Utilising mark-recapture data for Bayesian modelling of fish mortality

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Summary in English

In this work, the aim was to produce a realistic assessment of yearly mortality of Archipelago Sea pike perch during the period 1997-2012. The utilized data origins from the mark-recapture experiment carried out by the Finnish Game and Fisheries Research Institute (FGFRI). In this mark-recapture experiment, returnings of the marks were based on voluntary tag reporting by the fishermen gaining small monetary rewards. In this study design, the count of returned tags is affected by the size of the release cohort, efficiency of the fishing method used by a fisherman and the fisherman's willingness to return the tag. In addition, each year a proportion of the tags become detached from fish, which means that those tags cannot be returned. All these factors were taken into account in a hierarchical model, which was developed in the same fashion as the well-known Cormack-Jolly-Seber model. Data from the yearly total catch were not used in this work because those data will be used in the subsequent research utilizing results of this work.

The objective of this work was to estimate fishing gear specific catchability coefficients and mortality rates, including natural mortality rate. The amount of data and number of parameters to be estimated set their own limitations, so it was decided to estimate parameters of interest by splitting the data into only three fishing fleets: professional fishermen, recreational net fishermen and recreational line fishermen.

The estimability of the hierarchical model developed for mark-recapture data was studied using simulation experiments. One was able to find such a model configuration, where the parameters concerning mortality estimates may be estimated without significant systematic errors in the estimated posterior distributions. Simultaneously, the tag reporting probabilities were estimated for each of the three fishing fleets although systematic errors remained for these parameters.

The final mortality estimate indicates that about half of the Archipelago Sea pike perch population is removed annually. For the recent years about half of this mortality was caused by professional fishing, and almost the same amount was due to natural death. The mortality caused by recreational fishing is the smallest mortality component. The estimate concerns population similar to released cohorts. The produced estimate is sensitive to many factors, whereas effects of environmental change, or changes in seal or cormorant abundances, were beyond the scope of this work.

Summary in Finnish

Tässä työssä pyrittiin tuottamaan mahdollisimman todenmukainen arvio Saaristomeren kuhan vuosittaiselle kuolleisuudelle ajanjaksolla 1997-2012. Työssä käytettiin Riista- ja kalatalouden tutkimuslaitoksen (RKTL) suorittamista merkintä-takaisinpyyntikokeesta saatua aineistoa. Kyseessä olevalle merkintä-takaisinpyyntikokeelle merkkien palautuminen perustui kalastajien vapaaehtoiseen pyydettyjen merkkien raportointiin pientä rahallista korvausta vastaan. Tällaisessa tutkimusasetelmassa palautuneiden merkkien määrään vaikuttaa kalakohortin koon lisäksi myös kalastajan käyttämän pyyntitavan tehokkuus sekä halukkuus palauttaa merkki. Lisäksi vuosittain osasta kaloista merkki irtoaa, jolloin kyseinen merkki ei palaudu. Kaikki nämä tekijät otettiin huomioon hierarkkisessa mallissa, joka kehitettiin aiemmin tunnetun Cormack-Jolly-Seber -mallin pohjalta. Tietoa vuosittaisesta ammatti- ja vapaa-ajankalastajien kokonaissaaliista ei tässä työssä käytetty, sillä kyseistä tietoa hyödynnetään myöhemmässä tämän työn tuloksia hyväksikäyttävässä tutkimuksessa.

Tavoitteena oli estimoida kalastustapakohtaiset pyydettävyys- ja kuolleisuusparametrit mukaanlukien luonnollinen kuolleisuus. Aineiston koko ja estimoitavien parametrien määrä asetti kuitenkin omat rajoitteensa, joten tyydyttiin estimoimaan halutut parametrit vain kalastajaryhmittäin käyttäen kolmea ryhmää: ammattikalastajat, vapaa-ajan verkko- ja rysäkalastat ja vapaa-ajan siimakalastajat.

Kehitetyn hierarkkisen mallin estimoitavuutta tutkittiin simulointikokeilla, joissa onnistuttiin löytämään sellainen mallikonfiguraatio, jolle kuolleisuuteen vaikuttavien muuttujien estimoinnissa ei synny merkittävää systemaattista virhettä estimoituihin posteriorijakaumiin. Ohessa estimoitiin myös merkin palauttamishaluukkuus kolmelle kalastajaryhmälle, mutta niiden osalta systemaattisesta virheestä ei päästy kokonaan eroon.

