normal approaches, than for very high capture probabilities (0.8), where though the SE is small the small bias causes poor coverage. In this case coverage can be as small as 25%. However, the confidence intervals at small capture probabilities are too wide for the model to be useful (recapture rates are too low for reliable estimates). Standard errors and coverage rates of confidence intervals for capture probability between 0.2 and 0.6 (even though they are too liberal) still suggest that the estimation method works reasonably well for these values of $\Pr(c)$. A smaller CI coverage rate is also usually observed for the second and the ninth capture occasions. Finally, using the normal scale or a log-normal transformation to construct the confidence intervals does not appear of major importance once the capture probability is 0.1 or greater. Below that the log-normal CI clearly performs better.

In the light of the present results, the TSJS estimator presents no serious error for capture probabilities $\Pr(c)$ equal or higher than 0.2, for a simultaneous sampling probability $\Pr(s_3)$ above the critical value of 0.2, over a 10-occasion period, when all assumptions are met and when the population (*N*) is greater than 500 individuals. In such conditions, for capture probabilities $\Pr(c)$ smaller than 0.2, nothing can be stated as the estimated values can be unbiased or severely biased and the large standard errors underline a poor precision of the estimator. For very large capture probabilities (e.g. $\Pr(c) = 0.8$), while the estimates appear unbiased, the true value may often not be included in the confidence interval due to a very underestimated standard error, but the issue of poor confidence interval coverage at large capture probability seems to be overcome when $\Pr(s_3) = 0.5$ (Appendix 5).

2.4.2. With unequal single sampling probabilities

The TSJS model will often have intrinsic heterogeneity since the two sampling methods are unlikely to present the same capture probability. Therefore, in this section, I investigate the performance of the TSJS estimator with scenarios where $\Pr(s_1)$ and $\Pr(s_2)$ are not equal. In the previous section, I was investigating mainly the effect of $\Pr(s_3)$, setting $\Pr(s_1)$ and $\Pr(s_2)$ equal. However, having $\Pr(s_1)$ and $\Pr(s_2)$ exactly equal is rather unlikely in reality. Moreover, $\Pr(s_1)$ and $\Pr(s_2)$ will also influence the proportion of unresolved latent histories (number of individuals in F, see chapter one, section 1.4.3) which is when the TSJS should perform at its best compared with the other uncorrected methods. It is expected that the simultaneous sampling probability $\Pr(s_3)$ will be the factor conditioning the marginal ratio between the two single sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ that can still lead to useful estimates with the TSJS estimator.

When the ratio between the single sampling probabilities is 3:1

Table 2-2 shows that, when the simultaneous sampling probability $\Pr(s_3)$ is as high as 0.5, results are the same in terms of relative error, standard error and CI coverage rate, when the single sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ are equal or when one is three times more likely to occur than the other, i.e. $\Pr(s_1) = 3\Pr(s_2)$ or $3\Pr(s_1) = \Pr(s_2)$: estimated population size might be slightly biased at small capture probabilities $\Pr(c)$ but the error is negligible on any capture occasion for a capture probability higher than 0.1.

Table 2-2- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-year study for a 3:1 ratio in single sampling probabilities and with a simultaneous sampling probability of 0.5 (sampling scenario 50-37.5-12.5 or 50-12.5-37.5) and a starting population of 500 individuals.

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(c)=0.05							
$\hat{N}_2$	485	626	-0.23	256	0.61	54	77
$\hat{N}_3$	626	655	-0.04	299	0.8	72	84
$\hat{N}_4$	714	694	0.03	323	0.69	81	85
$\hat{N}_5$	847	718	0.18	374	0.98	82	85
$\hat{N}_6$	771	742	0.04	335	0.98	78	88
$\hat{N}_7$	848	761	0.11	371	0.81	81	84
$\hat{N}_8$	834	793	0.05	358	0.94	70	79
$\hat{N}_9$	749	828	-0.1	324	0.76	64	69
Pr(c)=0.075							
$\hat{N}_2$	638	626	0.02	215	0.67	67	68
$\hat{N}_3$	740	654	0.13	220	0.7	79	80
$\hat{N}_4$	754	695	0.08	219	0.49	85	88
$\hat{N}_5$	779	719	0.08	220	0.46	85	84

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_6$	785	746	0.05	221	0.47	82	87
$\hat{N}_7$	849	763	0.11	236	0.54	85	83
$\hat{N}_8$	847	796	0.06	238	0.5	80	85
$\hat{N}_9$	862	831	0.04	240	0.59	76	76
Pr(*c*)=0.1							
$\hat{N}_2$	699	627	0.12	165	0.67	67	73
$\hat{N}_3$	734	656	0.12	158	0.55	82	81
$\hat{N}_4$	756	695	0.09	157	0.33	87	85
$\hat{N}_5$	793	721	0.1	164	0.32	92	88
$\hat{N}_6$	806	747	0.08	164	0.3	89	88
$\hat{N}_7$	843	767	0.1	171	0.35	90	86
$\hat{N}_8$	866	798	0.09	177	0.36	86	83
$\hat{N}_9$	891	834	0.07	183	0.48	68	68
Pr(*c*)=0.2							
$\hat{N}_2$	667	625	0.07	62	0.27	60	62
$\hat{N}_3$	690	654	0.06	61	0.17	78	78
$\hat{N}_4$	752	692	0.09	68	0.17	79	76
$\hat{N}_5$	755	718	0.05	67	0.13	87	85
$\hat{N}_6$	782	745	0.05	71	0.13	86	86
$\hat{N}_7$	813	763	0.07	74	0.16	80	79
$\hat{N}_8$	844	795	0.06	78	0.16	84	81
$\hat{N}_9$	866	830	0.04	82	0.19	73	73
Pr(*c*)=0.3							
$\hat{N}_2$	662	626	0.06	32	0.14	54	56
$\hat{N}_3$	681	653	0.04	33	0.1	68	71
$\hat{N}_4$	733	693	0.06	37	0.1	77	78
$\hat{N}_5$	743	718	0.04	39	0.08	86	86
$\hat{N}_6$	773	744	0.04	42	0.08	86	85
$\hat{N}_7$	791	762	0.04	44	0.08	87	85
$\hat{N}_8$	823	794	0.04	47	0.08	87	85
$\hat{N}_9$	863	828	0.04	51	0.12	66	67
Pr(*c*)=0.4							
$\hat{N}_2$	647	627	0.03	18	0.09	53	53
$\hat{N}_3$	679	655	0.04	20	0.06	68	67

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_4$	721	696	0.04	24	0.06	72	72
$\hat{N}_5$	743	721	0.03	26	0.05	86	86
$\hat{N}_6$	771	747	0.03	28	0.05	83	81
$\hat{N}_7$	790	764	0.03	29	0.05	88	87
$\hat{N}_8$	824	797	0.03	32	0.06	78	77
$\hat{N}_9$	857	832	0.03	35	0.08	75	75
Pr(c)=0.5							
$\hat{N}_2$	643	628	0.02	11	0.06	40	41
$\hat{N}_3$	672	655	0.03	13	0.05	56	57
$\hat{N}_4$	712	694	0.03	16	0.04	75	75
$\hat{N}_5$	739	719	0.03	18	0.04	78	78
$\hat{N}_6$	763	746	0.02	19	0.04	83	83
$\hat{N}_7$	780	764	0.02	21	0.04	85	84
$\hat{N}_8$	814	796	0.02	23	0.04	85	85
$\hat{N}_9$	847	830	0.02	26	0.05	78	79
Pr(c)=0.6							
$\hat{N}_2$	636	625	0.02	6	0.05	36	37
$\hat{N}_3$	666	652	0.02	8	0.03	49	49
$\hat{N}_4$	705	690	0.02	11	0.03	64	65
$\hat{N}_5$	728	715	0.02	12	0.03	80	80
$\hat{N}_6$	755	740	0.02	14	0.03	79	79
$\hat{N}_7$	769	756	0.02	15	0.03	89	89
$\hat{N}_8$	805	789	0.02	17	0.03	84	84
$\hat{N}_9$	837	823	0.02	19	0.04	79	81
Pr(c)=0.8							
$\hat{N}_2$	631	626	0.01	1	0.02	23	20
$\hat{N}_3$	657	653	0.01	2	0.01	39	39
$\hat{N}_4$	698	693	0.01	5	0.01	68	69
$\hat{N}_5$	722	717	0.01	6	0.01	81	83
$\hat{N}_6$	750	744	0.01	7	0.01	88	88
$\hat{N}_7$	766	761	0.01	8	0.01	95	95
$\hat{N}_8$	799	793	0.01	10	0.01	97	97
$\hat{N}_9$	832	827	0.01	12	0.01	93	94

$\hat{N}_2$, …, $\hat{N}_9$ =population size estimate at time 2, …, 9.

However, when $\Pr(s_3)$ is equal to 0.2 (table 2-1), the model appears unable to provide reasonably unbiased results for capture probabilities $\Pr(c)$ smaller than 0.2. Fig.2-9 (see also Appendix 4) displays the severe relative error that occurs with $\Pr(s_3) = 0.2$ compared to $\Pr(s_3) = 0.5$ when the ratio between the two single sampling probabilities is 3:1, i.e. $\Pr(s_1) = 3\Pr(s_2)$ or $3\Pr(s_1) = \Pr(s_2)$.

When $\Pr(s_3) = 0.2$, a ratio between $\Pr(s_1)$ and $\Pr(s_2)$ as great as 3:1, i.e. $\Pr(s_1) = 3\Pr(s_2)$ or $3\Pr(s_1) = \Pr(s_2)$, can be handled by the estimator for capture probabilities $\Pr(c)$ greater than 0.2: in such cases the relative error is no greater than 0.1. When $\Pr(s_3) = 0.2$, Fig.2-10 (see also Appendix 4) shows that a smaller ratio between the two single sampling probabilities of 1.5:1 can be handled by the estimator, even for small capture probabilities.

So it seems that the greater $\Pr(s_3)$ is, the greater the ratio between $\Pr(s_1)$ and $\Pr(s_2)$ can be, for a given capture probability, Pr(c). Increasing $\Pr(s_3)$ enables the model to support a greater ratio between $\Pr(s_1)$ and $\Pr(s_2)$: 1.5:1 when $\Pr(s_3) = 0.2$ up to 1:3 when $\Pr(s_3) = 0.5$.

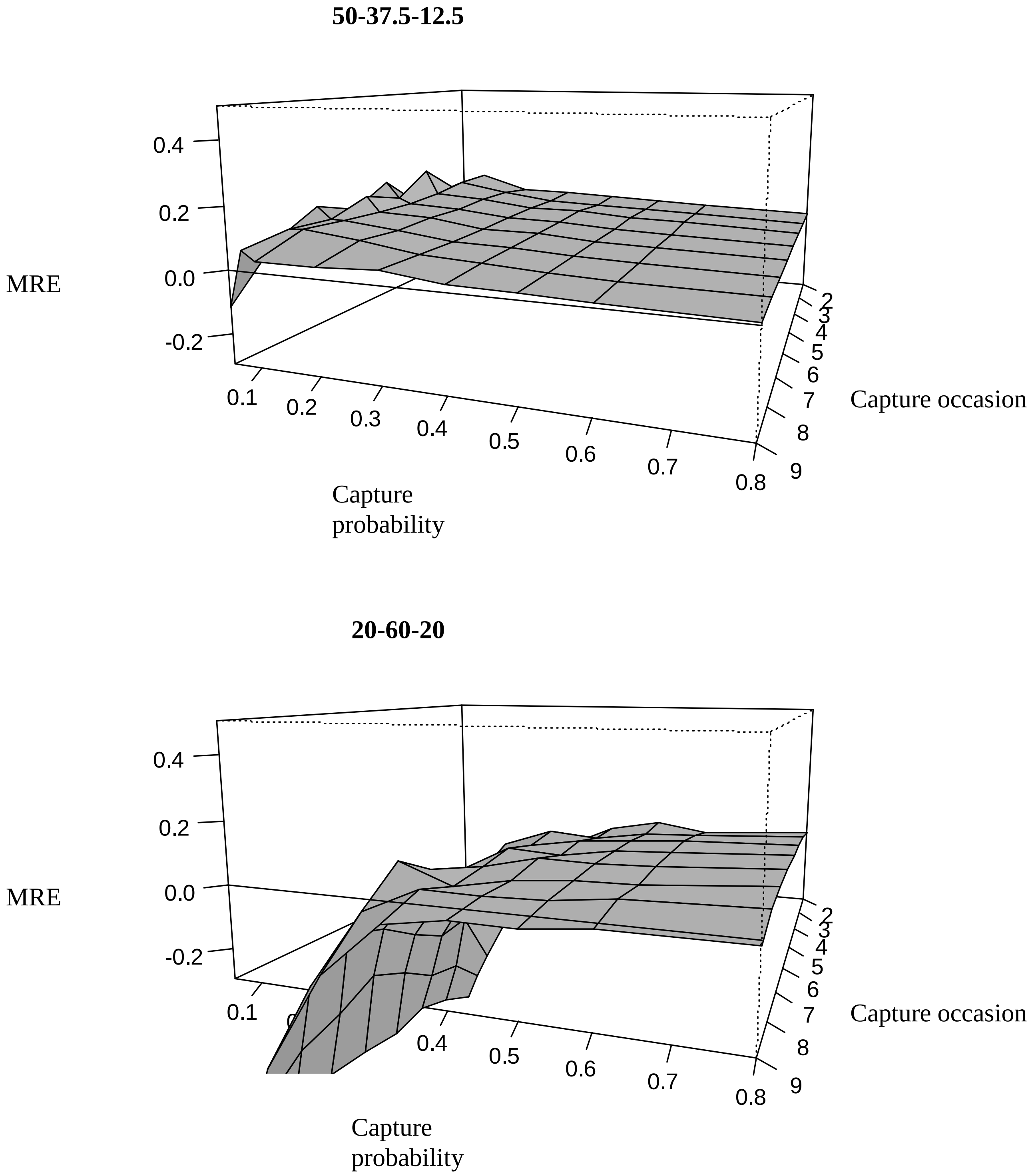


Fig.2-9- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 500 individuals for scenarios of sampling probabilities 50-37.5-12.5 and 20-60-20**.**

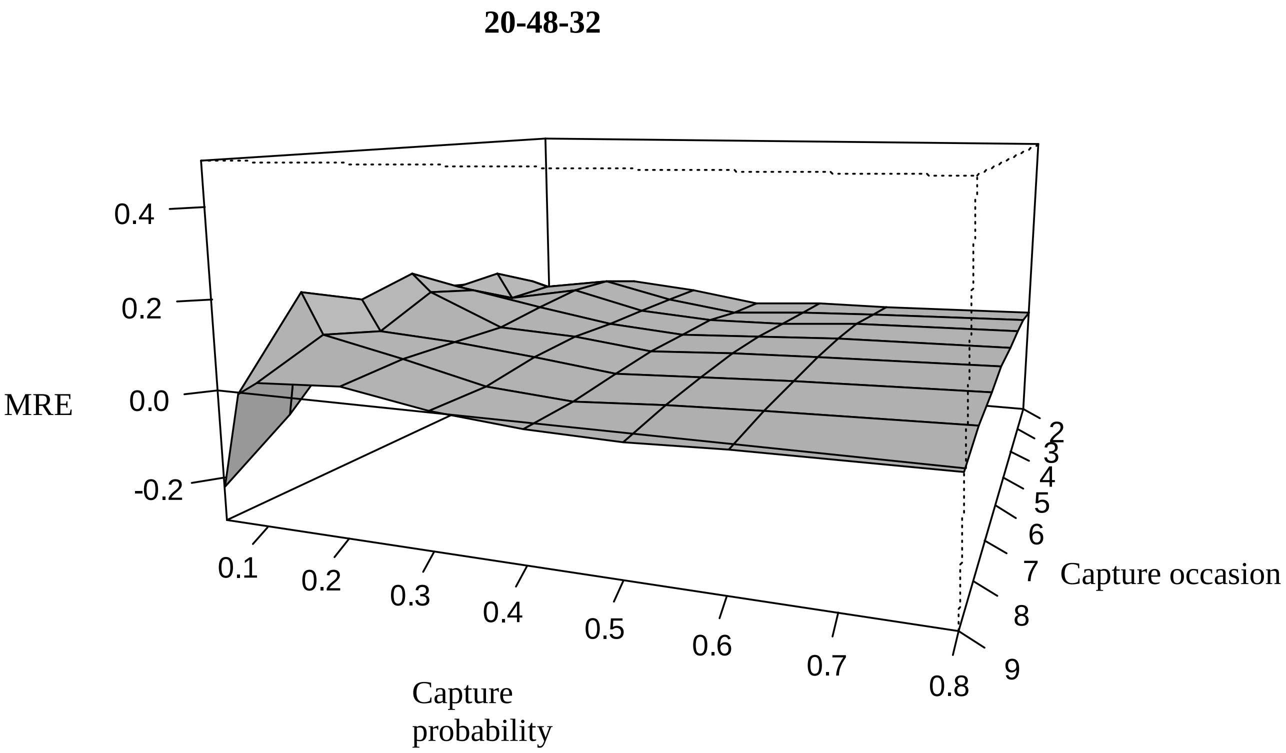


Fig.2-10- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 500 individuals for scenarios of sampling probabilities 20-48-32 a ratio of 1.5:1.

2.5. Effect of population size

In small sample situations

The TSJS model is investigated here in small population situations, with a starting population of N=50 individuals and over T=10 occasions. It is important to note that at small capture probabilities ($\Pr(c)$<0.2), some statistics and/or parameters described in the Methods part of this chapter can be zero on some occasions and in such conditions the estimation of the population size can not be computed. Fig.2-11 (see also Appendix 4) clearly shows when $\Pr(s_3) = 0.2$, the estimator is severely negatively biased for capture probabilities below 0.2. However, if the capture probability is equal or higher than 0.2, the estimator provides reasonable, though over-estimated, population size estimates.

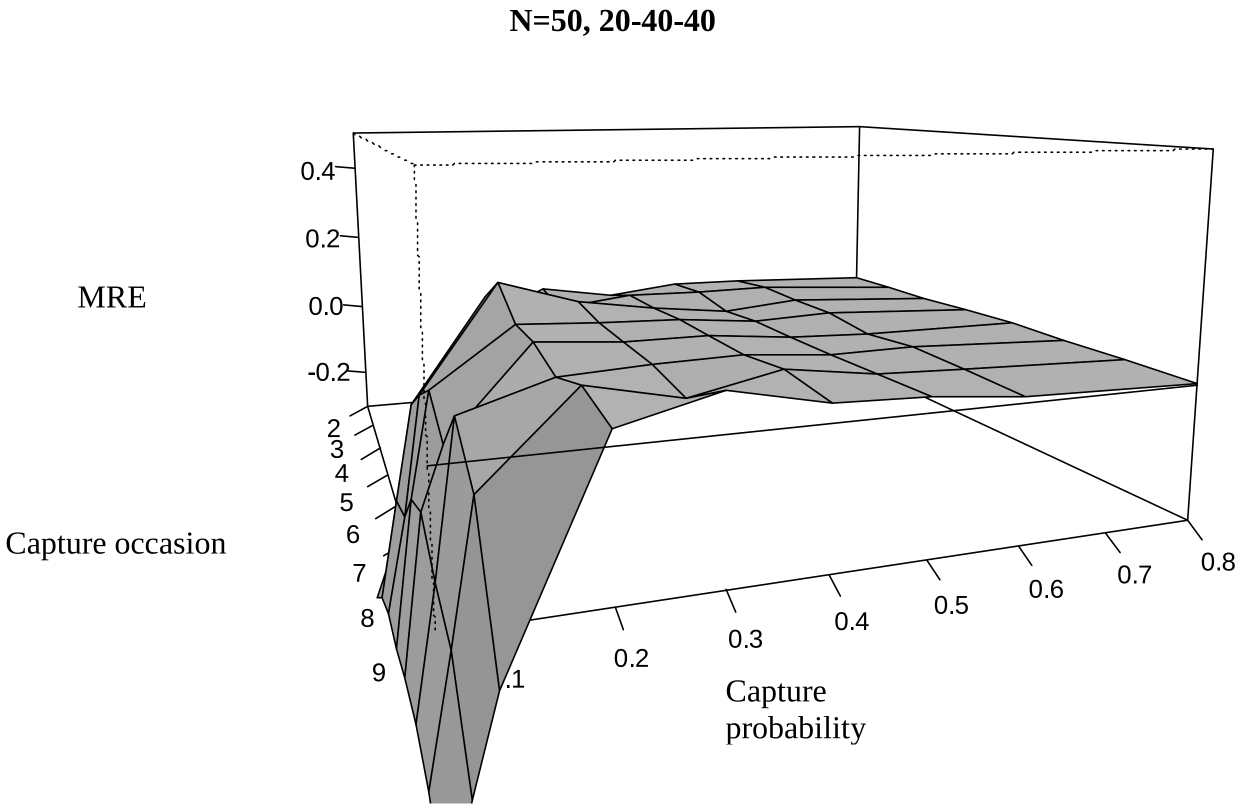


Fig.2-11- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 50 individuals for scenarios of sampling probabilities 20-40-40.

Table 2-3 shows that, with $\Pr(s_3) = 0.5$ and a starting population of 50 individuals, the problem of the severe underestimation encountered at small capture probabilities ($\Pr(c)$<0.2) still remains: for capture probability of 0.05 and 0.075 the MRE is never smaller than -0.32 and can be as high as -0.82. At capture probability $\Pr(c)$=0.1, it is still severely biased at the first and last estimation but it is unbiased for the intermediate capture occasions 5, 6 and 7. Then, for capture probability $\Pr(c)$>0.2, the MRE is smaller and quickly becomes negligible (<0.1). However, the RMSRE is higher than 0.23 for capture probability $\Pr(c)$<0.3

suggesting that, for small populations, a high capture probability might be required to get reliable estimates.

As observed previously, standard errors decrease significantly with the increase of the value of the capture probability and increase with the capture occasions for all capture probabilities. A log-normal transformation for the confidence intervals seems to be important at small capture probabilities ($\Pr(c) < 0.1$) and small sample size. Indeed the CI coverage rate never exceeds 67% and can be as low as 29% for the normal confidence intervals while it is never smaller than 52% and can be as high as 84% with log-normal confidence intervals. Then, for higher capture probabilities, the CI coverage rate is generally similar for the normal and log-normal approaches and generally fluctuates between 70% and 95% on the intermediate capture occasions (second and ninth capture occasions often have smaller CI coverage rates).

Table 2-3- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-year study for sampling scenario 50-25-25 and a starting population of 50 individuals.

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(*c*)=0.05							
$\hat{N}_2$	14	63	-0.78	22	0.81	29	61
$\hat{N}_3$	17	65	-0.75	27	0.8	40	62
$\hat{N}_4$	21	69	-0.7	31	0.77	42	69
$\hat{N}_5$	25	71	-0.65	35	0.8	44	69
$\hat{N}_6$	23	74	-0.69	32	0.8	44	71
$\hat{N}_7$	22	75	-0.71	34	0.79	44	71
$\hat{N}_8$	20	78	-0.75	29	0.83	36	64
$\hat{N}_9$	18	81	-0.82	27	0.86	31	52
Pr(*c*)=0.075							
$\hat{N}_2$	22	63	-0.65	24	0.77	40	64
$\hat{N}_3$	32	65	-0.52	32	0.69	54	74
$\hat{N}_4$	40	69	-0.43	38	0.7	58	74
$\hat{N}_5$	45	71	-0.37	43	0.69	62	82
$\hat{N}_6$	50	74	-0.32	48	0.68	65	84
$\hat{N}_7$	50	76	-0.34	46	0.68	67	81

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_8$	46	79	-0.42	44	0.69	55	77
$\hat{N}_9$	30	83	-0.65	30	0.73	40	67
Pr(*c*)=0.1							
$\hat{N}_2$	29	62	-0.53	23	0.69	53	65
$\hat{N}_3$	46	65	-0.29	33	0.66	62	79
$\hat{N}_4$	51	69	-0.25	36	0.65	66	81
$\hat{N}_5$	68	72	-0.05	46	0.83	74	88
$\hat{N}_6$	72	74	-0.05	48	0.86	76	88
$\hat{N}_7$	69	76	-0.1	48	0.87	71	86
$\hat{N}_8$	66	79	-0.18	45	1.07	72	84
$\hat{N}_9$	54	82	-0.36	40	0.7	57	76
Pr(*c*)=0.2							
$\hat{N}_2$	56	63	-0.1	17	0.56	61	64
$\hat{N}_3$	70	65	0.06	19	0.7	70	70
$\hat{N}_4$	76	69	0.1	22	0.67	77	78
$\hat{N}_5$	72	72	0.01	20	0.38	83	87
$\hat{N}_6$	76	75	0.03	22	0.43	86	89
$\hat{N}_7$	83	76	0.08	24	0.47	89	88
$\hat{N}_8$	90	80	0.13	27	0.6	82	86
$\hat{N}_9$	88	83	0.04	26	0.85	64	69
Pr(*c*)=0.3							
$\hat{N}_2$	63	62	0.01	9	0.47	54	54
$\hat{N}_3$	66	65	0.01	10	0.32	66	68
$\hat{N}_4$	74	69	0.08	12	0.3	79	77
$\hat{N}_5$	74	72	0.03	12	0.23	88	87
$\hat{N}_6$	78	75	0.05	13	0.23	87	89
$\hat{N}_7$	79	76	0.03	13	0.26	87	84
$\hat{N}_8$	83	80	0.05	15	0.29	86	85
$\hat{N}_9$	86	83	0.03	16	0.38	74	72
Pr(*c*)=0.4							
$\hat{N}_2$	63	62	0.01	6	0.3	49	47
$\hat{N}_3$	66	65	0.01	6	0.2	70	68
$\hat{N}_4$	72	69	0.04	7	0.18	78	75
$\hat{N}_5$	75	72	0.05	8	0.16	88	86

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_6$	76	74	0.02	8	0.14	90	90
$\hat{N}_7$	78	76	0.03	9	0.14	91	90
$\hat{N}_8$	83	80	0.03	10	0.16	89	90
$\hat{N}_9$	85	84	0.02	11	0.24	75	78
Pr(c)=0.5							
$\hat{N}_2$	63	62	0.01	4	0.18	53	52
$\hat{N}_3$	65	65	0.01	4	0.12	71	73
$\hat{N}_4$	70	69	0.02	5	0.1	81	78
$\hat{N}_5$	72	71	0.02	6	0.09	88	89
$\hat{N}_6$	76	74	0.03	6	0.1	86	87
$\hat{N}_7$	77	76	0.02	7	0.09	91	89
$\hat{N}_8$	80	79	0.01	7	0.11	86	88
$\hat{N}_9$	84	83	0.02	8	0.15	81	83
Pr(c)=0.6							
$\hat{N}_2$	62	62	0	2	0.12	41	43
$\hat{N}_3$	65	65	0	3	0.09	62	62
$\hat{N}_4$	69	68	0.01	3	0.08	73	74
$\hat{N}_5$	73	71	0.02	4	0.08	84	84
$\hat{N}_6$	75	73	0.02	4	0.07	86	87
$\hat{N}_7$	76	75	0.01	5	0.08	90	89
$\hat{N}_8$	80	79	0.02	5	0.08	94	93
$\hat{N}_9$	83	82	0.01	6	0.1	82	83
Pr(c)=0.8							
$\hat{N}_2$	63	63	0	1	0.05	36	36
$\hat{N}_3$	66	66	0	1	0.04	50	51
$\hat{N}_4$	70	70	0	1	0.03	74	75
$\hat{N}_5$	73	72	0	2	0.03	84	84
$\hat{N}_6$	75	75	0.01	2	0.03	94	94
$\hat{N}_7$	77	77	0.01	3	0.03	95	95
$\hat{N}_8$	80	80	0.01	3	0.04	95	95
$\hat{N}_9$	83	83	0	4	0.04	93	93

$\hat{N}_2$, …, $\hat{N}_9$ =population size estimate at time 2, …, 9.

In large sample situations

As expected, increasing the population size N decreases the relative error in the estimation: Fig.2-12 (see also Appendix 4) shows that, when $\Pr(s_3) = 0.2$ and $\Pr(s_1) = \Pr(s_2)$, the MRE is no more than 0.2 for all capture probabilities $\Pr(c)$ on any capture occasion which, though still large for small $\Pr(c)$, is relatively much smaller than many other scenarios tried earlier.

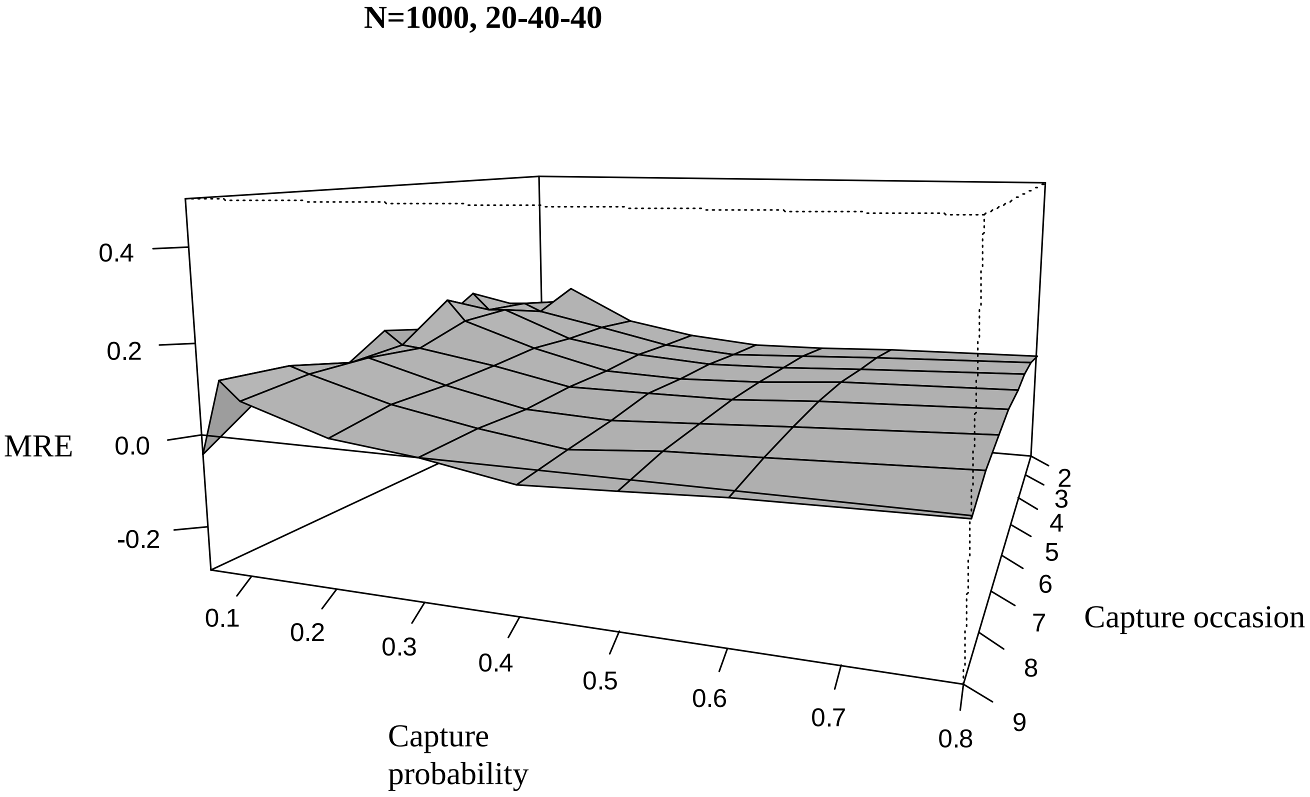


Fig.2-12- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 1000 individuals for scenarios of sampling probabilities 20-40-40.

The effect of the population size on the estimator performances is also relevant in terms of robustness to ratios between $\Pr(s_1)$ and $\Pr(s_2)$: in the last section, the model could not handle a ratio of 1:3 for capture probabilities $\Pr(c)$ smaller than 0.4 when $\Pr(s_3) = 0.2$ and a starting population of 500 individuals. Fig.2-13 shows that with a starting population of

N=1000 individuals, the TSJS approach produces estimates with a MRE no higher than 0.2 for all capture probabilities on any capture occasion.

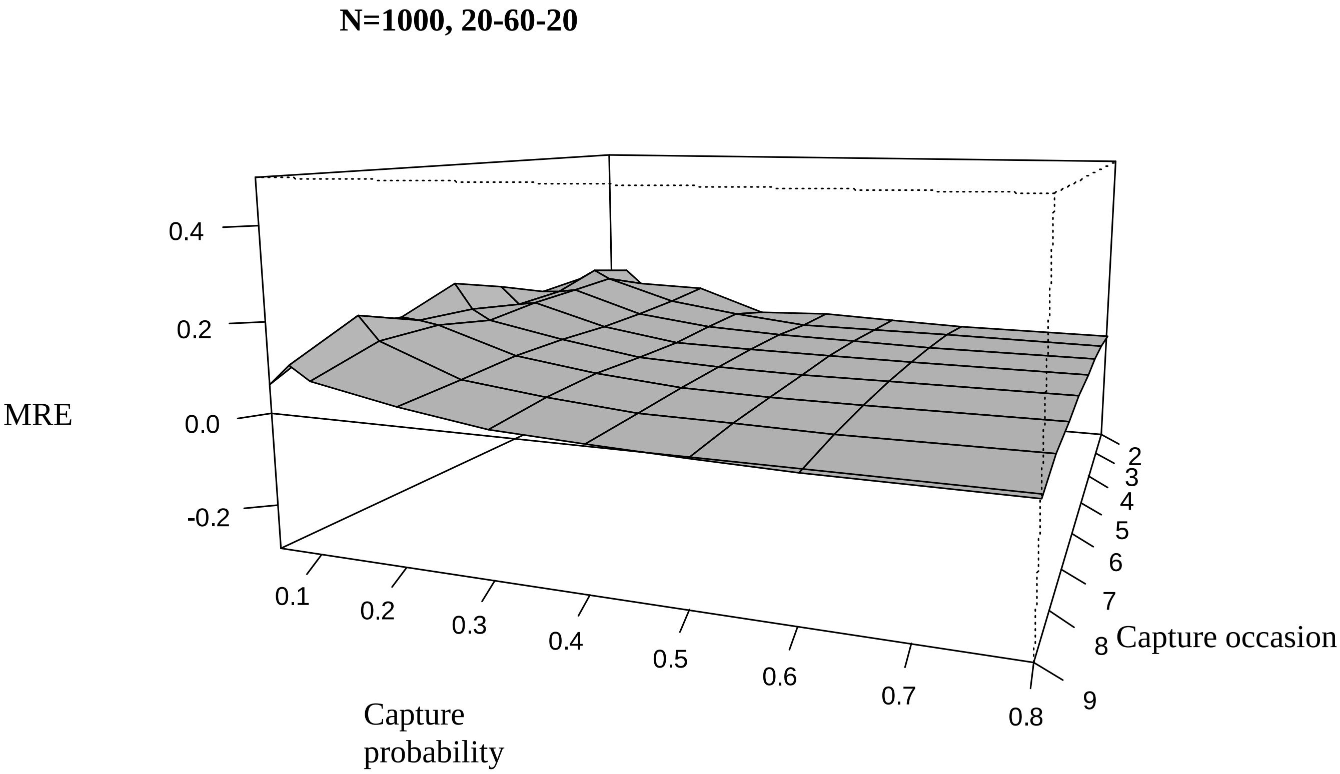


Fig.2-13- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 1000 individuals for scenarios of sampling probabilities 20-60-20.

So it seems that the bigger the population *N* is, the more robust the model is to differences in the values of $\Pr(s_1)$ and $\Pr(s_2)$. With large populations, the estimator can still produce valuable results with greater ratios between $\Pr(s_1)$ and $\Pr(s_2)$ (e.g. with a ratio of 3:1 when $\Pr(s_3) = 0.2$ up to a ratio of 1:4 when $\Pr(s_3) = 0.5$, as shown in Fig.2-14).

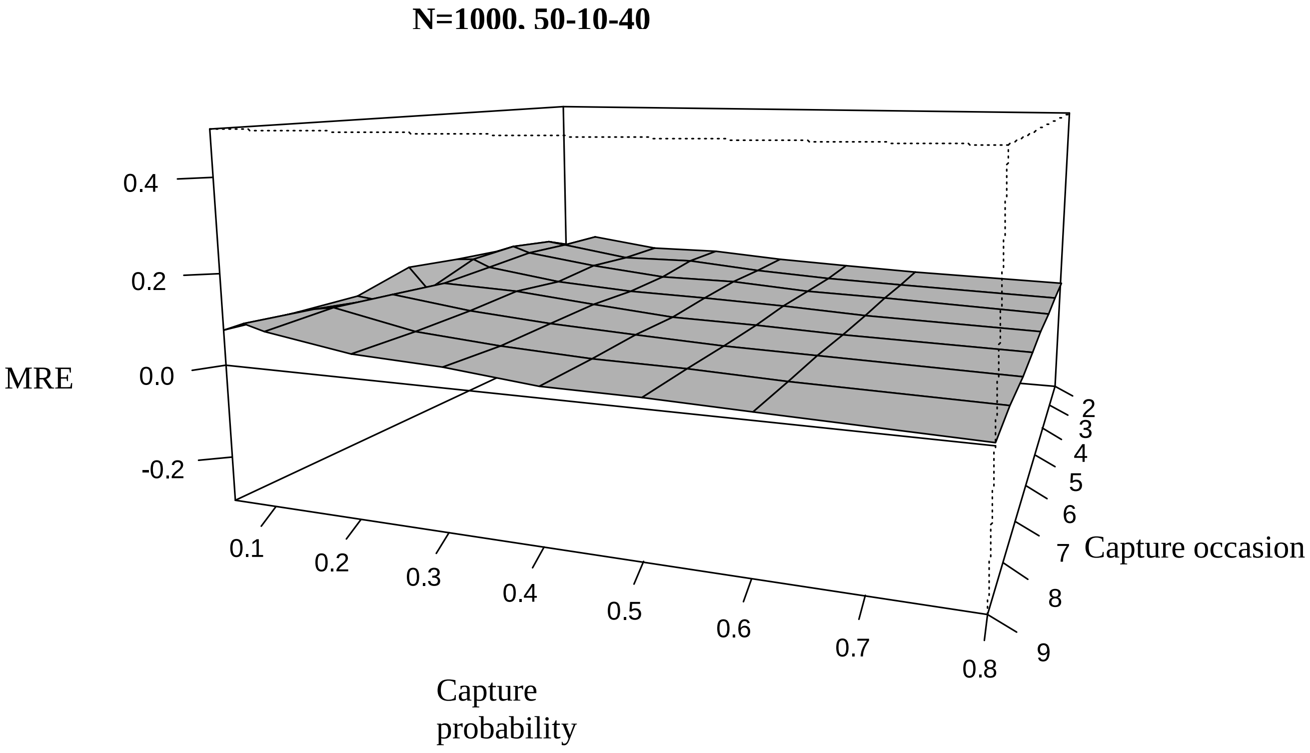


Fig.2-14- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 1000 individuals for scenarios of sampling probabilities 50-10-40.

In a high turnover and declining population situation

This situation was created in order to show the generality of the results provided in this chapter. I show that, when all assumptions are met, the performances of the present estimator are independent from the parameters set for the simulated animal population: here the survival rate is 0.4 for all the individuals and the birth rate is 0.8 for all mature females. Given the survival rate, the population is declining over the T=10 occasions of the experiment: in the present simulation, the population starts at N=2000 individuals, is down to approximately 500 at capture occasion 4, 150 at capture occasion 6 and below 70 at capture occasion 9. Therefore, at the start of the simulation, the situation is that of a large declining population and of a small population on the last capture occasions.

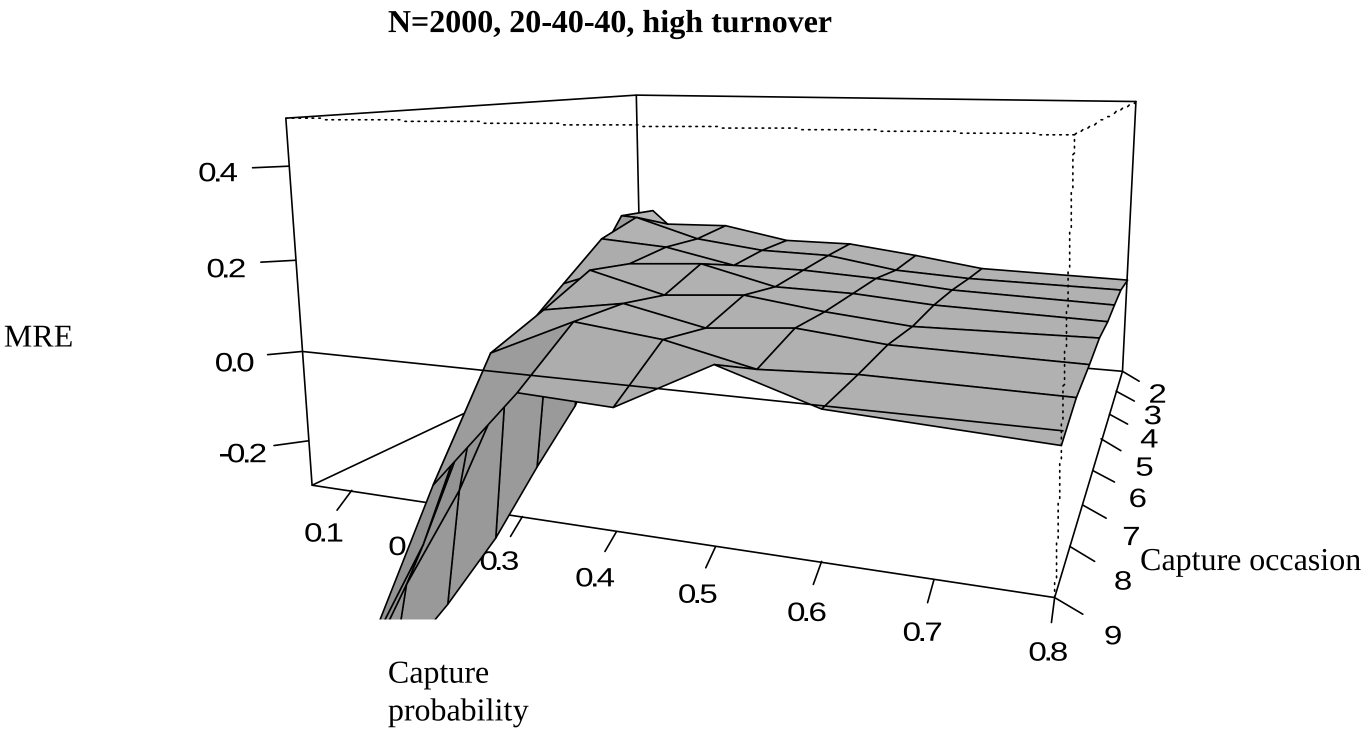


Fig.2-15- MRE as a function of the capture probability and capture occasion over 10 years, with a starting population of 2000 individuals for scenario of sampling probabilities 20-40-40**.**

As shown in Fig.2-15 (see also Appendix 4), for all capture probabilities $\Pr(c)$, the error is always greater on the last capture occasions which is not surprising since the situation in the last capture occasions is the one of small populations described above. For capture probabilities smaller than 0.1, the MRE is above 0.1 for all capture occasions. Then, as the capture probability $\Pr(c)$ increases, the error on the last occasions decreases and from a capture probability of 0.2, the MRE is smaller than 0.1 on all capture occasions (except at capture occasion 9 for a capture probability of 0.2).