Tuloksena saatu kuolleisuusarvio osoittaa, että Saaristomeren kuhakannasta noin puolet menehtyy vuosittain. Viime vuosina noin puolet kuolleisuudesta on aiheutunut ammattikalastuksesta ja lähes yhtä suuri osa luonnollisista syistä. Vapaa-ajankalastajien aiheuttama kuolleisuus kuhalle on vähäistä. Arviossa otaksutaan, että populaatio on samanlainen vapautettuihin kohortteihin nähden. Saatu estimaatti on sensitiivinen useille tekijöille eikä esimerkiksi ympäristön muutoksen tai hylje- ja merimetsokantojen kehityksen vaikutusta ole huomioitu mallintamisessa lainkaan.

Contents

1 Introduction

Understanding the size of a fish population is of economical and ecological importance. The increased risk of over-exploitation of fish populations has raised an interest towards developing more efficient methods in fish stock assessment.

In the ECOKNOWS (*Effective Use of Ecosystem and Biological Knowledge in Fisheries*) -project the goal is to develop methods for efficient measures of the size of commercially exploited fish populations, and for doing this, information about fish mortality is needed. Another source of interest towards fish populations is to base and control the regulations and directives set by the European Union.

Two kinds of data may be used to measure the size of fish populations; catch-effort data or mark-recapture data. Often only catch-effort data are used in Catch per unit effort -analysis (CPUE). If certain assumptions hold, the CPUE approach gives information about the population trend. The problem is that it is not possible to check if the needed assumptions hold. The mark-recapture approach is more efficient (Seber, 1982). In mark-recapture, first a group of fish is being tagged with individually identifiable tags and released into the population. Then the tagged fish are being monitored either via sampling or commercial fishing. The counts of the tagged and untagged fish in the samples give us information about the population size.

The objective of this study is to construct prior distributions for a stock assessment model, being posteriors derived from the mark-recapture data. The objective of the mark-recapture analysis is to estimate gear-specific fishing mortality rates and the natural mortality rate by age classes. All the analyses will be based on mark-recapture and fishing effort data and on prior knowledge. Prior knowledge may come from earlier studies or expert judgement. An essential part of this work is sensitivity analyses, the purpose of which are to show how prior information affects our final results (posterior probability distributions).

If the time between the release and the recapture is not very short, then at the time of the recapture some of the tagged fish are likely to be removed from the population due to fishing, natural death or emigration. Mortality is important because, in the mark-recapture, the number of the tagged fish in the population must be known to be able to estimate the population abundance. Thus, without taking mortality into account, abundance estimators will be incorrect. However, if one can provide information about mortality and give an estimate about the number of the tagged fish in the waters, the information about population abundance can be gathered even though the number of tags in the waters is uncertain.

Let us now demonstrate the idea behind the mark-recapture shortly. Petersen estimator $\hat{N}$ is an estimator of the true population size N. Let us denote the number of animals in the first sample as n_1, in the second sample as n_2, and the number of the tagged animals in the second sample as m_2, see Table 1. Then under the assumptions (Appendix B) ratios between the samples are expected to be the same, or more formally $\frac{m_2}{n_2} \approx \frac{n_1}{\hat{N}}$. Therefore, Petersen estimator of

Table 1: Contingency table associated with Petersen estimator with one unknown cell value. N is true population abundance and thus unknown.

	Second sample		
First sample	Present	Absent	Total
Present	m_2	$n_1 - m_2$	n_1
Absent	$n_2 - m_2$	-	
Total	n_2		N

the population abundance is

$$\hat{N} = \frac{n_1 n_2}{m_2}. \tag{1}$$

After the long period of applying traditional frequentist methodology to this type of problems, the Bayesian approach is nowadays more common. Examples of Bayesian analysis of tagging experiments are e.g. Whitlock and McAllister 2009, Whitlock et al. (2012). If the population remains unchanged during the study period such that there is no migration, mortality nor recruitment, then the population is called closed. In practice, this is often the case when the study period is short and when there is no fishing in the study area. Whenever heavy fishing takes place, tags are removed from the waters by many reasons. Then, we say that population is open. The best-known open population approach is the Jolly-Seber -method, but also many modified versions of Jolly-Seber have been used. Jolly-Seber allows fish to die and migrate (permanently) from the study population. In this study, we will base the model development on the Cormack-Jolly-Seber model (CJS-model), which was first introduced by R.M. Cormack (1964). The paper by Brooks et al. (2000) shows how CJS-model can be used in the Bayesian frame.