2.6. Effect of number of capture occasions

In this section, the error of the TSJS estimator is explored for *T*=5 occasions. As for *T*=10 occasions and $\Pr(s_3) = 0.5$ in the dataset, MRE were found to be relatively small for $\Pr(c)$>0.1 but the direction of the average relative error varies, as shown in Fig.2-16. For $\Pr(c)$<0.1, increasing the length *T* of the experiment can reduce the error substantially. For low capture probabilities, this is consistent with Jolly's (1965) conclusion that the bias of the JS model decreases as the number of the capture occasions *T* increases.

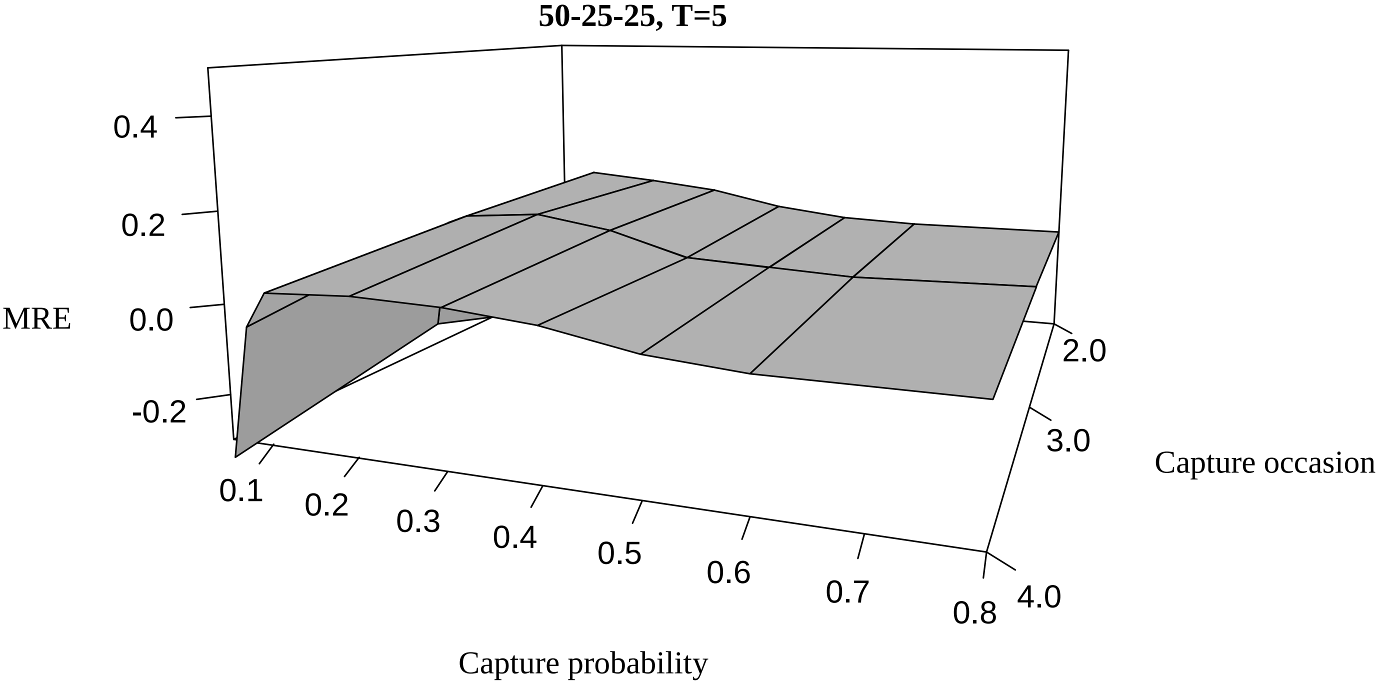


Fig.2-16- MRE as a function of the capture probability and capture occasion over 5 years, with a starting population of 500 individuals for scenarios of sampling probabilities 50-25-25.

When $\Pr(s_3) = 0.2$ and a minimum *N*=500, the MRE is not more than 10% of the true population size which is similar to the results with $\Pr(s_3) = 0.5$. As shown in Table 2-4, when $\Pr(s_3) = 0.2$, the RMSRE is below 0.3, on any capture occasion, with $\Pr(c)$>0.1. At smaller capture probabilities, i.e. $\Pr(c)$<0.2, the MRE is generally below 0.1 when $\Pr(c)$>0.075 but the RMSRE is always greater than 0.6.

Large variances arise at small capture probabilities ($\Pr(c)$<0.1), leading to 95% confidence intervals containing the true population size more than 62% of the time with the normal approach and more than 80% for the log-normal transformation. However, for $\Pr(c)$<0.1, the confidence intervals are too wide for the method to be useful. As previously, standard errors decrease as the capture probability increases. Values of the standard error equal to no more than 12% of the population size are obtained with $\Pr(c)$>0.2 and CI coverage rate is never below 70% though seldom above 90%. Moreover, for $\Pr(c)$>0.2, the choice of the log-normal transformation over the normal approximation for the construction of the confidence intervals is not necessary, as both approaches lead to very similar coverage rates. For large capture probability ($\Pr(c) = 0.8$), the issue of small standard errors leads to low CI coverage rate (54% to 69% for the normal approximation and 56% to 71% for the log-normal transformation).

Table 2-4- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 5-capture-occasion study with sampling scenario 20-40-40 and a starting population of 500 individuals.

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(c)=0.05							
$\hat{N}_2$	323	626	-0.48	352	0.7	62	83
$\hat{N}_3$	411	653	-0.37	410	0.91	65	81
$\hat{N}_4$	424	692	-0.39	439	0.76	67	86
Pr(c)=0.075							
$\hat{N}_2$	527	626	-0.16	348	0.7	73	86
$\hat{N}_3$	604	655	-0.08	347	0.74	72	80
$\hat{N}_4$	741	694	0.07	411	1.06	76	80
Pr(c)=0.1							
$\hat{N}_2$	681	627	0.09	315	1.02	86	85
$\hat{N}_3$	726	656	0.11	297	0.76	80	83
$\hat{N}_4$	703	695	0.01	282	0.68	73	76
Pr(c)=0.2							
$\hat{N}_2$	643	626	0.03	130	0.32	80	79
$\hat{N}_3$	711	653	0.09	129	0.29	88	84
$\hat{N}_4$	735	691	0.06	130	0.29	86	82

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(c)=0.3							
$\hat{N}_2$	641	626	0.02	75	0.21	80	80
$\hat{N}_3$	677	653	0.04	73	0.17	84	84
$\hat{N}_4$	722	692	0.04	78	0.18	83	82
Pr(c)=0.4							
$\hat{N}_2$	641	627	0.02	48	0.13	78	78
$\hat{N}_3$	664	654	0.01	48	0.11	86	86
$\hat{N}_4$	701	694	0.01	51	0.12	78	79
Pr(c)=0.5							
$\hat{N}_2$	619	626	-0.01	31	0.08	80	79
$\hat{N}_3$	654	653	0	33	0.07	83	83
$\hat{N}_4$	688	693	-0.01	35	0.08	80	80
Pr(c)=0.6							
$\hat{N}_2$	613	625	-0.02	21	0.06	68	68
$\hat{N}_3$	646	654	-0.01	23	0.05	78	79
$\hat{N}_4$	679	695	-0.02	25	0.06	77	78
Pr(c)=0.8							
$\hat{N}_2$	610	626	-0.03	10	0.04	54	56
$\hat{N}_3$	644	653	-0.01	12	0.03	69	71
$\hat{N}_4$	672	693	-0.03	14	0.04	58	60

$\hat{N}_2, \ldots, \hat{N}_4$=population size estimate at time 2, …, 4.

The effect of a shorter experiment (here 5 capture occasions compared to previously 10 capture occasions) on the TSJS estimator performance lies mainly in an increase of the RMSRE: approximately 1.5 higher than the RMSRE in Table 2-1. For all Pr(c), standard errors are generally larger than the standard errors found on the capture occasions 7, 8 and 9 for the same Pr(c) in Table 2-1. CI coverage rate is lower than in Table 2-1.

2.7. Discussion

In this chapter, I have presented the results of simulations on the TSJS estimator when all assumptions are met. This simulation model is an attempt to recreate a subset of realistic animal populations. With this simulation model, there are no totally-uncatchable animals in the population: any individual is available for sampling on each capture occasion. I did not consider the case where there might be untrappable animals because I believe that the chance of having such individuals is considerably reduced with double-sampling experiments. Moreover in the simulation model, individuals can only be detected once and sampled by only one method on each occasion. Therefore, I did not model long sampling occasions during which secondary sampling occasions might occur even though that is the sampling situation in chapter five where each sampling occasion covers approximately two months. Indeed, I considered that, if an individual is available by both capture methods separately during a long sampling occasion, it means that it is available by the simultaneous method and then, if it is captured, it should be by both methods simultaneously at least once during this long sampling occasion. The single captures that might have occurred during this sampling occasion should be ignored and only the simultaneous event should figure in the capture history for this sampling occasion.

The simulations show that the TSJS estimator presents generally a small error for capture probabilities $\Pr(c)$ equal or greater than 0.2. The estimator is, however, severely biased and produces wide, and therefore useless, confidence intervals for capture probabilities smaller than 0.1. Increasing the population size N results in a substantial reduction of the error and permits a greater inequality between the values of the single sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ that the model can handle.

Important results include:

*With T=**10** and N=**500** and* $\Pr(s_1) = \Pr(s_2)$*:*

Minimum/critical probability of double tagging following a capture $\Pr(s_3) = 0.2$

*With T=**10** and N=**500** and* $\Pr(s_3)$ *=0.2:*

Most extreme ratio between the two single sampling probabilities that could be handled = 1:1.5 or 1.5:1, i.e. $\Pr(s_1) = 1.5\Pr(s_2)$ or $1.5\Pr(s_1) = \Pr(s_2)$

*With T=**10** and N=**500** and* $\Pr(s_3)$ *=0.5:*

Ratio handled by the model between $\Pr(s_1)$ and $\Pr(s_2)$ = 3:1, i.e. $\Pr(s_1) = 3\Pr(s_2)$ or $3\Pr(s_1) = \Pr(s_2)$

*With T=**10** and N=**1000** and* $\Pr(s_3)$ *=0.2:*

Ratio handled by the model between $\Pr(s_1)$ and $\Pr(s_2)$ = 3:1, i.e. $\Pr(s_1) = 3\Pr(s_2)$ or $3\Pr(s_1) = \Pr(s_2)$

*With T=**10** and N=**1000** and* $\Pr(s_3)$ *=0.5:*

Ratio handled by the model between $\Pr(s_1)$ and $\Pr(s_2)$ = 1:4, i.e. $\Pr(s_1) = 4\Pr(s_2)$ or $4\Pr(s_1) = \Pr(s_2)$

*With T=**10** and N=**50** and* $\Pr(s_1) = \Pr(s_2)$*:*

Minimum $\Pr(s_3) = 0.5$

Severe negative bias (MRE>50%) for $\Pr(c)$<0.2.

CIs consistently too liberal, sometimes extremely.

The relative error can be small (<10%) and the precision is good when the capture probability is high and there is no violation of assumptions. These results are similar to those of Gilbert’s (1973) on the standard JS model, the only differences here being that the error is not systematically symmetrical with respect to capture occasion. Increasing the length of the study also results in a reduction of the error (RMSRE) which underlines the fact that the estimator becomes more useful as the length of the experiment increases. As in Gilbert (1973) the relative error is no greater than 10% when the capture probability is greater than 0.2 and the simultaneous sampling probability is above the critical value, i.e. $\Pr(s_3)>0.2$. With 10 capture occasions, $\Pr(c)=0.5$ and $\Pr(s_3)=0.5$, 95% of all animals would be double tagged at least once if the population was closed. So, in such case, even though the population is open, the number of individuals in F (see chapter one, section 1.4.3) can be expected to be very low and thus, in the simulations, the JS model could perhaps be applied instead of the TSJS model.

Confidence interval coverage could be reasonably good (e.g. 90%), indicating a good reliability of the estimation with the TSJS approach, although first and last estimation occasions generally present smaller CI coverage rates, but most of the times confidence interval coverage was poor. Using the log-normal approach to construct the confidence interval leads to a slight increase in the CI coverage rate especially at the smaller capture probabilities and population sizes. The estimated value of population size is usually believed to be a log-normally-distributed parameter, which explains why log-normal confidence intervals display better coverage rates than normal confidence intervals. In my thesis, I used a frequentist approach for the confidence intervals rather than Bayesian statistics. The interpretation, usefulness and application of these two approaches (frequentist vs Bayesian) are nowadays debated. Credible intervals based on Bayes’ theorem are considered to have a more straightforward and practical interpretation than confidence intervals based on sampling distributions do: with credible intervals the interpretation is usually of the form “My degree of belief that the true parameter is in fact in the interval is …%”. With 95% confidence intervals, results can only be interpreted as “The interval will contain the true value 95% of the time if the study were repeated many times using samples from the same population”. However, the use of credible intervals requires a prior probability prone to subjectivity, which inevitably provokes controversy. Avoiding subjectivity in the credible intervals would be equivalent of setting an uninformative prior probability, therefore leading to the credible interval corresponding to the confidence interval. Confidence intervals are more commonly used by biologists, hence it seemed more appropriate to use the frequentist approach. However, here confidence interval coverage rate was, in most scenarios, poor. Indeed, the idea for the 95% nominal confidence interval in the frequentist approach is that confidence intervals will include the true value 95% of the time, so it does not seem satisfying for the TSJS method that the coverage rate barely reaches the 95% threshold in most of the cases explored here. However, confidence intervals were obtained by invoking the asymptotic properties of maximum likelihood estimates (MLEs), and more precisely the property that the estimates are asymptotically normally distributed. However, the TSJS estimator is not an MLE and as quoted earlier in this section, population size estimates are believed to be log-normally distributed but the use of a log-normal confidence interval does not significantly improve the confidence coverage rate. Furthermore, the method of profile likelihood that applies to all MLEs and usually improves the confidence interval coverage cannot be used since the TSJS estimator is not an MLE. Therefore, a major improvement for the TSJS method to be more useful would be a valid interval estimator. Nevertheless, as shown in chapter four, none of the current models leads to satisfying confidence interval coverage rate underlying the difficulty of getting a valid interval estimator.

Problems in the estimation are also inevitable if the simultaneous sampling probability is too small. It is important for the general design of the study that the investigators put as much effort as possible in the double-tagging part of the experiment which will determine the robustness of the model. Depending on field conditions, it is also preferable not to favor one sampling method, make sure the sampling is opportunistic but keep a reasonable ratio between the two tagging methods when the simultaneous sampling probability is expected to be moderate.

The performance of the model also depends on the validity of the underlying assumptions in the experiment and therefore the behaviour of the estimator is investigated in chapter three in various situations of departure from the model assumptions. If small rates of simultaneous marking can not be avoided, researchers must be aware that the estimator may also be more sensitive to violation of assumptions. The results of the TSJS estimator when model assumptions are violated will then be compared to those of classic closed-population models in the same situations in chapter four.

3. Chapter Three

When things go wrong: heterogeneity among individuals in capture or sampling probabilities and tag misreading

3.1. Abstract

A common problem in capture-mark-recapture (CMR) studies is the presence of heterogeneous capture probabilities among individuals of a population. If not modelled, the magnitude of the resulting bias usually depends on the degree and characteristics of the heterogeneity in capture probabilities among individuals. Simulations described in chapter two are used here to test the performance of the Two-Source Jolly-Seber (TSJS) estimator when the assumption of equal catchability among individuals is violated, when the single-sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ are not equal among the individuals and when there is a tag misreading issue. To provide a relevant pattern of heterogeneity, knowledge from a humpback whale population is used to specify the model. The mean relative error (MRE), the root mean square relative error (RMSRE) and the confidence interval coverage rate are used to provide information on the suitability of the estimator under different scenarios believed to represent a simplifying approximation of the sampling situation in humpback whale populations. The TSJS model is fairly robust when the heterogeneity in catchability is small to moderate. Given the present simulation structure, this extension of the Jolly-Seber (JS) model gives little error when all individuals have capture probabilities greater than 0.5 on all capture occasions. As expected, the average negative error increases as the magnitude of the heterogeneity rises and serious negative error can occur when the average capture probabilities are small. In the presence of heterogeneity in sampling probabilities among classes of individuals, the estimator usually performs well. Finally, for the tag misreading issue, the TSJS estimator demonstrates no error for a homogeneous tag misreading rate. These results are probably relevant to a range of large mammal populations and possibly, given a proportional time scale shift, to some other groups as well. However, only a small range of

the possible parameters and model space has been explored so these conclusions inevitably have limited generality.

3.2. Introduction

One of the challenges when estimating population size using CMR methodology is the ubiquity of heterogeneity in capture probabilities in field studies, where individuals of the same population often exhibit different degrees of catchability (Roff, 1973). These heterogeneous capture probabilities most likely depend on biological factors such as sex, size, reproductive status, age and it typically leads to negatively biased abundance estimates (Amstrup et al., 2005; Chao, 1987; Hwang and Chao, 1995; Otis et al., 1978; Seber, 1986; Williams et al., 2002). The magnitude of the bias usually depends also on the characteristics of the heterogeneity itself. If some individuals of a population exhibit low capture probability on different trap occasions and a high capture probability on some others, there should be little bias in the abundance estimator (Williams et al., 2002). On the other hand, if, throughout the whole study, some individuals tend to have a relatively low capture probability while others exhibit a high probability of being caught, the magnitude of the error should be more important.

Hwang and Chao (1995), Otis et al. (1978), Carothers (1973) and Gilbert (1973) showed that the heterogeneity in capture probabilities did not affect the estimates given by the JS model when all animals had high capture probabilities (>0.5). However, a high degree of heterogeneity can cause severe underestimation in the population size estimates with the JS model and new techniques to reduce the bias have been developed. Hwang and Chao (1995) developed a method using the sample coverage approach to minimize the bias. Pledger and Efford (1998) used a method aiming at correcting the abundance estimates for bias via inverse prediction. Both approaches performed well in simulation studies but have seen little use so far.

In this chapter, the coefficient of variation is used to measure the degree of heterogeneity in capture probability present within the simulated populations. Many different patterns of heterogeneity in capture and sampling probability can occur and it is important to tailor the analysis of the error to the specific type of biological problem encountered. Due to the biological purpose of the model, values of biological parameters related to humpback whales and found in the literature were used to create the animal population in the simulations for the purpose of chapters three and four. The aim was to ensure that the model was tested on a biologically relevant combination of parameters.

In the simulations, I have chosen to divide the population into four demographic classes based on the reproductive status (adult males, non-breeding females, breeding females and calves) to test the effect of heterogeneity in capture and sampling probabilities between the classes. This pattern of heterogeneity seems to better suit the biological situation of the humpback whales, especially to test the heterogeneity in sampling probabilities $\Pr(s_1)$, $\Pr(s_2)$ and $\Pr(s_3)$ (see chapter one) which are probably related to the reproductive status for this species. Two types of heterogeneity will be analyzed here: heterogeneity in capture probabilities and heterogeneity in sampling probabilities. This keeps the problem tractable and allows us to investigate the separate effects of each source of error described above. It is also necessary to avoid confounding them in the analysis. Therefore, each type of heterogeneity is explored independently in this chapter. As shown in chapter two, the TSJS method does not perform well if the capture probability is too low ($\Pr(s_3)<0.2$). A logical step here is also to avoid confounding this type of problem with any problems coming from the failure of one or more of the underlying assumptions of the model. Thus, only some scenarios of sampling probabilities, described in chapter two and producing almost no error when all assumptions are met, are used to account for the effect of the heterogeneity on the abundance estimator.

The possibility of heterogeneous capture probability among individuals of a population leads to the need to modify the simulations to account of the effect on the abundance estimator of the violation of the underlying assumption. The simulation structure described in chapter two, however, remains unchanged up to the sampling part where individuals are randomly captured.

Two forms of heterogeneity can be tested within the present simulation experiment: heterogeneity in capture probabilities and heterogeneity in sampling probabilities. Due to the structure of the simulation, the animal population is divided into four classes g, based on sex, age and reproductive status, which will be characterized by specific capture or sampling probabilities $\Pr(c)_g$, $\Pr(s_1)_g$, $\Pr(s_2)_g$ and $\Pr(s_3)_g$ for the purpose of this chapter.

Another form of violation of assumption known to induce bias in precision in JS estimates is tag loss (Arnason and Mills, 1981; McDonald et al., 2003). In the context of humpback whale studies, tags are mainly lost by misreading and thus the loss may only be temporary (similar to the misreading of rings in bird studies). While some morphological patterns of the fluke, such as the trailing edge, do not naturally change with time, some ventral fluke features, such as the pigmentation and superficial scars, have been found to be age-dependent and to become stable usually after sexual maturation (Blackmer et al., 2000; Carlson and Mayo, 1990). Tag misreading typically occurs during the matching process but experience of the matchers and photographic quality has proven to be an important factor to avoid tag misreading (Carlson and Mayo, 1990; Friday et al., 2000). As for the genetic tagging process in humpback whale studies, this can be done either via the invasive process of skin sampling biopsy or by a noninvasive one after a breach when it is possible to harvest some sloughed skin (Valsecchi et al., 1998). Tag loss in genetic mark-recapture studies is mostly due to allelic dropout, and for tag misreading that leads to false alleles, misinterpretation of allele banding patterns, product size, locus polymorphism (Hoffman and Amos, 2005; Taberlet et al., 1999). These sources of tag loss and tag misreading concern mainly noninvasive tagging for which the quality of the DNA is lowered. However, they should not be ignored for data arising from invasive sampling (McKelvey and Schwartz, 2004; Roon et al., 2005; Taberlet et al., 1999).

Arnason and Mills (1981) stated, in the first paper on the bias induced in the JS estimator by tag loss, that "$\hat{N}$ […] is not biased by tag loss". This finding has been discussed by McDonald et al. (2003) who showed that this result was only true for a tag loss situation where all the individuals were equally likely to lose their tag. A coding modification of the basic simulation structure is outlined in the present chapter to account for the effect of homogeneous tag misreading on the TSJS estimator.

It is worth noting that tag misreading is only considered here as a way to produce new individuals, i.e. false-negative errors, and which will thereby induce an overestimation of the population size. Tag misreading can occur in the other direction, i.e. false-positive errors, leading to an underestimation, also known as the "shadow effect", when several individuals have the same genetic tag as a result of using too few loci or loci with a low heterozygosity (Mills et al., 2000; Waits et al., 2001). However, this is not believed to be an issue in the context of mature research programs (such as humpback whale studies), as microsatellites will usually be well developed.

The aim of this chapter is to assess the degree of error and precision of the population size estimator, using the TSJS model, generated under different cases of heterogeneity in capture and sampling probabilities among the classes and under tag misreading situations. Given the multitude of possible scenarios and cases that could be investigated, it is very important to keep in mind that I chose to focus on scenarios and cases relevant to the study of long-lived animal populations.

3.3. Heterogeneity in capture probabilities

3.3.1. Materials and Methods

Biological context of the simulation

The humpback whale (*Megaptera novaeangliae*) is a baleen whale belonging to the Balaenopteridae family. Present in both hemispheres and in all oceans, it is a migratory species that alternates between warm waters in low latitude for breeding in winter and cold waters in high latitude for feeding in summer (Baker et al., 1986; Brown et al., 1995; Clapham, 2002; Clapham et al., 1993a; Darling and McSweeney, 1984; Garrigue et al., 2002; Katona and Beard, 1990). The seasonal cycle makes the Northern Hemisphere and South Hemisphere populations distinct stocks that never mix (Lockyer, 1984). Humpback whales exhibit a seasonal change in behavior linked with the migratory cycle and congregate in groups both in the feeding and breeding areas: cooperation for coordinated feeding has been observed in high latitude while competitive reproductive groups are likely to appear in breeding grounds (Baraff et al., 1991; Clapham, 1993; Clapham et al., 1993b; Stevick et al., 2006; Tyack and Whitehead, 1982; Valsecchi et al., 2002).

Application to the simulations

Sex ratio

Chittleborough’s study (1965) suggested a sex ratio very slightly biased towards males at birth. So a sex ratio of 52% of males was applied to the population at the beginning and to determine the sex of the new born.

Survival rate

The following (over)simplifying assumption is made: survival probability is constant over all time periods and equal for all individuals. An equal survival rate is used for the population: 0.91, even though the calves (younger than 2 years-old) might have a slightly smaller survival probability (Buckland, 1990; Chittleborough, 1965; Gabriele et al., 2001; Mizroch et al., 2004).

Reproductive rate

In each year, except for the first year, mature females, the ones being more than 5 years old (Chittleborough, 1965; Clapham and Mayo, 1990), could potentially give birth to a calf at a rate of 0.8 if they did not have a calf the year before or 0.1 if they did (Barlow and Clapham, 1997; Chittleborough, 1965; Clapham and Mayo, 1987, 1990). In the first year, the birth history for females is not available so a mean annual reproductive rate for females of 0.37 is used (Barlow and Clapham, 1997; Chittleborough, 1965; Clapham and Mayo, 1987, 1990).

Sampling methods

Two sampling methods are frequently used to generate capture histories for humpback whale populations: photo-identification and genotyping from skin biopsy. Then method 1 described above could be assimilated to photo-identification and method 2 could correspond to genetic sampling.

Heterogeneity in capture probability

The model was designed in the context of the sampling protocol used in surveys of humpback whale populations but is relevant to a broad range of long-lived animals. Reproducing a realistic field sampling situation, though simplified, was an important consideration in the simulations to investigate the performance of the model when specific model assumptions were not met in the field.

In this section, the simulated population is split into four classes g of animals: female breeding adults, female non-breeding adults, male adults, calves. Each class g is given a capture probability $\Pr(c)_g$ which stays constant over time. Indeed, in the biological context of the present model, it is believed that capture probabilities might be dependent on the reproductive status rather than depending randomly on time alone. Six cases of heterogeneity within the population are considered in this chapter. To make the comparison possible between the cases of heterogeneity and the homogeneity counterpart, four scenarios of heterogeneity with an average capture probability for the population set at 0.2, and two scenarios with an average capture probability of 0.7 are explored. The average capture probability of 0.2 was believed to be in agreement with the average capture probability found in the biological population to which the model is later applied in chapter five. I chose also to test the performance of the estimator with a high average capture probability (0.7) and individual capture probabilities greater than 0.5 in the presence of heterogeneity. The purpose is to see whether, even with high capture probabilities, any potential problem still exists.

Thus, for each scenario, a degree of heterogeneity is calculated. This degree of heterogeneity can be expressed by the coefficient of variation CV of the distribution of the capture probabilities over individuals, i.e.: $\mathrm{CV} = \sigma / \mu$

As stated above, in the simulated population, four subpopulations can have a distinct capture probability: calves (under 2 years-old), breeding females, non-breeding females, males.

For a starting population comprising 500 individuals, the numbers of individuals in each class at the beginning of the simulations (during year 1) are approximated to be: 72 calves, 72 breeding females, 168 non breeding females, 260 males. Then, the general equation to get all the capture probabilities and coefficient of variation for each case is given by:

$$1)\quad \frac{72\times \Pr(c)_{ca} + 72\times \Pr(c)_{Bf} + 168\times \Pr(c)_{NBf} + 260\times \Pr(c)_{m}}{572} = 0.2 \qquad (1)$$

where $\Pr(c)_{ca}$ is the capture probability of the calves,

$\Pr(c)_{Bf}$ is the capture probability of the breeding females,

$\Pr(c)_{NBf}$ is the capture probability of the non-breeding females,

$\Pr(c)_{m}$ is the capture probability of the males.

N.B.: “*m*” corresponds to adult males, “NBF” to non-breeding mature females, “BF” to breeding females and “ca” to calves.

Note that the starting number is 500 but the reproductive process takes place just before the sampling process, adding approximately 72 calves to the population. Therefore, the total number of individuals just before sampling is not 500 but approximately 572.

I am aware that this is an open population but the mortality rate is assumed to be very low (0.09) and the same for all classes – emigration is being ignored (see chapter five for a discussion of these values for the New Caledonian population of humpback whales). So, even though the population increases through the simulation, this equation is assumed to approximately hold at later time periods.

2) $\mu = 0.2$

$$\sigma = \sqrt{\frac{1}{572} \times \left[72 \times (\Pr(c)_{ca} - \mu)^2 + 72 \times (\Pr(c)_{Bf} - \mu)^2 + 168 \times (\Pr(c)_{NBf} - \mu)^2 + 260 \times (\Pr(c)_{m} - \mu)^2\right]}$$

The capture probabilities for the four heterogeneity cases are the following:

Table 3-1- Capture probability for each class for every case of heterogeneity considered at an average capture probability of 0.2.

	$\Pr(c)_m$	$\Pr(c)_{NBf}$	$\Pr(c)_{Bf}$	$\Pr(c)_{ca}$	**CV**
Case 1	0.21	0.22	0.15	0.15	0.14
Case 2	0.24	0.24	0.1	0.05	0.37
Case 3	0.25	0.25	0.05	0.05	0.43
Case 4	0.35	0.1	0.05	0.05	0.68

Case 1 has a small heterogeneity, cases 2 and 3 illustrate moderate heterogeneity and cases 4 presents what would be regarded as severe heterogeneity in capture probabilities.

The same procedure is applied with an average capture probability of 0.7 and capture probabilities for each class of individuals all greater than 0.5 to create two cases of heterogeneity:

Table 3-2-Capture probability for each class for every case of heterogeneity considered at an average capture probability of 0.7.

	$\Pr(c)_m$	$\Pr(c)_{NBf}$	$\Pr(c)_{Bf}$	$\Pr(c)_{ca}$	**CV**
Case 5	0.8	0.5	0.5	0.5	0.23
Case 6	0.5	0.86	0.86	0.86	0.26

Note that in case 5 the average capture probability is not 0.7 but 0.64.

Only two cases with small heterogeneity are created here because with a high mean capture probability (0.7 or 0.64) and the necessity of having all capture probabilities higher than 0.5, it was not possible to obtain a big coefficient of variation.

3.3.2. Results

Estimation with heterogeneity in capture and equal sampling probabilities

The results of the simulation to estimate the error and the precision of the TSJS estimator in the presence of heterogeneity in capture probability are summarized in Table 3-3. The six cases of heterogeneity described in Table 3-1 and Table 3-2 are tested under the scenario 20-40-40 and a starting population of 500 individuals. Illustrating the performances of the TSJS model using scenario 20-40-40 presents two advantages: there is no other form of heterogeneity (i.e. no heterogeneity between the two sampling methods, i.e. $\Pr(s_1) = \Pr(s_2)$) and the use of the smallest probability of double tagging handled by the model, i.e. $\Pr(s_3) = 0.2$. This scenario should thus provide, under heterogeneity in capture probability, the biggest error given by the estimator that can be expected.

Table 3-3- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-occasion study for different cases of heterogeneity in capture probabilities with scenario 20-40-40 and a starting population of 500 individuals.

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 $\mathrm{CV} = 0.14$ $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	608	627	-0.03	73	0.3	64	65
$\hat{N}_3$	638	654	-0.02	71	0.2	72	76
$\hat{N}_4$	660	693	-0.05	74	0.17	75	76
$\hat{N}_5$	696	719	-0.03	79	0.17	81	85
$\hat{N}_6$	738	745	-0.01	84	0.16	87	89
$\hat{N}_7$	745	763	-0.02	86	0.17	80	82
$\hat{N}_8$	774	794	-0.03	90	0.18	75	80
$\hat{N}_9$	815	830	-0.02	97	0.22	73	79

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 2 CV =0.37 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	513	626	-0.18	57	0.26	43	47
$\hat{N}_3$	490	653	-0.25	50	0.28	27	30
$\hat{N}_4$	529	693	-0.24	56	0.27	29	34
$\hat{N}_5$	566	718	-0.21	63	0.25	39	44
$\hat{N}_6$	602	745	-0.19	68	0.23	45	52
$\hat{N}_7$	622	763	-0.18	73	0.22	49	55
$\hat{N}_8$	642	795	-0.19	75	0.24	44	50
$\hat{N}_9$	714	830	-0.14	85	0.24	56	59
Case 3 CV =0.43 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	508	627	-0.19	57	0.29	38	41
$\hat{N}_3$	490	655	-0.25	51	0.29	25	30
$\hat{N}_4$	523	694	-0.25	56	0.28	26	30
$\hat{N}_5$	568	718	-0.21	64	0.24	40	46
$\hat{N}_6$	597	744	-0.2	69	0.23	41	49
$\hat{N}_7$	626	761	-0.18	74	0.21	48	57
$\hat{N}_8$	626	793	-0.21	75	0.25	35	42
$\hat{N}_9$	730	827	-0.12	88	0.23	57	60
Case 4 CV =0.68 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	343	627	-0.45	29	0.46	1	1
$\hat{N}_3$	354	653	-0.46	27	0.46	0	0
$\hat{N}_4$	364	694	-0.48	29	0.48	0	0
$\hat{N}_5$	410	717	-0.43	36	0.43	0	0
$\hat{N}_6$	426	745	-0.43	39	0.43	0	0
$\hat{N}_7$	443	763	-0.42	42	0.42	1	1
$\hat{N}_8$	465	795	-0.42	45	0.42	1	1
$\hat{N}_9$	479	828	-0.42	47	0.43	2	2

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 5 CV =0.23 $\overline{\Pr}(c)_g = 0.64$							
$\hat{N}_2$	556	626	-0.11	6	0.12	2	2
$\hat{N}_3$	605	653	-0.07	7	0.08	5	5
$\hat{N}_4$	654	692	-0.05	10	0.06	20	21
$\hat{N}_5$	685	718	-0.05	13	0.05	32	33
$\hat{N}_6$	712	744	-0.04	14	0.05	41	43
$\hat{N}_7$	723	761	-0.05	15	0.06	32	37
$\hat{N}_8$	738	793	-0.07	17	0.07	17	17
$\hat{N}_9$	741	828	-0.11	18	0.11	3	3
Case 6 CV =0.26 $\overline{\Pr}(c)_g = 0.7$							
$\hat{N}_2$	599	627	-0.05	4	0.05	9	9
$\hat{N}_3$	653	655	0	7	0.02	64	66
$\hat{N}_4$	712	695	0.02	10	0.03	62	62
$\hat{N}_5$	743	719	0.03	11	0.04	45	45
$\hat{N}_6$	771	746	0.03	13	0.04	55	55
$\hat{N}_7$	782	764	0.02	1	0.03	75	75
$\hat{N}_8$	795	795	0	15	0.02	93	93
$\hat{N}_9$	793	830	-0.04	16	0.05	35	35

$\hat{N}_2$, …, $\hat{N}_9$ =population size estimate at time 2, …, 9.

As already reported in other studies, the error for $\hat{N}$ was found, in all heterogeneity cases explored, to be negative, bigger in the RMSRE and in the absolute value of the MRE than in the case of homogeneity reported in Table 2-1, where capture probability is also 0.2 (for comparison with the heterogeneity case 1 to 4) or higher than 0.5 (for comparison with the heterogeneity case 5 and 6) (Carothers, 1973; Gilbert, 1973). As expected the more severe the heterogeneity within the population is, the bigger the underestimation. Case 1 exhibits a low degree of heterogeneity and as such the error is no more than the one produced by the homogeneous counterpart where the constant capture probability $\Pr(c)$ equals 0.2. Cases 2 and 3 demonstrate a moderate heterogeneity but both the MRE and the RMSRE are considerably larger (|MRE|>0.1 and RMSRE>0.22) than the homogeneous case. Case 4 shows a high degree of heterogeneity leading to very large MRE and RMSRE (|MRE|>0.42 and RMSRE>0.42).

In terms of standard error, case 1 does not differ from the homogeneous case but from case 2 onwards the standard errors decrease substantially as the degree of heterogeneity increases, becoming less than half the size in case 4 than the homogeneous counterpart (Table 2-1): the values go from 8% of the population size on the first occasion to almost 10% on the last occasion against approximately 12% of the population at any given occasion when there is no heterogeneity.

Concerning the CI coverage rate, in the case 1, it is similar to the ones reported in Table 2-1 for a capture probability $\Pr(c)$ of 0.2, varying from 64% on the first estimation occasion to 87% on the fifth estimation occasion for the normal approximation. Both the normal and log-normal approaches to construct the confidence intervals perform very similarly with the log-normal method having slightly higher CI coverage rates. CI coverage rate decreases in case 2 and 3, being half of the value found for case 1. In the most extreme case of heterogeneity (case 4), the CI coverage rate is zero on almost all capture occasions. This seems to be due to a mixture of error in the population estimates and in the standard errors. With a higher capture probability and a reasonable heterogeneity in capture probability (case 5 and 6), standard errors tend to be small, the consequence of which is a very poor CI coverage on some capture occasions, especially on the early and last capture occasions. In these two cases, this seems to be due to error in the standard errors only as the RMSRE reports only a minimal error in the estimates.

Finally, cases 5 and 6 present on average a high capture probability as all individuals have a probability of being caught equal or higher than 0.5. The estimator appears relatively unbiased in both cases with the MRE usually smaller than 0.1 and the overall error is small with the RMSRE below 0.1, except on the first and last occasions of case 5.

As expected, the TSJS model performs better with high capture probability (i.e. 0.5) and small coefficient of variation.

Estimation with heterogeneity in capture and unequal sampling probabilities

The TSJS model was investigated under heterogeneity in capture and sampling scenario 50-37.5-12.5 and the results are displayed in Table 3-4. The estimator is still robust to the inequality in the probabilities between the two sampling methods with a ratio 3:1 as long as the probability of double capture is not smaller than 0.5 (Table 2-2) . Here the aim is to see if adding another disturbance (i.e. the heterogeneity in capture probabilities) would interfere with the performance of the estimator.

Table 3-4- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-occasion study for different cases of heterogeneity in capture probabilities with scenario 50-37.5-12.5 and a starting population of 500 individuals.

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 CV =0.14 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	640	626	0.02	59	0.23	63	65
$\hat{N}_3$	658	653	0.01	57	0.16	71	73
$\hat{N}_4$	704	692	0.02	63	0.15	81	80
$\hat{N}_5$	713	716	0	65	0.12	86	88
$\hat{N}_6$	745	743	-0.01	69	0.12	86	87
$\hat{N}_7$	753	761	0	71	0.11	89	90
$\hat{N}_8$	808	794	0.02	77	0.13	88	88
$\hat{N}_9$	831	827	0	81	0.19	73	73
Case 2 CV =0.37 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	526	624	-0.16	45	0.23	34	38
$\hat{N}_3$	505	652	-0.22	41	0.25	22	25
$\hat{N}_4$	539	691	-0.22	45	0.24	23	26
$\hat{N}_5$	591	716	-0.17	53	0.2	32	43
$\hat{N}_6$	610	742	-0.18	56	0.21	37	41
$\hat{N}_7$	644	761	-0.15	61	0.18	46	53
$\hat{N}_8$	663	792	-0.16	64	0.19	45	50
$\hat{N}_9$	729	826	-0.12	71	0.21	50	52

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 3 $\mathrm{CV} = 0.43$ $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	529	626	-0.15	45	0.24	40	40
$\hat{N}_3$	504	652	-0.23	41	0.25	20	23
$\hat{N}_4$	542	692	-0.22	44	0.24	23	25
$\hat{N}_5$	581	717	-0.19	52	0.21	34	38
$\hat{N}_6$	607	743	-0.18	56	0.21	36	38
$\hat{N}_7$	631	761	-0.17	61	0.2	39	46
$\hat{N}_8$	663	792	-0.16	64	0.21	44	47
$\hat{N}_9$	718	827	-0.13	70	0.21	48	52
Case 4 $\mathrm{CV} = 0.68$ $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_2$	362	626	-0.42	24	0.43	0	0
$\hat{N}_3$	367	653	-0.44	22	0.44	0	0
$\hat{N}_4$	385	693	-0.44	25	0.45	0	0
$\hat{N}_5$	424	716	-0.41	30	0.41	0	0
$\hat{N}_6$	438	743	-0.41	32	0.41	0	0
$\hat{N}_7$	474	760	-0.38	37	0.38	0	0
$\hat{N}_8$	482	793	-0.39	38	0.4	0	0
$\hat{N}_9$	511	827	-0.38	42	0.39	2	3
Case 5 $\mathrm{CV} = 0.23$ $\overline{\Pr}(c)_g = 0.64$							
$\hat{N}_2$	576	628	-0.08	4	0.09	1	1
$\hat{N}_3$	619	655	-0.05	5	0.06	8	9
$\hat{N}_4$	665	695	-0.04	8	0.05	18	20
$\hat{N}_5$	691	719	-0.04	10	0.04	32	33
$\hat{N}_6$	716	745	-0.04	12	0.04	34	36
$\hat{N}_7$	733	763	-0.04	13	0.05	41	43
$\hat{N}_8$	756	796	-0.05	15	0.05	26	28
$\hat{N}_9$	773	832	-0.07	16	0.08	16	16

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 6 CV =0.26 $\overline{\Pr}(c)_g = 0.7$							
$\hat{N}_2$	617	626	-0.01	3	0.03	24	24
$\hat{N}_3$	658	655	0.01	5	0.02	55	56
$\hat{N}_4$	712	695	0.03	7	0.03	40	41
$\hat{N}_5$	738	718	0.03	9	0.03	38	39
$\hat{N}_6$	766	745	0.03	10	0.03	45	46
$\hat{N}_7$	778	763	0.02	11	0.02	75	76
$\hat{N}_8$	801	795	0.01	12	0.02	95	95
$\hat{N}_9$	809	828	-0.02	14	0.03	67	70

$\hat{N}_2,\ldots,\hat{N}_9$ =population size estimate at time 2,…,9.

The TSJS estimates appear unbiased only in the cases of high average capture probability (cases 5 and 6). For cases 1 to 4, the error increases with the degree of heterogeneity. For cases 2 and 3, the MRE is on average below 0.18 and the RMSRE is always below 0.25. However, for case 4 representing a high heterogeneity in capture probabilities, the estimates are severely negatively biased (|MRE|>0.38 and 0.38<RMSRE<0.45). Compared to the results under the same scenario (50-37.5-12.5) with no heterogeneity (Table 2-2), case 1 of heterogeneity displays, for MRE and RMSRE, similar values to the values of the counterpart case with no heterogeneity with $\Pr(c) = 0.2$. Cases 2 and 3 of heterogeneity present similar RMSRE but the values of the MRE greatly differ compared to the case with $\Pr(c) = 0.2$ in Table 2-2. Case 4 shows RMSRE values more than twice bigger (except in the second occasion) and MRE values more than 7 times bigger in almost all capture occasions than the values of, respectively, RSMRE and MRE reported in Table 2-2 for $\Pr(c) = 0.2$. In cases 5 and 6, values of MRE and RMSRE are similar to the values of MRE and RMSRE found in Table 2-2 for $\Pr(c) \geq 0.5$.