Pike perch data were collected in years 1997-2012 from Archipelago Sea. All released fish were hatchery-reared. The first release is in 1997 and the last one in 2008. There is one five year gap in releases during 2001-2005. This does not affect analysis methods, only weakens the accuracy. The last reported fish is recaptured on June 2012. Each of the released pike perch was tagged by a Carlin tag having individual identification number. There is total of 4412 released tagged pike perch, and 591 reported recaptures of pike perch in data. This gives a rate of return 13.4 % which is a rather high rate compared with many other studies. There is a substantial amount of missing values in the important parameters: LENGTH 25.2 %, WEIGHT 32.9 %, GEAR 15.4 % and MESH 50.2 %. According to data, the most intensively used fishing gear on capturing pike perch were: gill net (77.4 %), fyke net (8.1 %) and trolling (6.6 %).

The natural choice for estimation is Bayesian methods because of the use of multiple data sources having completely unobserved variables in the model, possibly causing confounding between some of the variables. Furthermore, we have useful additional information from earlier studies, which gives us information about the actual state of the parameters before observing the actual mark-recapture data. Also, by using Bayesian estimation methods, taking into account dominant uncertainties is rather straightforward.

In the next chapter, the detailed description of the data and a study area are given. Chapter 3 describes the Cormack-Jolly-Seber model as a starting point for modelling purposes. Further, the development of the fish mortality model is described in detail in Chapter 3. Chapter 4 shows simulation experiment where the efficiency of estimation is studied. Chapter 5 presents results and posteriors, and Chapter 6 gives a discussion over the work done in the thesis. Throughout text, it is assumed that the reader understands basic principles of Bayesian statistical methodology and theory.

2 Description of data

In this section, tagging and effort data and theirs missingness are described. Additional sources of information and challenges affecting the modelling task are discussed. Catch data are available but not discussed here because it is not used in the model. This is to avoid double use of data in the ECOKNOWS -project, and thus to keep the understanding about uncertainties realistic in a subsequent work utilizing the results of this thesis.

2.1 Tagging data

The mark-recapture data are collected on pike-perch in the Archipelago Sea. The markings have been done using a single Carlin tag per fish in the years 1997-2000 and 2006-2008, and the recaptures cover the period from 1997 to 2012. All the tagged fish were two years old, and 50.7 % of them were released into the ICES (*International Council for the Exploration of the Sea*) fishing rectangle area 47 and the rest 49.3 % into the rectangle area 52. The ICES fishing rectangles are represented in Figure 4 (page 9).

Fish groups were released into the population at spring or early summer. The earliest within the calendar year release date was 28th of May and the latest 16th of June. The release-recapture matrix is given in Table 1. Most of the recaptures, about 83 %, are captured during the first year from the release date. There also seems to be within-year seasonal pattern in the recaptures, see Figure 1. In total, the 40.8 % of the recaptures reported with location were from the rectangle 47 (north), 21.0 % from the rectangle 51 (south-east) and 38.2 % from the rectangle 52 (east).

2.2 Effort data

There are two kinds of fishing effort data: professional and recreational. Professional fishing effort is measured in detail because professional fishermen are obligated to report the amount of their fishing (e.g. Söderkultalahti, 2013). Recreational fishing effort is based on survey samples, where answering is voluntary. The measurement units of the professional and recreational efforts are different: the professional effort is in terms of the number of gear days, whilst the recreational effort is in terms of fishing days. Fishing days counts only those days used for fishing, but the number of gears used does not affect the effort. Gear days count both days and gears used for fishing. For example, if there is in total five fishermen and each of them has been fishing for three days (no matter how many hours per day they were fishing) using two gears, then the total fishing effort is $5 \times 3 \times 2 = 30$ in gear days and $5 \times 3 = 15$ in fishing days.

The professional effort is also measured for all of the ICES fishing rectangles and about thirty most used fishing gear types. The professional fishing gear types are separated, for example, as five gill nets groups with different mesh sizes and four different types of trap nets. The combined measurements of gill nets and trap nets over the three study rectangles and temporal time frame are

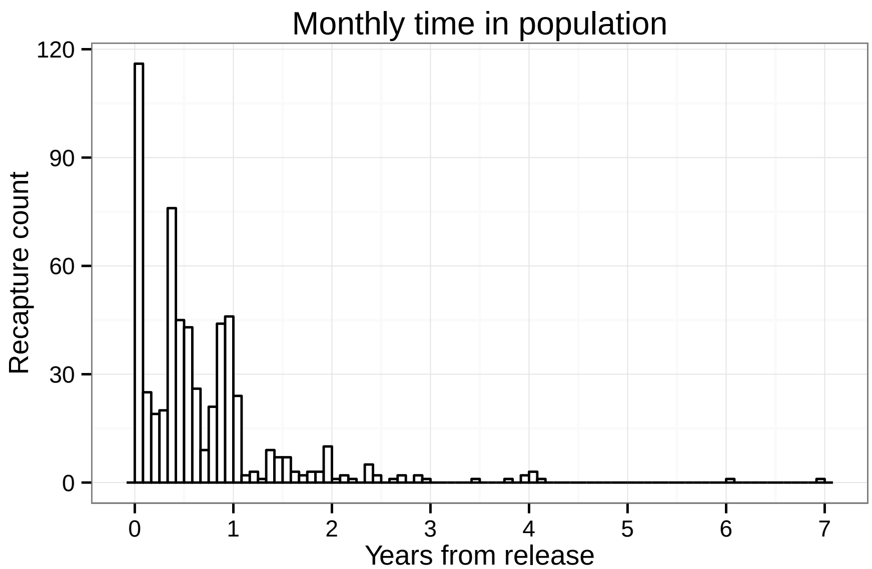


Figure 1: Histogram of differences between release and recapture. Each bar represents a month, but the start of a year is the date of the earliest release, which is 28th of May.

described in Figure 2 for the professional effort. The professional fishing effort used in this study consists of a gill net effort and a trap net effort relevant for pike perch fishing.

The recreational effort bases on survey sampling executed by FGFRI every second year (Moilanen, 2000, 2002, 2004, 2005, 2007, 2009, 2011). The applicable surveys are from the even years of 1998-2010. The gear types reported in the survey are: gill net; fish trap, crayfish trap or trap net; jig; hook and line; spinning rod; fly rod; trolling gear and other gear. The survey report gives fishing days estimates and appropriate coefficients of variation (CV). Estimates are given for seven gear groups: gill net, jig, hook and line, spinning rod, fly rod, trolling gear and other. These are combined into two gear groups in this: nets (gill net, trap net and other) and lines (jig, hook and line, spinning rod, fly rod and trolling gear). For some gears and years the uncertainties are very high, which means that the survey sampling estimates are not accurate. The recreational efforts combined into two gear groups and their approximate 95 % confidence intervals (using rule $\mathrm{CV} = \frac{\sigma}{E[X]} \Rightarrow \sigma = \mathrm{CV}E[X]$ and $CI \approx (E[X] - 1.96\sigma, E[X] + 1.96\sigma)$) are in Figure 3.

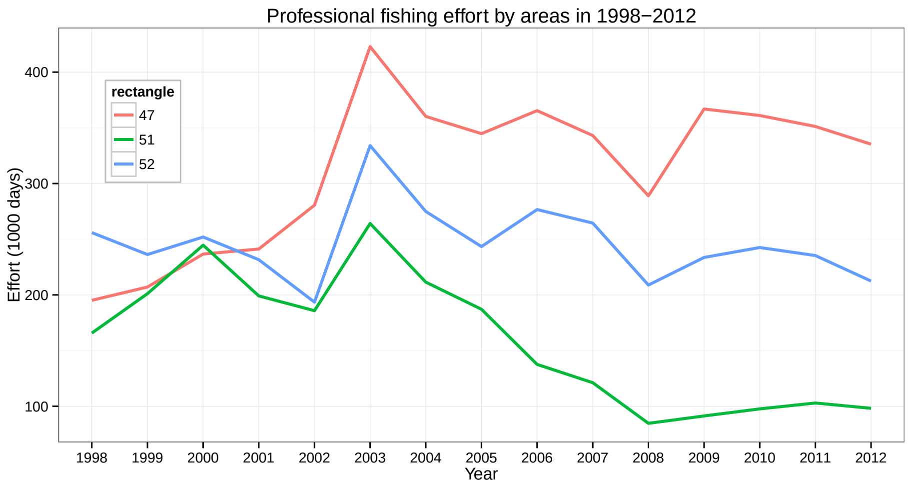


Figure 2: Point estimates of professional fishing effort by fishing rectangles over the study time period. The effort consists of the fyke net and gill net efforts.

2.3 Missing tagging and effort data

Missing values exist both in the effort and mark-recapture data. In the recreational effort data, all the odd years $1997, 1999, \ldots, 2011$ and the year 2012 are missing. In the professional effort data, the effort of the year 1997 is a missing value, but the values corresponding to the other years are observed. In mark-recapture data, the fishing gear is missing in 10.7 % of the cases and the recapture location in 11.2 % of the cases. Also, all the unreported captured tags can be thought as missing values, but also their number is unknown. In some sense, the data are similar to the presence-only data (Divino et al., 2013) because only the reported tags (presences) may be observed.