The CI coverage rate is equivalent to the one with equal sampling probabilities under scenario 20-40-40: in case 1, it is similar to the ones reported in Table 2-1 for a capture probability of 0.2. However, it quickly decreases in case 2 and 3, being half of the value found for case 1. CI coverage rates are also smaller in cases 2 and 3 of heterogeneity than they are in Table 2-2 with $\Pr(c) = 0.2$. In the most extreme cases of heterogeneity (case 4), the CI coverage rate is zero on almost all capture occasions. With a higher capture probability and a reasonable heterogeneity in capture probability (case 5 and 6), standard errors tend to be very small and the CI coverage rate is generally poor. Moreover, in cases 5 and 6, CI coverage rates are smaller than those found in Table 2-2 for $\Pr(c) \geq 0.5$, although better in case 6 than in case 5. As observed earlier, the normal approximation and the log-normal transformation perform very similarly for the construction of the confidence intervals, with the log-normal approach leading to slightly higher coverage rates.

Finally, results in Table 3-4 are similar to the results in Table 3-3, presenting respectively cases with heterogeneity and unequal sampling probabilities and cases with heterogeneity and equal sampling probabilities. Therefore, errors in the estimates arise from the heterogeneity in capture probabilities and having unequal sampling probabilities with heterogeneous capture probabilities does not affect furthermore the performance of the TSJS model.

3.4. Heterogeneity in sampling probabilities

3.4.1. Materials and Methods

Another degree of heterogeneity can be achieved by setting different sampling probabilities between the four classes which could be present in a humpback population. In this section, all the animals have the same probability of being caught (or detected) $\Pr(c)$ and the “heterogeneity” is characterized by a difference in sampling probabilities $\Pr(s_1)$, $\Pr(s_2)$, $\Pr(s_3)$ between the classes g. Two cases representing the heterogeneity in sampling are tested for a capture probability $\Pr(c)$ of 0.2 and 0.5. In both cases, each class is given as sampling probabilities $\Pr(s_1)_g$, $\Pr(s_2)_g$, $\Pr(s_3)_g$ either the scenario 20-40-40 or 50-25-25, i.e. for class g $\Pr(s_3)_g = 0.2$, $\Pr(s_1)_g = 0.4$, $\Pr(s_2)_g = 0.4$ or $\Pr(s_3)_g = 0.5$, $\Pr(s_1)_g = 0.25$, $\Pr(s_2)_g = 0.25$.

The starting population just before the sampling process of the first sampling occasion comprises again approximately 572 individuals, and the number of individuals in each class at the beginning of the simulations is set at: 72 calves, 72 breeding females, 168 non breeding females, 260 males. This gives the possibility of calculating a ratio for the sampling heterogeneity scenarios. This ratio simply describes the amplitude of the heterogeneity in sampling probability in the population in the absence of a statistic equivalent to the coefficient of variation.

Table 3-5- Sampling scenario for each class *g* for the four cases investigated.

	$Pr(s_3)_m$, $Pr(s_1)_m$, $Pr(s_2)_m$	**$Pr(s_3)_{NBF}$, $Pr(s_1)_{NBF}$, $Pr(s_2)_{NBF}$**	**$Pr(s_3)_{BF}$, $Pr(s_1)_{BF}$, $Pr(s_2)_{BF}$**	**$Pr(s_3)_{ca}$, $Pr(s_1)_{ca}$, $Pr(s_2)_{ca}$**	**Pr(*c*)**	**ratio**
Case 1	50-25-25	20-40-40	20-40-40	20-40-40	0.2	2:2
Case 2	50-25-25	20-40-40	20-40-40	20-40-40	0.5	2:2
Case 3	20-40-40	50-25-25	20-40-40	20-40-40	0.2	3:1
Case 4	20-40-40	50-25-25	20-40-40	20-40-40	0.5	3:1

Cases 1 and 2 have a less severe heterogeneity in sampling probabilities than cases 3 and 4.

3.4.2. Results

Following the investigation of the TSJS model under four cases of heterogeneity in sampling probabilities among classes of individuals described in Table 3-5, results of the performance of the estimator when there is heterogeneity in sampling probabilities are shown in Table 3-6.

Table 3-6- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-occasion study for 2 cases of heterogeneity in sampling probabilities between the 4 classes of individuals with capture probability of 0.2 and 0.5 and a starting population of 500 individuals.

Sampling case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 Ratio=2 :2 Pr(*c*)=0.2							
$\hat{N}_2$	611	639	-0.04	59	0.24	52	55
$\hat{N}_3$	656	692	-0.05	61	0.19	64	68
$\hat{N}_4$	718	757	-0.05	69	0.16	70	75
$\hat{N}_5$	779	804	-0.03	78	0.15	79	80
$\hat{N}_6$	834	851	-0.02	85	0.16	87	87
$\hat{N}_7$	872	886	-0.02	91	0.16	85	87
$\hat{N}_8$	936	943	0	100	0.19	80	81

Sampling case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_9$	1015	1003	0.01	110	0.24	74	75
Case 2 Ratio=2 :2 Pr(c)=0.5							
$\hat{N}_2$	593	639	-0.07	7	0.06	23	24
$\hat{N}_3$	632	693	-0.09	9	0.04	6	7
$\hat{N}_4$	697	757	-0.08	14	0.04	16	17
$\hat{N}_5$	762	806	-0.05	20	0.04	41	44
$\hat{N}_6$	809	852	-0.05	23	0.04	54	56
$\hat{N}_7$	859	888	-0.03	27	0.04	73	78
$\hat{N}_8$	901	943	-0.04	31	0.04	71	74
$\hat{N}_9$	961	1004	-0.04	35	0.05	71	72
Case 3 Ratio=3 :1 Pr(c)=0.2							
$\hat{N}_2$	619	639	-0.03	61	0.21	54	54
$\hat{N}_3$	634	692	-0.08	60	0.16	59	61
$\hat{N}_4$	707	757	-0.07	69	0.16	67	72
$\hat{N}_5$	752	804	-0.06	76	0.14	77	81
$\hat{N}_6$	818	849	-0.04	85	0.13	83	86
$\hat{N}_7$	861	885	-0.03	91	0.14	87	90
$\hat{N}_8$	922	940	-0.02	99	0.16	81	84
$\hat{N}_9$	958	1002	-0.04	106	0.2	75	78
Case 4 Ratio=3 :1 Pr(c)=0.5							
$\hat{N}_2$	584	640	-0.09	7	0.06	12	13
$\hat{N}_3$	626	694	-0.1	9	0.04	6	6
$\hat{N}_4$	688	757	-0.09	15	0.04	12	12
$\hat{N}_5$	747	805	-0.07	19	0.04	23	26
$\hat{N}_6$	796	851	-0.07	23	0.04	39	42
$\hat{N}_7$	834	886	-0.06	26	0.03	48	50
$\hat{N}_8$	887	940	-0.06	30	0.03	57	61
$\hat{N}_9$	935	1002	-0.07	34	0.05	49	50

$\hat{N}_2$, …, $\hat{N}_9$ =population size estimate at time 2, …, 9.

The heterogeneity in sampling probabilities among the classes of individuals as presented here does not seem to affect the performance of the TSJS estimator at both capture probabilities 0.2 and 0.5 in terms of bias: the estimates are slightly negatively biased (MRE no more than -0.1 and values for the RMSRE on average below 0.1). For both ratios (2:2 and 3:1) of heterogeneity in sampling probabilities among the classes, as one might expect, the cases with a capture probability of 0.5 give better results in terms of RMSRE with values below 0.06 (against values between 0.13 and 0.24 for a capture probability of 0.2). The higher capture probability produces smaller standard errors, as reported for earlier tables, i.e. Table 2-1, Table 2-2, Table 2-3.

In the presence of heterogeneity in sampling probabilities among the classes, as expected, increasing the capture probability leads to a decrease of the error, i.e. larger capture probabilities result in more precise estimates. So, if the error is small, the CI coverage rate should still be good. The problem here is that increasing the capture probability also leads to an excessive decrease in the standard errors which systematically results in a smaller CI coverage: for a capture probability of 0.2 the CI coverage rate varies, with the normal approximation to construct the confidence intervals, from 52% to 87% (55% to 90% with the log-normal transformation) while it ranges from 6% to 73% (7% to 78% with the log-normal transformation) for a capture probability of 0.5.

3.5. Tag misreading

3.5.1. Materials and Methods

A tag is defined as any marking, natural or added to the individuals during capture that allows the identification of each animal specifically in later recapture. In order to evaluate the impact of tag misreading in this chapter, tag misreading was included in the simulation. The tag misreading concerns only the single-type of capture as I assume that, with simultaneous marking, i.e. marking by both methods on the same occasion, tags cannot be lost as one method backs-up the other. A probability of missing the tag or not recognizing it is introduced by creating a matrix of 0-1 uniform random numbers of the same dimensions as the CMR matrix (created after the situation of overlap). Then, if the random number is smaller than a set tag misreading rate and if the event corresponds to a recapture by method 1 or 2 (namely to a “4”, “5”, “17” or “18”) (see chapter two), the tag is considered lost, is erased from the history of the individual and a new line is added to the CMR matrix. This new line only contains “0” and the capture event erased previously. So here I consider the situation where the tag misreading results from a false negative matching mistake (for visual tags such as ringing and photo-identification data), i.e. the visual tag is misread and not correctly matched, or a laboratory mistake (for genetic data such as scat or hair data), i.e. a new false genotype appears instead of the proper one. Therefore, individuals that lose their tag on one occasion do not retain this new identity for subsequent recaptures but could possibly lose again their tag on a later occasion. This configuration was chosen for the simulation as I believe that, in many vertebrate studies (e.g. humpback whales), it is the most likely scenario and that it is unlikely that an individual which has lost its tag (either the photo or the genetic one) retains this false identity for subsequent recaptures, except maybe if there is a new feature causing the mismatch (e.g. new scar resulting from an injury…). In the presence of tag misreading, the matrix created after the tag misreading process is used to estimate population size.

The tag misreading rate is assumed homogeneous over the population, set at 5% per occasion which is believed to be above the rate of error present in humpback whale studies but might be plausible for other tag systems (Carlson and Mayo, 1990; Palsbøll et al., 1997; Stevick et al., 2001).

3.5.2. Results

The results obtained with a tag misreading situation in the case of equal catchability under the sampling scenario 20-40-40 and 50-25-25 are illustrated in Table 3-7 for a starting population of 500 (572 really) over 10 capture occasions.

Table 3-7- MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors of the estimated values and nominal and log-normal CI coverage rates at each capture occasion of a 10-occasion study with a tag misreading rate of 5% homogeneous within the population and a starting population of 500 individuals.

Case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 20-40-40 Pr(c)=0.2							
$\hat{N}_2$	647	641	0.01	68	0.26	56	58
$\hat{N}_3$	699	694	0.01	71	0.17	77	79
$\hat{N}_4$	771	758	0.02	81	0.15	87	88
$\hat{N}_5$	807	805	0	86	0.14	88	89
$\hat{N}_6$	869	852	0.02	94	0.14	91	92
$\hat{N}_7$	919	887	0.03	100	0.15	91	88
$\hat{N}_8$	961	942	0.02	107	0.16	86	85
$\hat{N}_9$	1017	1002	0.01	115	0.19	76	78
Case 2 20-40-40 Pr(c)=0.5							
$\hat{N}_2$	621	638	-0.03	9	0.14	29	30
$\hat{N}_3$	675	691	-0.02	13	0.12	49	49
$\hat{N}_4$	75	755	0	19	0.1	80	79
$\hat{N}_5$	803	803	0	22	0.1	86	87
$\hat{N}_6$	847	849	0	26	0.09	93	94
$\hat{N}_7$	877	886	-0.01	28	0.09	94	94
$\hat{N}_8$	919	939	-0.02	31	0.11	83	85
$\hat{N}_9$	966	999	-0.03	35	0.13	70	72
Case 3 50-25-25 Pr(c)=0.2							
$\hat{N}_2$	674	627	0.07	65	0.26	64	64
$\hat{N}_3$	706	655	0.08	64	0.18	76	76
$\hat{N}_4$	757	694	0.09	69	0.17	79	76
$\hat{N}_5$	774	719	0.08	71	0.16	80	78
$\hat{N}_6$	789	745	0.06	73	0.14	84	84
$\hat{N}_7$	827	763	0.08	77	0.15	86	83
$\hat{N}_8$	855	795	0.08	82	0.16	82	82
$\hat{N}_9$	879	829	0.06	86	0.19	78	75

Case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 4 50-25-25 Pr(c)=0.5							
$\hat{N}_2$	643	626	0.03	11	0.07	35	36
$\hat{N}_3$	674	656	0.03	13	0.05	64	64
$\hat{N}_4$	715	694	0.03	16	0.05	72	72
$\hat{N}_5$	742	718	0.03	18	0.04	72	72
$\hat{N}_6$	771	743	0.04	20	0.05	74	73
$\hat{N}_7$	786	760	0.03	21	0.05	72	71
$\hat{N}_8$	819	792	0.03	24	0.05	79	76
$\hat{N}_9$	854	826	0.03	26	0.06	75	75

$\hat{N}_2$, …, $\hat{N}_9$ =population size estimate at time 2, …, 9.

With both scenarios, the results are similar to what was found in other studies: except under scenario 20-40-40 for a capture probability of 0.5 for which the error was negative or 0, tag misreading usually induces positive bias because capture probability $\Pr(c)$ tends to be underestimated (Williams et al., 2002). The error is negligible for both capture probabilities, 0.2 and 0.5 (|MRE|<0.1). The overall error is below 0.2 for all intermediate capture occasions and gets smaller as the capture and the simultaneous sampling probabilities $\Pr(c)$ and $\Pr(s_3)$ get bigger. In terms of CI coverage, the results are similar to those found in the equivalent cases with no misread tag (Table 2-1 and Appendix 5), except in the case with a capture probability of 0.5 and scenario 20-40-40 where the results are better when there is tag misreading occurring. The CI coverage appears to be better than usual for this method (>80%) in most cases, except in case 4 (with capture probability $\Pr(c)$ =0.5 and sampling scenario 50-25-25) where it does not exceed 79%.

3.6. Discussion

Heterogeneity in capture probabilities

Violation of the assumption of homogeneity in capture probability usually prevents or restricts the use of the classic JS model for the purpose of population size estimation in many wildlife studies. This chapter shows, however, that the TSJS estimator is fairly robust when the heterogeneity in catchability among classes of individuals is small. Studies focusing on the JS model report minor bias on the population size estimate when all individuals have capture probabilities greater than 0.5 on all capture occasions (Carothers, 1973; Gilbert, 1973; Hwang and Chao, 1995). Similarly here the extension of the JS model, the TSJS model, gives negligible error when all individuals have capture probabilities greater than 0.5 on all capture occasions. As expected, the negative error increases as the magnitude of the heterogeneity rises and serious negative error can occur when the average capture probabilities are small. The structure of this heterogeneity is also a factor to take into account when evaluating the impact of heterogeneous capture probabilities. Here, I chose to model the heterogeneity in capture among classes of individuals rather than among individuals and therefore to set the value of the capture probability of the individuals based on biological features rather than randomly as we suspect it to be the case in the population studied in chapter five. Another source of heterogeneity that should probably be explored in future studies when two sources of data are to be combined is where the degree of individual heterogeneity is not the same in the two sampling methods.

The performance of the model depends on its assumptions and further work is required to develop an open-population model that can handle heterogeneity in capture probability which is one of the most frequent sources of bias in abundance estimators (Boulanger et al., 2004c; Crespin et al., 2008; Hammond, 1986; Link, 2004; Prévot-Julliard et al., 1998).

Heterogeneity in sampling probabilities

In the presence of heterogeneity in sampling probabilities among classes of individuals, the estimator is usually relatively unbiased.

As mentioned earlier, temporal variation *per se* in capture or sampling probability was not considered here. However, in the present Monte Carlo experiment, some individuals can have different sampling and capture probabilities over the course of the study, depending on their reproductive status. A new-born female will have a different capture probability when it becomes adult and during the adult phase may change its probability of capture several times, depending on whether it is breeding or not. General patterns of heterogeneity in capture probability are difficult to predict because they may also depend on the magnitude of specific trends of temporal variation. In this chapter, I tried to reproduce a simplified pattern of heterogeneity in catchability that I think is relevant to the population studied in chapter five in order to extrapolate the results on the error of the TSJS estimator to real data.

Tag misreading

There are several ways tags can be misread: (1) an existing tag can be wrongly assigned to another individual, (2) a tag can be unrecognized, i.e. not matched where it should be, and a new individual is created, (3) the tag of a new individual can be assigned to an existing individual, (4) a tag that does not exist can be created, (5) a tag that does not exist can be assigned to an existing individual. Errors (4) and (5) correspond to what Creel et al. (2003) referred to as “ghost” to represent a non-existing genotype. With natural marking there is no list that is error-free and it is typically very hard to know when an error has occurred. In photo-matching, the only way to reduce the matching error rate is to have a team of experienced people and good-quality photographs. With genetic data, when possible, two runs of analysis could help minimizing the lab error. In their study of humpback whales double-tagged by photo-identification and genetics, Stevick et al. (2001) did not find any false-positive error, i.e. errors (1), (3), (5) and I also believe that in such studies, if the protocol is rigourous, false-positive error is unlikely in matching photographs, at least for this species. In genetic data, false-positive error is also very unlikely as the number of possible genotypes usually greatly exceeds the number of genotypes in the population. Therefore, for the present simulation experiment I only considered false-negative errors. However, the shadow effect is not really tag misreading but rather an example of a study design flaw, even though it was included in the tag misreading issue. In photo-identification, with non-evolving natural marks, as in the humpbacks (unless the animal is injured, e.g. shark bites), the matching error is unlikely to be repeated and the individual should not retain this new identity for subsequent recaptures. However, in an effort to be more general, I considered the possibility in the simulation that an individual might be missed again creating another individual. Similarly, in genetic tagging, the chance of a false DNA fingerprint being assigned again is very small given the number of loci is adequate. I again considered potential false negative error for the same individual in subsequent recaptures. Finally, the tag misreading rate was assumed constant although this might not always be the case, especially in photo-identification data where animals with indistinct marks may be more likely to be misread.

With a tag misreading issue, errors in identification generally leads to an overestimation of the population size (Stevick et al., 2001). The TSJS estimator demonstrates no error due to a homogeneous tag misreading rate, like the JS estimator (Arnason and Mills, 1981). However, as stated in McDonald et al. (2003), these results should not be extrapolated to other situations for which they would be inappropriate: the magnitude of the error in abundance estimates certainly depends on the tag misreading rate (see Appendix 6) which should be kept as low as possible. In the matching of photographs, these errors can be substantially reduced, however, when the photo-quality standard is high. This has the disadvantage of reducing the sample size, leading to a decrease in precision. The magnitude of the error in population size estimate may also depends on the way the tags are lost in the population (whether it is homogeneous or not). Unlike the abundance estimators using one set of data, the TSJS estimator already makes full use of the double-marking. Double marking has been previously used to circumvent the problem of tag misreading in population size estimation and reduce the bias (Stevick et al., 2001). In the TSJS model, double-tagging is already integrated in the population size calculation and, given a sufficient simultaneous sampling probability, it should help overcome the tag misreading issue and similarly any form of tag loss.

In the simulation model, I decided to use a survival rate of 0.91 (p.105) rather than the published value of 0.96 for adult humpback whales or higher (Buckland, 1990 Gabriele et al., 2001; Mizroch et al., 2004) to have a population a little more open demographically to the death or permanent emigration process. At first sight, I may be biasing the simulation against closed population models. However, the “death” process that closed population models are responding to in many species (particularly long lived ones as are primarily considered here) is dominated by emigration and in the simulation I have not included a separate permanent emigration process. Therefore, by lowering the survival rate I integrate a process of permanent emigration and the value of 0.91 is actually an apparent survival value somewhat larger than the estimates from the CJS (apparent survival=true survival + permanent emigration). In chapter five, apparent survival estimates with the CJS show that the humpback whale population used in this study appears to be even more open than that.

These results are probably relevant to a range of large mammal populations and possibly, given a proportional time scale shift, to some other groups as well. However, only a small range of the possible parameters and model space has been explored so these conclusions inevitably have limited generality.

4. Chapter Four

Model Comparison

4.1. Abstract

At present, many population size estimates are obtained using one set of data with closed population models. Some of those multiple-recapture closed-population models can handle individual or temporal heterogeneity in capture probabilities. These models could thus be appealing when estimating animal population size when capture probability likely varies among individuals or over time. However, such models most likely violate the closure assumption and only provide a single point estimate over the whole study period. On the other hand, the two-source Jolly-Seber (TSJS) model is an open-population model providing an estimate for every capture occasion (except the first and the last one) but is not able to handle a great degree of individual heterogeneity. Thus, it is of interest to compare, in the presence of heterogeneity among classes of individuals as described in chapters two and three, the results of the TSJS, the Jolly-Seber (JS) model and of the closed population models handling heterogeneity in capture probabilities that are commonly used even with open populations: M_h and M_{th} by Chao and M_t by Darroch. Given the structure of the heterogeneity in the simulation, the estimator for model M_h is expected to perform better than the one for model M_t. However, the estimator for model M_h only performs better than the one of model M_t when the heterogeneity is extreme (case 4). The TSJS estimator seems to be the most appropriate model when the individual heterogeneity is small and the capture probability high and is in most of the cases the best estimator among the JS type of models presented here. However, the closed population estimates and the average open-population estimates do not have the same meaning and should be compared with caution. If heterogeneity is believed to be important, effort should focus on the study design in order to meet the basic assumption of closure to use closed-population models handling heterogeneity or in order to use a model based around the robust design. If the population is open during the experiment and two sources of data available, the TSJS model is the most advisable among the JS models.

4.2. Introduction

At present, many population size estimates are based on closed population models. The classical two-occasion models include Chapman’s, the Petersen two-sample capture-recapture method or Bailey’s modification of the previous method (Buckland and Duff, 1989; Calambokidis and Barlow, 2004; Calambokidis et al., 1990; Felix and Haase, 2001a, b; Garrigue et al., 2004; Larsen and Hammond, 2004). Those models assume that all animals have the same capture probability on each capture occasion and that the population is closed demographically and geographically. Of the multiple-recapture closed-population models often used, the simplest model, denoted M_0 (0 for no variation in capture probability) can be inappropriate for many wildlife studies where variation in capture probability is likely to occur. Therefore, more realistic multiple-recapture closed-population models are used to take account of this possible variability by allowing capture probabilities to vary with time, and/or among animals. Those last models could be appealing when estimating population size where capture probability most likely varies among individuals:

M_t: capture probabilities vary over time,

M_h: capture probabilities vary among animals but are constant across time for each individual,

M_{th}: capture probabilities vary among animals and with time.

However, closed-population models might have little relevance or might be hard to interpret for some populations due to the long monitoring period, migratory behavior of the species, sampling design (e.g. small grid size, inappropriate grid placement in bear studies) for instance and therefore due to the violation of the closure assumption (Boulanger et al., 2004b; Calambokidis and Barlow, 2004; Calambokidis et al., 1990; Cerchio, 1998; Meekan et al., 2006; Smith et al., 1999). Kendall (1999) evaluated the robustness of closed-population methods with various types of departure from the closure assumption: in the present simulation study, the closure violation can be assimilated to the case of “one entry and one exit”. Kendall concluded that for this type of closure violation no closed-population method provides an unbiased estimate of abundance. Generally closure violation results in a positive bias in abundance estimation because it inflates the number of marked animals and negatively biases capture probability estimates (Boulanger and McLellan, 2001).

In some studies, researchers use two sampling methods for mark-recapture experiments and two sets of data are available (Forcada and Robinson, 2006; Garrigue et al., 2004; Laiolo et al., 2007; Smith et al., 1999; Urbán et al., 1999). My objective here is to see whether the assumption of closure is more important than the assumption of equal capture probability and if using two datasets could overcome the systematic underestimation in the JS estimates in presence of heterogeneity in capture probability among individuals (Carothers, 1973, 1979; Hwang and Chao, 1995).

In this chapter, the performance of some closed-population models and of the JS model to estimate abundance using one set of data is compared to the new models combining the 2 sources of data, i.e. the TSJS model and the two-source M_0 model, using the simulation described in Chapters two and three. The robustness of the two-source M_0 estimator was checked and the two-source M_0 estimator is unbiased when all the model assumptions are met (see Appendix 7). In this chapter, the closed-population methods are first briefly described before being compared to the JS model and the new framework developed in chapter one and the validity and usefulness of such a comparison is discussed.

4.3. Materials and Methods

4.3.1. Closed population models

For comparison purposes, multiple-recapture models M_t, M_h and M_{th} and the JS model, the variance-weighted JS model and the two-source M_0 model were coded to be used in the simulations. This choice was based upon the closed-population models used in abundance assessment of many animal populations such as polar bears, whales, sharks (Calambokidis et al., 1990; Cerchio, 1998; Derocher and Stirling, 1995; Meekan et al., 2006; Parra et al., 2006). A number of approaches have been developed for models M_t and M_h (Chao, 2001; Williams et al., 2002). The Darroch approach for model M_t and the sample coverage method developed by Chao for model M_h were chosen, among the various approaches available: the Darroch approach for model M_t because it is the most widely used for this class of models and model M_h by Chao because I anticipated the situation faced with the data analyzed in chapter five where most of the individuals are only caught once or twice. Therefore, Chao's model M_h would appear to better suit the applied case (Chao, 1988).

Temporal variation: Model M_t by Darroch

Under model M_t, animals have the same capture probability but this capture probability varies from one occasion to another. Darroch (1958) demonstrated that *N* could be estimated by solving the following equation:

$1-\frac{M_{T+1}}{\hat{N}}=\prod_{t=1}^{T}\left(1-\frac{n_t}{\hat{N}}\right)$ where $\hat{N}$ is the estimated population size, T the number of capture occasions during the study, M_{T+1} the total number of unmarked individuals that are caught for the first time during the study and n_t the number of animal caught at occasion *t*.

Daroch (1958) gave an asymptotic variance estimator of the form:

$$v(\hat{N})=\left[\frac{1}{\hat{N}-n}+\frac{T-1}{\hat{N}}-\sum\left(\frac{1}{\hat{N}-n_t}\right)\right]^{-1}$$

Here I use a more recent approximation for the variance for model M_t given by the formula (Amstrup et al., 2005):

$Var(\hat{N})=\frac{\hat{N}}{\exp(n/\hat{N})-1-n/\hat{N}}$ where $\hat{N}$ is the estimated population size and n the total number of animals caught during the study.

Heterogeneity among individuals: Model M_h by Chao

Under model M_h, every animal has its own capture probability but there is no temporal variation in capture probabilities. Chao (1988) proposed a moment estimator to estimate *N*, under model M_h, based on a method known as the sample coverage *C*. The sample coverage *C* can be calculated via frequency data:

$\hat{C}=1-\frac{f_1}{\sum_{t=1}^{T}t\times f_t}$ where T is the number of capture occasions during the study and f_t is the number of animals caught on exactly t occasions.

Then the estimate of the sample coverage can be used to estimate the population size N as following: $\hat{N}=\frac{M_{T+1}}{\hat{C}}$ where M_{T+1} is the total number of unmarked individuals that are caught for the first time during the study.

The variance estimator under model M$_h$ is provided using an asymptotic approach (Chao, 1989):

$$Var(\hat{N}) = f_2\left[0.25\left(\frac{f_1}{f_2}\right)^4 + \left(\frac{f_1}{f_2}\right)^3 + 0.5\left(\frac{f_1}{f_2}\right)^2\right]$$

Temporal variation and heterogeneity among individuals: Model M$_{th}$ by Chao

The model described below is a version of model M$_{th}$. Both temporal and individual variations in capture probability are allowed by model M$_{th}$: each individual *i* can have its own capture probability which can also vary over time with *t* = 1, …, *T*. At the time Otis et al. (1978) introduced model M$_{th}$, no estimation procedure for population size was available. Under such a model, the capture probabilities p_i are viewed as random elements from some probability distribution $F(p)$ and are contained in the resulting set of capture histories $\{x_i\}$ such that:

$p_{it} = p_i e_t$ where $0 \le p_i e_t \le 1$ with *i* = 1, ..., *N* and *t* = 1, …, *T*

e denotes a capture probability that varies over time.

$$P[x_{it}] = P[x_{it}|M_{T+1}]P[M_{T+1}]$$

and

$$P[\{x_{it}\}|M_{T+1}] = \left[\prod_{t=1}^{T} e_t^{n_t}\right]\left[\prod_{i=1}^{M_{T+1}}\int_0^1 p^{y_i}[\prod_{t=1}^{T}(1-pe_t)^{1-x_{it}}]dF(p)\right]$$

where y_i is the number of times animal *i* is captured, $P[M_{T+1}]$ the probability distribution of the number of animals that are caught for the first time which depends on the parameters $N, e_1, ..., e_T$ and the distribution $F(p)$, M_{T+1} is the total number of unmarked individuals that are caught for the first time during the study.

Later Chao and Lee (1992) proposed an estimator for model M$_{th}$ based on the sample coverage approach: $\hat{N} = \frac{M_{T+1}}{\hat{C}} + \frac{f_1\hat{\gamma}^2}{\hat{C}}$ where $\hat{\gamma}^2$ is an estimate of the coefficient of variation of the individual capture probabilities and $\hat{C}$ an estimate of the sample coverage, both estimated as follows:

$$\hat{\gamma}^2 = \max\left\{\left(\frac{M_{T+1}}{\hat{C}}\right)\frac{\sum_{k=1}^{T} k(k-1) f_k}{2\sum_{t=1}^{T}\sum_{k=t+1}^{T} n_t n_k} - 1, 0\right\}$$

and

$$\hat{C} = 1 - \frac{f_1 - 2 f_2 /(T-1)}{\sum_{k=1}^{T} k f_k}$$

where f_k is the number of classes that have exactly k elements in the sample.

4.3.2. Heterogeneity cases

For this analysis, I only consider the cases of heterogeneity in capture probability described in chapter three:

i. Four cases of heterogeneity where the average capture probability $\Pr(c)$ is 0.2.

Table 4-1- Capture probability for each class for every case of heterogeneity considered at an average capture probability of 0.2.

	$\Pr(c)_m$	$\Pr(c)_{NBf}$	$\Pr(c)_{Bf}$	$\Pr(c)_{ca}$	**CV**
Case 1	0.21	0.22	0.15	0.15	0.14
Case 2	0.24	0.24	0.1	0.05	0.37
Case 3	0.25	0.25	0.05	0.05	0.43
Case 4	0.35	0.1	0.05	0.05	0.68

ii. Two cases where the average capture probability $\Pr(c)$ is 0.7 (actually 0.64 in case 5) with all capture probabilities above 0.5.

Table 4-2- Capture probability for each subpopulation for every case of heterogeneity considered at an average capture probability of 0.7.

	$\Pr(c)_m$	$\Pr(c)_{NBf}$	$\Pr(c)_{Bf}$	$\Pr(c)_{ca}$	**CV**
Case 5	0.8	0.5	0.5	0.5	0.23
Case 6	0.5	0.86	0.86	0.86	0.26

N.B.: in the previous tables, "*m*" corresponds to adult males, "NBF" to the non-breeding mature females, "BF" to the breeding females and "ca" to the calves.

4.3.3. Tag misreading

As stated in chapter three, tag misreading concerns only the single-type of capture as I assume that, with the simultaneous double captures, tags cannot be lost: with simultaneous double capture, if one tag is misread, it is unlikely for the tag from the other method to also be misread. Individuals that lose their tag on one occasion do not retain this new identity for subsequent recaptures but could possibly lose again their tag at a later occasion. The tag misreading rate is homogeneous over the population, set at 5% per occasion which is believed to be above the rate of error present in studies, such as studies in humpback whales (Carlson and Mayo, 1990; Palsbøll et al., 1997; Stevick et al., 2001).

4.3.4. Expected trends in population size estimates

In the simulation, the heterogeneity is mainly among individuals of the population. There is, however, a small heterogeneity in capture probabilities due to calves becoming adults and adult females shifting between the states of non-breeding and breeding. Model M_t does not seem very appropriate with the present simulation structure and is not expected to work very well in any case here. Models M_h and M_{th} might also be biased by the heterogeneity in capture probability among individuals (Kendall, 1999; Lee and Chao, 1994) but I expect them to perform better as the individual heterogeneity in capture probabilities gets bigger, compared to models not accommodating heterogeneity in capture probabilities among individuals (i.e. all the JS models, the two-source M_0 model and the M_t model). The main impact of heterogeneous capture probabilities among individuals on models that are not robust to this type of heterogeneity in capture probabilities (i.e. the JS model, the weighted JS model, the TSJS model and the two-source M_0 model) is a negative error in both population estimates and associated variances (Carothers, 1973; Hwang and Chao, 1995; White et al., 1982). Therefore, the JS model, the weighted JS model, the TSJS model and the two-source M_0 model are expected to underestimate the true population size, with the severity of the error in the estimates depending on the degree of heterogeneity in capture probabilities among individuals.

Tag misreading as simulated here should intuitively result in underestimated capture probabilities and therefore should inflate the population size estimates. However, Arnason and Mills (1981) and later McDonald et al. (2003) showed that a homogeneous tag loss does not result in error of the JS estimates so long as the capture probability is high. Consequently, when the capture probabilities are high in the simulation, the JS, the weighted JS and the TSJS estimates should be unbiased.

The closed-population estimators produce a single estimate for the whole study period and in the case of an open population these estimators should be interpreted with caution. When using closed-population methods for the estimation of an open population size, the group of animals in the study area at any given capture occasion t belongs to a notional superpopulation assumed to be closed (Kendall, 1999). Therefore, in the simulation, closed-population estimates should be interpreted as being the size of the entire closed superpopulation during the course of the experiment. Furthermore the TSJS and the JS estimators produce an estimate for each capture occasion, except the first and the last ones. To make possible the comparison of the open-population models with the closed population ones, the estimates, the MRE, RMSRE, standard errors and 95% confidence intervals given by the TSJS and the JS estimators are averaged over the 10 occasions as well as the true population size. Confidence intervals for the closed-population models are obtained using the traditional form: $\hat{N} \pm 1.96 \times se$ and the log normal approximation: $(\hat{N}_t / C; \hat{N}_t \times C)$

where $C = \exp\left\{ 2\sqrt{\log(1 + \frac{Var(\hat{N}_t)}{\hat{N}_t^{\,2}})} \right\}$

4.4. Results

4.4.1. With heterogeneity in capture probability among individuals

Table 4-3 shows that $\hat{N}_{TSJS}$ is only the best estimator when the heterogeneity is small and the capture probabilities high (case 1, 6 and 7) with respect to MRE, RMSRE and CI coverage. Then, for cases 2 and 3, $\hat{N}_{TSM_0}$ appears like the best estimator in terms of MRE (<0.1) and RMSRE(<0.11). However, in cases 2 and 3, the second best estimator $\hat{N}_t$ in terms of MRE and RSMRE is the best in terms of CI coverage rate with more than 87% of CI coverage rate ($\hat{N}_{TSM_0}$ only has 10% of CI coverage in case 2 and 50% in case 3 with both approaches). In cases 2, 3, and 4, the closed-population estimators are better than the open-population estimators, with the TSJS estimator always being the best of the JS models (which is obviously because it is using more data). However, in case 3, $\hat{N}_{TSJS}$ and $\hat{N}_h$ seem similar in RMSRE and absolute value of MRE ($\hat{N}_{TSJS}$ underestimates while $\hat{N}_h$ overestimates) and $\hat{N}_{TSJS}$ even appears slightly better than $\hat{N}_h$ in case 3, in terms of CI coverage rate: normal and log-normal CI coverage rates are respectively 39% and 44% while being 34% and 32% for $\hat{N}_h$, though this could be just sampling error.

All the estimators are expected to underestimate the true parameter when CV>0 (Carothers, 1973; Hwang and Chao, 1995; Otis et al., 1978; Pollock et al., 1990) but most of the closed-population estimators $\hat{N}_t$, $\hat{N}_h$, $\hat{N}_{th}$ and $\hat{N}_{TSM_0}$ present a positive error (MRE>0.1) for most cases of heterogeneity ($\hat{N}_t$, $\hat{N}_h$, $\hat{N}_{th}$ and $\hat{N}_{TSM_0}$ in cases 1, 2; $\hat{N}_t$, $\hat{N}_h$, $\hat{N}_{th}$ in case 3 and $\hat{N}_{th}$ in case 4) and when the average capture probability is high (all closed-population estimators in cases 5, 6). When the heterogeneity is high (case 4), $\hat{N}_h$ and $\hat{N}_{th}$ provide a very good CI coverage (with the normal approximation and the log-normal transformation respectively 99 and 100% for $\hat{N}_h$ and 95% and 85% for $\hat{N}_{th}$). The JS estimator leads to estimates systematically more negatively biased than the ones given by the TSJS estimator but better CI coverage rates in cases 2, 3 and 4.

It is very interesting to note that $\hat{N}_t$ and $\hat{N}_{TSM_0}$ behave very similarly even though $\hat{N}_{TSM_0}$ has no correction for temporal heterogeneity. One reason might be that $\hat{N}_{TSM_0}$ uses almost twice as more data as any of the other closed-population models.

That the mean of the variance-weighted means for the two single JS simulations does not fall between the two separate JS averages might seem surprising. This comes from the fact that, even though each of the 1600 (8 estimates and 200 runs of simulation) individual weighted means is indeed between the values of the two corresponding estimates, one of the JS estimates ($\hat{N}_{JS1}$ from method 1 or $\hat{N}_{JS2}$ from method 2) is not systematically smaller than the other. For example see Appendix 8. Moreover the fact that the average weighted JS estimate is always less than the smallest of the two single means of $\hat{N}_{JS1}$ and $\hat{N}_{JS2}$, is because the weight is always largest for the smallest mean (SE correlated with estimate) so the weighted mean is always closer to the lowest estimate in the pair. This introduces a systematic tendency to be small and explains why the average weighted mean is never higher than the two averages of the JS estimates $\hat{N}_{JS1}$ and $\hat{N}_{JS2}$.

Table 4-3- Comparison of mean estimates under 6 cases of heterogeneity in capture probabilities of closed-population and JS models based on the dataset 1 and the weighted JS model, the two-source M_0 model, the TSJS model under scenario 20-40-40, over 10 occasions and with a starting population of 500 individuals.

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 CV =0.14 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	709	728	-0.03	82	0.19	76	79
$\hat{N}_{JS1}$	689		-0.06	113	0.27	72	76
$\hat{N}_{JS2}$	682		-0.06	112	0.26	71	75
$\hat{N}_{wJS}$	646		-0.11	75	0.22	60	64
$\hat{N}_t$	962		0.33	75	0.36	2	2
$\hat{N}_h$	1053		0.46	82	0.48	0	0
$\hat{N}_{th}$	1073		0.46	68	0.66	0	0
$\hat{N}_{TSM_0}$	943		0.31	34	0.31	0	0

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 2 CV =0.37 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	585	728	-0.2	66	0.25	41	46
$\hat{N}_{JS1}$	566		-0.22	92	0.32	43	51
$\hat{N}_{JS2}$	569		-0.22	92	0.31	44	51
$\hat{N}_{wJS}$	534		-0.27	62	0.31	24	28
$\hat{N}_t$	799		0.11	69	0.16	94	92
$\hat{N}_h$	871		0.21	72	0.24	34	27
$\hat{N}_{th}$	847		0.17	52	0.19	50	50
$\hat{N}_{TSM_0}$	810		0.1	30	0.11	10	10
Case 3 CV =0.43 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	583	727	-0.2	67	0.26	39	44
$\hat{N}_{JS1}$	561		-0.23	92	0.33	41	48
$\hat{N}_{JS2}$	558		-0.23	91	0.32	40	47
$\hat{N}_{wJS}$	524		-0.28	61	0.32	21	26
$\hat{N}_t$	802		0.11	70	0.16	91	87
$\hat{N}_h$	877		0.22	75	0.25	34	32
$\hat{N}_{th}$	866		0.18	55	0.2	31	31
$\hat{N}_{TSM_0}$	773		0.08	27	0.09	50	50
Case 4 CV =0.68 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	411	728	-0.44	37	0.45	1	1
$\hat{N}_{JS1}$	401		-0.45	54	0.47	5	7
$\hat{N}_{JS2}$	398		-0.45	54	0.48	5	7
$\hat{N}_{wJS}$	382		-0.48	36	0.49	0	0
$\hat{N}_t$	628		-0.13	55	0.16	43	49
$\hat{N}_h$	700		-0.03	66	0.11	99	100
$\hat{N}_{th}$	761		0.06	48	0.1	95	85
$\hat{N}_{TSM_0}$	616		-0.16	16	0.16	0	0

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 5 CV =0.23 $\overline{\Pr}(c)_g = 0.64$							
$\hat{N}_{TSJS}$	677	727	-0.07	13	0.07	19	20
$\hat{N}_{JS1}$	558		-0.23	20	0.24	0	0
$\hat{N}_{JS2}$	561		-0.23	20	0.23	0	0
$\hat{N}_{wJS}$	557		-0.24	14	0.24	0	0
$\hat{N}_{t}$	1068		0.48	44	0.5	0	0
$\hat{N}_{h}$	1159		0.61	42	0.63	0	0
$\hat{N}_{th}$	1275		0.74	37	0.75	0	0
$\hat{N}_{TSM_0}$	1059		0.47	6	0.47	0	0
Case 6 CV =0.26 $\overline{\Pr}(c)_g = 0.7$							
$\hat{N}_{TSJS}$	731	729	0	11	0.04	55	55
$\hat{N}_{JS1}$	581		-0.2	18	0.21	0	0
$\hat{N}_{JS2}$	580		-0.21	17	0.21	0	0
$\hat{N}_{wJS}$	578		-0.21	12	0.21	0	0
$\hat{N}_{t}$	1214		0.68	43	0.7	0	0
$\hat{N}_{h}$	1310		0.61	38	0.83	0	0
$\hat{N}_{th}$	1412		0.93	35	0.93	0	0
$\hat{N}_{TSM_0}$	1224		0.66	6	0.66	0	0

$\hat{N}_{TSJS}$, $\hat{N}_{JS1}$, $\hat{N}_{JS2}$, $\hat{N}_{wJS}$, $\hat{N}_{t}$, $\hat{N}_{h}$, $\hat{N}_{th}$, $\hat{N}_{TSM_0}$ = population size estimate for model TSJS, JS model by sampling method 1 and 2, weighted JS, M_t by Darroch, M_h by Chao, , M_{th} by Chao, and two-source M_0 models.

4.4.2. With heterogeneity in capture probability and unequal sampling probability

Compared to the previous section, another disturbance known to be detrimental to the TSJS estimator (see chapter three) is added to the simulation experiment the results of which are shown in Table 4-4. This disturbance introduced in the form of unequal sampling probabilities $\Pr(s_1)$ and $\Pr(s_2)$ should only penalize the TSJS estimator. However, it should benefit the other models in the way that the sample size increases, because data for those single-source models will be based on the largest of the two datasets available: with the previous scenario of 20-40-40 the dataset 1 covers 60% of all the data available for the TSJS model. Under the scenario of 50-37.5-12.5, the dataset 1 accounts for 87.5% of the total amount of data used in the TSJS model.

Table 4-4- Comparison of mean estimates under 6 cases of heterogeneity in capture probabilities of closed-population and JS models based on the dataset 1 and the weighted JS model, the two-source M_0 model, the TSJS model under scenario 50-37.5-12.5, over 10 occasions and with a starting population of 500 individuals**.**

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 CV =0.14 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	732	726	0.01	68	0.16	79	80
$\hat{N}_{JS1}$	709		-0.02	74	0.17	72	75
$\hat{N}_{JS2}$	668		-0.08	105	0.27	68	74
$\hat{N}_{wJS}$	679		-0.07	59	0.18	59	62
$\hat{N}_{t}$	977		0.36	53	0.36	2	2
$\hat{N}_{h}$	1062		0.47	53	0.48	0	0
$\hat{N}_{th}$	1082		0.5	49	0.69	0	0
$\hat{N}_{TSM_0}$	968		0.34	28	0.57	0	0
Case 2 CV =0.37 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	601	725	-0.17	54	0.22	36	41
$\hat{N}_{JS1}$	583		-0.2	60	0.25	35	41
$\hat{N}_{JS2}$	543		-0.25	84	0.32	37	44
$\hat{N}_{wJS}$	559		-0.23	48	0.27	22	24
$\hat{N}_{t}$	815		0.13	46	0.15	86	81
$\hat{N}_{h}$	884		0.23	43	0.24	38	30
$\hat{N}_{th}$	882		0.21	37	0.44	0	0
$\hat{N}_{TSM_0}$	827		0.14	24	0.35	0	0

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 3 CV =0.43 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	597	726	-0.18	54	0.22	35	39
$\hat{N}_{JS1}$	580		-0.2	60	0.25	33	39
$\hat{N}_{JS2}$	536		-0.26	83	0.32	38	44
$\hat{N}_{wJS}$	553		-0.24	49	0.28	20	23
$\hat{N}_{t}$	813		0.13	46	0.16	86	82
$\hat{N}_{h}$	882		0.22	44	0.25	33	25
$\hat{N}_{th}$	878		0.22	39	0.45	0	0
$\hat{N}_{TSM_0}$	812		0.13	23	0.34	0	0
Case 4 CV =0.68 $\overline{\Pr}(c)_g = 0.2$							
$\hat{N}_{TSJS}$	430	726	-0.41	31	0.41	0	1
$\hat{N}_{JS1}$	424		-0.42	36	0.43	1	1
$\hat{N}_{JS2}$	377		-0.48	48	0.49	2	3
$\hat{N}_{wJS}$	403		-0.45	29	0.45	0	0
$\hat{N}_{t}$	668		-0.07	37	0.15	48	58
$\hat{N}_{h}$	746		0.04	47	0.1	99	99
$\hat{N}_{th}$	850		0.16	47	0.4	20	20
$\hat{N}_{TSM_0}$	679		-0.07	15	0.25	30	30
Case 5 CV =0.23 $\overline{\Pr}(c)_g = 0.64$							
$\hat{N}_{TSJS}$	691	729	-0.05	10	0.06	22	23
$\hat{N}_{JS1}$	649		-0.11	13	0.12	8	10
$\hat{N}_{JS2}$	523		-0.28	17	0.29	0	0
$\hat{N}_{wJS}$	597		-0.18	10	0.19	1	1
$\hat{N}_{t}$	1156		0.6	41	0.51	0	0
$\hat{N}_{h}$	1241		0.72	42	0.64	0	0
$\hat{N}_{th}$	1400		0.81	38	0.96	0	0
$\hat{N}_{TSM_0}$	1134		0.54	NA	0.74	NA	NA

Heterogeneity case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 6 CV =0.26 $\overline{\Pr}(c)_g = 0.7$							
$\hat{N}_{TSJS}$	735	728	0.01	8.82	0.03	55	56
$\hat{N}_{JS1}$	680		-0.07	11.3	0.07	23	24
$\hat{N}_{JS2}$	537		-0.26	14.13	0.27	0	0
$\hat{N}_{wJS}$	623		-0.14	8.76	0.15	0	0
$\hat{N}_t$	1303		0.8	43.32	0.71	0	0
$\hat{N}_h$	1386		0.92	35.09	0.84	0	0
$\hat{N}_{th}$	1499		1.07	31.88	1.04	0	0
$\hat{N}_{TSM_0}$	1266		0.77	NA	0.88	NA	NA

$\hat{N}_{TSJS}$, $\hat{N}_{JS1}$, $\hat{N}_{JS2}$, $\hat{N}_{wJS}$, $\hat{N}_t$, $\hat{N}_h$, $\hat{N}_{th}$, $\hat{N}_{TSM_0}$ = population size estimate for model TSJS, JS model by sampling method 1 and 2, weighted JS, M_t by Darroch, M_h by Cha**o**, , M_{th} by Cha**o,** and two-source M_0 models. NA= not available, because maximum likelihood has occurred on the boundary of the parameter space, e.g. one of the probabilities is estimated very close to 0 or 1.

$\hat{N}_{TSJS}$ appears again to be the best estimator in cases 1, 5 and 6 in term of RMSRE, MRE and CI coverage, then the second best estimator after $\hat{N}_t$ in cases 2 and 3. In case 3, $\hat{N}_{JS1}$ and $\hat{N}_h$ perform equally in terms of RMSRE and absolute value of MRE but $\hat{N}_{JS1}$ has slightly better log-normal CI coverage rates. When the heterogeneity in capture probabilities $\mathrm{P}(c)$ is the highest, i.e. case 4, the closed-population estimators $\hat{N}_t$ and $\hat{N}_h$ are the best although only $\hat{N}_h$ provides a very good CI coverage in case 4 (with the log-normal transformation 99% for $\hat{N}_h$ and only 58% for $\hat{N}_t$). However, in contrast to the previous section, $\hat{N}_{th}$ and $\hat{N}_{TSM_0}$ do not perform well in any case. Results (RMSRE, MRE and CI coverage rates) with the variance-weighted mean estimator always appear between the results of the two JS estimators, with better estimates for the JS estimator based on dataset 1. It is interesting to highlight that the JS estimator based on the largest dataset, $\hat{N}_{JS1}$, always performs better than $\hat{N}_{JS2}$ in terms of MRE and RMSRE but $\hat{N}_{JS2}$ provides better CI coverage rate in cases 2, 3 and 4. As before, when the average capture probability is high, i.e. cases 5 and 6, all the open-population estimators perform far better than the closed-population estimators.

4.4.3. With tag misreading

In this simulation, all animals have the same chance of having their tag misread and could possibly lose it several times. Under the homogeneous tag misreading experiment, Table 4-5 shows that all estimators perform poorly for $\Pr(c) \le 0.1$ and then for $\Pr(c) \ge 0.2$, the open-population estimators perform far better than all the closed-population estimators. For small capture probabilities, i.e. $\Pr(c) \le 0.1$, $\hat{N}_{TSJS}$ displays better than usual CI coverage rates (more than 78%). For $\Pr(c) \le 0.5$, all open-population estimators generally have CI coverage rates between 50% and 84%. Then, with the increase of the capture probability, the standard errors, as in earlier chapters (e.g. Table 2-1, Table 3-3) decrease excessively for all estimators leading to poor CI coverage rates at $\Pr(c) \ge 0.5$.

All closed-population estimators are systematically severely positively biased (MRE>0.3 and RMSRE>0.4): for $\hat{N}_h$, $\hat{N}_t$ and $\hat{N}_{th}$, the overestimation increases both in terms of RMSRE and MRE as the capture probability $\Pr(c)$ increases. For $\hat{N}_{TSM_0}$, the error is constant for $\Pr(c)$ <0.5, although higher for $\Pr(c)$ =0.05.

Table 4-5- Comparison of mean estimates, with a 5% tag misreading rate under constant capture probability, of closed-population and JS models based on the dataset 1 and the weighted JS model, the two-source M_0 model, the TSJS model under scenario 50-25-25, over 10 occasions and with a starting population of 500 individuals.

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\Pr(c)$=0.05							
$\hat{N}_{TSJS}$	785	727	0.03	348	0.8	81	84
$\hat{N}_{JS1}$	613		-0.17	360	0.71	68	82
$\hat{N}_{JS2}$	601		-0.18	352	0.72	66	83
$\hat{N}_{wJS}$	504		-0.31	222	0.59	52	66
$\hat{N}_t$	1033		0.43	188	0.5	1	10
$\hat{N}_h$	1146		0.59	230	0.66	0	3
$\hat{N}_{th}$	1165		0.6	221	0.76	42	32
$\hat{N}_{TSM_0}$	1122		0.55	271	0.73	82	78

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(*c*)=0.075							
$\hat{N}_{TSJS}$	802	729	0.1	240	0.6	82	80
$\hat{N}_{JS1}$	703		-0.01	267	0.61	77	81
$\hat{N}_{JS2}$	721		-0.01	277	0.66	78	81
$\hat{N}_{wJS}$	640		-0.12	182	0.48	65	71
$\hat{N}_{t}$	1019		0.41	128	0.45	0	1
$\hat{N}_{h}$	1125		0.56	151	0.74	0	0
$\hat{N}_{th}$	1143		0.57	142	0.75	0	0
$\hat{N}_{TSM_0}$	992		0.35	134	0.57	56	49
Pr(*c*)=0.1							
$\hat{N}_{TSJS}$	806	730	0.1	174	0.41	83	78
$\hat{N}_{JS1}$	738		0	203	0.44	80	81
$\hat{N}_{JS2}$	742		0.02	205	0.48	78	81
$\hat{N}_{wJS}$	699		-0.04	144	0.39	69	72
$\hat{N}_{t}$	1036		0.41	101	0.46	0	0
$\hat{N}_{h}$	1140		0.57	117	0.61	0	0
$\hat{N}_{th}$	1160		0.62	110	0.77	0	0
$\hat{N}_{TSM_0}$	953		0.33	85	0.57	12	11
Pr(*c*)=0.2							
$\hat{N}_{TSJS}$	783	728	0.07	73	0.17	74	71
$\hat{N}_{JS1}$	729		0	91	0.2	80	80
$\hat{N}_{JS2}$	728		0	91	0.2	80	80
$\hat{N}_{wJS}$	737		0.01	68	0.19	82	70
$\hat{N}_{t}$	1048		0.45	61	0.47	0	0
$\hat{N}_{h}$	1144		0.58	64	0.61	0	0
$\hat{N}_{th}$	1274		0.77	69	0.87	0	0
$\hat{N}_{TSM_0}$	1010		0.38	36	0.59	0	0

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(c)=0.3							
$\hat{N}_{TSJS}$	796	730	0.09	47	0.14	64	62
$\hat{N}_{JS1}$	738		0	59	0.13	79	78
$\hat{N}_{JS2}$	738		0	59	0.13	80	79
$\hat{N}_{wJS}$	734		0	41	0.1	84	72
$\hat{N}_{t}$	1144		0.58	53	0.6	0	0
$\hat{N}_{h}$	1254		0.73	56	0.75	0	0
$\hat{N}_{th}$	1409		0.96	58	0.98	0	0
$\hat{N}_{TSM_0}$	1046		0.44	21	0.64	0	0
Pr(c)=0.4							
$\hat{N}_{TSJS}$	758	728	0.04	27	0.07	50	49
$\hat{N}_{JS1}$	697		-0.04	37	0.09	76	77
$\hat{N}_{JS2}$	697		-0.04	37	0.09	75	76
$\hat{N}_{wJS}$	722		-0.01	28	0.08	64	63
$\hat{N}_{t}$	1109		0.54	45	0.56	0	0
$\hat{N}_{h}$	1201		0.66	41	0.68	0	0
$\hat{N}_{th}$	1535		1.08	54	1.04	0	0
$\hat{N}_{TSM_0}$	972		0.35	14	0.69	0	0
Pr(c)=0.5							
$\hat{N}_{TSJS}$	751	727	0.03	19	0.05	33	33
$\hat{N}_{JS1}$	675		-0.07	26	0.08	66	68
$\hat{N}_{JS2}$	673		-0.08	26	0.1	67	68
$\hat{N}_{wJS}$	704		-0.03	21	0.07	54	55
$\hat{N}_{t}$	1148		0.59	43	0.61	0	0
$\hat{N}_{h}$	1241		0.72	40	0.74	0	0
$\hat{N}_{th}$	1681		1.33	59	1.17	0	0
$\hat{N}_{TSM_0}$	1115		0.55	19	0.72	0	0

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Pr(*c*)=0.6							
$\hat{N}_{TSJS}$	750	730	0.02	16	0.04	22	22
$\hat{N}_{JS1}$	656		-0.1	19	0.11	46	47
$\hat{N}_{JS2}$	655		-0.1	19	0.13	46	47
$\hat{N}_{wJS}$	684		-0.06	15	0.09	33	34
$\hat{N}_{t}$	1190		0.64	43	0.66	0	0
$\hat{N}_{h}$	1283		0.77	41	0.79	0	0
$\hat{N}_{th}$	1818		1.48	66	1.26	0	0
$\hat{N}_{TSM_0}$	1129		0.55	7	0.73	0	0
Pr(*c*)=0.8							
$\hat{N}_{TSJS}$	738	728	0.01	9	0.02	6	6
$\hat{N}_{JS1}$	602		-0.17	10	0.18	7	7
$\hat{N}_{JS2}$	602		-0.17	10	0.18	7	7
$\hat{N}_{wJS}$	643		-0.12	9	0.13	3	3
$\hat{N}_{t}$	1258		0.74	43	0.76	0	0
$\hat{N}_{h}$	1346		0.87	44	0.88	0	0
$\hat{N}_{th}$	2150		1.96	83	1.51	0	0
$\hat{N}_{TSM_0}$	1180		0.63	4	0.78	0	0

$\hat{N}_{TSJS}$, $\hat{N}_{JS1}$, $\hat{N}_{JS2}$, $\hat{N}_{wJS}$, $\hat{N}_{t}$, $\hat{N}_{h}$, $\hat{N}_{th}$, $\hat{N}_{TSM_0}$ = population size estimate for model TSJS, JS model by sampling method 1 and 2, weighted JS, M_t by Darroch, M_h by Chao, , M_{th} by Chao**,** and two-source M_0 models.

4.5. Discussion

The relevance of this chapter is based on the observation that researchers knowingly use closed-population models on open populations (Boulanger et al., 2002; Calambokidis and Barlow, 2004; Cerchio, 1998; Karanth and Nichols, 1998; Meekan et al., 2006). Therefore, I was interested in seeing which of the closed-population or the open-population approaches were the most appropriate with an open population in various cases of heterogeneous capture probabilities among individuals and tag misreading. The aim was to identify general guidelines in the use of closed and open-population models in the case of an open heterogeneous population, as well as to be able to extrapolate the magnitude and direction of the bias to results based on real data in chapter five. Consequently, the results in this chapter illustrate the need to carefully measure the balance between the bias caused by the violation of the assumption of closure with closed-population models and the bias caused by the violation of the assumption of homogeneous capture probabilities with open-population models on abundance estimates. It is not surprising here that for an open population it is more appropriate to use open-population estimators when the degree of heterogeneity in capture probabilities among individuals is fairly small or the average capture probability very high or the degree of openness high. As expected, the results show that when the heterogeneity in capture probabilities among individuals is small in an open population, the violation of the closure assumption leads to more biased estimates of population size with closed-population models than the abundance estimates with open-population models despite the violation of equal capture probability. It also seems straightforward that, when the heterogeneity in capture probabilities is high, using a closed-population estimator handling heterogeneity in capture probability is the best approach, even though the population is open, especially if the openness is not great.

A major point about the interpretation of the results in this chapter is that closed population estimates and the average open-population estimates do not have the same meaning and should always be compared with caution. The closed population models estimate the total population size during the time of data collection, so over 10 occasions in the simulations. In fact, when closure is violated, closed population estimates often apply to the size of a superpopulation, from which animals in the sampling area are a random sample at each capture occasion, that is assumed closed (Boulanger and McLellan, 2001; Kendall, 1999). On the other hand, open-population models estimate the size of the open population for each capture occasion and I calculated the average over all occasions to get a single point estimate. Consequently, two different notions of population size are compared: the average size of an open population over the whole experiment with an open-population model and the closed superpopulation estimates provided by the closed-population models in this chapter. However, in the simulation, the population is only open demographically, there is no movement in and out the theoretical study area and no uncatchable individuals. Therefore, estimates of population size, with closed and open population models, should not be taken for the estimates of a superpopulation.

An important point to highlight here is the direction of the error that systematically differs between open and closed-population models: except in case 4 (high heterogeneity), all closed-population estimators tend to overestimate the abundance while all open-population estimators consistently underestimate it. Underestimation was expected here with all the population size estimators when capture probabilities are heterogeneous among individuals (Carothers, 1973; Hwang and Chao, 1995; Kendall, 1999; Lee and Chao, 1994; White et al., 1982). On the other hand, closure violation, especially of the kind of “one entry (i.e. birth) and one exit (i.e. death)” is known to introduce an overestimation in the population size estimates with closed-population models by negatively biasing the capture probability estimates (Kendall, 1999; Boulanger and McLellan, 2001). Therefore, the observed overestimation with closed-population models indicate that, for closed-population models, the positive bias induced by the violation of the closure assumption, even though limited in this simulation, is larger than the negative bias induced by the violation of the homogeneous capture probability assumption.

In the presence of a moderate to high degree of heterogeneity (cases 2, 3, 4) in capture probabilities, all closed population estimators perform better in terms of the error on the abundance estimates than any of the open-population estimators presented here. However, with a relatively small degree of heterogeneity (case 1) or a high average capture probability (cases 5, 6), all the open-population estimators perform better than any of the closed-population estimators. So it seems that the degree of heterogeneity in capture probabilities, the average capture probability and the degree of openness, if they can be measured or estimated, would be sensible criteria to decide if it is more important to hold the assumption of closure or the assumption of equal capture probability and therefore choose between open or closed-population models. The degree of heterogeneity is an especially hard feature to estimate in field studies but the use of individual covariates recorded during the experiment could be an efficient way of explicitly modeling the heterogeneity in capture probability among individual (Huggins, 1991). The degree of openness can sometimes be estimated in the field with additional investigations (e.g. radiocollared bears (Boulanger et al., 2002)) or can be tested using specific tests for closure (Otis et al., 1978; Stanley and Burnham, 1999).

With this structure of heterogeneity in capture probabilities, the new estimators combining both sources of data seem to be the most suitable estimators in most of the cases presented here. Therefore, combining both sources of data in a model to estimate population size appears to be an efficient way to reduce the error and, in some cases, enables researchers to use an open-population model with heterogeneous capture probabilities among individuals of the population without facing an unreasonable underestimation. The TSJS model was generally better with a small heterogeneity in capture probabilities among individuals (case 1) and high average capture probability (cases 5 and 6) while the two-source M_0 model was the best model in terms of magnitude of the error when the heterogeneity was moderate (cases 2 and 3). However, if the CI coverage rate is the criterion, the traditional closed-population estimator $\hat{N}_t$ is the best estimator when the heterogeneity is moderate (cases 2 and 3). In case 4 (high heterogeneity), there is no ambiguity: $\hat{N}_h$ and $\hat{N}_{th}$ are the best estimators.

While it seems that the TSJS estimator is always the best estimator among all the JS-related estimators presented here, it is not necessarily obvious which of the closed-population estimators is the most reliable when closed-population models should be used, i.e. low population turnover with high heterogeneity. In the presence of a moderate to high degree of heterogeneity in capture probabilities, $\hat{N}_{TSM_0}$ and $\hat{N}_t$ appear fairly consistent in the error while the results with $\hat{N}_h$ and $\hat{N}_{th}$ seem to greatly depend on the degree of heterogeneity. I would have expected $\hat{N}_t$ to perform not that well given the very small temporal heterogeneity and the increasing individual heterogeneity in capture probabilities and I would have expected

$\hat{N}_h$ to perform better than $\hat{N}_t$. However, as anticipated, $\hat{N}_h$ turns out to be the most appropriate estimator when the heterogeneity is the most extreme.

The TSJS estimator also appears to be better in handling tag misreading compared to closed population estimators. The single JS model could also be used with regards to CI coverage rate as, in most cases, it produces the best CI coverage rate.

Researchers should keep in mind that, if the studied population is open during the data collection, results based on closed-population models can be difficult to interpret and the direction and magnitude of the bias will depend on possible violation of other assumptions, especially the assumption of homogeneous capture probability. If heterogeneity in capture probabilities, either temporal or among individuals or both, is an important source of bias in population size estimates, the study design should focus on meeting the assumption of closure so that closed-population models handling heterogeneity could be appropriately used. However, using the TSJS model proposed in the present dissertation leads to improvements in abundance estimation as compared to applying the classic JS estimator to a single source of data. From a monitoring point of view, an open-population model, for an open population, is sensible and interpretable, even though estimates might be biased by heterogeneity. The direction of the error is known when heterogeneity in capture probabilities is suspected and therefore, the estimates can be interpreted in consequence as being an underestimate of the true population size which is, in some cases, to be preferred in population size assessment for precautionary reasons, i.e. for an endangered species, quota management.

5. Chapter Five

Analysis of the abundance of the New Caledonian humpback whale population

5.1. Abstract

The two-source Jolly-Seber (TSJS) and the two-source M_0 models are applied to data from the humpback whale, *Megaptera novaeangliae*, population in New Caledonia (South Pacific). This globally distributed species undertakes systematic yearly migrations between feeding and breeding grounds: in the South Hemisphere, the feeding taking place in the Antarctic, so the whales are mainly accessible for sampling on the breeding grounds located in lower latitudes. On the breeding ground of New Caledonia, whales are usually present from July to September and a sampling protocol combining photo-identification and skin-biopsy has been used since 1999 to sample the population. This sampling protocol leads to the creation of two datasets: a dataset for the photo-identified whales and a dataset for the genotyped ones. Individuals are frequently, but not always, photographed and genotyped on the same capture occasion; the TSJS and the two-source M_0 approaches thus seem ideal for analysis of these data. Estimates of abundance provided by these new approaches are compared to population sizes given by traditional methods: relevant multiple-occasion closed-population models (M_t by Darroch, M_t by Chao, M_h by Chao, M_h using the jackknife method and M_{th}), the Chapman modified Lincoln-Petersen and the Jolly-Seber (JS) estimators. Those traditional estimators give very different results depending on the dataset used (photographic data 1999-2005, photographic data 1999-2004 with only quality-controlled (QC) photographs or genetic data 1999-2005) while the TSJS and the two-source M_0 estimators disagree but are separately quite consistent between the two datasets available (combined dataset 1999-2005 and combined 1999-2005 with only the QC photographs). Sources of bias for the different estimators are explored. Closed-population estimates are probably overestimated due to the violation of the closure assumption. Investigation on a larger spatial scale including data from neighboring breeding grounds (Tonga, Cook Island and French Polynesia) indicates that temporary emigration takes place, which violates the assumption of geographical closure for

the closed-population models. Results for apparent survival with the Cormack-Jolly-Seber (CJS) model also suggest that long-term emigration may occur in the population. Evidence of temporal heterogeneity and individual variation in capture probability is highlighted by the CJS model and the tests for temporal variation in trapping probabilities in program CAPTURE. The temporal heterogeneity in capture probabilities seems to arise from a heterogeneous sampling effort throughout the years (2002 and 2004 presenting considerably less effort than the other years) and could be avoided with a standardized sampling effort. Finally, tests with U-CARE indicate the presence of transient individuals (significant for males) passing through New Caledonia once with a very low probability of being captured again on a subsequent occasion. This heterogeneity in capture probabilities among individuals most likely results in an underestimation of the population size with the TSJS model.

5.2. Introduction

Humpback whales were heavily hunted from the end of the 19th century through the 20th century. Chittleborough assessed this population to be 22,000-34,000 in the 1930's (Chittleborough, 1965). In the 20th century alone, 200,000 individuals were killed in the Southern Hemisphere, more than 48,000 were illegal Soviet catches from which 30,000 were killed between summers 1960 and 1962 (Clapham, 2002; Clapham and Baker, 2002; Findlay, 2000; Walsh, 1999). Post-exploitation stocks might have been as low as 10% of the pre-exploitation stocks for some populations. Humpback populations are nowadays recovering and rates of recovery might be as high as 10% per year in some cases (Zerbini et al., 2008). However, concerns remain for some subpopulations of humpback whales, i.e. the Arabian Sea, the western North Pacific, the West coast of Africa and the South Pacific subpopulations, for which information about status is lacking (Reilly et al., 2008). To monitor the recovery of these discrete subpopulations, it is therefore important to have reliable and precise estimates of population size.

In the Southern Hemisphere, the Antarctic feeding area is divided into six areas (I to VI) and humpback whales are classified into seven groups (A to G) in the breeding ground. Humpback whales breeding in New Caledonia are believed to feed in area V and belong to the breeding group E (IWC, 1998). Two sampling methods are used to individually identify whales and gather data during the breeding season (July to September): photo-identification and skin biopsy (Garrigue et al., 2001). When humpback whales dive, they usually raise their flukes and enable researchers to photograph the markings and unique pigmentation patterns on the ventral surface: all whales in New Caledonia have a distinct marking that allows to uniquely identify them. In New Caledonia, whales are also genotyped via a tissue sample collected using a crossbow with an adapted bolt or, very opportunistically, via a skin sample that can be harvested with a net after the whale has breached. However, on a given capture occasion, some whales may not fluke so they cannot be photographed and some others cannot be approached to be genotyped. Using both photo-identification and the genotype via skin biopsy sampling during a vessel survey has proven effective to gather more data and is used to survey the humpback whale population in New Caledonia. This sampling protocol leads to the creation of two datasets, one for each sampling method: a dataset for the photo-identified whales and a dataset for the genotyped ones. Individuals are frequently but not always photographed and genotyped on the same capture occasion. The TSJS and the two-source M_0 methods thus seem particularly well suited for analysis of these data.

In this chapter, I start by estimating the abundance of the population using the traditional closed-population estimators, the traditional JS estimator estimator using each dataset independently, before comparing those results with those provided by the variance-weighted mean of the JS estimators, the two-source M_0 estimator and the TSJS estimator on the combined dataset. I then explore the possible sources of bias in those estimates due to violation of the demographic and geographic closure assumptions and to the possible heterogeneous capture probabilities and I make inferences on survival using the TSJS corrected estimator and an approximated CJS likelihood. Finally, I discuss the validity of these abundance estimates in the case of the humpback whale population of New Caledonia.

5.3. Materials and Methods

5.3.1. Field methods

Since 1999, the same field protocol has been used in New Caledonia to gather data (Garrigue et al., 2001). The sampling season usually takes place from July to September and the team goes to sea every day, unless sea conditions are too bad, in an outboard-powered semi-inflatable boat. The boat randomly surveys an area of roughly 1,000 km² and can be directed towards whales by a land-based team monitoring the same area (Fig.5-1). When a whale or a pod of whales is encountered, an attempt is made to get a photograph and a skin sample of the solitary individual or of each of the individuals present in the group. Sampling ends when a photograph and a skin sample have been taken, or after approximately one hour of attempts.

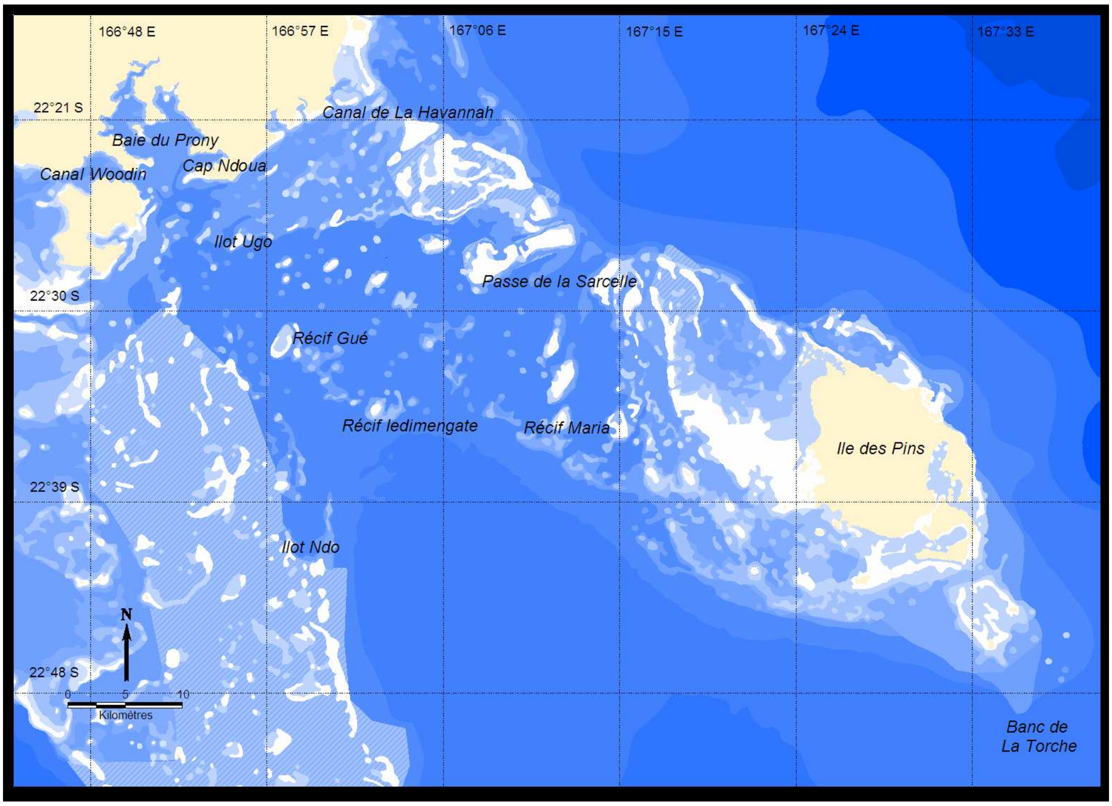


Fig.5-1- Sampling area in the South lagoon of New Caledonia.

5.3.2. Matching process

Flukes were classified by their degree of whiteness to make the matching process easier (Carlson and Mayo, 1990; Friday et al., 2000). Every photo was matched against the existing catalogue by at least two experienced persons.

Eleven published microsatellite loci were used by Garrigue et al. (2004) for genotyping matching. Alleles were sized with the software packages GENESCAN and GENOTYPER 2.5 (Applied Biosystems). Individual matching was done using CERVUS 2.0 and GenAIEX. A genotype was a match when identical to another one. To decrease the risk of genotyping errors, two analyses were usually run for each biopsy sample.

Finally, to avoid photo-matching and laboratory (or field recording) errors, genetic and photo records were also compared when available.

For further information on the photographic material used and molecular analysis see Garrigue et al. (2004). I was involved in later field work in New Caledonia and I did not contribute to the collection of the 1999-2005 data used in this chapter.

5.3.3. Datasets

Photo-identification catalogue

Two photographic catalogues were available at the time of the thesis:

1) the photographic catalogue 1999-2005 where all photos are included,

2) the photographic catalogue 1999-2005 where photos have been checked for quality under a protocol for ranking the quality of each photograph (Calambokidis et al., 2001) (also referred to as quality control (QC) protocol). The purpose of this protocol is to make all photographic catalogues in the South Pacific homogeneous to ease the comparison and research of matches within and between the breeding grounds in this area. Under this protocol photographs are given a number between 1 and 5 (1 being good and 5 being bad) for different characteristics: exposure, fluke angle, percentage of the fluke that is visible, focus and lateral angle. If a photo receives at least one 5 or 4, it is deleted from the catalogue.

Fig.5-2- Example of a photograph (on the left) removed under the quality-control protocol against a good-quality one (on the right).

The photographic catalogue 1999-2005 contained a total of 227 capture histories: from this complete catalogue (with all the photos) 1999-2005, 29 photographs were deleted because of the photographic QC protocol, resulting in the suppression of 26 capture histories. Indeed, of those 29 deleted photographs, only three were part of a multiple capture history and so 26 capture histories were actually deleted as their unique capture by photograph was deleted.

Genetic database

Genetic data were available for the years 1999 to 2005 which comprised 313 capture histories. In addition to capture-recapture information, the genetic database provided information on the sex of each biopsied individual.

Combined datasets for the two-source Jolly-Seber model

Since there were two photographic catalogues available in addition to the genetic database, there were two possible combined datasets for use with the TSJS model and the two-source M_0 model:

a) The genetic dataset 1999-2005 and the photographic catalogue 1999-2005, with all the photographs, which comprised 331 capture histories from which 107 have been genotyped only, 18 photographed only and the remaining 206 capture histories contained at least one double sampling capture,

b) The genetic dataset 1999-2005 and the photographic catalogue 1999-2005 where photographs have been checked for quality. This combined dataset included 328 capture histories from which 128 have been genotyped only and 12 photographed only. From the 29 photographs deleted under the quality-control protocol, only three capture histories were deleted from the data in the combined dataset 1999-2005 under the quality protocol.

The compiled datasets with photographic and genetic data were formatted using the encounter history code detailed in chapter two. A computer program has been written (Appendix 9) to allow users to easily format their data in this way.

5.3.4. Capture-Recapture estimates

Besides the TSJS estimator and the two-source M_0 model, multiple-occasion closed-population models, the Chapman modified Lincoln-Petersen estimator and the JS model were used to estimate the whale population size from the photographic datasets 1999-2005 with all the photographs, 1999-2005 with only the good-quality photographs and the genetic database 1999-2005. The multiple-occasion closed-population estimates were produced using program CAPTURE included in the option “closed capture” in program MARK. Program CAPTURE computes the estimation of population size for models: M_t by Darroch ($M_{tDarroch}$), M_t by Chao (M_{tChao}), M_h by Chao (M_{hChao}), M_h using the jackknife method ($M_{hjackknife}$), M_{th}, M_0, M_b by Zippin, generalized removal M_{bh}, Pollock and Otto’s M_{bh}, M_{tb} by Burnham. Models including a behavioral response (denoted by a “b” in the subscript) were not explored because trap response is not believed to occur during sampling in humpback populations: studies have shown that biopsy sampling may cause a short-term minimal disturbance that typically does not affect later recaptures by biopsy or photo (Clapham and Mattila, 1993; Weinrich et al., 1991). Here I considered models $M_{tDarroch}$, M_{tChao}, M_{hChao}, $M_{hjackknife}$ and M_{th} (Amstrup et al., 2005; Borchers et al., 2002; Seber, 1986; Seber, 2002). Models $M_{tDarroch}$, M_{hChao} and M_{th} are described in chapter four and the JS in chapter one.

Closed-population models

Model M_t by Chao

Under model M_t, all individuals have the same capture probability on a given capture occasion but this capture probability can vary over time. The general model M_t and the corresponding multinomial likelihood can be viewed as a *T*-sample version of the Lincoln-Petersen estimator (Darroch, 1958; Williams et al., 2002):

$$L(N, p_1, ..., p_T) = \frac{N!}{(N - M_{T+1})! \prod_h a_h!} \prod_{t=1}^{T} \left[p_t^{n_t} (1 - p_t)^{N - n_t} \right]$$

where N denotes the population size, p the capture probability, M_{T+1} the number of individuals recaptured at occasion *T+1*, a_h the frequency of observable capture history *h*, and $n = n_1 + n_2 + ... + n_T$ the total number of captures.

Chao (1989) developed an estimator for model M_t, which is especially useful with sparse data: when the number of recaptures is small on each capture occasion, most of the individuals do not have many captures in their capture histories. Chao's purpose was to base the estimator on the lower-order frequency counts with:

$$N = S + f_0$$

where S is the number of distinct individuals captured in the T samples and f_0 is the number of animals never captured. To do so, it is necessary to estimate $E(f_0)$ from f_1 and f_2 which are, respectively, the number of animals captured exactly once and twice. This leads to an estimator for N of the form:

$$\hat{N} = S + \frac{f_1^2 - \sum_{t=1}^{T} Z_t^2}{2 f_2}$$

where Z_t is the number of animals caught only in the *t*th capture occasion.

A bias-corrected form of the previous estimator was provided by Chao:

$$\hat{N} = S + \frac{f_1^2 - \sum_{t=1}^{T} Z_t^2}{2(f_2 + 1)}$$

Under model $M_{t\ \mathrm{Chao}}$, variance is given by:

$$\mathrm{var}_{est}\left(\hat{N}\right) \approx \left(\hat{N} - S\right) + \left(\hat{N} - S\right)^2 \left(\frac{1}{f_2 + 1} + \frac{4}{\hat{N}}\right) + \frac{\sum_{t=1}^{T} (f_1 - Z_t)^2 Z_t - \left[\sum_{t=1}^{T} (f_1 - Z_t) Z_t\right]^2 / \hat{N}}{(f_2 + 1)^2}$$

Model M_h using the jackknife method

Under model M_h, every individual has its own capture probability which does not vary over time. The vector of capture probabilities $\{p_i\}$ is viewed as a random sample of size *N* from some probability distribution $F(p)$ defined on the interval [0,1] (Burnham and Overton, 1978; Burnham and Overton, 1979; Otis et al., 1978). The corresponding model is of the form:

$$P\left(f_1,\ldots,f_T \middle| F\right)=\frac{N!}{\left(N-M_{T+1}\right)!\prod_{j=1}^{T} f_j!}\pi_0^{N-M_{T+1}}\prod_{j=1}^{T}\pi_j^{f_j}$$

where $\pi_j=\int_0^1 \frac{T!}{\left(T-j\right)!\,j!}p^j\left(1-p\right)^{T-j}dF(p)$

π_j can be viewed as the average probability that an animal is caught exactly *j* times.

The approach for M$_h$ using the jackknife statistic (Quenouille, 1949, 1956) gives M_{T+1} as a naïve estimator of *N*, and the bias is reduced using a linear function of the capture frequencies f_j such that: $\hat{N}_k=\sum_{j=1}^{T}a_{jk}f_j$ where *k* is the “order” of the jackknife estimator and a_{jk} the coefficients generated by the jackknife procedure.

For the variance, I chose to present the results using the profile likelihood approach as recommended in Cormack (1992) and applied in Otis et al. (1978).

The Chapman modified Lincoln-Petersen estimator

The Chapman modified Lincoln-Petersen estimator is also used on the same datasets (Borchers et al., 2002):

$$\hat{N}=\frac{\left(n_1+1\right)\left(n_2+1\right)}{m+1}-1$$

where $\hat{N}$ is the estimated population size for the considered capture occasion, n_1 is the total number of capture on the previous capture occasion, n_2 the total number of capture on the considered capture occasion and m the number of marked animals captured on the considered capture occasion. For estimation purposes, the data from one capture occasion were used as first-capture data for the estimate of the next capture occasion and as recapture data for the estimate of the relevant capture occasion (except the first capture occasion,i.e. year 1999 which can only be used as first capture data for the estimation of year 2000).

The approximately unbiased estimator of the variance of Chapman modified Lincoln-Petersen estimator is as follows (Wittes, 1972):

$$Var\left[\hat{N}\right] = \frac{(n_1+1)(n_2+1)(n_1-m)(n_2-m)}{(m+1)^2(m+2)}$$

Confidence interval

For all models, confidence intervals displayed in the results are classical approximate 95% confidence intervals of the form: $estimate \pm 1.96 \times se$. A log-transformation approximation was also used to get improved 95% confidence intervals as $(\hat{N}/C; \hat{N} \times C)$ where $C = \exp\left\{2\sqrt{\log(1+\frac{Var(\hat{N})}{\hat{N}^2})}\right\}$.

Growth rate

The Chapman modified Lincoln-Petersen, the JS and the TSJS estimators lead to an estimated population size for each capture occasion of a study (except on the first and last occasions for the JS and TSJS, and except on the first occasion for the Chapman modified Lincoln-Petersen). For those three estimators, it is then possible to get the finite rate of population increase. The growth rate λ_t at time *t* is defined here as the ratio of abundances N_t in two successive capture occasions *t* and *t*+1: $\lambda_t = N_{t+1}/N_t$.

The associated approximate standard error is defined as follows (Kendall and Stuart, 1969): $se_{N_{t+1}/N_t} = \frac{N_{t+1}}{N_t}\sqrt{\left(\frac{se_{N_{t+1}}}{N_{t+1}}\right)^2 + \left(\frac{se_{N_t}}{N_t}\right)^2 - 2r \times \frac{se_{N_{t+1}}}{N_{t+1}} \times \frac{se_{N_t}}{N_t}}$

where *r* is the unknown but most likely positive correlation between N_{t+1} and N_t. Therefore, I choose to assume independence to get a conservative standard error and set $r = 0$.

To investigate the abundance trend and see whether the three models (the Chapman modified Lincoln-Petersen, the JS and the TSJS models) provide the same evidence for the dynamics of the present population, the population growth rate and associated standard error were calculated and presented in the corresponding abundance table.

5.3.5. Exploration of model selection and assumption violation

Goodness of fit and model selection with program CAPTURE

Program CAPTURE includes, for closed-population models, goodness of fit and specific tests (Otis et al., 1978) based on standard Chi-square tests which allow a user:

1) to test the fit of a given model to the data

2) to test a model against a more general one.

These tests provides information that can be used to determine the most appropriate model: the test for heterogeneity of trapping probabilities and the one for time specific variation in trapping probabilities might give insight on whether some kind of heterogeneity was present in the data. Program CAPTURE also implements a procedure to select the appropriate model based on a linear discriminant classifier.

The Cormack-Jolly-Seber approach: a way to get information on the capture and survival probabilities

As for closed population models, the original CJS model uses multinomial distributions to model captures and recaptures. The CJS model is related to the JS model as it was originally derived from one of the likelihood components of the JS containing the capture and the survival probabilities that are time-dependent. It requires information only on the marked individuals of the population and Lebreton et al. (1992) developed an approach allowing the modeling of survival and capture probability. The component L_3 of the JS model was originally derived by Cormack (1964), and contains the recapture information conditional on the numbers of marked animals released at each occasion:

$$P_3\left(\{m_{tj}\} \mid \{R_t\},\{\phi_t\},\{p_t\}\right) = \prod_{t=1}^{T-1} \frac{R_t}{(m_{t,t+1})!(m_{t,t+2})!\ldots(m_{t,T})!(R_t - r_t)!}(\phi_t p_{t+1})^{m_{t,t+1}}$$

$$\times\{\,[\phi_t(1-p_{t+1})\phi_{t+1}p_{t+2}]^{m_{t,t+2\ldots}}\,[\phi_t(1-p_{t+1})\ldots\times\phi_{T-1}p_T]^{m_{t,T}}\,\chi_t^{R_t-r_t}\,\}$$

where R_t denote the number of releases at time *t*, r_t the number of R_t captured again later, ϕ_t the apparent survival at time *t* and χ_t the probability that an animal alive and in the study population at time *t* is not caught or observed again at any time after capture occasion *t*.

Two parameters are used in the model: the capture probability p_t that a marked individual at time *t* is captured at time *t* and the probability of survival ϕ_t that a marked individual alive at time *t* survives until time *t*+1 and does not temporarily emigrate. This second probability combines the probability of survival *per se* and the probability of not emigrating from the sampling area between capture occasions and hence represents the probability of apparent survival.

The use of the CJS model here could allow the estimation of the capture probabilities and survival rates from an open-population model. The first advantage of this model is the direct estimation of capture probabilities for the marked individuals of the population. This will provide valuable information to relate to the results of chapters three and four on the simulation of the TSJS given the estimated value of the capture probabilities obtained with the CJS. Then, because it allows the modeling of the capture probabilities, it will be possible to investigate whether the capture probability is time-specific using the photographic catalogue. Using the genetic data will provide additional information on the capture probability and survival: not only will it be possible to see if there is a temporal variation for capture probabilities and survival, but also to see if females and males have different capture and survival probabilities.

The fully parameterized CJS model is usually denoted $\{p_t, \phi_t\}$ (subscript *t* for time-specific survival and encounter probability), and from this model, reduced parameterized models that allow for stationary values of $p_.$ and $\phi_.$ or both, can be used. With the genetic dataset it is possible to build more complex models using the effect of the two groups, males or females, denoted “g”, in addition to time, as well as combination or interaction of those two factors: “*” denotes an interaction between the factors and “+” a linear combination of the effects. Therefore, a model such as model $\{p_{t+g}, \phi_.\}$ indicates that capture probabilities depends on combinations of group and time and that survival is constant. Then the model-selection procedure uses the Akaike’s Information Criterion (AIC) of the general form: $AIC = 2k - 2\ln(L)$ where *k* is the number of parameters in the model and *L* the maximized value of the likelihood function for the estimated model. The smallest AIC usually points out the model that best explains the data with a minimum of parameters. A rule of thumb is useful to assess the strength of evidence between the best models: a difference of 2 or less between AIC of models usually gives support to both models while a difference greater than 2 in AIC gives considerably less support to the next best model (Burnham and Anderson, 2004). This helps to decide which model is the most parsimonious and thus how the capture probability should be modeled given the data.

Finally, survival is a fundamental process governing population dynamics and is intuitively inherent to the population. Therefore, if the photographic and genetic sampling methods indeed sample the same population, both sampling methods should provide very close estimates of survival. It would therefore be of interest to compare the fit of models where survival varies by sampling method with models where the survival is constrained to be the same across the sampling methods. However, at present, except for the TSJS version of the JS survival estimator described in chapter one, I am unaware of a framework that allows the estimation of survival by combining two overlapping datasets. So I use the TSJS survival estimator and a likelihood-based approach based on an approximation: the idea is to multiply the likelihoods of the CJS models based on the genetic and photographic data and constrain the survival parameter to be the same across the two datasets. This can be done using program MARK and setting the photographic and genetic data as two distinctive groups. Using such an approximation leads to two major disadvantages: some individuals will knowingly be counted twice and multiplying likelihoods based on the two datasets also implies that the two sampling methods are assumed to be unconditionally independent. So results of the analysis should be interpreted with caution. In program MARK, the model-selection procedure is based on the AICc which is the AIC with a second order correction for small sample size such that: $AICc = AIC + \frac{2k(k+1)}{n-k-1}$ where k is the number of parameters in the model and n the sample size. As n gets large AICc converges to AIC.

Temporary emigration

A Markovian multi-state counterpart of the CJS, the Conditional-Arnason-Schwarz (CAS) model was used to estimate the probabilities of transition of humpback whales between breeding grounds in the South Pacific, between 1999 and 2004 (Arnason, 1972, 1973; Brownie et al., 1993; Hestbeck et al., 1991; Lebreton et al., 1992; Schwarz et al., 1993).

In this class of model, the state of an animal at time *t*+1 is stochastically determined as a function of its state at time *t*. Here the study site is the South West Pacific which can be split into *r* distinct, non-overlapping regions: New Caledonia, French Polynesia, Tonga and Cook Island. Animals are assumed to be able to move freely around the study area denoted *R* between sampling events: the transition between one region to another is Markovian and the region where the animals are caught at time *t* does not depend on the region where the animals previously were. The difficulty lies in the formulation of the likelihood since, for most studies, the complete data detailing the location of each animal is not available for the capture occasions where the animals were not observed. King and Brooks (2003) proposed likelihood forms for such a model. Where times of recapture are recorded and there is no dead recovery like in the present case, the likelihood takes the following form with :

$$L(\theta; v, n, d) = \prod_{r \in R} \left[\prod_{t=1}^{T} \{\chi_t(r)\}^{v_t(r)} \times \prod_{l=1}^{T-1} \prod_{t=l}^{T-1} \prod_{s \in R} \{O_{(l,t)}(r,s)\}^{n_{(l,t)}(r,s)} \right]$$

where $v_t(r)$ is the number of animals that are recaptured for the last time in region *r* at time *t*; $\chi_t(r)$ the probability that an animal seen at time *t* in region $r \in R$ is not seen again in the study, given by

$$\chi_t(r) = \begin{cases} 1 & (t = T), \\ 1 - F_t(r)\left[1 - \sum_{s \in R} \psi_t(r,s)\{1 - p_{t+1}(s)\}\chi_{t+1}(s)\right] & (t \leq T), \\ -\{1 - F_t(r)\} & (t < T); \end{cases}$$

$O_{(l,t)}$ the probability that an animal observed in region *r* at time *l* ($l \in \{1, ..., T\}$ is unobserved until time *t*+1, for $t \in \{l, ..., T-1\}$, and is sighted in $s \in R$, given by

$$O_{(l,t)}(r,s) = p_{t+1}(s) Q_{(l,t)}(r,s),$$

where $Q_{(l,t)}$ denotes the probability that an individual migrates from region *r* at time *l* ($l \in \{1, ..., T\}$ to region $s \in R$ at time *t*+1, for $t \in \{l, ..., T-1\}$, and is unobserved between these times, such that: $Q_{(l,t)}(r,s) = \begin{cases} F_l(r)\psi_l(r,s) & (l = t), \\ F_l(r)\sum_{r \in R}\{1 - p_{l+1}(l)\}\psi_l(r,l)\, Q_{(l+1,t)}(l,s) & (l < t); \end{cases}$

The set of parameters therefore comprises:

$F_t(r) = \Pr(\text{an animal in region } r \text{ at time } t \text{ survives until time } t+1);$

$p_t(r) = \Pr(\text{an animal in region } r \text{ at time } t \text{ is captured at time } t)$;

$\psi_t(r,s) = \Pr(\text{an animal in region } r \text{ at time } t \text{ moves to region } s \text{ by time } t+1, ;$

$\text{given that it is alive at time } t)$

Besides estimating capture probability, the CAS model with general notation $\{F, \psi, p\}$ also allows a break-down of the probability ϕ of apparent survival in the general CJS model into the two components which can be state-specific: true survival *F* and transition probability ψ. Different subscripts are used to parameterize *F,* ψ, and *p*: "from" indicates a variation in the parameter dependent on the previous region the animal was, "to" a variation dependent on the current region where the individual is, "time" a time-dependent variation. Moreover, two operators can be used to combine the effect of previous region, current region and time to build more complex models: "*" denotes an interaction between factors and "+" a linear combination of the effects. Therefore, a model such as model $\{F_{.}, \psi_{from+to}, p_{to*time}\}$ used later on, indicates a constant survival, a probability of transition depending on the linear combination of site of departure with site of arrival and a probability of capture depending on the interaction between site of arrival and on the time.

It is of interest to model and estimate the transition probability for a better understanding of the stock structure of humpback whales in the South Pacific and to see if there is temporary emigration between different breeding grounds that would constitute a violation of the assumptions of both geographic closure for closed population models and of temporary emigration for the open-population JS and the TSJS models. Knowledge of occasional interchanges among neighboring breeding grounds (New Caledonia, Samoa, Cook Island, Tonga and French Polynesia) has been documented from individual identification photographs: 12 whales have been sighted in the two different areas between 1999 and 2004. The data were collected during synoptic surveys conducted by researchers from the South Pacific Whale Research Consortium (SPWRC) in each of the breeding grounds between 1999 and 2004 (Garrigue et al., 2002; Garrigue et al., 2007; Garrigue et al., 2000). The quality protocol described above was used to homogenize all photographic catalogues and a search of matches, by researchers from the SPWRC, within and between the breeding grounds in this area permitted the building of multi-state capture-recapture histories (each breeding ground is considered as a state). The joined catalogue comprises 684 individual capture histories with a total of 778 sightings. The number of sightings and re-sightings per region are summarized in Table 5-1.

Table 5-1- Summary of photographic captures and recaptures by study site between 1999 and 2004.

region	Number of capture histories	Number of resights within region
New Caledonia	160	33
Tonga	285	25
Cook Islands	37	0
French Polynesia	159	20

The AIC criterion was again used to select the most appropriate model.

The software M-SURGE was used for building and selecting CAS models (Choquet et al., 2004).

Transient individuals and trap-dependence

It is of interest to detect if there are transients among the population: animals that pass through the sampling area once with negligible probability of being caught again at a subsequent capture occasion. Their presence would lead to heterogeneity in capture probabilities between transients and residents. The transience issue has been previously noted based on genetic data for the humpbacks in New Caledonia between 1995 and 2001 (personal work, not published) but at that time, genetic samples were not taken systematically.

Program U-Care version 2.2 (Choquet et al., 2005) conducts goodness-of-fit tests as well as specific tests for transience (test 3.SR) and trap-dependence (test 2.CT). Both tests are based on 2x2 contingency tables:

1) one of observed values such as:

Table 5-2- 2x2 contingency table for test 3.SR based on the individuals encountered at capture occasion *i*.

	Seen later	Never seen later	Total
“new” or “newly marked”	o_{11}	o_{12}	$o_{1.}$
“old” or “already marked”	o_{21}	o_{22}	$o_{2.}$
Total	$o_{.1}$	$o_{.2}$	$o_{..}$

2) one of expected values such as:

Table 5-3- 2x2 contingency table for test 3.SR of expected numbers of individuals encountered at capture occasion *i*.

	Seen later	Never seen later	Total
"new" or "newly marked"	$e_{11} = o_{.1} \times o_{1.} / o_{..}$	$e_{12} = o_{.2} \times o_{1.} / o_{..}$	$e_{1.}$
"old" or "already marked"	$e_{21} = o_{.1} \times o_{2.} / o_{..}$	$e_{22} = o_{.2} \times o_{2.} / o_{..}$	$e_{2.}$
Total	$e_{.1}$	$e_{.2}$	$e_{..}$

Hypotheses to be tested are:

1) In test 3.SR

H_0: there is no difference between the "new" and the "old" individuals captured at occasion *t* in the probability of being later encountered.

Alternatively

H_1: there is a difference in the probability of being later encountered between the new and the "old" individuals captured at occasion *t*.

2) In test 2.CT

H_0: there is no difference between those encountered and not encountered at occasion *t* in the probability of being reencountered at *t*+1 conditional on presence at both occasions.

Alternatively

H_1: there is a difference in the probability of being reencountered at *t*+1 between those encountered and not encountered at occasion *t* conditional on presence at both occasions.

For both tests, the usual χ^2 statistic is obtained as:

$$\chi^2(t) = \frac{\sum (o_{jk} - e_{jk})^2}{e_{jk}}$$

where o_{jk} is the observed value corresponding to the cell *jk* in the 2x2 contingency table of observed values and e_{jk} the expected value corresponding to the cell *jk* in the 2x2 contingency table of expected values.

Under H_0, the $\chi^2(t)$ follows a χ^2 distribution with 1 degree of freedom. Here those two tests were used to investigate possible sources of bias in the population size estimates. Even though trap response is believed not to be an issue in humpback whale studies, the data were checked for this.

5.4. Results

5.4.1. Survey effort

Over the 7 years of the survey in the South lagoon, 290 boat trips were carried out and a total of 331 whales have been sampled in approximately 2138 hours of navigation. Year 2002 was a “bad” year for field work, due to weather conditions, with not as many days at sea as the other years and 2004 had very few days in the South lagoon because field work was conducted in another part of New Caledonia for most of the season. Table 5-4 shows details of the effort deployed per year.

Table 5-4- Sampling effort in the South lagoon of New Caledonia between 1999 and 2005.

Year	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**
Number of days at sea	46	50	62	36	42	11	43
Number of hours at sea	308h05	356h21	487h25	265h08	326h58	77h34	317h05
Number of nautical miles	2581	2661	3717	2109	2316	567	2492
Number of individual whales photographed	21	38	72	22	48	36	63
Year-to-year resights with photo-identification		4	8	6	3	4	6
Number of individual whales photographed under the QC protocol	19	35	64	22	43	32	46
Year-to-year resights with photo-identification under the QC protocol		4	8	5	3	4	3
Number of individual whales genotyped	27	46	88	33	63	39	84
Year-to-year resights with genetic		3	7	5	3	2	4

5.4.2. Abundance

Results based on photographic catalogues

a) *Under the photographic ranking protocol: QC photographs only*

As shown in Table 5-5, for the period 1999-2005, among the multiple-occasion closed-population models, the $M_{tDarroch}$ gave the smallest estimate and standard error (402 ± *39*) and the M_{hChao} and M_{th} the largest estimates and standard-errors (respectively 646 ± *112* and 625 ± *102*) which was consistent with the removal of negative bias resulting from heterogeneity. It resulted that the largest multiple-occasion closed-population estimate (M_{hChao}) was larger that the smallest one ($M_{tDarroch}$) by a factor 1.6, leading to a wide range of estimates with the closed-population models. With the present dataset, the two approaches for model M_t (Darroch and Chao) and M_h (Chao and jackknife) also gave results that disagreed within each model, with the approach of Chao always leading to larger estimates and standard-errors: 1.37 greater than the other approach for model M_t and 1.12 for model M_h.

With the Chapman modified Lincoln-Petersen (Table 5-6) and the JS estimator (Table 5-7), based on this QC photographic catalogue 1999-2005, the whale population was estimated to be respectively 143 ± *47* and 151 ± *50* in 2000. In 2004, the estimators were far from agreeing: the population was down to 76 ± *18* with the JS estimator and up to 289 ± *103* with the Chapman modified Lincoln-Petersen estimator. While the Chapman modified Lincoln-Petersen estimator seemed to underline a quasi constant increase of the population from 1999 to 2005, the JS estimator showed a different pattern with an increase until 2002 and then a decrease. Up to 2002, the abundance estimate and the growth rate were similar to those of the Chapman modified Lincoln-Petersen. Then, with the JS estimator, the population declined by half every year but increased with the Chapman modified Lincoln-Petersen with a growth rate also increasing every year from 1.02 ± *0.51* in 2003 to 1.34 ± *0.72* in 2005.

b) *With all photographs: catalogue 1999-2005*

Compared to the results based on the photographic catalogue 1999-2005 with only good-quality photos (Table 5-5), i.e. under the photographic QC protocol, the results produced by the same multiple-occasion closed-population estimators on a dataset including all quality photographs always appeared larger (Table 5-8): only by a factor 1.04 for model $M_{tDarroch}$ which encountered the smallest increase and by 1.33 for model M_{hChao} which displayed the largest increase. The only similarity between the results based on the two photographic catalogues was that $M_{tDarroch}$ also gave the smallest estimate and standard-errors (419 ± 36) and the M_{hChao} and the M_{th} the largest ones (respectively 858 ± 160 and 806 ± 129). However, with the photographic catalogue 1999-2005 with all photographs, the M_{hChao} estimate was larger than the $M_{tDarroch}$ one by a factor 2.05 whereas it was only larger than the $M_{tDarroch}$ estimate by a factor 1.61 with the QC catalogue 1999-2005. Moreover, the M_{tChao} estimate was larger than the $M_{hjackknife}$ estimate and had a larger standard-error while, with the photographic QC protocol catalogue 1999-2005, the M_{tChao} estimate was smaller than the $M_{hjackknife}$ estimate but still had a larger standard-error. Here, as with the photographic catalogue 1999-2005 under the photographic QC protocol, the two approaches for model M_t and M_h gave very different estimates within each kind of models (M_t or M_h), with the approach of Chao always leading to larger estimates: 1.72 greater than the other approach for model M_t and 1.27 for model M_h.

As shown in Table 5-10, except in 2002 and 2004, the JS estimator gave very similar results as those based on the catalogue 1999-2005 under the photographic QC protocol. The population started at 166 ± 50 and was estimated in 2004 at 281 ± 67. Here the growth rate was, however, more stable and did not show an apparent decline from 2002 as did the growth rate with the photographic catalogue 1999-2005 under the photographic QC protocol. Here the growth rate fluctuated and the increase was less clear than with the previous results with the Chapman modified Lincoln-Petersen estimator on both photographic catalogues. The yearly JS estimates were below those of the Chapman modified Lincoln-Petersen estimator by a factor 0.98 (in 2000) to 0.59 (in 2002) (Table 5-9). The growth rate varied with the same trend for both models (population size increased except in 2002 where $\hat{\lambda} < 1$) with the increase being greater with the JS estimator in 2003 and 2004.

The Chapman modified Lincoln-Petersen estimator was consistent with both photographic catalogues leading to similar results: the population was estimated to be 171 ± 58 in 2000 reaching 337 ± 102 in 2005.

Results based on the genetic data

As shown in Table 5-11, the estimates based on the genetic dataset were ranked in the same order as the photographic catalogue 1999-2005 with only good-quality photographs (under the photographic QC protocol) (Table 5-5) but appeared more than twice larger than those based on both photographic catalogues (Table 5-5, Table 5-8), ranging from 847 ± 88 with model $M_{tDarroch}$ to 1592 ± 285 with the M_{hChao}.

With the Chapman modified Lincoln-Petersen estimator, the situation was the same as with the multiple-occasion closed-population models, with results based on the genetic (Table 5-12) twice as large as the population size given by the photographic data: from 328 ± 130 in 2000 to 679 ± 252 in 2005. With the Chapman modified Lincoln-Petersen estimator, though photographic and genetic datasets did not agree on the estimates, they both showed an increase of the population size, except in 2002 even though this decrease was only really noticeable for the photographic catalogue with all photographs.

When using the classical Jolly-Seber model separately on the three datasets (the two photo-identification ones (Table 5-7, Table 5-10) and the genetic one (Table 5-13)), the population size obtained using the genetic data was always larger than its photo-identification counterpart for the same year, agreeing with all the previous results with other models for the discrepancy between the size given by the genetic and the photo-id database. In 2002 and 2004, the genetic dataset indicated a population twice as large as that produced by the photo-identification data with all photographs (respectively 315 ± 80 and 559 ± 153). The standard error produced with the genetic dataset was as well always larger than the photo-identification one. Except in 2003 with the photographic data 1999-2005 with all photographs and in 2002 with the QC photographic data 1999-2005 (under the photographic QC protocol), the growth rate estimated from the genetic data (Table 5-13) was always larger than its photographic counterpart (Table 5-7, Table 5-10).

The JS estimates with the genetic dataset (Table 5-13) were again smaller than the Chapman modified Lincoln-Petersen estimator (Table 5-12) by a factor 0.54 (in 2003) to 0.81 and than all closed-population estimates for the same dataset (Table 5-11) by a factor as high as 3. However, growth rates from the JS model were larger than with the Chapman modified Lincoln-Petersen estimator in 2001 and 2004 where they almost reached a value of 2 (respectively 1.99 ± 1.16 and 1.9 ± 0.48), being the largest rates of increase so far.

Results based on combined datasets

The TSJS model (Table 5-16, Table 5-17) seemed to produce estimates that were a intermediate among all the estimates based on the photographic data and genetic data separately but the two-source M_0 estimator gave two of the largest estimates (Table 5-18). As expected, the weighted mean of the Jolly-Seber estimator (Table 5-14, Table 5-15) gave intermediate estimates between the estimates from the photographic and the genetic datasets separately and smaller standard errors.

Compared to the results given by the JS and the Chapman modified Lincoln-Petersen estimators for the genetic and the photographic data separately, the TSJS estimates were closer to the ones provided by the genetic dataset (Table 5-12, Table 5-13): estimates varied, with dataset 1999-2005 with all photographs (Table 5-17), between $222 \pm \mathit{68}$ in 2000 and $445 \pm \mathit{103}$ in 2004. However, the weighted estimates (Table 5-14, Table 5-15) were always closer to the photographic ones following the trend of the photographic estimates (Table 5-7, Table 5-10) but roughly consistent in 2000, 2001 and 2003 whether the complete or QC photographic dataset was used. The TSJS estimates were also consistent in 2000, 2001 and 2003 between the combined data with all photographs (Table 5-17) and the one under the QC protocol (Table 5-16). In 2002, however, the TSJS estimates varied between the datasets by a factor 1.42: being $412 \pm \mathit{97}$ for the dataset under the QC protocol and $289 \pm \mathit{58}$ for the one with all photographs. In 2004 the situation was reversed, the estimate with the dataset under the QC protocol being 0.59 smaller than the one produced with the dataset with all photographs (respectively $262 \pm \mathit{70}$ and $445 \pm \mathit{103}$). Concerning the standard errors, the order of magnitude was equivalent between the two combined datasets and the standard errors produced with the TSJS estimator fell between the standard errors of the JS estimates given by the photographic data (Table 5-7, Table 5-10) and the ones given by the genetic data (Table 5-13).

For the data 1999-2005 with all photographs, the growth rate in 2001 for the TSJS model (Table 5-17) was equal to that for the JS model with the genetic data (Table 5-13). The growth rates for the TSJS were very close to those provided by the Chapman’s estimator on the photographic dataset 1999-2005 with all photographs (Table 5-9). For the Chapman modified Lincoln-Petersen model, the growth rate indicated, in 2002, a slight decrease of the population with the two photographic and the genetic datasets (Table 5-6, Table 5-9, Table 5-12). With the combined dataset under the QC protocol (Table 5-16), however, the population estimates from the TSJS showed an apparent constant decline since 2001 which was also found with the JS estimator on the photographic data 1999-2005 under the QC protocol (Table 5-14) and on the weighted mean of the JS estimates from the QC photographic data and the genetic data (Table 5-14).

Compared to the results of the multiple-occasion closed-population models, the abundance given by the TSJS estimator (Table 5-16, Table 5-17) and the weighted mean of the JS model (Table 5-14, Table 5-15) were generally smaller than any closed-population estimate for the same data, except for the estimates given by the $M_{tDarroch}$ on both photographic catalogues (Table 5-5, Table 5-8). The two estimates produced by the two-source M_0 estimator (Table 5-18) on the combined datasets (with all photographs and under the QC protocol) were consistent, respectively 1116 ± 231 and 1238 ± 274, and the largest estimates after the estimates based on the M_{tChao}, the M_{hChao} and the M_{th} models on the genetic dataset 1999-2005 (Table 5-11). The associated standard errors produced by the two-source M_0 estimator on the combined datasets were also amongst the largest ones. Contrary to these closed-population models giving very different results depending on the dataset, the TSJS estimator and the two-source M_0 estimator appeared fairly consistent over the different datasets available.

Generally there was no major difference between the classical approximate 95% confidence intervals and the log-normal ones.

Table 5-5- Population size, associated standard error and confidence intervals (nominal and log-normal) for closed population models based on the 1999-2005 QC photographic catalogue.

Model	$\hat{N}$	*se*	Nominal lower CI	Nominal Upper CI	Log-normal lower CI	Log-normal upper CI
Mt Chao	**551**	*88*	379	723	401	757
Mt Darroch	**402**	*39*	325	479	331	488
Mh jackknife	**576**	*44*	490	662	495	671
Mh Chao	**646**	*112*	426	866	458	912
Mth	**625**	*102*	425	825	452	863

Table 5-6- Population size, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error with the Chapman's estimator based on the 1999-2005 QC photographic catalogue.

year	2000	2001	2002	2003	2004	2005
$\hat{N}$	**143**	**259**	**248**	**252**	**289**	**387**
se	*47*	*66*	*77*	*98*	*103*	*155*
Nominal lower CI	50	129	97	60	88	82
Nominal upper CI	236	389	399	444	491	692
Log-normal lower CI	75	157	135	119	145	179
Log-normal upper CI	272	428	455	534	576	839
$\hat{\lambda}$		1.81	0.96	1.02	1.15	1.34
se($\hat{\lambda}$)		*0.75*	*0.38*	*0.51*	*0.6*	*0.72*

Table 5-7- Population size, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error with the JS model on the QC photographic catalogue 1999-2005.

year	2000	2001	2002	2003	2004
$\hat{N}$	**151**	**246**	**264**	**134**	**76**
se	*50*	*93*	*59*	*38*	*18*
Nominal lower CI	53	63	149	60	40
Nominal upper CI	249	429	379	208	111
Log-normal lower CI	79	118	170	77	48
Log-normal upper CI	288	512	409	233	121
$\hat{\lambda}$		1.63	1.07	0.51	0.56
se($\hat{\lambda}$)		*0.82*	*0.47*	*0.18*	*0.21*

Table 5-8- Population size, associated standard error and confidence intervals (nominal and log-normal) for closed population models based on the complete 1999-2005 photographic catalogue.

model	$\hat{N}$	*se*	Nominal lower CI	Nominal upper CI	Log-normal lower CI	Log-normal upper CI
Mt Chao	**721**	*125*	476	966	511	1017
Mt Darroch	**419**	*36*	349	489	354	496
Mh jackknife	**676**	*46*	585	767	589	775
Mh Chao	**858**	*160*	544	1172	592	1243
Mth	**806**	*129*	553	1059	587	1107

Table 5-9- Population size, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error with the Chapman's estimator based on the complete 1999-2005 photographic catalogue.

year	2000	2001	2002	2003	2004	2005
$\hat{N}$	**171**	**315**	**239**	**281**	**362**	**337**
se	*58*	*82*	*67*	*110*	*130*	*102*
Nominal lower CI	58	154	107	66	106	138
Nominal upper CI	283	476	371	498	617	536
Log-normal lower CI	89	189	138	132	180	187
Log-normal upper CI	329	526	415	597	728	608
$\hat{\lambda}$		1.85	0.75	1.18	1.29	0.93
$se(\hat{\lambda})$		*0.79*	*0.29*	*0.57*	*0.68*	*0.44*

Table 5-10- JS estimates, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error based on the complete 1999-2005 photographic catalogue.

year	2000	2001	2002	2003	2004
$\hat{N}$	**166**	**299**	**141**	**182**	**281**
se	*50*	*104*	*24*	*47*	*67*
Nominal lower CI	69	95	95	90	151
Nominal upper CI	264	503	187	274	412
Log-normal lower CI	92	152	101	110	176
Log-normal upper CI	298	588	196	302	448
$\hat{\lambda}$		1.8	0.47	1.29	1.55
$se(\hat{\lambda})$		*0.83*	*0.18*	*0.4*	*0.54*

Table 5-11- Population size, associated standard error and confidence intervals (nominal and log-normal) for closed population models based on the 1999-2005 genetic dataset.

model	$\hat{N}$	*se*	Nominal lower CI	Nominal upper CI	Log-normal lower CI	Log-normal upper CI
Mt Chao	**1338**	*266*	816	1860	902	1985
Mt Darroch	**847**	*88*	674	1020	688	1042
Mh jackknife	**1018**	*57*	907	1128	911	1138
Mh Chao	**1592**	*285*	1033	2150	1116	2271
Mth	**1519**	*248*	1033	2005	1098	2102

Table 5-12- Population size, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error with the Chapman's estimator based on the 1999-2005 genetic dataset.

year	2000	2001	2002	2003	2004	2005
$\hat{N}$	**328**	**522**	**503**	**543**	**852**	**679**
se	*130*	*151*	*24*	*221*	*401*	*252*
Nominal lower CI	73	225	176	109	67	185
Nominal upper CI	583	819	831	977	1638	1173
Log-normal lower CI	153	296	458	248	349	381
Log-normal upper CI	705	922	552	1189	2083	1212
$\hat{\lambda}$		1.59	0.96	1.08	1.57	1.26
$se(\hat{\lambda})$		*0.78*	*0.28*	*0.44*	*0.98*	*0.48*

Table 5-13- JS estimates, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error based on the 1999-2005 genetic dataset.

year	2000	2001	2002	2003	2004
$\hat{N}$	**211**	**420**	**315**	**294**	**559**
se	*82*	*181*	*80*	*93*	*153*
Nominal lower CI	50	65	158	112	260
Nominal upper CI	372	774	471	476	859
Log-normal lower CI	100	184	191	159	327
Log-normal upper CI	447	958	519	544	956
$\hat{\lambda}$		1.99	0.75	0.93	1.9
$se(\hat{\lambda})$		*1.16*	*0.38*	*0.8*	*0.48*

Table 5-14- Population size, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error with the weighted mean of the JS model on the QC photographic catalogue and the genetic dataset 1999-2005.

year	2000	2001	2002	2003	2004
$\hat{N}$	**167**	**283**	**282**	**157**	**83**
se	*43*	*83*	*47*	*35*	*18*
Nominal lower CI	83	120	189	88	48
Nominal upper CI	251	446	375	226	118
Log-normal lower CI	101	159	202	101	55
Log-normal upper CI	276	502	393	244	125
$\hat{\lambda}$		1.69	1	0.56	0.53
$se(\hat{\lambda})$		*0.66*	*0.34*	*0.15*	*0.16*

Table 5-15- Population size, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error with the weighted mean of the JS model on the complete photographic catalogue and the genetic dataset 1999-2005.

year	2000	2001	2002	2003	2004
$\hat{N}$	**178**	**329**	**141**	**205**	**325**
se	*43*	*90*	*23*	*42*	*61*
Nominal lower CI	95	152	97	123	205
Nominal upper CI	261	506	185	287	445
Log-normal lower CI	111	192	103	137	224
Log-normal upper CI	285	564	193	307	472
$\hat{\lambda}$		1.85	0.43	1.45	1.56
$se(\hat{\lambda})$		*0.67*	*0.14*	*0.38*	*0.44*

Table 5-16- TSJS estimates, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error between 1999 and 2005 with the combined dataset under the photographic QC protocol.

year	2000	2001	2002	2003	2004
$\hat{N}$	**222**	**421**	**412**	**366**	**262**
se	*76*	*160*	*97*	*104*	*70*
Nominal lower CI	74	107	222	161	125
Nominal upper CI	371	735	602	570	398
Log-normal lower CI	114	202	259	206	155
Log-normal upper CI	432	878	655	631	442
$\hat{\lambda}$		1.89	0.98	0.89	0.72
se($\hat{\lambda}$)		*0.97*	*0.44*	*0.33*	*0.28*

Table 5-17- TSJS estimates, associated standard error, confidence intervals (nominal and log-normal), growth rate and associated standard error between 1999 and 2005 with the combined dataset with all the photographs.

year	2000	2001	2002	2003	2004
$\hat{N}$	**222**	**442**	**289**	**338**	**445**
se	*68*	*151*	*58*	*87*	*103*
Nominal lower CI	88	145	177	168	243
Nominal upper CI	355	738	402	507	648
Log-normal lower CI	122	227	195	204	281
Log-normal upper CI	405	859	429	559	704
$\hat{\lambda}$		1.99	0.66	1.17	1.32
se($\hat{\lambda}$)		*0.91*	*0.26*	*0.38*	*0.46*

Table 5-18- Two-source M_0 estimates, associated standard errors, confidence intervals (nominal and log-normal) and capture probabilities between 1999 and 2005 with the combined datasets with all photographs and under the photographic QC protocol.

Combined Dataset 1999-2005	$\hat{N}$	*se*	Nominal lower CI	Nominal upper CI	Log-normal lower CI	Log-normal upper CI	Capture probability					
							$\hat{p}$	*se*($\hat{p}$)	$\hat{g}$	*se*($\hat{g}$)	$\hat{\alpha}$	*se*($\hat{\alpha}$)
With all photographs	**1116**	*231*	663	1569	740	1681	0.03	*0.01*	0.04	*0.01*	0.85	*0.02*
With good photographs only	**1238**	*274*	701	1775	799	1917	0.03	*0.01*	0.04	*0.01*	0.87	*0.02*

$\hat{p}$ = probability of capture by photo-identification; $\hat{g}$ = probability of capture by genetics; $\hat{\alpha}$ = probability of capture by genetics given a capture by photo-identification on the same occasion.

5.4.3. Model selection for closed-population models

In all three datasets (photographic catalogues 1999-2005 with all photographs and under the QC protocol, and the genetic data 1999-2005), the test for heterogeneity in capture probabilities in population for model M_h and for time specific variation in capture probabilities for model M_t were both significant (p-value<<0.05). Thus, not surprisingly, for the three datasets, the linear classifier from program CAPTURE systematically selected model M_{th} as the most appropriate model.

Goodness-of-fit tests in program CAPTURE consistently rejected the null hypothesis when testing the fit of model M_h and M_t. However, there is no goodness-of-fit available in program CAPTURE for model M_{th}.

5.4.4. Capture probability

Estimation using photographic data

The CJS model $\{p_t, \phi_t\}$ and the three other models possible with time-dependency ($\{p_., \phi_.\}$, $\{p_t, \phi_.\}$, $\{p_., \phi_t\}$) were run on the photographic catalogue 1999-2005 with all photographs and under QC protocol. Results are displayed in Table 5-19. For the dataset 1999-2005 with all photographs, from the AIC, 3 models were similarly supported by the data and two out of the three models ($\{p_., \phi_t\}$, $\{p_., \phi_.\}$) seemed to demonstrate that capture probability was constant and did not depend on time: under the best model $\{p_., \phi_.\}$, capture probability was estimated to be 0.17 ± 0.03. Models with constant survival ($\{p_., \phi_.\}$, $\{p_t, \phi_.\}$) were better than models with time-specific survival ($\{p_t, \phi_t\}$, $\{p_., \phi_t\}$): under model $\{p_., \phi_.\}$ survival was estimated to be 0.65 ± 0.11 and under model $\{p_t, \phi_.\}$ to be 0.68 ± 0.12.

The quality-control protocol procedure applied on the photographic data 1999-2005 resulted in a more ambiguous situation for the capture probability and survival with the two best models disagreeing: one in favour of capture probabilities depending on time (Fig.5-3) and constant survival, i.e. model $\{p_t, \phi_.\}$ and the other one in favour of a constant capture probability and time-specific survival $\{p_., \phi_t\}$. The survival estimated under model $\{p_t, \phi_.\}$ was 0.92 ± 0.091, greater and with a smaller standard error than previously reported by this model with the dataset with all photographs. With the second best model $\{p_., \phi_t\}$ capture probability was estimated to be 0.2 ± 0.04 which was very close to the best model with the dataset with all photographs. Survival under model $\{p_{.},\phi_{t}\}$ varied between 0.34 ± 0.16 and 1, showing the unreliability of the estimation as such variation for survival (even though apparent survival) is unlikely to occur in the present case.

Capture probabilities based on the best model from the dataset under the quality-control protocol $\{p_{t},\phi_{.}\}$ and second best for the complete dataset 1999-2005 also $\{p_{t},\phi_{.}\}$ are shown in Fig.5-3. Capture probabilities were very close except in 2005 where the capture probability given by the dataset with all photographs was more than four times higher than the one provided by the data under the quality-control protocol, respectively 0.17 ± 0.06 and 0.04 ± 0.02. A glance at table 5-4 shows that this is most likely due to the QC protocol excluding half the resighted animals in that year, though in most years no resightings are excluded.

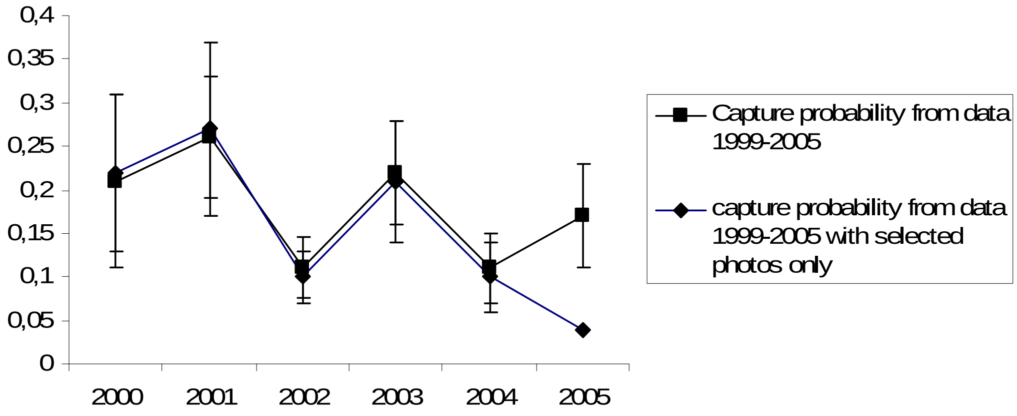


Fig.5-3- Capture probability estimates and standard errors from model $\{p_{t},\phi_{.}\}$ for complete photographic data 1999-2005 and for QC-photographic data 1999-2005.

Given the present results with both photographic datasets, it was not clear whether capture probability was dependent on time. However, there were two “abnormal” years (2002 and 2004: resulting from a shorter field work season) in the data always displaying smaller capture probabilities, and I suspected these values to be the origin of time-dependent capture probability. Hence, I removed those two years from each dataset and re-ran the models as shown in Table 5-19. Without those two years, from the AIC with the dataset under the quality-control protocol, three models demonstrated a similar adequacy to the data and two out of the three models $\{p_t, \phi_.\}$ and $\{p_t, \phi_t\}$ seemed to indicate that capture probability was still dependent on time and it was unclear whether the survival depended on time, although it is unlikely here. On the other hand, without those two years, with the dataset with all photographs, the two best models ($\{p_., \phi_.\}$, $\{p_., \phi_t\}$) agreed on constant capture probability but still disagreed on the survival. So, from the photographic data, it was not clear whether there was temporal heterogeneity in capture probability. Removing 2002 and 2004 from the dataset had an opposite effect depending on the dataset. With the dataset with all the photographs, survival was increased (0.78 ± 0.11 under model $\{p_., \phi_.\}$ and 0.86 ± 0.13 under model $\{p_t, \phi_.\}$) while survival estimates were lesser with the dataset with QC photographs: 0.87 ± 0.17 under model $\{p_t, \phi_.\}$ and 0.62 ± 0.11 under model $\{p_., \phi_.\}$. Under model $\{p_., \phi_t\}$ with the dataset under the quality-control protocol, survival estimates varied between 0.08 ± 0.05 and 0.97 ± 0.26. The first important thing to note about these very small survival rates is that with the CJS model the parameter of survival actually mixes two processes: true survival and permanent (or at least long term) emigration. Therefore, if an estimate of 0.78 ± 0.11 seems small for a whale, it may actually underline that emigration is important and not that true survival is low. However, under the CJS model, an estimate of 0.08 ± 0.05 for apparent survival for humpback whales simply seems unreliable and most likely indicates difficulties for the model to estimate this parameter with values very close to the boundaries.

Table 5-19- AIC for the CJS and related models for photographic catalogues 1999-2005 under the QC protocol ("Selected 1999-2005"), 1999-2005 with all photographs ("All 1999-2005") and both without 2002/2004.

	AIC			
Model	Selected 1999-2005	Selected 1999-2005 without 2002 and 2004	All 1999-2005	All 1999-2005 without 2002 and 2004
p_t, ϕ_t	379.63	202.59	473.9	288.52
$p_t, \phi_.$	376.33	202.74	467.91	286.42
$p_., \phi_t$	378.67	202.07	469.66	285.25
$p_., \phi_.$	387.23	219.92	467.75	283.04

Estimation using genetic data

A deeper analysis was possible with the genetic data because it includes information about the sex of the individuals. From the genetic database 1999-2005, of the 308 animals that were sexed, 129 were females and 179 males. It was possible to model survival and capture probability with separate parameters for each time and group (females or males) denoted "*g*" in Table 5-20 which presents the 6 first best models in terms of AIC.

I disregarded further time-dependent survival models as such models previously gave inconsistent and unreliable estimation of survival and always had bigger AIC than time-constant survival models with the genetic data.

For the genetic data 1999-2005, two models with constant survival, based on the AIC, seemed appropriate: the best model was model $\{p_t, \phi_.\}$ where capture probability only depended on time and second best model was model $\{p_{t+g}, \phi_.\}$ where capture probabilities were group and time-dependent. Under the later model, which may have more biological relevance in the context of humpback whales (Garrigue et al., 2004; Smith et al., 1999), males and females had different capture probabilities that also varied with time and equal survival probabilities. Estimates of capture probabilities under model $\{p_{t+g}, \phi_.\}$ are displayed in Fig.5-4. Under model $\{p_t, \phi_.\}$ and $\{p_{t+g}, \phi_.\}$, survival was estimated to be respectively 0.68 ± 0.12 and 0.68 ± 0.13. Again these low values for survival with the CJS model may indicate that emigration from this population is an important process of loss for this population.

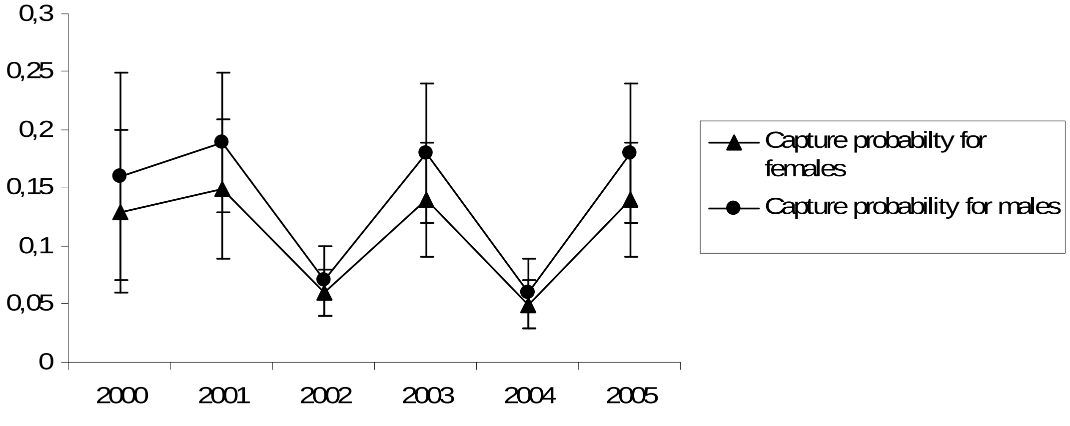


Fig.5-4- Capture probability estimates for males and females from model $\{p_{t+g}, \phi_.\}$ using genetic data in 1999-2005.

Under this model, males had systematically higher capture probabilities than females, usually above 0.1. Given the fact that years 2002 and 2004 again gave very small estimates compared to the other years, I again removed those two capture occasions and re-ran all models to check whether the temporal variation in capture probabilities was still holding. As found with the photographic data, once those two years were removed, the best model did not include time-dependent capture probabilities. Instead, the best model was either model $\{p_., \phi_.\}$ where survival and capture probability were constant over time; or model $\{p_g, \phi_.\}$ where survival was constant over time and capture probability depended on the sex; or model $\{p_., \phi_g\}$ where survival depended on sex and capture probability was constant. Under model $\{p_., \phi_.\}$ and $\{p_., \phi_g\}$, the capture probability was estimated to be $0.2 \pm \mathit{0.06}$ and model $\{p_g, \phi_.\}$, males had again a higher capture probability: $0.22 \pm \mathit{0.07}$ against $0.16 \pm \mathit{0.06}$ for the females.

Constant survival was estimated to be $0.65 \pm \mathit{0.11}$ and $0.66 \pm \mathit{0.11}$ under respectively model $\{p_., \phi_.\}$ and $\{p_g, \phi_.\}$. Under model $\{p_., \phi_g\}$, males had a higher survival probability: $0.69 \pm \mathit{0.12}$ against $0.59 \pm \mathit{0.13}$ for females. This discrepancy between males and females may suggest two things: either the females have a lower true survival rate or they have a higher chance of leaving the population permanently (or for long periods).

Table 5-20- AIC for the CJS and related models for genetic data 1999-2005 and 1999-2005 without 2002/2004.

	AIC	
Model	1999-20005	1999-2005 without 02 & 04
$p_., \phi_.$	451.06	272.54
$p_g, \phi_.$	452.45	273.47
$p_., \phi_g$	453,05	273.88
$p_t, \phi_.$	447.82	277.95
$p_{t+g}, \phi_.$	449.09	278.93
p_g, ϕ_g	455.37	275.46

The capture probabilities estimated with the two-source M_0 model applied to the photographic data in Table 5-18 appeared very small compared to the corresponding capture probabilities estimated with the CJS model, although very close to the estimated capture probability in 2005 with the photographic data and in 2002 and 2004 with the genetic data: the probability p and g that a whale was sampled respectively by photo-identification and genetics on any occasion was estimated to be 0.03 ± 0.01 and 0.04 ± 0.01. However, the probabilities α that a whale was sampled by photo-identification given it has been sampled by genetics on the same occasion were very high: 0.85 ± 0.02 and 0.87 ± 0.02 with respectively the combined dataset with all photographs and under the quality-control protocol.

Information provided by the analysis with the CJS framework on capture probabilities from photographic and genetic data with single-state open-population models led to four conclusions:

1) there might be a small heterogeneity in capture probability among individuals of the population, that could be based on sex, although no other source of heterogeneity could be tested,

2) there might be temporal heterogeneity in capture probabilities, most likely arising from an heterogeneous sampling effort,

3) estimated capture probabilities in genetics are slightly smaller than those obtained with photo-identification, and

4) capture probabilities for marked individuals are around 0.05-0.26 within both sampling methods.

5.4.5. Two-set estimation of Survival

In the previous section, capture probabilities and apparent survival probabilities were estimated using CJS-class of models run separately on the genetic and photographic data and estimates of survival based on the genetic data often appeared lower than those based on photographic data. As described earlier, in section 5.3.5, the approximation with the multiplication of the likelihoods of the CJS models on both sampling methods allowed the comparison between models where the parameter of apparent survival was constrained to be the same across the two sampling methods (denoted $\phi_.$) and those where it varied with the sampling methods (ϕ_m). As capture probabilities surely cannot be the same between the two sampling methods, only models where capture probabilities differed between the methods, i.e. $p_{m.}$, $p_{m.*t}$, were considered.

First of all, as shown in Table 5-21 and Table 5-22, program MARK often returned a survival estimate of 1 with a corresponding standard error of 0 (more precisely in the order of

10^{-7}) in models where survival varied with time, i.e. models $(p_{m.}, \phi_t)$, $(p_{m*t.}, \phi_t)$, $(p_{m.}, \phi_{m*t})$ and $(p_{m.*t}, \phi_{m*t})$. Such values for the SEs could be caused by some aspects of the data which prevented the parameter from being estimated. One solution would be to use the option of profile likelihood CI available in MARK. Unfortunately, the software systematically returned an error message when using this option. Moreover, with models $(p_{m*t.}, \phi_t)$ and $(p_{m.*t}, \phi_{m*t})$, program MARK returned small estimates with unreliable standard errors for year 2004 probably due sparse data. Therefore, as in the previous section, models where survival varied with time are not discussed further and four models were retained for comparison: models (p_m, ϕ_m), $(p_m, \phi_.)$, $(p_{m*t.}, \phi_m)$ and $(p_{m*t.}, \phi_.)$.

Models were classified based on the AICc: model $(p_{m*t.}, \phi_.)$ was the best model (respectively with all photographs and selected photographs, AICc= 924.11 or 833.03) followed by model $(p_{m*t.}, \phi_m)$ (AICc=926.12 or 834.57). Under the best model, model $(p_{m*t.}, \phi_.)$, the apparent survival was estimated to be 0.85 ± *0.05* with the genetic dataset and the dataset including all photographs (Table 5-21) and 0.87 ± *0.06* with the genetic dataset and the dataset under the QC protocol (Table 5-22). Under the second best model, model $(p_{m*t.}, \phi_m)$ which supports the inference of a different apparent survival between the two sampling methods, the apparent survival was estimated to be: 0.83 ± *0.08* with the genetic sampling (Table 5-21 and Table 5-22), 0.87 ± *0.07* and 0.92 ± *0.09* with the photographic sampling based respectively on all photographs (Table 5-21) and selected photographs (Table 5-22). These values for the survival were higher than those found in the previous section (Section 5.4.4) and standard errors smaller, for both the genetic data and the photographic data with all photographs: previously, with the best models for the genetic data, models $\{p_t, \phi_.\}$ and $\{p_{t+g}, \phi_.\}$, the apparent survival was estimated to be respectively 0.68 ± *0.12* and 0.68 ± *0.13*; and previously, with the best models for the complete photographic data, models $\{p_., \phi_.\}$ and $\{p_t, \phi_.\}$, the apparent survival was estimated to be respectively 0.65 ± *0.11* and 0.68 ± *0.12* (Table 5-24).

The value of apparent survival with the approximation of the CJS based on the genetic and the QC photographic datasets for the photographic method under model $(p_{m*t.}, \phi_m)$ was, however, exactly the same as previously reported with the QC photographic method alone (Table 5-24) with model $\{p_t, \phi_.\}$, i.e. 0.92 ± *0.09*.

Table 5-21- “Approximated” two-set CJS models and corresponding value of AICc and survival estimates with standard error and 95% CI lower and upper bounds with the genetic dataset and the dataset with all photographs.

Model	AICc	Year	Survival for photographic data				Survival for genetic data			
			Estimate	*se*	95% CI lower	95% CI upper	Estimate	*se*	95% CI lower	95% CI upper
$(p_{m*t.},\phi_{.})$	924.11	NA	**0.85**	*0.05*	0.73	0.93	**0.85**	*0.05*	0.73	0.93
$(p_{m.},\phi_{t})$	924.3	1999	**0.93**	*0.17*	0.07	1	**0.93**	*0.17*	0.07	1
		2000	**1**	*0*	1	1	**1**	*0*	1	1
		2001	**0.62**	*0.08*	0.44	0.76	**0.62**	*0.08*	0.44	0.76
		2002	**1**	*0*	1	1	**1**	*0*	1	1
		2003	**0.64**	*0.1*	0.43	0.81	**0.64**	*0.1*	0.43	0.81
		2004	**1**	*0*	1	1	**1**	*0*	1	1
$(p_{m*t.},\phi_{m})$	926.12	NA	**0.87**	*0.07*	0.68	0.95	**0.83**	*0.08*	0.63	0.94
$(p_{m.},\phi_{.})$	926.86	NA	**0.85**	*0.04*	0.75	0.92	**0.85**	*0.04*	0.75	0.92
$(p_{m.},\phi_{m})$	928.89	NA	**0.85**	*0.06*	0.7	0.93	**0.86**	*0.07*	0.67	0.95
$(p_{m*t.},\phi_{t})$	931.03	1999	**0.9**	*0.19*	0.12	1	**0.9**	*0.19*	0.12	1
		2000	**0.97**	*0.19*	0	1	**0.97**	*0.19*	0	1
		2001	**0.66**	*0.15*	0.35	0.88	**0.66**	*0.15*	0.35	0.88
		2002	**0.95**	*0.26*	0	1	**0.95**	*0.26*	0	1
		2003	**0.91**	*0.32*	0	1	**0.91**	*0.32*	0	1
		2004	**0.24**	*33.68*	0	1	**0.24**	*33.68*	0	1
$(p_{m.},\phi_{m*t})$	936	1999	**1**	*0*	1	1	**0.76**	*0.24*	0.19	0.98
		2000	**1**	*0*	1	1	**1**	*0*	1	1
		2001	**0.62**	*0.11*	0.4	0.81	**0.61**	*0.13*	0.35	0.82
		2002	**1**	*0*	1	1	**1**	*0*	1	1
		2003	**0.62**	*0.13*	0.35	0.83	**0.66**	*0.16*	0.33	0.88
		2004	**1**	*0*	1	1	**1**	*0*	1	1
$(p_{m.*t},\phi_{m*t})$	940.5	1999	**1**	*0*	1	1	**0.68**	*0.26*	0.17	0.96
		2000	**0.99**	*0.23*	0	1	**0.98**	*0.3*	0	1
		2001	**0.63**	*0.15*	0.32	0.86	**0.73**	*0.26*	0.16	0.97
		2002	**1**	*0*	1	1	**0.85**	*0.34*	0.03	1
		2003	**0.79**	*0.33*	0.07	0.99	**1**	*0*	1	1
		2004	**0.41**	*177.1*	0	1	**0.34**	*60.53*	0	1

NA=not applicable

Table 5-22- “Approximated” two-set CJS models and corresponding value of AICc and survival estimates with standard error and 95% CI lower and upper bounds with the genetic dataset and the dataset with selected photographs (QC protocol).

Model	AICc	Year	Survival for photographic data				Survival for genetic data			
			Estimate	*se*	95% CI lower	95% CI upper	Estimate	*se*	95% CI lower	95% CI upper
$(p_{m*t.}, \phi_{.})$	833.03	NA	**0.87**	*0.06*	0.71	0.95	**0.87**	*0.06*	0.71	0.95
$(p_{m*t.}, \phi_{m})$	834.57	NA	**0.92**	*0.09*	0.49	0.99	**0.83**	*0.08*	0.63	0.94
$(p_{m*t.}, \phi_{t})$	839.76	1999	**0.95**	*0.2*	0	1	**0.95**	*0.2*	0	1
		2000	**0.96**	*0.19*	0	1	**0.96**	*0.19*	0	1
		2001	**0.95**	*0.26*	0	1	**0.95**	*0.26*	0	1
		2002	**0.65**	*0.21*	0.22	0.92	**0.65**	*0.21*	0.22	0.92
		2003	**0.8**	*0.34*	0.06	1	**0.8**	*0.34*	0.06	1
		2004	**0.51**	*77.29*	0	1	**0.51**	*77.29*	0	1
$(p_{m.}, \phi_{t})$	843.82	1999	**1**	*0*	0	1	**1**	*0*	0	1
		2000	**1**	*0*	1	1	**1**	*0*	1	1
		2001	**0.68**	*0.1*	0.46	0.84	**0.68**	*0.1*	0.46	0.84
		2002	**1**	*0*	1	1	**1**	*0*	1	1
		2003	**0.52**	*0.1*	0.33	0.71	**0.52**	*0.1*	0.33	0.71
		2004	**0.92**	*0.21*	0.07	1	**0.92**	*0.21*	0.07	1
$(p_{m.}, \phi_{m*t})$	845.06	1999	**1**	*0*	1	1	**0.76**	*0.24*	0.19	0.98
		2000	**1**	*0*	1	1	**1**	*0*	1	1
		2001	**0.72**	*0.14*	0.39	0.91	**0.61**	*0.13*	0.35	0.82
		2002	**1**	*0*	1	1	**1**	*0*	1	1
		2003	**0.46**	*0.14*	0.22	0.72	**0.66**	*0.16*	0.33	0.88
		2004	**0.35**	*0.16*	0.11	0.69	**1**	*0*	1	1
$(p_{m.*t}, \phi_{m*t})$	846.32	1999	**1**	*0*	1	1	**0.68**	*0.26*	0.17	0.96
		2000	**1**	*0*	1	1	**0.98**	*0.3*	0	1
		2001	**1**	*0*	1	1	**0.73**	*0.26*	0.16	0.97
		2002	**0.61**	*0.23*	0.19	0.91	**0.85**	*0.34*	0.03	1
		2003	**0.35**	*0.23*	0.07	0.79	**1**	*0*	1	1
		2004	**0.31**	*57.84*	0	1	**0.34**	*60.53*	0	1
$(p_{m.}, \phi_{.})$	846.64	NA	**0.83**	*0.05*	0.71	0.9	**0.83**	*0.05*	0.71	0.9
$(p_{m.}, \phi_{m})$	848.37	NA	**0.8**	*0.07*	0.64	0.9	**0.86**	*0.07*	0.67	0.95

NA=not applicable

So the approximation with the multiplication of the likelihoods based on the two sampling methods usually led to greater estimates of apparent survival than those from the separate models based on each type of data (photographic or genetic). This may be due to many individuals appearing in both datasets. When the two-set model with the approximation indicated that the apparent survival was not the same between the two sampling methods, the estimate based on the genetic data was, as previously reported, smaller than the estimate based on the photographic data. This probably suggested that the loss of animals by emigration was more easily detected with the genetic sampling than it was with the photographic sampling.

Corrected estimates for survival $\hat{\phi}_t$ could also be obtained with the TSJS model as shown in chapter one. Except in 2003, the survival estimates reported in Table 5-23 were very similar whether they were based on the combined dataset with all photographs or with selected photographs. These survival estimates were also of the same order as those reported previously with the approximation of the CJS model, i.e. greater than 0.8. However, standard errors of the TSJS estimates of survival were large (>0.2), generally at least 3 times greater than those obtained with the approximation of the CJS model. This is consistent with the approximation of the CJS model using data where some individuals are counted twice and therefore using more data than it should be while the TSJS model corrects for duplicated animals and therefore have larger confidence intervals.

In the case of whales, it is reasonable to assume that survival is independent of time and to use a straight arithmetic mean of the estimates of survival (Buckland, 1990). Buckland (1990) also showed that survival estimates corresponding to the last few occasions of sampling can be smaller than earlier estimates in the presence of heterogeneous capture probabilities which was likely to be the case here. If the unreasonable estimate of 2003 was deleted, the annual survival rate, i.e. mean(2), was estimated to be 0.86 ± 0.05 (combined dataset with genetic and all photographs) and 0.86 ± 0.03 (combined dataset with genetic and selected photographs). These estimates might be expected to be underestimates of the true survival although the confidence intervals included most of the estimates found in the literature for humpback whales (Buckland, 1990; Chittleborough, 1965; Gabriele et al., 2001; Mizroch et al., 2004). But, as explained before, these parameters are really estimating loss to the population.

Table 5-23- Survival estimates and corresponding standard error (se) and 95% CI lower and upper bounds under the TSJS model for the combined datasets 1999-2005 with all photographs and selected photographs.

Dataset	genetic and all photographs				genetic and selected photographs			
Year	$\hat{\phi}_t$	*se*	95% CI lower	95% CI upper	$\hat{\phi}_t$	*se*	95% CI lower	95% CI upper
1999	**0.84**	*0.22*	0.4	1	**0.86**	*0.23*	0.41	1
2000	**0.93**	*0.23*	0.49	1	**0.9**	*0.23*	0.45	1
2001	**0.85**	*0.24*	0.38	1	**0.86**	*0.32*	0.23	1
2002	**0.84**	*0.3*	0.25	1	**0.83**	*0.42*	0.01	1
2003	**0.44**	*0.21*	0.03	0.85	**0.42**	*0.29*	0	0.99
Mean	**0.78**	*0.19*	0.41	1	**0.77**	*0.2*	0.38	1
Mean(2)	**0.86**	*0.05*	0.76	0.96	**0.86**	*0.03*	0.8	0.92

Finally, Table 5-24 summarizes the survival estimates given by the best models (based on the AIC or the AICc) under the CJS, TSJS (ignoring 2003) and two-set CJS approaches, highlighting the broad range of values and the inconsistency between the different approaches.

Table 5-24-Survival estimates or range of survival estimates and corresponding standard error with the best model(s) under the CJS, TSJS and two-set CJS approaches with the different datasets 1999-2005**.**

Dataset - Approach	All photographs	Selected photo-graphs	Genetic	genetic and all photographs	genetic and selected photographs
CJS	**0.65**(*0.11*)-**0.68**(*0.12*)	**0.92**(*0.09*)	**0.68**(*0.12*)	-	-
TSJS	-	-	-	**0.84**(*0.3*)-**0.93**(*0.23*)	**0.83**(*0.42*)-**0.9**(*0.23*)
two-set CJS	-	-	-	**0.62**(*0.08*)-1	**0.83**(*0.08*)-**0.92**(*0.09*)

5.4.6. Temporary emigration

Multistate models give an opportunity to investigate factors controlling, in particular, the process of movement of humpback whales between breeding grounds in the South Pacific. Using the multi-site capture history dataset 1999-2004 (where the sites are New Caledonia, French Polynesia, Tonga and Cook Island) models were built and run in M-SURGE. The six best models based on the AIC are displayed in Table 5-25 where F is the true survival, ψ is the transition probability, p is the capture probability. Different subscripts are used here to parameterize F, ψ, and p: “from” indicates a variation in the parameter dependent on the previous region the animal was, “to” a variation dependent on the current region where the individual is, “time” a time-dependent variation. Two operators can be used to combine the effect of previous region, current region and time to build more complex models: “*” denotes an interaction between factors and “+” a linear combination of the effects.

Table 5-25- AIC for multistate models using multi-site capture history data of Humpback whales between 1999 and 2004.

Model	Number of parameters	AIC
$F_{.}, \psi_{from+to}, p_{to*time}$	28	824.3
$F_{.}, \psi_{to}, p_{from*to*time}$	25	829.95
$F_{.}, \psi_{from+to+time}, p_{from*to*time}$	32	830
$F_{.}, \psi_{from}, p_{from*to*time}$	25	831.12
$F_{from+to}, \psi_{from+to}, p_{from*to*time}$	35	834.11
$F_{.}, \psi_{to}, p_{from+time}$	9	839.69

Based on the AIC, the best model was the CAS model $\{F_{.}, \psi_{from+to}, p_{to*time}\}$ for which the true survival was constant over the years and did not depend on the site of departure or the site of arrival ($F_{.} = 0.99 \pm 0.00$), the transition depended on the combination of site of departure with site of arrival and the probability of capture depended on the interaction between the site of arrival and on the year. The probabilities of interchange from one breeding ground to another are displayed in Table 5-26. The diagonal corresponds to the site fidelity. In the case of New Caledonia, there seemed to be interchange only with Tonga. Then, a whale first sighted in New Caledonia had a probability of 0.95 ± 0.03 of being seen again there, of 0.05 ± 0.01 of being seen in Tonga afterwards and of 0.01 ± 0.01 of having been seen before in Tonga.

Table 5-26- Estimates of the probabilities of transition of humpback whales between breeding grounds in the South Pacific, between 1999 and 2004, from the CAS model $\{F_{.}, \psi_{from+to}, p_{to*time}\}$.

from/to	NC	Tg	FP	CI
NC	**0.95** *(se=.03)*	**0.05** *(se=.03)*	**0**	**0**
Tg	**0.01** *(se=.01)*	**0.83** *(se=.15)*	**0.03** *(se=.02)*	**0.13** *(se= .15)*
FP	**0**	**0**	**1**	**0**
CI	**0**	**0.31** *(se=.43)*	**0**	**0.69** *(se=.43)*

NC = New Caledonia; Tg = Tonga; FP = French Polynesia; CI = Cook Island.

5.4.7. Transience and trap-dependence

The test 3.SR provided by U-CARE on the combined (photo and genetic) dataset 1999-2005 revealed a transience problem (2-sided test: p-value<< 0.000): some individuals passed through New Caledonia once with a very low probability of being captured again on a subsequent occasion.

Two separate datasets being available, it was interesting to see whether it was an issue with the genetic or the photo-identification data or with both or if this transience problem in the combined data was the result of many individuals appearing twice in the combined dataset. Test 3.SR run on the photographic catalogue 1999-2005 and on the genetic database 1999-2005 separately showed that the transience problem was present for both kinds of data (p-value<<0.05). Within the genetic dataset it was, however, possible to go deeper in the analysis of the transience: two groups (males and females) could be distinguished and test 3.SR was run on each group separately. From those tests, it appeared that the transient individuals were the males (p-value<<0.05), while the group of females did not show a detectable issue with transience (2-sided test p-value= 0.25).

As expected, trap-response was not a significant feature of the data from test 2.CT run on the combined data (2-sided test: p-value=0.2), i.e. biopsy sampling does not seem to detectably affect recapture.

5.5. Discussion

Several population size estimates have, in the past, been produced for the humpback population of New Caledonia using photo-identification or genetic data (Garrigue et al., 2004). While genetic and photographic data have been collected consistently since 1999, no attempt has been made yet to combine them in capture-recapture models to produce population size estimates. However, the need to merge both sources of data to estimate population was emphasized in Garrigue et al. (2004) and, from this example, questions arise in the absence of a way to use both datasets in one abundance model: which dataset to use and which model to believe? Would an average value be better? Average between sampling methods? Average between models for the same sampling method?

Investigations in the thesis have shown that both temporal variability and heterogeneity among individuals in capture probability appear to be present in the data, therefore violating the assumption of the JS and TSJS models of homogeneous capture probability among individuals and over time. Some multi-occasion closed population models have the advantage of handling heterogeneity. Here, however, the closure assumption is most likely violated given the length of the study (7 years) and the migratory behavior of the animals. Therefore, the problem in this analysis is similar to the question investigated in chapter four: does the violation of the assumption of closure have more impact on the population size estimates of the closed-population models than the violation of the assumption of homogeneous capture probability on the TSJS estimates?

The TSJS does not handle a high degree of heterogeneity among individuals in capture probability (see chapter three) but is more robust than the closed population estimators when this kind of heterogeneity in capture probability is small or the capture probability high (see chapter four). In the case of the humpback population in New Caledonia, heterogeneity among individuals in capture probability is certainly a factor to take into account but the degree is not known. Previous studies showed that females tend to have a lower capture probability than males on breeding ground, and that the number of individuals genotyped is biased towards males and that individuals are usually unequally available for the two sampling methods (Garrigue et al., 2004; Smith et al., 1999). For the structure of the heterogeneity in capture probability, investigations suggest that males tend to have a higher capture probability than females, especially in biopsy sampling (Garrigue et al., 2004; Smith et al., 1999). However, the discrepancy between capture probabilities of males and females is not large, which could give evidence towards a small to moderate heterogeneity in capture probability. Moreover, capture probabilities of marked individuals are estimated around 0.05-0.26 in both datasets and the average capture probability used in chapter four falls in this interval, even though the capture probabilities estimated with the CJS should be taken with caution as the extrapolation is valid only if the marked individuals are representative of the whole population. Thus, unless there are uncatchable animals, an issue that should be minimized by the double-sampling design, the situation in the data could be extrapolated from the results of the CJS model to be close to the simulation structure in chapter four in case 1, 2 or 3 under heterogeneity in capture probability and unequal sampling probability for the TSJS model: in such a case the TSJS estimator appears to be a fairly good estimator and to underestimate the abundance on average (possibly from 1 to 18% of the true population size but a greater underestimation is probably to be expected as the simulation results were based on a 10-occasion experiment and here the study was over 7 occasions). Moreover, the TSJS model assumes that the probability of capture is the same across sampling methods and differences in capture by each sampling method are only dealt with in the estimation of the I_{id} parameter. So heterogeneity is to be expected in the TSJS model since the sampling methods will usually be different. However, with an appropriate rate of simultaneous capture (see chapters two and three), this heterogeneity is handled by the TSJS model.

Given the present evidence of temporal variation in capture probability probably due to the small sampling effort in 2002 and 2004 compared to the other years, it might be advisable to ignore estimates from 2002 and 2004 in the open-population and Chapman modified Lincoln-Petersen estimators or to interpret them with caution. My results suggest that the temporal heterogeneity in capture probability may not be due to any biological reason but due to the sampling effort that varied yearly. Therefore, standardizing sampling effort over years in future work would be desirable.

Speculation about the kind of heterogeneity in capture probabilities forces us to run at least 5 closed-population models for both sampling methods (the genetic and the photographic data) and thus give a variety of estimates that the researcher has to choose from. Indeed these estimators are not MLEs so the classic model selection approach with the Akaike's Information Criterion is therefore not possible. The classifier from program CAPTURE selected model M_{th} as the most appropriate given the present data, which is not surprising given the evidence of a temporal and individual variability in capture probability found by other methods. As mentioned in Otis (1978), the usefulness of such a classifier declines with the capture probability: here evidence shows that the data could be of medium quality (following the Otis data qualifier) with an approximate average of capture probability of approximately 0.2. There is, thus, considerably less chance that the program selects an inappropriate model compared to the situation with poor data (average capture probability around 0.05) where it can select 34.7% of the time a model which is only appropriate 12.5% of the time as stated in Otis (1978). Model M_{th} could be the most suitable in the present case. Furthermore, with the three datasets available, models M_h by Chao and M_h using the Jackknife method may not perform well, as the tests in CAPTURE suggested. Generally, heterogeneity in capture probability results in negatively-biased estimates and, as shown in chapter four, closed population models perform well in some situations and poorly in others. The sample coverage approach developed by Chao (M_{hChao}) is usually biased downward when there is heterogeneity in capture probability among the members of the population (Chao and Lee, 1992), which is the case here. Model M_h using the Jackknife method performs poorly and can exhibit negative bias when data are sparse, a situation in which model M_h by Chao performs better, or when some individuals are not catchable (Otis et al., 1978), which is most likely the case here as well, as it appears that many individuals are catchable only by biopsy or only by photo-identification. However, the latter issue is probably only of concern for the photographic data, as there are considerably less individuals catchable only by photo-identification than there are by genetics alone. On the other hand, model M_h using the Jackknife method can overestimate the population size when almost all the individuals have been caught (Amstrup et al., 2005), which I do not think is likely here. Model M_{th} seems to be able to handle a greater degree of heterogeneity but between the three datasets available for multiple-occasion closed-population models, model M_{th}, supposedly the most suitable of the closed population ones using the classifier from program CAPTURE, gave very different results: firstly between the two photographic catalogues with estimates apart by a factor 1.29 and then between genetic and photographic datasets with population size greater for the genetic dataset by a factor 1.88 to 2.43. Moreover, in chapter four, model M_{th} was never the best model in the 6 cases of heterogeneity in capture probability. Consequently, I would not consider model M_{th} as reliable in the present analysis. The two-source M_0 model leads to results very similar to the results with model M_{th}, so very high compared to the results with the TSJS model. Under the two-source M_0 model, the probability of being sampled by both methods is very high and it was shown, in chapter four, that the two-source M_0 model leads to highly positively biased results when there is heterogeneity and a high average capture probability (cases 6 and 7, see chapter four), while the TSJS estimator gave very good results in such cases. Results from simulation in chapter four suggest that model M_t by Darroch performs well in the presence of a small heterogeneity and this model appeared fairly consistent through the simulation study. Therefore, I would consider model M_t by Darroch as a good candidate among the closed-population models. Finally, the modified Chapman's estimator seems to also greatly depend on the data it is based on and like the other models based on one type of data, the inconsistency between the two photographic catalogues and with the genetic data, along with the extraordinary range of estimates, can only confuse the ecologist.

The violation of the closure assumption leads to difficulties in interpreting closed-population model estimates and such estimates should be regarded as estimators for an entire superpopulation whose members move in and out of the study area (Kendall, 1999). In this study the assumption of closure is violated both geographically and demographically. The demographic non-closure, here through the process of death and birth, is similar to the scenario of "one entry and one exit" during the course of the experiment, therefore leading to biased closed-population estimates (Kendall, 1999). Violation of the geographical closure assumption has also been brought to light by the evidence of interchange between New Caledonia and neighboring breeding grounds shown in this chapter: this study is the first attempt to understand the stock structure of humpback whales in the South Pacific and has not been published at the time of the writing of the present thesis. The interchange probabilities could be larger than the ones provided here. Indeed there is variation among the study areas in sampling effort, size of the area, geographic accessibility. Despite those sampling difficulties, it is clear that interchange, hence temporal emigration, exists and should not be ignored in the discussion of assumption violations. However, it is not known whether this emigration is completely at random, Markovian, or driven by climatic pseudocycles like the ENSO. The consequences of the violation of the geographical closure assumption for closed-population models depend on the nature of the movement process: if the emigration movement is random, unless there is heterogeneity among individuals in capture probability, there should be no bias in closed-population estimators (Kendall, 1999). Finally, results on the apparent survival estimated with the CJS model could also highlight geographic openness of the population. Since it is almost certain that the true survival is high (also highlighted by the CAS model where true survival was estimated as 0.99) for the humpbacks, the relatively low apparent survival would reflect a probable high rate of permanent or long term emigration during the course of this study (again in the form of “one exit”, therefore leading to bias in the closed-population estimates). Therefore, the appropriate closed-population estimates here are most-likely positively biased by the violation of the assumption of closure, with a presumably larger overestimation than the overestimation found in chapter four since the population here seems more open than the simulated population. The TSJS model is certainly negatively biased by the violation of the assumption of homogeneous capture probability.

Combining the photographic and the genetic sources using the approximated CJS models or the corrected TSJS estimates of survival generally led to smaller survival estimates than those found in the literature (Buckland, 1990; Chittleborough, 1965; Gabriele et al., 2001; Mizroch et al., 2004). However, Buckland (1990) recommended, for reliable survival estimation, capture probabilities higher than 0.2 (here capture probabilities were estimated around 0.05-0.26) and ideally at least 10 years of an intensive research program (here only 7 years were available, with two years, 2002 and 2004, with a small sampling effort). Results on the apparent survival suggested that estimates differed between the genetic sampling and the photographic sampling, with an apparent survival probability always greater with the photographic sampling than with the genetic sampling. It is unlikely that, for a species such as humpback whale, the true survival differed between the two sampling methods because that would mean that these sampling methods sampled two populations with different survival rates. However, it is possible that this discrepancy between apparent survival estimates indicated that the loss of animals through permanent emigration was higher with the genetic sampling and that there was a portion of the population that were transient individuals more likely to be sampled by the genetic sampling. In such case, a combined analysis where the survival is constrained to be the same across the sampling methods leads to the loss of valuable information.

One of the assumptions of the model is that captures are independent of one another. This suggests that individuals should be independent of each other. However, even in remotely sociable species, there is always some degree of relationship between individuals that begets the violation of this assumption. The humpback whale is no exception. Associations between adults are known to be temporary but mother and calf association on breeding grounds are stable throughout the season. Thus it might be advisable to ignore calves for the purpose of population size estimation with the TSJS model, even though the consequences of keeping them in the datasets are unknown.

Among the possible violation of assumptions of the TSJS model, the misreading of tags is believed to be negligible in both the genetic and photographic data thanks to a rigorous laboratory protocol and to the experience of the team in matching. However, if misreading of tags is technically inevitable, researchers should take their results with caution as this may lead to overestimated population sizes along with a loss in precision in the estimation and therefore potentially affect conclusions and mislead researchers. In the case of the New Caledonian humpback whale population, estimation using all the photographs does not lead to a clear trend in the population dynamics. However, all open population models (JS, weighted JS and TSJS models) using the photographic data based on the most rigorous protocol (i.e. the QC protocol, therefore removing the chance of misread tags with the photographic data) agree on the fact that, since 2001 or 2002, the sampled population is declining.

With the evidence provided by the present TSJS model, the humpback whale population of New Caledonia was estimated at less than 500 individuals in 2004 and may be declining. In addition, the population size between 1995 and 2001 was estimated by Garrigue et al. (2004) using two closed-population models: the weighted mean of the Petersen model and the Chapman's modification of the Petersen 2-sample model. With the former, the abundance was 533 (CV=0.15) with the genetic data and 327 (CV=0.11) with the photographic data, and with the later 643 (CV=0.18) and 574 (CV=0.18), respectively. So, even though the estimation using the TSJS model is probably negatively biased by heterogeneity in capture probability among individuals, these new results emphasize the potential vulnerability of the New Caledonian humpback whale population and the need for a longer and rigorous monitoring study. Future work in this region would benefit from a different sampling design. A robust-design type of experiment (Pollock, 1982) would be especially recommended here as in the long term the population is open but during the capture occasions that usually take place over a period of two months, the demographic closure assumption holds. The robust design could help recognizing and measuring temporary immigration that is suspected in the humpback whale population in New Caledonia and would allow the estimation of more population parameters than the present study design reasonably permits. Then the estimation of population size at each secondary period with closed-population models could be faithfully compared to the abundance given on the primary periods by open-population estimators such as the TSJS estimator. Capture probabilities for primary periods should increase resulting in more precise estimates and better discrimination among models. A pitfall of the robust design is the extra sampling effort compared to a JS experiment because the design implies sampling at both primary and secondary time scales but in this case, it is being done anyway.

CONCLUSIONS

The aim of the present thesis is to provide a solution to the extremely difficult task associated with the estimation of abundance while adding another difficulty to it with the use of two partially-overlapping sources of information. One objective was to emphasize to researchers the potential benefits of combining sources of information (Barker, 1997; Barker et al., 2004; Barker and White, 2001; Forcada and Robinson, 2006; Salewski et al., 2007) versus the traditional approaches based on one source. In this context, a new assessment methodology for the estimation of abundance could be useful for many species that are sampled by different methods: birds (ringing and acoustics) (Laiolo et al., 2007; Salewski et al., 2007), bats (ringing and genetics) (Rivers et al., 2005; Senior et al., 2005), whales (photo-identification and genetics) (Garrigue et al., 2004), seals (tagging and photo-identification) (Forcada and Robinson, 2006). The novel approach proposed here, the two-source Jolly-Seber (TSJS) model, is an extension of the classic Jolly-Seber model and is therefore relevant to open population and to long-term monitoring studies on long-lived animals for which the classic JS model is often used.

Although mathematical models inevitably simplify the biological complexity characterizing these animal populations, one has to identify the goal to pursue in order to choose which of the multiple approaches available today to use. Do we wish to obtain the size of the population at specific times? Do we wish to compare the actual abundance with the one of 10 years ago? Do we want to monitor a population over a period of time? And so on. In many cases even answering these questions to narrow the choice of models still leads to a broad list of possible methods. And the multiple sources of uncertainty about biological process describing these animal populations do not help identifying the optimal approach. Nevertheless, I attempted here to provide another method to answer a relatively-new situation in population size assessment: when two datasets based on two different sampling methods are available for the same population, which one should we use to estimate the size of this population? I suggest a sensible solution is that all sources of information should be used to make inference on abundance. Moreover, double sampling is an efficient approach to increase the sample size without increasing the length of the experiment.

This estimation method using the original Jolly-Seber moment estimator in which the I_{id} parameter is plugged-in is a simple modification of a well accepted and widely used method and may not face the usual reluctance on the part of the field ecologists. It avoids intensive computer work and provides simple calculations that can even be checked by hand. However, I am aware that such a method does not make full use of the modern statistical tools available (Bayesian framework (Brooks et al., 2004; King and Brooks, 2001; Schofield and Barker, 2008), more sophisticated likelihood-based methods (Barker and White, 2004; Schwarz and Arnason, 1996)…). Nevertheless, I chose, with the present method, to match the complexity of the model with the intended use to create a model no more complex than necessary. I also show how survival and recruitment can be estimated using the TSJS approach, therefore extending the use of the model to more than just abundance estimation.

In the present thesis, the verification of the robustness of the method to departure from the underlying assumptions was done using a specific simulation structure. This particular simulation structure is, however, relevant to a broad range of populations, i.e. relatively long-lived, slow-reproducing with short sampling frequency relative to longevity. It is always hard to generalize results when it comes to heterogeneity in capture probabilities. Ideally simulations matching as closely as possible the situation should be run to test the population size estimators and the aim here was to be able to extrapolate (while being careful with the extrapolation) the results found in the simulation to the case study in chapter five.

Unbiased estimates were obtained through the simulation study when all assumptions of the TSJS model held, for a range of parameter values. However, a researcher will be more interested in the validity of the method when underlying assumptions are violated, often the case in ecological studies. Interpretation of the analytical results depends on the validity of the underlying assumptions. For the TSJS model, the assumptions are: (1) the capture probabilities are the same over time and across individuals within each capture method, (2) all animals have the same probability of survival between occasion t and occasion t+1, (3) marked animals do not lose their mark and marks are not overlooked, (4) sampling periods are short enough to avoid death during the sampling period, (5) emigration is permanent, (6) capture probabilities are independent of each other, (7) a sampling period can include multiple capture occasions: in this case only one event is recorded, the others ignored. If the individual is available by both methods and is captured at least once, then it should be captured by both simultaneously at least once during this sampling period, (8) having a capture by one method in the capture history does not depend on whether or not the animal has been captured by any other method.

Studies have shown the limits of the robustness of the Jolly-Seber estimator due to the failure of assumption (1) (Carothers, 1973; Gilbert, 1973) and simulation studies on the TSJS estimator showed similar limitations. This assumption is the most likely to be violated and therefore the validity of the TSJS model was thoroughly checked with departure from this assumption. The TSJS model proves to be relatively efficient when heterogeneity is small or when the average capture probability is high (>0.5) (see chapter three). When heterogeneity in capture probability among individuals is expected or suspected, researchers should be aware that the population size will be underestimated with a degree depending on the degree of heterogeneity. There are two sources of heterogeneity in capture probabilities (Crespin et al., 2008). The first source is the extrinsic heterogeneity that results from the design experiment. For example, bear studies where grid-sampling is used usually exhibits an edge effect (Jensen, 1975): bears whose home ranges are entirely on the grid are at a higher risk of capture than those whose home ranges straddle the grid (Boulanger et al., 2004b). A sampling design where some regions (or habitats) are more extensively sampled than others and where data are pooled at a regional or habitat level will also necessarily display extrinsic heterogeneity (Mizroch et al., 2004; Thompson, 2004). Care should be given to the sampling design to decrease extrinsic heterogeneity. For instance, in bat studies, effort should be made to construct an appropriate sample frame which matches as closely as possible the target population (Thompson, 2004); in bear studies, grid design should take into account the topography and the number of bears expected (Boulanger et al., 2002). The second source of heterogeneity in capture probability is the intrinsic heterogeneity which conveys biological information and depends on observable characteristics, such as gender, colours (Pradel et al., 1997), and on less obvious features such as social or reproductive status (Summerlin and Wolfe, 1973). In chapter four, I show that using each type of data separately could be less efficient, in terms of both precision and bias, than the combined approach developed here. I show that the underestimation with the TSJS model will always be lesser than the one with the classic JS model on just one source of information when the capture probabilities vary among individuals. Results of chapter four also demonstrate that, for closed-population estimators, the balance of the underestimation due to the heterogeneous capture probability and the overestimation expected due to the violation of the closure assumption (of the form of one entry and one exit during the study period, e.g. (Kendall, 1999)) falls in favour of an overall overestimation. Therefore, with an open-population with a high survival rate and exhibiting heterogeneous capture probabilities among individuals, closed-population estimators are likely to overestimate the population size at that site. The calculated value should be interpreted as a superpopulation estimate (Boulanger and McLellan, 2001; Boulanger et al., 2002; Kendall, 1999).

The use of multiple sampling methods is therefore potentially a good approach in sampling design to maximize effectively the number of catchable animals, thus decreasing heterogeneity in capture probabilities and ensuring that marked and unmarked animals in the sampled population have similar probabilities of entering the sample, without having to dilute the sampling effort over a large area. And as it is important to control variation in a sampling design, this methodology could provide a useful way to reduce variation by increasing the sample size and, hence, to increase the estimator precision.

Assumption (2) concerns the survival that is assumed equal among individuals. While violation of this assumption should not bias the population size estimate and was not explored in the present thesis, survival is an important parameter in population dynamics that can increase understanding of causes of variation in population size and therefore requires consideration. With two overlapping sources of data, there are, at present, two ways survival can be estimated: using the approach of the TSJS model based on the ad hoc JS model (see p.34) and using an approximation based on the CJS framework (see p.160). The first approach uses the probabilistic framework with the I_{id} parameter to correct the classic JS estimates for overlap. The second approach is based on a more flexible framework, allowing both capture probabilities and survival to be modeled as functions of external covariates but ignores the potential overlapping between the two sources of data. Therefore, I would not recommend the survival to be estimated this way. Moreover, results in chapter five highlight that a combined analysis, like the TSJS method, where the survival is constrained to be the same across the sampling method could lead to the loss of valuable information on the characteristics of the populations sampled by the two sampling methods. Therefore, researchers should combine data with caution in survival analysis.

Assumptions (3) can be violated in various cases. In studies using photographic tags of natural marks (Karanth and Nichols, 1998; Meekan et al., 2006), marks can be unrecognized because of a natural change of patterns or because of a human matching mistake. The violation of this assumption in such studies can therefore be minimized by a rigorous matching protocol involving at least two experienced workers and by using only good quality photographs (Stevick et al., 2001). Studies with visual recaptures, e.g. visual recapture of seals (Schwarz and Stobo, 1999) or visual recapture in bird ringing studies will tend to be more prone to violation of this assumption than photographic tagging. In genetic studies, misidentification will be most likely of the form of false negative error and result in the creation of new “ghost” individuals (Stevick et al., 2001). Misidentification that results in the creation of new individuals will result in an overestimation of the population size (Stevick et al., 2001; Yoshizaki et al., 2009). In chapters three and four, I show that the TSJS model is relatively efficient in handling such misidentification as long as the misidentification is homogeneous within the population. This is not surprising because the TSJS model is prone to an underestimation of the population size which can be counterbalanced by the overestimation due to tag misreading. Therefore, the presence of a small homogeneous misidentification rate (<5%) in the data should not be an issue with the TSJS approach, similar to what was found for JS estimates (Arnason and Mills, 1981) as long as researchers are aware of it. In the specific case of the New Caledonian humpback whale study, photographic matching involves a minimum of two experienced researchers so mismatch is unlikely. Concerning the genetic data, the field protocol provides good-quality DNA (i.e. skin biopsy) and re-run of problematic samples is systematic, so mismatch is also unlikely.

The TSJS model allows for an entry and one exit from the study area during the length of the experiment and therefore assumption (5) will be violated in studies where temporary emigration is present, i.e. individuals enter and exit the study sites several times (Kendall and Bjorkland, 2001). This temporary emigration can have an ecologically meaningful interpretation, e.g. home range of individuals extending outside the study area (Boulanger et al., 2002), being a temporary emigrant is equivalent to being a non-breeder in bird studies

(Pradel and Lebreton, 1999). Concerning the case study in the present thesis, some individuals have been sighted in other grounds in the South Pacific. Although the mechanism of the interchange between neighboring breeding grounds has just started to be studied, it seems unlikely that emigration is permanent. However, this needs to be confirmed and a similar sampling effort should be undertaken in each breeding ground not to minimize this possible issue.

Assumption (6) requires independence of the individuals for capture. Surely this assumption can rarely hold for social species that live in groups, e.g., gorillas, elephants, wolves. This assumption can also be violated to some extent in species that display temporary associations.

Non-violation of assumption (7) is directly contingent on the sampling protocol used in the field and is at risk of violation when the primary sampling occasions include several secondary sampling occasions, such as in a robust design experiment, or/and when several “teams” survey simultaneously the same area, i.e. the same population.

Assumption (8) will inevitably be at risk in studies where animals are likely to become trap-shy or trap-happy after a capture. Behavioral response can be a problematic source of variation and there is often no way to fully eliminate the response: prebaiting (placing traps few days prior to the actual trap is set) can help reducing the trap-happy behavior or minimizing trap-shy behaviour can be accomplished by reducing the handling time. Nevertheless, if trap-shy/happy behavior is suspected (e.g number of captures decreases with time, number of captures increases with time) in one of the two sampling methods or in both, I would not recommend the use of the TSJS model because, in many studies, behavioral response will not be the only source of variation and general patterns in the bias in the abundance estimates with multiple sources of variation are extremely difficult to predict.

There are therefore a large number of ways in which the TSJS can become biased. However, this is true of all the methods currently available. The case study on humpback whales in chapter five shows this clearly. However, there is here a consistent disagreement between datasets, between closed population models and between open and closed population models. These differences may suggest that there is more than just an issue with the estimation method: does this suggest two populations of whales, a change in whale behavior, or an unknown bias in the genetic data? This case study shows the consequences of the peculiarities of the situation being investigated and shows that, without a lot of extra information and simulations, the researchers may easily end up undecided as to what is happening.

I have shown through simulation studies, that the use of two sources of information rather than a single one can enhance the precision of the population size estimation. I also provide a comparison of the estimator with the Jolly-Seber model and closed-population methods and highlight the difficulty in comparing results coming from two approaches, i.e. open and closed population methodology. Matching sampling design with study goals is therefore essential for the validity of the data analysis and interpretation of the results. For monitoring purposes, the proposed method provides an efficient alternative to the existing approaches to deal with multiple sources of data to estimate abundance. At present, however, there is no way to evaluate the goodness-of-fit of the TSJS model. Therefore, a productive direction for future work would be the development of a goodness-of-fit procedure for the TSJS model in order to see if the model provides good adequacy in characterizing the field data. Future research on combining overlapping sources of information should also focus on the Crosbie-Manly-Arnason-Schwarz framework (Crosbie and Manly, 1985; Schwarz and Arnason, 1996) to develop a likelihood that would allow a more parsimonious modeling of population parameters than the TSJS model permits and would allow researchers to base their inference not only on the best model but on a set of models that seem to well fit the data.

However, ultimately, workers are at the mercy of their data. For example if the methods sample different populations then combining the two makes no sense. Similarly, long term studies for which open population methods are appropriate are vulnerable to changes in personnel, technology and the behavior of animals (even the effects of climate change on the sampling environment) that can lead to misleading conclusions, unless these are recorded and explicitly included in the analysis. It may be some time before methods have evolved sufficiently to accommodate all the things that can go wrong in a long term study – even if the information is available, for the entire study period, to model them. Until then, results from such studies must be interpreted with great caution.

A user's guide with R-codes implementing the two-source Jolly-Seber and the two-source M_0 models is available in Appendix 9.

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Appendix 1

Variances for Jolly-Seber parameters $\hat{M}_t$, $\hat{\phi}_t$, $\hat{B}_t$ and $\hat{p}_t$.

$$\operatorname{var}(\hat{M}_t | M_t) = [M_t - E(m_t)][M_t - E(m_t) + n_t]\left[\frac{1}{E(r_t)} - \frac{1}{n_t}\right]$$

$$\operatorname{var}(\hat{\phi}_t | \phi_t) = \phi_t^2 \left\{ \frac{[M_{t+1} - E(m_{t+1})] \times [M_{t+1} - E(m_{t+1}) + n_{t+1}]}{M_{t+1}^2} \times \left[\frac{1}{E(r_{t+1})} - \frac{1}{n_{t+1}}\right] \right.$$

$$\left. + \frac{[M_t - E(m_t)]}{[M_t - E(m_t) + n_t]} \times \left[\frac{1}{E(r_t)} - \frac{1}{n_t}\right] \right\}$$

$$\operatorname{var}(\hat{B}_t | B_t) = \left\{ \frac{B_t^2 [M_{t+1} - E(m_{t+1})] \times [M_{t+1} - E(m_{t+1}) + n_{t+1}]}{M_{t+1}^2} \right\} \times \left[\frac{1}{E(r_{t+1})} - \frac{1}{n_{t+1}}\right]$$

$$+ \frac{[M_t - E(m_t)]}{[M_t - E(m_t) + n_t]} \times \frac{[\phi_t n_t (N_t - M_t)]^2}{M_t^2} \times \left[\frac{1}{E(r_t)} - \frac{1}{n_t}\right]$$

$$+ \frac{[N_t - E(n_t)] \times (N_{t+1} - B_t) \times (N_t - M_t) \times (1 - \phi_t)}{N_t \times [M_t - E(m_t) + n_t]}$$

$$+ \frac{N_{t+1}[N_{t+1} - E(n_{t+1})] \times (N_{t+1} - M_{t+1})}{N_{t+1} \times E(m_{t+1})}$$

$$+ \frac{\phi_t^2 N_t [N_t - E(n_t)] \times (N_t - M_t)}{N_t E(m_t)}$$

$$\operatorname{var}(\hat{p}_t | p_t) = p_t^2 (1 - p_t)^2 \left[\frac{1}{E(r_t)} - \frac{1}{n_t} + \frac{1}{E(m_t)} + \frac{1}{E(z_t)}\right]$$

Appendix 2

R codes simulating the Venn diagram in Fig.1-1 and calculating the approximation of the proportion of individuals in F (Fig.1-1).

The following R code produces capture histories as illustrated in the Venn diagram Fig.1-1 and the calculation of the approximation of the proportion of individuals in F (see Fig.1-1):

```
out=NULL
histories=NULL
T=10          #NUMBER OF CAPTURE OCCASIONS
p=c(0.1, 0.1, 0.15)    #INSERT OCCASION-SPECIFIC CAPTURE PROBS HERE
respectively: prob getting a “1”, prob getting a “2”, prob getting a “3” on each
capture occasion

for (ind in 1:10000) # NUMBER OF DETECTED INDIVIDUALS during the
experiment
{
r=runif(T)
c=(r<p[1])*1
d=((r>p[1])&(r<sum(p[1:2])))*2
e= ((r>sum(p[1:2]))&(r<sum(p[1:3])))*3
f=c+d+e
histories=rbind(histories,f)
if (any(f==3) & !any(f==2) & !any(f==1)) {aa="A"} else
if (any(f==3) & !any(f==2) & any(f==1)) {aa="B"} else
if (any(f==3) & any(f==2) & !any(f==1)) {aa="C"} else
if (!any(f==3) & any(f==2) & !any(f==1)) {aa="D"} else
if (any(f==3) & any(f==2) & any(f==1)) {aa="E"} else
if (!any(f==3) & any(f==2) & any(f==1)) {aa="F"} else
if (!any(f==3) & !any(f==2) & any(f==1)) {aa="G"}
out=append(out,aa)
}

#GET THE TABLE OF FREQUENCIES OF A TO G
tt=table(out)

dd=rep(0,7)
names(dd)=c("A","B","C","D","E","F","G")
dd[match(names(tt),names(dd))]=tt
tt=dd #MAKING SURE THAT ANY ZERO OCCURRENCES ARE PUT IN SO
THAT A TO G ARE ALL THERE
zz1=sum(tt[c(2,5,6,7)])/ sum(tt) #P1=B+E+F+G
zz2=sum(tt[c(3:6)])/ sum(tt) #P2=C+D+E+F
zz3=sum(tt[c(1,2,3,5)])/sum(tt) #P3=A+B+C+E

#Get true F by subtraction
pp=tt/sum(tt) #GET PROBS OF A TO G
pp
#Get F by P1P2(1-P3)
zz1*zz2*(1-zz3)

#REAL VALUE
pp[6]
print("ratio of estimated to true value of F")
zz1*zz2*(1-zz3)/pp[6]

#histories[1:10,]
 P=(1-(1-p)^10)/(1-(1-sum(p))^10)
 round(P,digits=3)
round(c(zz1,zz2,zz3), digits=3)
```

Appendix 3

A linear model showing the effect of P_1, P_2, P_3 on the approximation of the proportion of individuals in F (Fig.1-1).

The effect of the probabilities P_1, P_2, P_3 on the adequacy of the approximation can be highlighted by fitting a simple linear model (to what is clearly non-linear, but apparently monotonic):

$$X_i = \beta_0 + \beta_1 (P_1 + P_2)_i + \beta_2 P_{3i} + \varepsilon_i \text{ (a)}$$

where X_i is the proportion of individuals in F,

β_0 is the intercept,

β_1 is the regression coefficient associated with $(P_1 + P_2)$,

β_2 is the regression coefficient associated with P_3,

ε_i is the error term.

N.B.: P_1 and P_2 are summed because they are interchangeable in the estimator.

Results in Table A and Table B show that P_3 has the greatest effect on the approximation of the proportion of unidentified overlap: as the value of P_3 increases, the value of the approximation of the proportion of individuals in F decreases, therefore leading to an increase of the value of the I_{id} parameter. This effect does not seem much affected by the number of capture occasions in the experiment. However, as the number of capture occasions increases, the positive effect of $(P_1 + P_2)$ increases, counterbalancing the negative effect of P_3 on the approximation of the proportion of unidentified overlap.

Table A- Results of the simple linear model (a) for a 5-occasion experiment.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	1.06028	0.07915	13.396	2.25E-09	***
sum(P1+P2)	0.09652	0.0384	2.513	0.0248	*
P3	-0.57812	0.07275	-7.947	1.48E-06	***

Table B- Results of the simple linear model (a) for a 10-occasion experiment.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	0.96062	0.10405	9.232	4.51E-07	***
Sum(P1+P2)	0.22375	0.03766	5.941	4.90E-05	***
P3	-0.54728	0.09352	-5.852	5.67E-05	***

Appendix 4

Additional 2D views for figures 2-4, 2-5, 2-7, 2-9, 2-10, 2-11, 2-12 and 2-15.

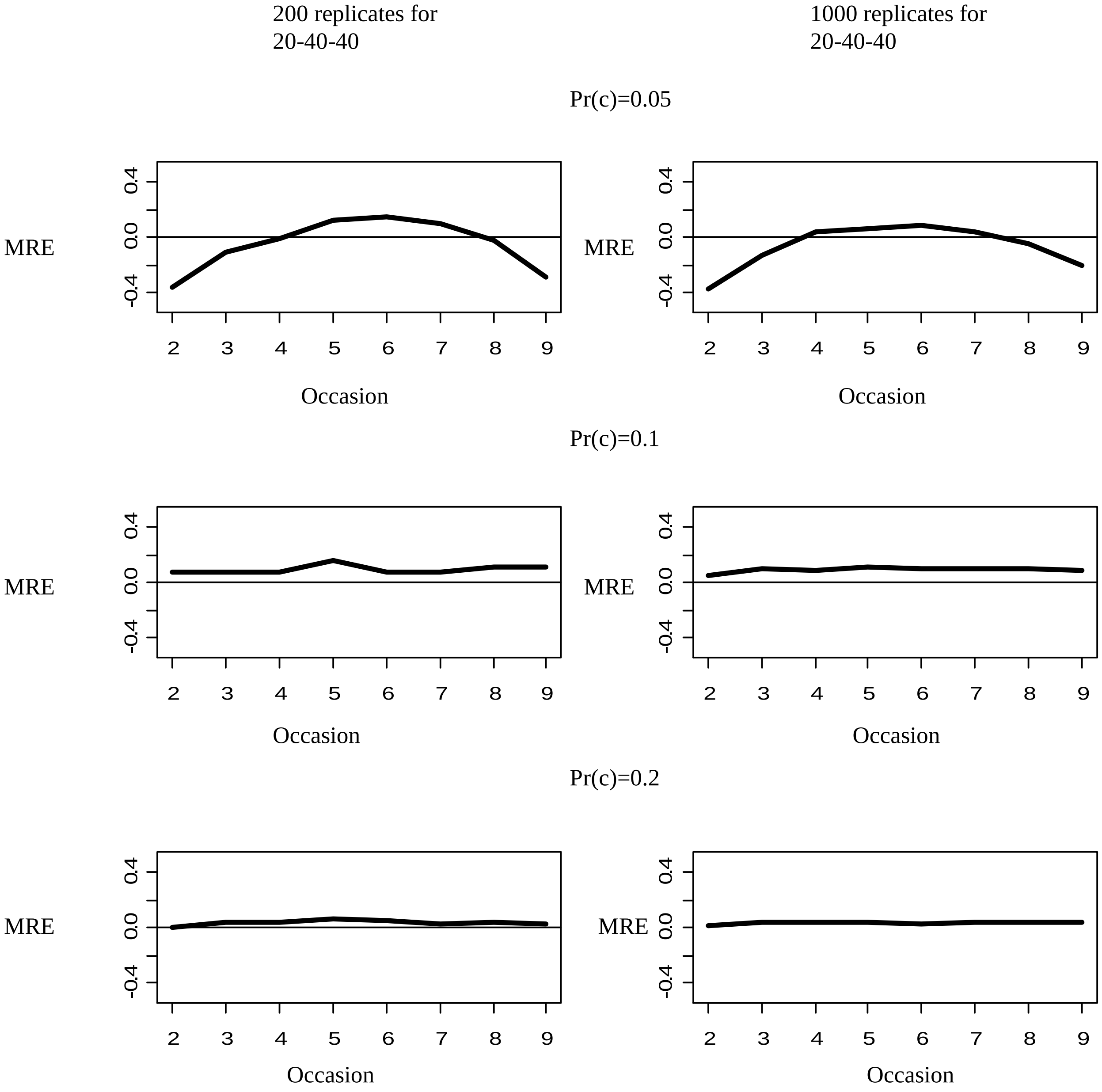


Fig.A- Additional 2D views for figures 2-4 and 2-5.

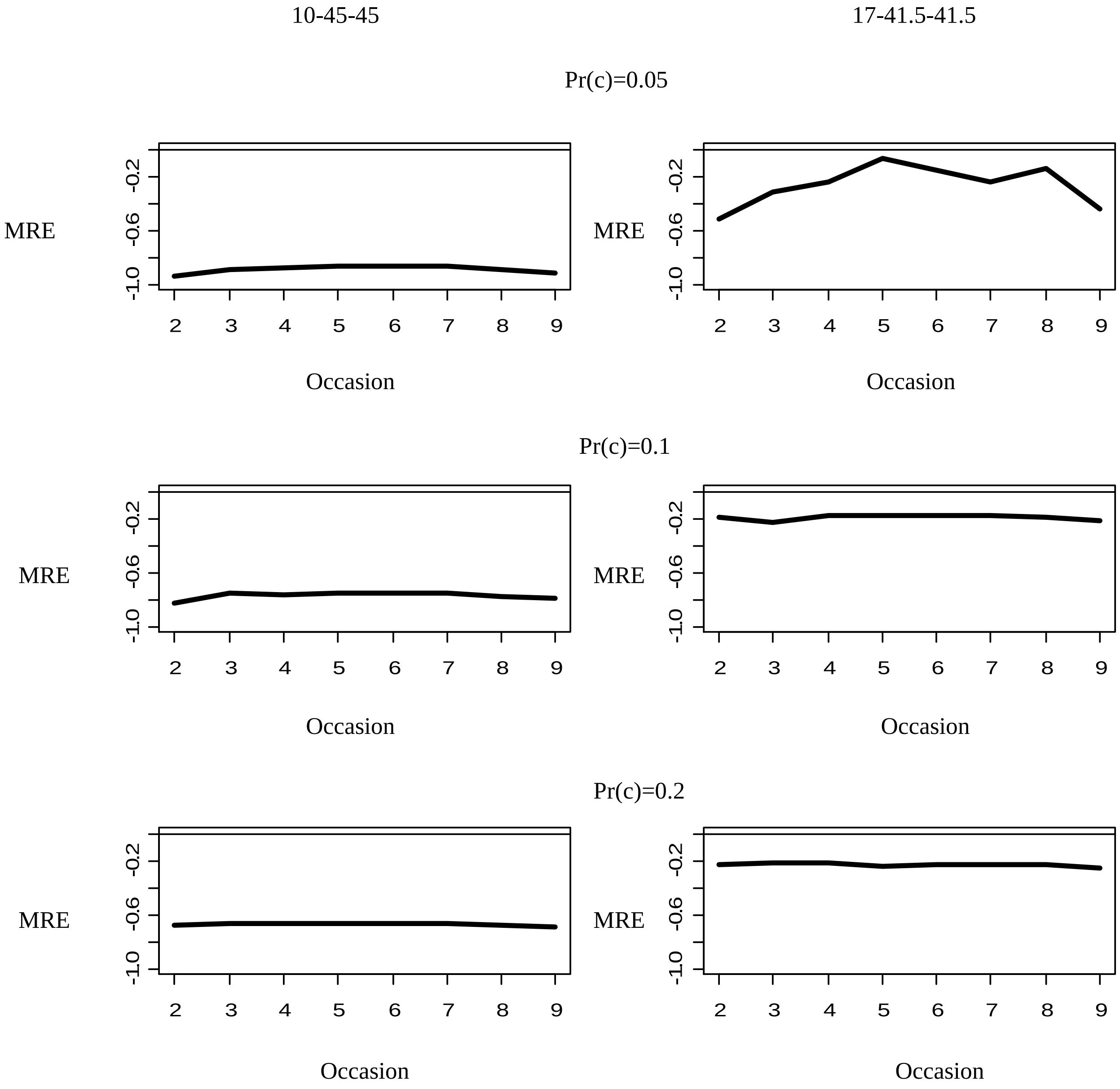


Fig.B- Additional 2D views for figure 2-7.

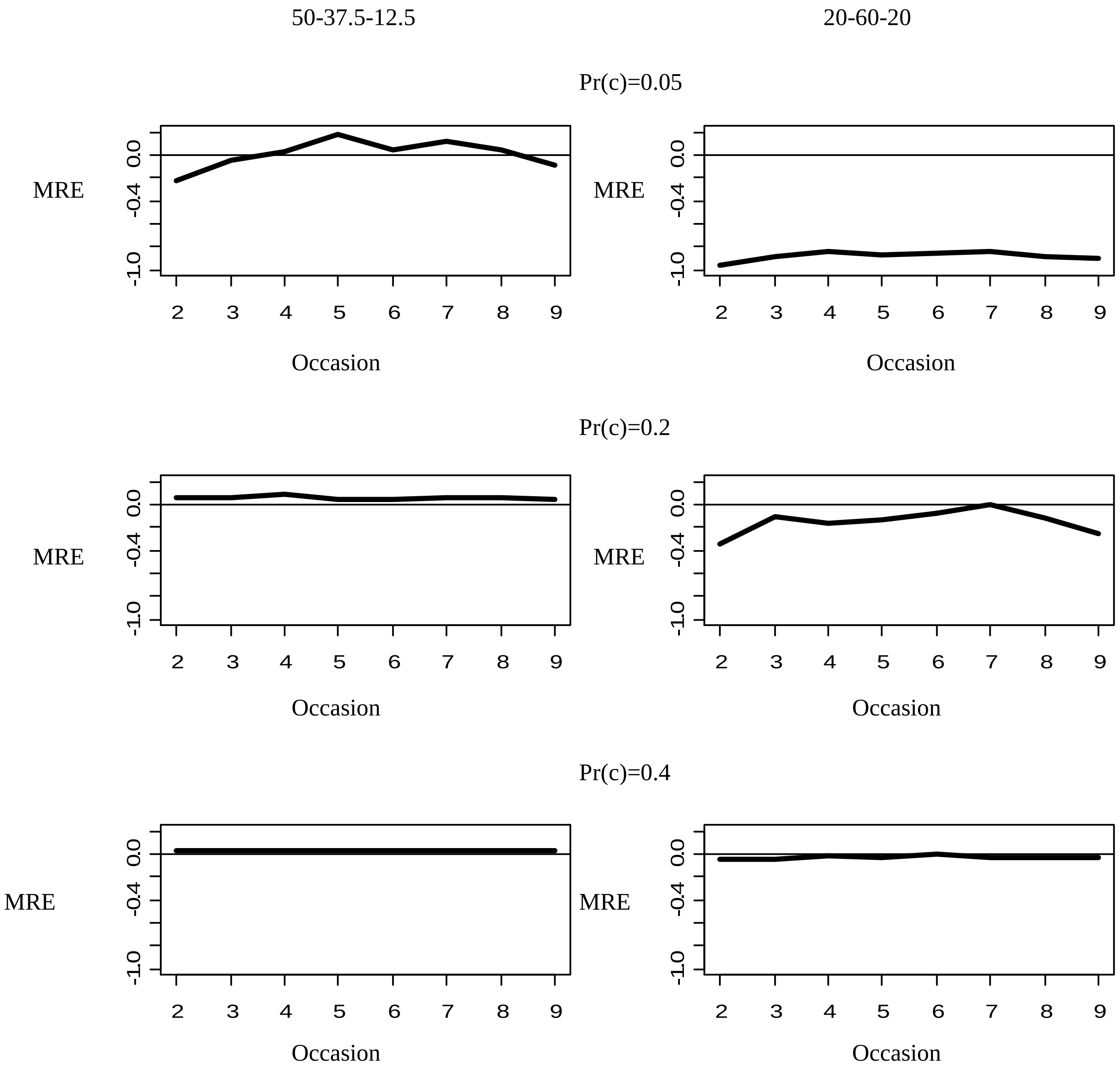


Fig.C- Additional 2D views for figure 2-9.

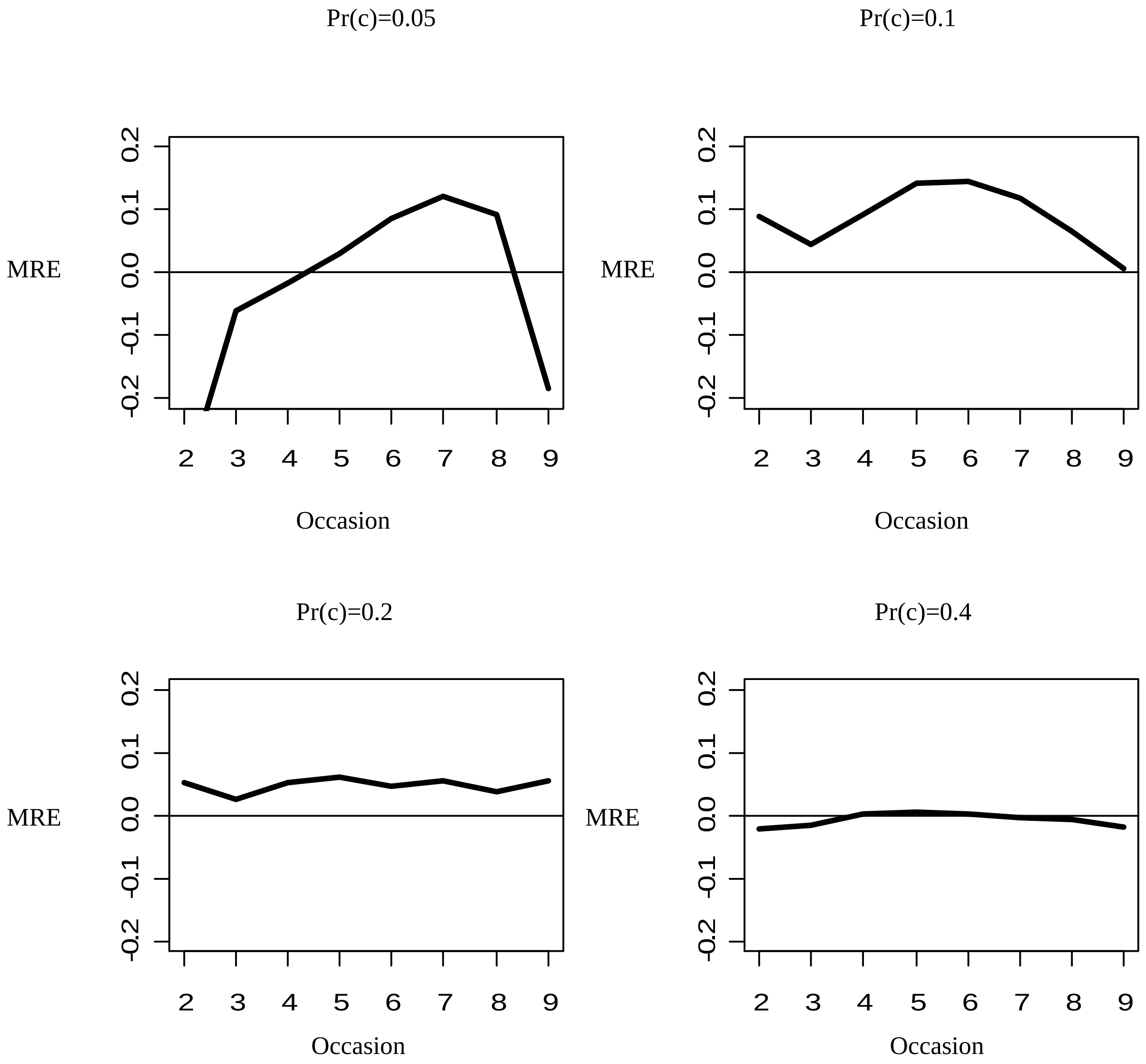


Fig.D- Additional 2D views for figure 2-10.

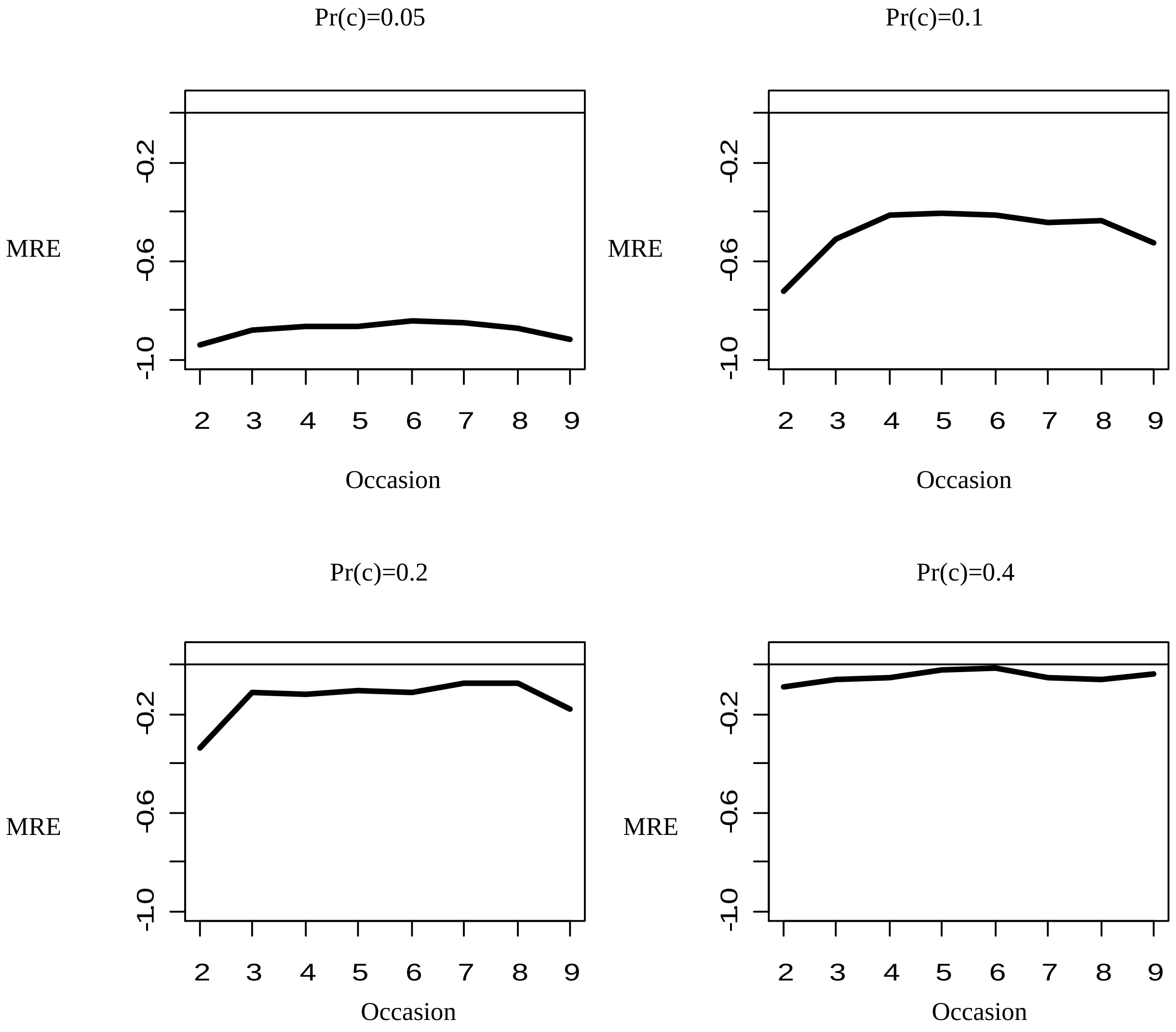
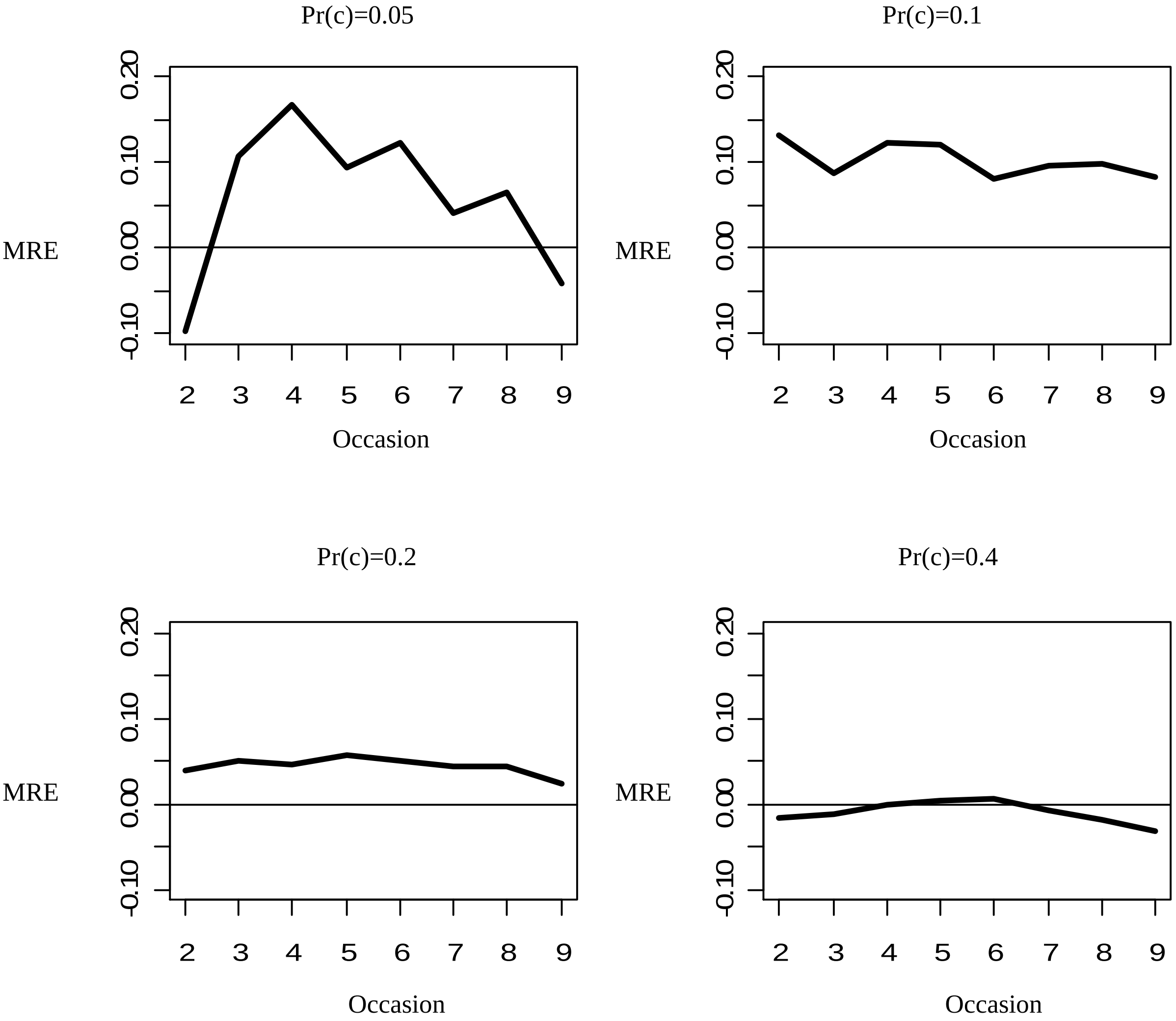


Fig.E- Additional 2D views for figure 2-11.


Pr(c)=0.05

Pr(c)=0.1

Pr(c)=0.2

Pr(c)=0.4

Fig.F- Additional 2D views for figure 2-12.

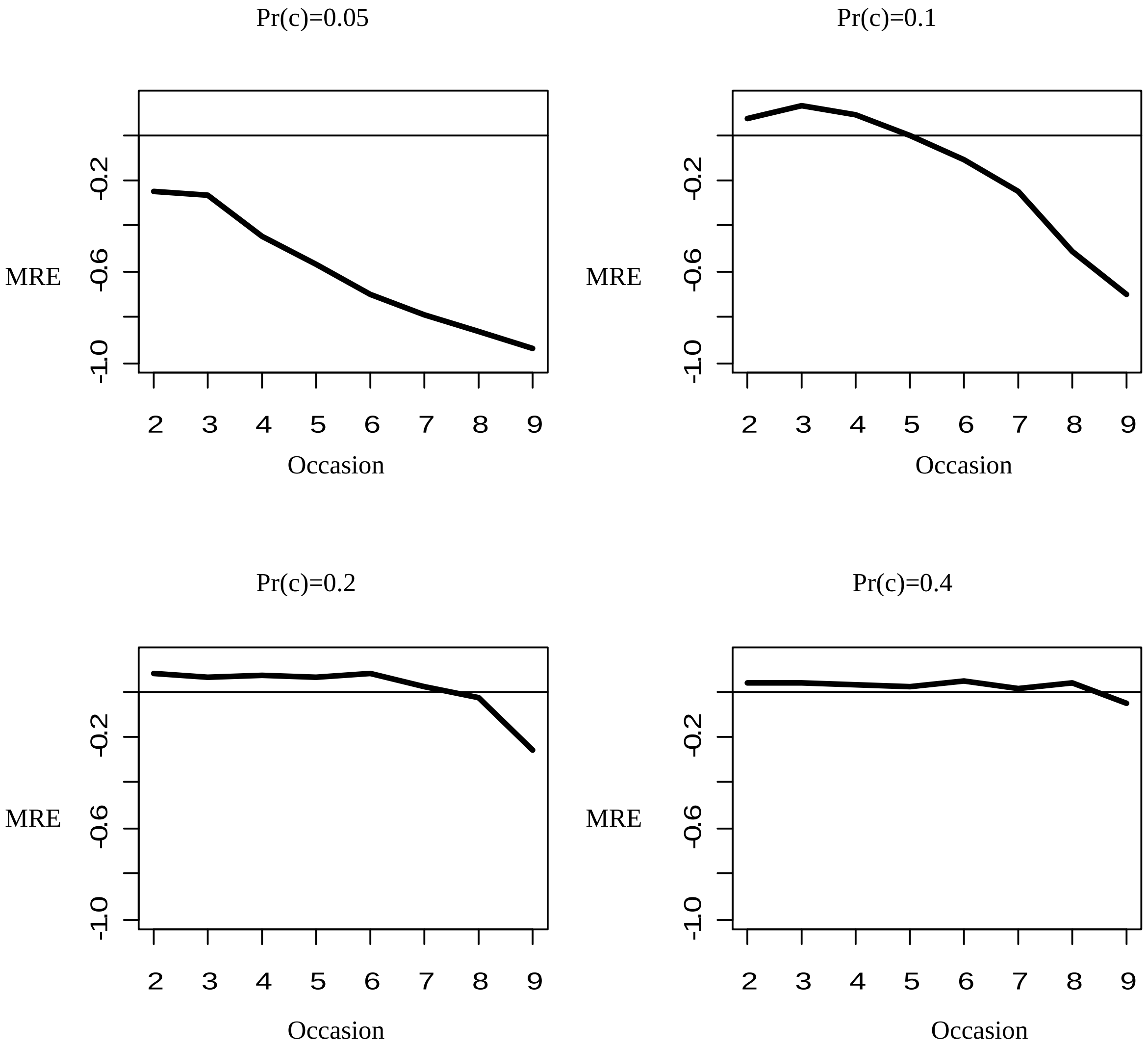


Fig.G- Additional 2D views for figure 2-15.

Appendix 5

MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors, normal and log-normal CI coverage rates of the estimated values, at each capture occasion of a 10-year study for different capture probabilities with scenario 50-25-25 and a starting population of 500 individuals.

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
P(*c*)=0.05							
$\hat{N}_2$	474	627	-0.24	246	0.59	62	75
$\hat{N}_3$	671	655	0.02	322	0.78	77	82
$\hat{N}_4$	720	694	0.04	352	0.86	75	83
$\hat{N}_5$	873	720	0.21	359	1.05	79	82
$\hat{N}_6$	819	746	0.1	385	0.68	80	82
$\hat{N}_7$	876	763	0.15	371	1.29	84	84
$\hat{N}_8$	906	795	0.14	369	1.07	79	82
$\hat{N}_9$	768	831	-0.08	335	0.73	67	78
P(*c*)=0.075							
$\hat{N}_2$	637	627	0.02	219	0.74	64	72
$\hat{N}_3$	767	654	0.17	236	0.66	78	80
$\hat{N}_4$	753	69	0.09	222	0.53	86	85
$\hat{N}_5$	804	718	0.12	235	0.56	85	84
$\hat{N}_6$	822	744	0.1	237	0.46	86	84
$\hat{N}_7$	873	762	0.15	250	0.61	84	84
$\hat{N}_8$	873	794	0.1	247	0.8	80	83
$\hat{N}_9$	993	827	0.2	281	1.1	71	70
P(*c*)=0.1							
$\hat{N}_2$	64	626	0.03	157	0.54	71	75
$\hat{N}_3$	711	654	0.09	157	0.47	76	74
$\hat{N}_4$	760	691	0.1	162	0.45	81	80
$\hat{N}_5$	779	717	0.09	165	0.3	91	90
$\hat{N}_6$	832	743	0.12	17	0.34	88	88
$\hat{N}_7$	808	760	0.06	168	0.31	87	84
$\hat{N}_8$	873	792	0.1	183	0.41	81	83
$\hat{N}_9$	927	826	0.12	194	0.49	73	72
P(*c*)=0.2							
$\hat{N}_2$	690	627	0.1	65	0.26	69	65
$\hat{N}_3$	693	656	0.06	61	0.18	71	73
$\hat{N}_4$	746	696	0.07	67	0.16	84	81
$\hat{N}_5$	773	720	0.07	71	0.15	83	82
$\hat{N}_6$	790	746	0.06	72	0.14	86	81
$\hat{N}_7$	816	765	0.07	75	0.15	83	82

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_8$	834	797	0.05	78	0.14	84	82
$\hat{N}_9$	896	834	0.07	86	0.23	67	65
P(*c*)=0.3							
$\hat{N}_2$	655	627	0.04	32	0.14	61	60
$\hat{N}_3$	684	653	0.05	33	0.1	65	63
$\hat{N}_4$	731	695	0.05	38	0.1	74	74
$\hat{N}_5$	752	719	0.04	40	0.08	83	83
$\hat{N}_6$	781	745	0.05	43	0.09	83	81
$\hat{N}_7$	799	763	0.05	44	0.09	82	81
$\hat{N}_8$	833	795	0.05	48	0.1	79	80
$\hat{N}_9$	880	830	0.06	52	0.13	69	68
P(*c*)=0.4							
$\hat{N}_2$	646	626	0.03	19	0.09	52	52
$\hat{N}_3$	679	653	0.04	20	0.07	58	57
$\hat{N}_4$	716	691	0.04	24	0.07	73	72
$\hat{N}_5$	747	717	0.04	26	0.06	77	77
$\hat{N}_6$	770	742	0.04	28	0.06	81	81
$\hat{N}_7$	791	760	0.04	30	0.06	80	79
$\hat{N}_8$	819	793	0.03	32	0.06	82	82
$\hat{N}_9$	853	827	0.03	35	0.08	73	75
P(*c*)=0.5							
$\hat{N}_2$	648	627	0.03	11	0.07	38	38
$\hat{N}_3$	669	653	0.03	13	0.04	64	64
$\hat{N}_4$	717	694	0.03	16	0.05	61	60
$\hat{N}_5$	740	718	0.03	18	0.04	73	72
$\hat{N}_6$	767	744	0.03	20	0.04	77	77
$\hat{N}_7$	781	761	0.03	21	0.04	85	85
$\hat{N}_8$	814	794	0.03	23	0.04	85	86
$\hat{N}_9$	850	828	0.03	26	0.06	77	77
P(*c*)=0.6							
$\hat{N}_2$	638	626	0.02	6	0.04	31	32
$\hat{N}_3$	669	655	0.02	8	0.03	50	51
$\hat{N}_4$	709	694	0.02	11	0.03	64	65
$\hat{N}_5$	732	719	0.02	12	0.03	77	77

Capture probability	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
$\hat{N}_6$	763	746	0.02	14	0.03	80	80
$\hat{N}_7$	779	764	0.02	15	0.03	88	88
$\hat{N}_8$	812	797	0.02	18	0.03	88	88
$\hat{N}_9$	847	831	0.02	20	0.04	78	78
P(*c*)=0.8							
$\hat{N}_2$	632	626	0.01	1	0.02	14	14
$\hat{N}_3$	659	653	0.01	3	0.01	36	37
$\hat{N}_4$	699	693	0.01	5	0.01	64	64
$\hat{N}_5$	725	719	0.01	6	0.01	73	73
$\hat{N}_6$	750	744	0.01	7	0.01	85	85
$\hat{N}_7$	769	763	0.01	8	0.01	93	93
$\hat{N}_8$	802	795	0.01	10	0.01	92	93
$\hat{N}_9$	838	830	0.01	12	0.02	88	89

$\hat{N}_2, \ldots, \hat{N}_9$ =population size estimate at time 2, …, 9.

Appendix 6

MRE, RMSRE, mean estimate and true value of the population size over the simulation runs, and standard errors, normal and log-normal CI coverage rates of the estimated values, at each capture occasion of a 10-occasion study with a tag misreading rate of 50%, homogeneous within the population and a starting population of 500 individuals.

Case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 1 20-40-40 P(c)=0.2							
$\hat{N}_2$	617	640	-0.03	79	0.35	51	56
$\hat{N}_3$	689	693	0	84	0.28	68	77
$\hat{N}_4$	757	757	0	93	0.26	69	87
$\hat{N}_5$	821	804	0.02	102	0.27	69	88
$\hat{N}_6$	883	852	0.03	110	0.26	69	91
$\hat{N}_7$	933	888	0.04	118	0.29	64	91
$\hat{N}_8$	997	943	0.05	128	0.31	60	86
$\hat{N}_9$	1053	1006	0.04	137	0.34	59	76
Case 2 20-40-40 P(c)=0.5							
$\hat{N}_2$	559	640	-0.13	12	0.14	11	11
$\hat{N}_3$	620	693	-0.11	16	0.12	15	16
$\hat{N}_4$	693	757	-0.08	22	0.1	29	30
$\hat{N}_5$	736	804	-0.08	25	0.1	28	30
$\hat{N}_6$	786	849	-0.07	28	0.09	41	42
$\hat{N}_7$	816	886	-0.08	31	0.09	37	40
$\hat{N}_8$	857	941	-0.09	34	0.11	35	38
$\hat{N}_9$	888	1002	-0.1	37	0.13	28	29
Case 3 50-25-25 P(c)=0.2							
$\hat{N}_2$	690	626	0.1	71	0.27	59	58
$\hat{N}_3$	725	653	0.11	70	0.22	71	68
$\hat{N}_4$	749	693	0.08	73	0.18	80	77
$\hat{N}_5$	792	717	0.1	77	0.2	86	81
$\hat{N}_6$	836	744	0.12	82	0.2	84	81
$\hat{N}_7$	861	762	0.13	85	0.21	78	77
$\hat{N}_8$	901	794	0.14	90	0.21	70	66
$\hat{N}_9$	951	829	0.15	97	0.27	68	64

Case	Mean Estimate	Mean True Value	MRE	Mean estimated SE	RMSRE	Nominal 95% CI coverage rate (%)	Log-normal CI coverage rate (%)
Case 4 50-25-25 P(c)=0.5							
$\hat{N}_2$	648	627	0.03	14	0.07	42	43
$\hat{N}_3$	683	653	0.05	16	0.06	50	49
$\hat{N}_4$	741	693	0.07	19	0.08	51	51
$\hat{N}_5$	768	717	0.07	21	0.08	38	38
$\hat{N}_6$	803	743	0.08	23	0.09	32	31
$\hat{N}_7$	831	760	0.09	25	0.1	24	23
$\hat{N}_8$	880	792	0.11	28	0.12	23	23
$\hat{N}_9$	918	826	0.11	31	0.13	29	29

$\hat{N}_2, \ldots, \hat{N}_9$ =population size estimate at time 2, …, 9.

Appendix 7

Simulation results for the two-source M_0 model (200 simulation runs).

Number of capture occasions T	True abundance N	Mean estimate $\hat{N}$	Mean estimated SE	MRE	RMSRE	Mean CI lower bound	Mean CI upper bound	Normal CI coverage rate	True capture probabilities			Estimated capture probabilities and *se*		
									p	g	α	$\hat{p} \pm$ *se*	$\hat{g} \pm$ *se*	$\hat{\alpha} \pm$ *se*
10	500	502	19	0	0	491	514	100	0.25	0.12	0.2	0.25 ± *0.01*	0.12 ± *0.01*	0.19 ± *0.01*
10	50	49	2	0	0	44	53	100	0.25	0.12	0.2	0.23 ± *0.02*	0.11 ± *0.02*	0.12 ± *0.03*
5	500	482	16	-0.03	0.04	452	514	100	0.25	0.12	0.2	0.27 ± *0.01*	0.12 ± *0.01*	0.2 ± *0.02*
10	500	476	133	-0.05	0.05	278	815	100	0.05	0.01	0.025	0.04 ± *0.02*	0.008 ± *0.003*	0.017 ± *0.01*

Appendix 8

Sample of values of the two simulated JS estimates and corresponding weighted means under heterogeneity case 1, with scenario 20-40-40 and a starting population of 500 individuals.

The table below displays the three first values of the 1600 simulated estimates of population size obtained with the Jolly-Seber estimator on each of the two datasets available (dataset 1 from sampling method 1 and dataset 2 from sampling method 2) from a T=10-occasion capture-recapture experiment repeated 200 times and the variance-weighted means of each pair of the JS estimates. Each of the three $\hat{N}_{wJS}$ presented below is the variance-weighted mean of the $\hat{N}_{JS1}$ and $\hat{N}_{JS2}$ obtained on the same occasion and same run of the simulation, i.e. on capture occasion 2 and run of simulation 1, 2, 3. The table below shows that, despite the fact that each $\hat{N}_{wJS}$ falls between the value of the corresponding $\hat{N}_{JS1}$ and $\hat{N}_{JS2}$, it is possible that the arithmetic mean of the $\hat{N}_{wJS}$ does not fall between the arithmetic means of the $\hat{N}_{JS1}$ and $\hat{N}_{JS2}$.

Capture occasion 2	JS model on dataset 1		JS model on dataset 2		Variance weighted mean	
Run of simulation	$\hat{N}_{JS1}$	*se*	$\hat{N}_{JS2}$	*se*	$\hat{N}_{wJS}$	*se*
1	311	*50*	345	*60*	325	*38*
2	345	*52*	694	*120*	401	*48*
3	896	*171*	336	*55*	388	*52*
Arithmetic mean	517	*91*	458	*78*	371	*46*

Appendix 9

A USER'S GUIDE to the TWO-SOURCE JOLLY-SEBER MODEL and MODEL TWO-SOURCE M_0.

Permission is granted to copy this document, at no charge and in its entirety, provided that the copies are not used for commercial advantage, and that the source is cited. The manual is available upon request in an electronic format from the author.

STEP 1

Download and install the software R available at http://www.r-project.org/

Manuals are also available on this website for further information on the software.

STEP 2

Create the table to be used in the analysis:

- It must be a ".csv" file
- It must only contain one spreadsheet
- The table must contain no raw or column label
- Start the table in the A1 cell
- Write capture histories on raw, columns represent capture occasion
- A capture by method 1 (i.e. photo-id) = "4"
- A capture by method 2 (i.e. skin sampling) = "5"
- A simultaneous double capture = "8"
- Not captured = "0"
- Multiple captures on a capture occasion are to be ignored: only 1 capture per capture occasion allowed

STEP 3

Copy and past the following codes in the R-command space:

```
data.csv=function(data=data)(data=read.csv2(file.choose(),header=F))
target=data.csv()
```

STEP 4

Select the ".csv" file to be analyzed

STEP 5

Replace the x in the following code by the number of capture occasions in the study, copy and paste the updated code:

```
T<-x
```

STEP 6

Copy and paste the following codes (this will put the data in the appropriate format for the TSJS and the two-source M_0 model):

```
# Formatting the data for the two-source M0 model
                        # First separate matrix into 3 matrices: create dataP

                        newtargetP=target

                                        for(m in 1 :T) {
                                for(z in 1:nrow(newtargetP)) {

                                  x=newtargetP[z,]

                           if(x[m]==5) { newtargetP[z,m]=0}
                                                                          }}
                          for(m in 1 :T) {
                                for(z in 1:nrow(newtargetP)) {

                                  x=newtargetP[z,]

                           if((sum(x[1:T]==8)!=0)&(x[m]==4)) {newtargetP[z,m]=0}}}
                          for(m in 1 :T) {
                                for(z in 1:nrow(newtargetP)) {

                                  x=newtargetP[z,]
                           if(x[m]==8) {newtargetP[z,m]=0}}}


                        #to remove histories when whales had not been caught once to get the
matrix to be analyzed
                          sortout <- function(object)
                          {
                            condition <- function(row)
                            {
                              return(all(row==0))
                            }
                            rowindicator <- apply(object,1,condition)
                            return(object[!rowindicator,])
                          }
                          sortout(newtargetP)
                          dataP<- sortout(newtargetP)
```

```
# separate matrix into 3 matrices: create dataG

            newtargetG=target

                        for(m in 1 :T) {

                  for(z in 1:nrow(newtargetG)) {

                    x=newtargetG[z,]
              if(x[m]==4) { newtargetG[z,m]=0}
                                                       }}
              for(m in 1 :T) {
                  for(z in 1:nrow(newtargetG)) {

                    x=newtargetG[z,]

              if((sum(x[1:T]==8)!=0)&(x[m]==5)) {newtargetG[z,m]=0}}}
              for(m in 1 :T) {
                  for(z in 1:nrow(newtargetG)) {

                    x=newtargetG[z,]
             if(x[m]==8) {newtargetG[z,m]=0}}}


            #to remove histories when whales had not been caught once to get the matrix to be analyzed
              sortout <- function(object)
              {
                condition <- function(row)
                {
                  return(all(row==0))
                }
                rowindicator <- apply(object,1,condition)
                return(object[!rowindicator,])
              }
              sortout(newtargetG)
              dataG<- sortout(newtargetG)



            # separate matrix into 3 matrices: create dataB

            newtargetB=target

                        for(m in 1 :T) {

                  for(z in 1:nrow(newtargetB)) {

                    x=newtargetB[z,]

              if((sum(x[1:T]==8)==0)&(x[m]==4)) {newtargetB[z,m]=0}
              if((sum(x[1:T]==8)==0)&(x[m]==5)) {newtargetB[z,m]=0}
                                                       }}
```

```
#to remove histories when whales had not been caught once to get the matrix to be analyzed
sortout <- function(object)
{
  condition <- function(row)
  {
    return(all(row==0))
  }
  rowindicator <- apply(object,1,condition)
  return(object[!rowindicator,])
}
sortout(newtargetB)
dataB<- sortout(newtargetB)

dB2<-as.matrix(dataB)
dB<-as.vector(dB2)

dP2<-as.matrix(dataP)
dP<-as.vector(dP2)

dG2<-as.matrix(dataG)
dG<-as.vector(dG2)

opensim<-list(B=structure(dB,.Dim=as.integer(c(nrow(dB2),ncol(dB2)))),P=structure(dP,.Dim=as.integer(c(nrow(dP2),ncol(dP2)))),G=structure(dG,.Dim=as.integer(c(nrow(dG2),ncol(dG2)))),.Names=c("B","P","G"))
```

```
# Formatting the data for the TSJS model

for(y in 1:T) {

  for(z in 1:nrow(target)) {

     w= target [z,]

#at time 1
if(y==1) {
  if((w[y]==4)&(sum(w[(y+1):T]==8)==0)){ target[z,y]=1}
  if((w[y]==5)&(sum(w[(y+1):T]==8)==0)){ target[z,y]=2}
if((w[y]==5)&(sum(w[(y+1):T]==8)!=0)){target[z,y]=11}
if((w[y]==4)&(sum(w[(y+1):T]==8)!=0)){target[z,y]=10}
  if(w[y]==8){ target[z,y]=9}
}
#at subsequent occasion
else{
#if((sum(w[1:(y-1)])==0)&(w[y]== 4)) { target[z,y]= 1}
  if((sum(w[1:(y-1)]==4)==0)&(w[y]== 4)&(sum(w[1:(y-1)]==1)==0)&(sum(w[1:(y-1)]==8)==0)&(sum(w[1:(y-1)]==9)==0)) { target[z,y]= 1}
  if((sum(w[1:(y-1)]==5)==0)&(sum(w[1:(y-1)]==2)==0)&(sum(w[1:(y-1)]==8)==0)&(sum(w[1:(y-1)]==9)==0)&(w[y]== 5)) { target[z,y]= 2}
  if((sum(w[1:(y-1)]==9)==0)& (sum(w[1:(y-1)]==10)==0)& (sum(w[1:(y-1)]==11)==0)&(w[y]== 8)) { target[z,y]= 9}
}
  }
}
```

```
  for(m in 1 :T) {

  for(z in 1:nrow(target)) {

      x=target[z,]

 if((sum(x[1:(m-1)]==9)==1)&(x[m]==4)) { target[z,m]=6}
 if((sum(x[1:(m-1)]==9)==1)&(x[m]==5)) {target[z,m]=7}
 if((x[m]==1)&(sum(x[m:T]==9)!=0)){target[z,m]=10}
 if((x[m]==2)&(sum(x[m:T]==9)!=0)){target[z,m]=11}
 if((x[m]==9)&(sum(x[1:T]==10)!=0)){target[z,m]=14}
 if((x[m]==8)&(sum(x[1:T]==10)!=0)){target[z,m]=14}
 if((x[m]==9)&(sum(x[1:T]==11)!=0)){target[z,m]=14}
 if((x[m]==8)&(sum(x[1:T]==11)!=0)){target[z,m]=14}

}
}


for(m in 2 :T) {

  for(z in 1:nrow(target)) {

      x=target[z,]

 if((sum(x[1:(m-1)]==9)==1)&(x[m]==9)) { target[z,m]=8}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==14)!=0) &(x[m]==9)) { target[z,m]=19}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==14)==0)& (x[m]==9)) { target[z,m]=14}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==14)!=0)&(x[m]==8)) { target[z,m]=19}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==14)==0)&(x[m]==8)) { target[z,m]=14}

if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==14)!=0)&(x[m]==14)) { target[z,m]=19}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==14)!=0)&(x[m]==14)) { target[z,m]=19}

if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)==0) &(x[m]==10)) { target[z,m]=15}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)!=0) &(x[m]==10)) { target[z,m]=12}
if((sum(x[1:(m-1)]==11)==1)&(x[m]==11)) { target[z,m]=13}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)==0) &(x[m]==1)) { target[z,m]=15}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)!=0) &(x[m]==1)) { target[z,m]=12}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)==0) &(x[m]==4)) { target[z,m]=15}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)!=0) &(x[m]==4)) { target[z,m]=12}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)==0) &(x[m]==6)) { target[z,m]=15}
if((sum(x[1:(m-1)]==11)==1)& (sum(x[1:(m-1)]==15)!=0) &(x[m]==6)) { target[z,m]=12}

if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)==0) &(x[m]==11)) { target[z,m]=16}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)!=0) &(x[m]==11)) { target[z,m]=13}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)==0) &(x[m]==2)) { target[z,m]=16}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)!=0) &(x[m]==2)) { target[z,m]=13}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)==0) &(x[m]==5)) { target[z,m]=16}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)!=0) &(x[m]==5)) { target[z,m]=13}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)==0) &(x[m]==7)) { target[z,m]=16}
if((sum(x[1:(m-1)]==10)==1)& (sum(x[1:(m-1)]==16)!=0) &(x[m]==7)) { target[z,m]=13}

if((sum(x[1:(m-1)]==10)==1)&(x[m]==10)) { target[z,m]=12}
if((sum(x[1:(m-1)]==10)==1)&(x[m]==1)) { target[z,m]=12}
if((sum(x[1:(m-1)]==11)==1)&(x[m]==11)) { target[z,m]=13}
if((sum(x[1:(m-1)]==11)==1)&(x[m]==2)) { target[z,m]=13}
if((sum(x[1:(m-1)]==11)==1)&(x[m]==5)) { target[z,m]=13}
if((sum(x[1:(m-1)]==10)==1)&(x[m]==4)) { target[z,m]=12}
if((sum(x[1:(m-1)]==11)==1)&(x[m]==7)) { target[z,m]=13}
```

```
if((sum(x[1:(m-1)]==10)==1)&(x[m]==6)) { target[z,m]=12}

if((sum(x[1:(m-1)]==7)==1)&(x[m]==7)) { target[z,m]=17}
if((sum(x[1:(m-1)]==6)==1)&(x[m]==6)) { target[z,m]=18}

}
}

            newtarget=target
```

STEP 7

Copy and paste the following codes to run the models

to run the TSJS model

```
#calcul of probabilities
      Pp<-(sum(newtarget[,]==1)+ sum(newtarget[,]==10)+ sum(newtarget[,]==6)+
sum(newtarget[,]==15))/nrow(newtarget)
      Pg<- (sum(newtarget[,]==2)+ sum(newtarget[,]==11)+ sum(newtarget[,]==7)+
sum(newtarget[,]==16))/nrow(newtarget)
      Ppgtheo<-Pp*Pg
   Ppgdata<- (sum(newtarget[,]==9)+sum(newtarget[,]==14))/nrow(newtarget)

   #calcul of identity rate
f =
    function(I, Ppgtheo, Ppgdata)
    1 - (Ppgtheo/I^2 - Ppgtheo*Ppgdata/I^3)

g =
    function(I, Ppgtheo, Ppgdata)
    1 - (Ppgtheo/I^2 - Ppgtheo*Ppgdata/I^3) - I
plot(x, g(x, Ppgtheo, Ppgdata), type = "l", ylim = c(-1, 1))
abline(h = 0)

uniroot(g, c(.001, .999), Ppgtheo = Ppgtheo, Ppgdata = Ppgdata)

I<- uniroot(g, c(.001, .999), Ppgtheo = Ppgtheo, Ppgdata = Ppgdata)$root


#calcul pop size
m<-rep(0,T)
mP<-rep(0,T)
mG<-rep(0,T)

R<-rep(0,T)
RP<-rep(0,T)
RG<-rep(0,T)

n<-rep(0,T)
nP<-rep(0,T)
nG<-rep(0,T)

M<-rep(0,T)
MP<-rep(0,T)
MG<-rep(0,T)
```

```
N<-rep(0,T)
NP<-rep(0,T)
NG<-rep(0,T)

z<- rep(0,T)
zp<-rep(0,T)
zg<-rep(0,T)
zpg<-rep(0,T)
r<-rep(0,T)
rp<-rep(0,T)
rg<-rep(0,T)
rpg<-rep(0,T)
zP<-rep(0,T)
zG<-rep(0,T)
zPc<-rep(0,T)
zGc<-rep(0,T)

rP<-rep(0,T)
rG<-rep(0,T)

rPc<-rep(0,T)
rGc<-rep(0,T)

sum14Pfirst<-rep(0,T)
sum14Gfirst<-rep(0,T)
sum14Precapt<-rep(0,T)
sum14Grecapt<-rep(0,T)

sum15Pfirst<-rep(0,T)
sum16Gfirst<-rep(0,T)
sum15Precapt<-rep(0,T)
sum16Grecapt<-rep(0,T)

   for(i in 2:(T-1))  {
   for(j in 1:nrow(newtarget)) {
                         v=newtarget[j,]
                         if((v[i]==0)&(sum(v[1:(i-1)]==2)!=0)&(sum(v[(i+1):T]==5)!=0))
{zg[i]=zg[i]+1}

if((v[i]==0)&(sum(v[1:(i-1)]==6)!=0) &
(sum(v[(i+1):T]==8)==0)&(sum(v[(i+1):T]==18)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==10)!=0)&(sum(v[(i+1):T]==12)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==14)!=0)&
(sum(v[(i+1):T]==12)==0)&(sum(v[(i+1):T]==19)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==15)!=0)&(sum(v[(i+1):T]==12)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==9)!=0)&(sum(v[(i+1):T]==8)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==9)!=0)&
(sum(v[(i+1):T]==8)==0)&(sum(v[(i+1):T]==6)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==10)!=0)&
(sum(v[(i+1):T]==12)==0)&(sum(v[(i+1):T]==14)!=0)) {zPc[i]=zPc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==14)!=0)&
(sum(v[(i+1):T]==19)==0)&(sum(v[(i+1):T]==15)!=0)) {zPc[i]=zPc[i]+1}




if((v[i]==0)&(sum(v[1:(i-1)]==7)!=0) &
(sum(v[(i+1):T]==8)==0)&(sum(v[(i+1):T]==17)!=0)) {zGc[i]=zGc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==11)!=0)&(sum(v[(i+1):T]==13)!=0)) {zGc[i]=zGc[i]+1}
```

```
if((v[i]==0)&(sum(v[1:(i-1)]==14)!=0)&
(sum(v[(i+1):T]==13)==0)&(sum(v[(i+1):T]==19)!=0)) {zGc[i]=zGc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==16)!=0)&(sum(v[(i+1):T]==13)!=0)) {zGc[i]=zGc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==9)!=0)&(sum(v[(i+1):T]==8)!=0)) {zGc[i]=zGc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==9)!=0)&
(sum(v[(i+1):T]==8)==0)&(sum(v[(i+1):T]==7)!=0)) {zGc[i]=zGc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==11)!=0)&
(sum(v[(i+1):T]==13)==0)&(sum(v[(i+1):T]==14)!=0)) {zGc[i]=zGc[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==14)!=0)&
(sum(v[(i+1):T]==19)==0)&(sum(v[(i+1):T]==16)!=0)) {zGc[i]=zGc[i]+1}



              if((v[i]==0)&(sum(v[1:(i-1)]==1)!=0)&(sum(v[(i+1):T]==4)!=0))
{zp[i]=zp[i]+1}

                       if((v[i]==0)&(sum(v[1:(i-1)]==9)!=0)&(sum(v[(i+1):T])!=0))
{zpg[i]=zpg[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==10)!=0)&(sum(v[(i+1):T])!=0)) {zpg[i]=zpg[i]+1}
if((v[i]==0)&(sum(v[1:(i-1)]==11)!=0)&(sum(v[(i+1):T])!=0)) {zpg[i]=zpg[i]+1}

                        }

z[i]= zg[i]*I+ zp[i]*I+ zpg[i]
zP[i]= zp[i]+zPc[i]
zG[i]= zg[i]+zGc[i]
                        }


   for(i in 1:(T-1)) {
     for(j in 1:nrow(newtarget)) {
              w=newtarget[j,]
              if(w[i]==10)
                       {rpg[i]=rpg[i]+1}
              if(w[i]==11)
                       {rpg[i]=rpg[i]+1}
if((w[i]==9)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==12)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==13)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==14)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==7)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==6)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==8)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==15)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==16)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==17)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}

if((w[i]==18)&(sum(w[(i+1):T])!=0))
                       {rpg[i]=rpg[i]+1}
if((w[i]==19)&(sum(w[(i+1):T])!=0))
```

```
                    {rpg[i]=rpg[i]+1}

if((w[i]==1)&(sum(w[(i+1):T])!=0))
                    {rp[i]=rp[i]+1}
if((w[i]==2)&(sum(w[(i+1):T])!=0))
                    {rg[i]=rg[i]+1}

if((w[i]==9)&(sum(w[(i+1):T]==6)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==9)&(sum(w[(i+1):T]==6)==0)&(sum(w[(i+1):T]==8)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==8)&(sum(w[(i+1):T]==8)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==14)&(sum(w[(i+1):T]==19)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==19)&(sum(w[(i+1):T]==19)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==10)& (sum(w[(i+1):T]==12)==0) &(sum(w[(i+1):T]==14)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==12)&(sum(w[(i+1):T]==12)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==12)&(sum(w[(i+1):T]==12)==0) &(sum(w[(i+1):T]==19)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==12)&(sum(w[(i+1):T]==12)==0) &(sum(w[(i+1):T]==19)==0)
&(sum(w[(i+1):T]==14)!=0))
                    {rPc[i]=rPc[i]+1}


if((w[i]==6)&(sum(w[(i+1):T]==18)!=0))
                    {rPc[i]=rPc[i]+1}
if((w[i]==6)&(sum(w[(i+1):T]==18)==0)& (sum(w[(i+1):T]==8)!=0))
                    {rPc[i]=rPc[i]+1}

if((w[i]==18)&(sum(w[(i+1):T]==18)!=0))
                    {rPc[i]=rPc[i]+1}

if((w[i]==9)&(sum(w[(i+1):T]==7)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==9)&(sum(w[(i+1):T]==7)==0)&(sum(w[(i+1):T]==8)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==8)&(sum(w[(i+1):T]==8)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==14)&(sum(w[(i+1):T]==19)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==19)&(sum(w[(i+1):T]==19)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==11)& (sum(w[(i+1):T]==13)==0)&(sum(w[(i+1):T]==14)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==13)&(sum(w[(i+1):T]==13)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==13)&(sum(w[(i+1):T]==13)==0) &(sum(w[(i+1):T]==19)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==13)&(sum(w[(i+1):T]==13)==0) &(sum(w[(i+1):T]==19)==0)
&(sum(w[(i+1):T]==14)!=0))
                    {rGc[i]=rGc[i]+1}


if((w[i]==7)&(sum(w[(i+1):T]==17)!=0))
                    {rGc[i]=rGc[i]+1}
if((w[i]==7)&(sum(w[(i+1):T]==17)==0) &(sum(w[(i+1):T]==8)!=0))
```

```
                {rGc[i]=rGc[i]+1}

if((w[i]==17)&(sum(w[(i+1):T]==17)!=0))
                {rGc[i]=rGc[i]+1}

if((w[i]==19) & (sum(w[(i+1):T]==19)==0)&(sum(w[(i+1):T]==16)!=0))
                {rGc[i]=rGc[i]+1}
if((w[i]==19)& (sum(w[(i+1):T]==19)==0)&(sum(w[(i+1):T]==15)!=0))
                {rPc[i]=rPc[i]+1}

if((w[i]==14) & (sum(w[(i+1):T]==19)==0)&(sum(w[(i+1):T]==16)!=0))
                {rGc[i]=rGc[i]+1}
if((w[i]==14) & (sum(w[(i+1):T]==19)==0)&(sum(w[(i+1):T]==15)!=0))
                {rPc[i]=rPc[i]+1}
if((w[i]==14) & (sum(w[(i+1):T]==19)==0)& (sum(w[(i+1):T]==16)==0)&
(sum(w[(i+1):T]==13)!=0))
                {rGc[i]=rGc[i]+1}
if((w[i]==14) & (sum(w[(i+1):T]==19)==0)& (sum(w[(i+1):T]==15)==0)&
(sum(w[(i+1):T]==12)!=0))
                {rPc[i]=rPc[i]+1}


if((w[i]==10)&(sum(w[(i+1):T]==12)!=0))
                {rPc[i]=rPc[i]+1}
if((w[i]==11)&(sum(w[(i+1):T]==13)!=0))
                {rGc[i]=rGc[i]+1}
if((w[i]==15)&(sum(w[(i+1):T]==12)!=0))
                {rPc[i]=rPc[i]+1}
if((w[i]==16)&(sum(w[(i+1):T]==13)!=0))
                {rGc[i]=rGc[i]+1}

if((w[i]==15) & (sum(w[(i+1):T]==12)==0)&(sum(w[(i+1):T]==14)!=0))
                {rPc[i]=rPc[i]+1}
if((w[i]==16) & (sum(w[(i+1):T]==13)==0)&(sum(w[(i+1):T]==14)!=0))
                {rGc[i]=rGc[i]+1}

if((w[i]==8) & (sum(w[(i+1):T]==8)==0)&(sum(w[(i+1):T]==6)!=0))
                {rPc[i]=rPc[i]+1}
if((w[i]==8) & (sum(w[(i+1):T]==8)==0)&(sum(w[(i+1):T]==7)!=0))
                {rGc[i]=rGc[i]+1}

if((w[i]==8) & (sum(w[(i+1):T]==8)==0)& (sum(w[(i+1):T]==6)==0)&
(sum(w[(i+1):T]==18)!=0))
                {rPc[i]=rPc[i]+1}
if((w[i]==8) & (sum(w[(i+1):T]==8)==0)& (sum(w[(i+1):T]==8)==0)&
(sum(w[(i+1):T]==7)==0)& (sum(w[(i+1):T]==17)!=0))
                {rGc[i]=rGc[i]+1}


if((w[i]==4)&(sum(w[(i+1):T])!=0))
                {rp[i]=rp[i]+1}
if((w[i]==5)&(sum(w[(i+1):T])!=0))
                {rg[i]=rg[i]+1}



                             }

r[i]= rg[i]*l+ rp[i]*l+ rpg[i]
rP[i]= rp[i]+rPc[i]
```

```
rG[i]= rg[i]+rGc[i]

                                }
for(i in 1:T) {
        for(j in 1:nrow(newtarget)) {
                                                          w=newtarget[j,]
if((w[i]==14)&(sum(w[1:i]==10)==0))
                    {sum14Pfirst[i]=sum14Pfirst[i]+1}
if((w[i]==14)&(sum(w[1:i]==10)!=0))
                    {sum14Precapt[i]=sum14Precapt[i]+1}

if((w[i]==14)&(sum(w[1:i]==11)==0))
                    {sum14Gfirst[i]=sum14Gfirst[i]+1}
if((w[i]==14)&(sum(w[1:i]==11)!=0))
                    {sum14Grecapt[i]=sum14Grecapt[i]+1}

                    }
}

for(i in 1:T) {
        for(j in 1:nrow(newtarget)) {
                                                          w=newtarget[j,]
if((w[i]==15)&(sum(w[1:i]==14)==0))
                    {sum15Pfirst[i]=sum15Pfirst[i]+1}
if((w[i]==15)&(sum(w[1:i]==14)!=0))
                    {sum15Precapt[i]=sum15Precapt[i]+1}

if((w[i]==16)&(sum(w[1:i]==14)==0))
                    {sum16Gfirst[i]=sum16Gfirst[i]+1}
if((w[i]==16)&(sum(w[1:i]==14)!=0))
                    {sum16Grecapt[i]=sum16Grecapt[i]+1}

                    }
}


    for(i in 2:(T-1))  {

        if (i==2)
                    {
                    R[i-1]=sum(newtarget[,i-1]==9)+ sum(newtarget[,i-1]==10)+
sum(newtarget[,i-1]==11)+sum(newtarget[,i-1]==1)*l+sum(newtarget[,i-1]==2)*l;
RP[i-1]= sum(newtarget[,i-1]==1)+ sum(newtarget[,i-1]==10)+ sum(newtarget[,i-
1]==9)+ sum14Pfirst[i-1];
RG[i-1]= sum(newtarget[,i-1]==2)+ sum(newtarget[,i-1]==11)+ sum(newtarget[,i-
1]==9)+ sum14Gfirst[i-1];

m[i]=sum(newtarget[,i]==6)+sum(newtarget[,i]==4)*l+sum(newtarget[,i]==5)*l+sum(
newtarget[,i]==8)+sum(newtarget[,i]==7)+ sum(newtarget[,i]==12)+
sum(newtarget[,i]==13)+ sum(newtarget[,i]==14)+ sum(newtarget[,i]==15)+
sum(newtarget[,i]==16)+ sum(newtarget[,i]==17)+ sum(newtarget[,i]==18)+
sum(newtarget[,i]==19);

mP[i]= sum(newtarget[,i]==4)+ sum(newtarget[,i]==12)+ sum(newtarget[,i]==18)+
sum(newtarget[,i]==8)+ sum(newtarget[,i]==19)+ sum(newtarget[,i]==6)+
sum14Precapt[i]+ sum15Precapt[i];
mG[i]= sum(newtarget[,i]==5)+ sum(newtarget[,i]==13)+ sum(newtarget[,i]==17)+
sum(newtarget[,i]==8)+ sum(newtarget[,i]==19)+sum(newtarget[,i]==7)+
sum14Grecapt[i]+ sum16Grecapt[i];
```

```
                R[i]=sum(newtarget[,i]==9)+
sum(newtarget[,i]==10)+sum(newtarget[,i]==11)+sum(newtarget[,i]==1)*I+sum(new
target[,i]==2)*I;

RP[i]= sum(newtarget[,i]==1)+ sum(newtarget[,i]==10)+
sum(newtarget[,i]==9)+sum14Pfirst[i]+ sum15Pfirst[i];
RG[i]= sum(newtarget[,i]==2)+ sum(newtarget[,i]==11)+
sum(newtarget[,i]==9)+sum14Gfirst[i]+ sum16Gfirst[i];



                }
      else{

   m[i]=sum(newtarget[,i]==6)+sum(newtarget[,i]==4)*I+sum(newtarget[,i]==5)*I+su
m(newtarget[,i]==8)+sum(newtarget[,i]==7)+sum(newtarget[,i]==12)+
sum(newtarget[,i]==13)+ sum(newtarget[,i]==14) + sum(newtarget[,i]==15)+
sum(newtarget[,i]==16)+ sum(newtarget[,i]==17)+ sum(newtarget[,i]==18)+
sum(newtarget[,i]==19);
                R[i]=sum(newtarget[,i]==9)+
sum(newtarget[,i]==10)+sum(newtarget[,i]==11)+sum(newtarget[,i]==1)*I+sum(new
target[,i]==2)*I;

mP[i]= sum(newtarget[,i]==4)+ sum(newtarget[,i]==12)+ sum(newtarget[,i]==18)+
sum(newtarget[,i]==8)+ sum(newtarget[,i]==19)+ sum(newtarget[,i]==6)+
sum14Precapt[i]+ sum15Precapt[i];
mG[i]= sum(newtarget[,i]==5)+ sum(newtarget[,i]==13)+ sum(newtarget[,i]==17)+
sum(newtarget[,i]==8)+ sum(newtarget[,i]==19)+sum(newtarget[,i]==7)+
sum14Grecapt[i]+ sum16Grecapt[i];

RP[i]= sum(newtarget[,i]==1)+ sum(newtarget[,i]==10)+
sum(newtarget[,i]==9)+sum14Pfirst[i]+ sum15Pfirst[i];
RG[i]= sum(newtarget[,i]==2)+ sum(newtarget[,i]==11)+
sum(newtarget[,i]==9)+sum14Gfirst[i]+ sum16Gfirst[i];

                }

n[i]= m[i]+ R[i]
nP[i]= mP[i]+ RP[i]
nG[i]= mG[i]+ RG[i]

      M[i]=(z[i]*(n[i]+1))/(r[i]+1)+m[i]
                N[i]=(n[i]+1)*M[i]/(m[i]+1)

MP[i]=(zP[i]*(nP[i]+1))/(rP[i]+1)+mP[i]
                NP[i]=(nP[i]+1)*MP[i]/(mP[i]+1)

MG[i]=(zG[i]*(nG[i]+1))/(rG[i]+1)+mG[i]
                NG[i]=(nG[i]+1)*MG[i]/(mG[i]+1)          }
# Variance of Ni

n1=n[-1]
n2=n1[-(T-1)]
m1=m[-1]
m2=m1[-(T-1)]
r1=r[-T]
meanni=mean(n2)
meanmi=mean(m2)
meanri=mean(r1)
varNi=rep(0,T)
```

```
seNi=rep(0,T)

for (i in 2:(T-1)) {
varNi[i]=N[i]*(N[i]-meanni)*((M[i]-meanmi+n[i])/M[i])*(1/meanri-1/n[i])+((N[i]-
M[i])/(N[i]*meanmi))
seNi[i]=sqrt(varNi[i])
}
# Variance of NPi

nP1=nP[-1]
nP2=nP1[-(T-1)]
mP1=mP[-1]
mP2=mP1[-(T-1)]
rP1=rP[-T]
meannPi=mean(nP2)
meanmPi=mean(mP2)
meanrPi=mean(rP1)
varNPi=rep(0,T)
seNPi=rep(0,T)

for (i in 2:(T-1)) {
varNPi[i]=NP[i]*(NP[i]-meannPi)*((MP[i]-meanmPi+nP[i])/MP[i])*(1/meanrPi-
1/nP[i])+((NP[i]-MP[i])/(NP[i]*meanmPi))
seNPi[i]=sqrt(varNPi[i])
}

# Variance of NGi

nG1=nG[-1]
nG2=nG1[-(T-1)]
mG1=mG[-1]
mG2=mG1[-(T-1)]
rG1=rG[-T]
meannGi=mean(nG2)
meanmGi=mean(mG2)
meanrGi=mean(rG1)
varNGi=rep(0,T)
seNGi=rep(0,T)

for (i in 2:(T-1)) {
varNGi[i]=NG[i]*(NG[i]-meannGi)*((MG[i]-meanmGi+nG[i])/MG[i])*(1/meanrGi-
1/nG[i])+((NG[i]-MG[i])/(NG[i]*meanmGi))
seNGi[i]=sqrt(varNGi[i])

            }

taillepop<-N[-c(1,T)]
taillepopP<-NP[-c(1,T)]
taillepopG<-NG[-c(1,T)]
```

to run the two-source M_0 model

```
est.func<-function(dat, start.vec=missing())
{
	k <- ncol(dat$P)
	Pdat.tab <- table(dat$P)
	Gdat.tab <- table(dat$G)
	Bdat.tab <- table(dat$B)

	nB.0 <- Bdat.tab["0"]
	nB.1 <- Bdat.tab["1"]
	nB.2 <- Bdat.tab["2"]
	nB.3 <- Bdat.tab["3"]
	if(is.na(nB.0)) nB.0 <- 0
	if(is.na(nB.1)) nB.1 <- 0
	if(is.na(nB.2)) nB.2 <- 0

	nP.0 <- Pdat.tab["0"]
	nP.1 <- Pdat.tab["1"]
	if(is.na(nP.0)) nP.0 <- 0

	nG.0 <- Gdat.tab["0"]
	nG.2 <- Gdat.tab["2"]
	if(is.na(nG.0)) nG.0 <- 0

	hvec <- unlist(lapply(dat, nrow))
	hb <- hvec["B"]
	hp <- hvec["P"]
	hg <- hvec["G"]


	nllike.func <- function(pars)
	{
		p <- pars[1]
		g <- pars[2]
		phi <- pars[3]
		N <- pars[4]
		prob.inP <- (1 - phi * p)^k - (1 - p)^k
		pP.0 <- ((1 - p) * ((1 - phi * p)^(k - 1) - (1 - p)^(k - 1)))/prob.inP
		pP.1 <- 1 - pP.0

		loglik.P <- nP.0 * log(pP.0) + nP.1 * log(pP.1)
		prob.inG <- (1 - phi * p)^k - (1 - g)^k
		pG.0 <- ((1 - g) * ((1 - phi * p)^(k - 1) - (1 - g)^(k - 1)))/prob.inG
		pG.2 <- 1 - pG.0

		loglik.G <- nG.0 * log(pG.0) + nG.2 * log(pG.2)
		bk <- 1 - (1 - phi * p)^k
		bkm1 <- 1 - (1 - phi * p)^(k - 1)
		pB.0 <- (bkm1 * (1 - p - g + phi * p))/bk
		pB.1 <- (bkm1 * (1 - phi) * p)/bk
		pB.2 <- (bkm1 * (g - phi * p))/bk
		pB.3 <- (phi * p)/bk

		loglik.B <- nB.0 * log(pB.0) + nB.1 * log(pB.1) + nB.2 * log(
			pB.2) + nB.3 * log(pB.3)


		loglik.H <- log(histories.func(hB = hb, hP = hp, hG = hg, ps =
			p, gs = g, phis = phi, Nwh = N, ks = k))
```

```
        negloglik <- ( - loglik.H - loglik.B - loglik.P - loglik.G)
        negloglik
}
test.nll <- 0
if(!missing(start.vec)){
        test.nll <- nllike.func(start.vec)
        catline("Start.vec supplied:")
        print(c(start.vec, test.nll))
}
if(missing(start.vec) | test.nll==Inf){
        catline("Warning: start.vec missing or gives likelihood=0. Using ad-hoc start vector.")

        start.p <- (nP.1 - hp)/(length(dat$P) - hp) + 0.01
        start.g <- (nG.2 - hg)/(length(dat$G) - hg) + 0.01
        start.phi <- 0.5 * min(c(start.g/start.p, 1))
        start.N <- 20 + hb/(1 - (1 - start.phi*start.p)^k)
        start.vec <- c(start.p, start.g, start.phi, start.N)
        names(start.vec) <- c("start.p", "start.g", "start.phi", "start.N")
        catline("New start.vec:")
        print(start.vec)

}
Nmin <- hvec["B"] + max(c(hvec["P"], hvec["G"]))
MLE <- nlminb(start = start.vec, objective = nllike.func, control =
        list(iter.max = 2000, eval.max = 5000), lower = c(
        0, 0, 0, Nmin), upper = c(1, 1, 1, Inf))

MLE.params <- MLE$par
phat <- MLE.params[1]
ghat <- MLE.params[2]
phihat <- MLE.params[3]
Nhat <- MLE.params[4]
msgmax <- MLE$convergence
if(MLE$objective==Inf) msgmax <- "Inf"
ests <- c(MLE.params, msgmax)
names(ests) <- c("phat", "ghat", "phihat", "Nhat", "conv.0.good")
catline("------------------------------------")
catline("nlminb completed successfully: estimates are")
print(ests)
catline("------------------------------------")

nlm.hess.res <- nlm(f=nllike.func, p = MLE.params, iterlim = 2000,
        stepmax = 5000, hessian=T)
nlm.params <- nlm.hess.res$estimate
hess.warn <- 0

if((any(abs(MLE.params[1:3]-nlm.params[1:3])>0.001)) |
        abs(MLE.params[4]-nlm.params[4])>0.1) hess.warn <- 1
nlm.infmat <- solve(nlm.hess.res$hessian)
est.var.vec <- diag(nlm.infmat)
names(est.var.vec) <- c("varhat.p", "varhat.g", "varhat.phi", "varhat.N")
varhat.Nhat <- est.var.vec["varhat.N"]
ci.C <- exp(1.959964 * sqrt(log(1 + varhat.Nhat / Nhat^2)))
ci.lower <- Nhat / ci.C
ci.upper <- Nhat * ci.C
ci.vec <- c(ci.lower, ci.upper)
names(ci.vec) <- c("ciN.low", "ciN.hi")
res.all <- c(ests, est.var.vec, ci.vec, hess.warn=hess.warn)
print(res.all)
```

```
        res.all
}
```

STEP 8

To get the results for the population size, copy and paste the following codes:

```
#The population size given by the two-source Jolly-Seber model is estimated to be
from time 2 to (T-1):
taillepop
```

To get the associated standard error, copy and paste:

```
#The standard error given by the two-source Jolly-Seber model is estimated to be
from time 2 to (T-1):
seNi
```

From the present codes, it is also possible to get the estimates provided by the classical Jolly-Seber on each of the 2 separate datasets.

To get the results of the JS using the data associated to method 1, copy and paste:

```
#The population size given by the JS model with data from method 1 is estimated
to be from time 2 to (T-1):
taillepopP
```

To get the associated standard errors:

```
#The standard error given by the JS model with data from method 1 is estimated to
be from time 2 to (T-1):
seNPi
```

To get the results of the JS using the data associated to method 2, copy and paste:

```
#The population size given by the JS model with data from method 2 is estimated
to be from time 2 to (T-1):
taillepopG
```

To get the associated standard errors, copy and paste:

```
#The standard error given by the JS model with data from method 2 is estimated to
be from time 2 to (T-1):
seNGi
```

STEP 9

To get the population size, standard error, capture probabilities with the two-source M_0 model, copy and paste:

```
#The results with the two-source M0 model are:
    est.func(opensim)
```