2.4 Additional information

Mark-recapture and fishing effort data are not all the information on what the model is build. The biological aspects of the model have to be taken into account on the purpose that the model is biologically realistic. To do this, additional information, also known as biological data, has to be considered in the model building. The following claims are based on both cited articles and discussions with fish biologists. Many of the claims seem to be valid in data analysis made in this thesis. The biological information also gives us tools to interpret the results of the model. We have to emphasize that not all of the ideas presented here are based on the scientific studies but rather on deductive reasoning.

Seals seem to have increased their abundance in Baltic Sea aerial counts (Kauhala et al., 2012). Seals eat fish, and that is why they may have an effect

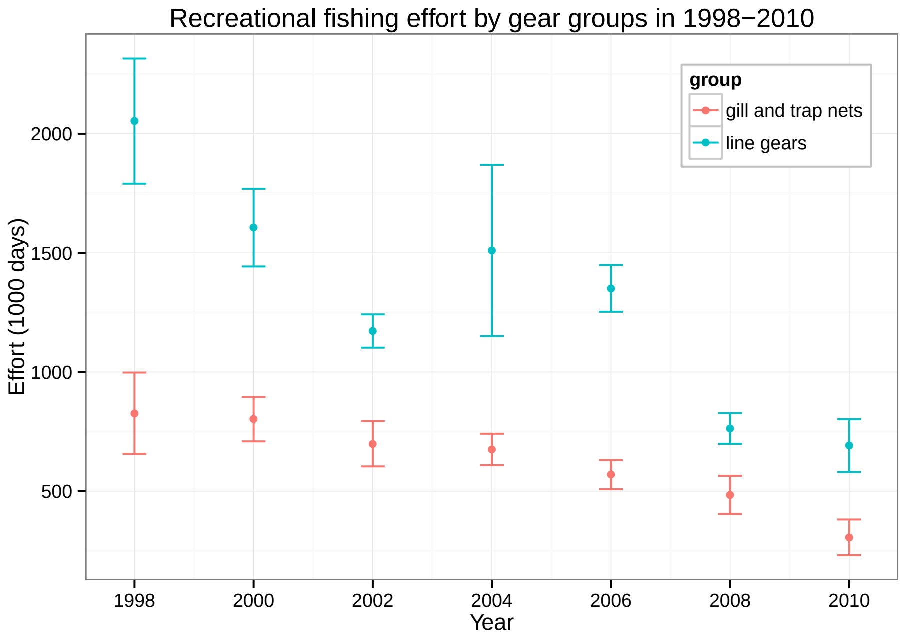


Figure 3: Estimates of recreational fishing effort in two gear type groups with approximate 95 % confidence intervals.

on fishing in the Archipelago. It has been claimed that seals cause harm to fish captured by gill net and those fish cannot be sold. According to experts, increased numbers of seals might have caused fishermen to change their preferred area of fishing towards coastline (areas 47 and 52). In the study rectangle 51, the fishing effort seems to have been decreased, see Figure 2.

Pike perch does migrate, but this cannot be generalized to whole fish population. Referring to Lehtonen et al. (1996) some proportion of the pike perch population does not migrate at all while others do. Migration is visible at the population level in Figure 4. Even though the individually recaptured fish are different between the two plots, this indicates that pike perch tend to stay in shallow waters more close to the coastline during the spring. In the autumn, many of the recaptures take place further away from the coast. Also density in the coastline is at least moderate in both plots, which supports the idea that not all the pike perch migrate.

Additional information about natural mortality of pike perch results from earlier meta-analysis study made by FGFRI researcher R. Whitlock. The methodology of the meta-analysis study is presented in the paper (Pulkkinen et al., 2011). The result of the study tells us that yearly natural mortality of about 18-25 percent of the living population is expected.

2.5 Challenges of detailed modelling

Using mark-recapture data we can only observe tags once, which is at the end of the life history of the captured fish. Process effecting the tags faith is complex, and many variables must be estimated to take into account all key aspects of that process. Mark-recapture data do not hold information about all of these variables, so external information is needed to prove realistic mortality estimate using this kind study design. External information may come from additional data sets, which are linked to this model and estimated simultaneously. Another way to add external knowledge is to build an informative prior distribution and let that prior affect one's final results.

Because data are rather small, the challenge is how to build a model describing the reality well enough and to be estimable at the same time. The phenomenon of fishing is complex and many of the parameters vary over the period. For example, catch probabilities differ for different gear types. In addition, professional and recreational fishermen are expected to have different tag reporting probabilities. It may be that not all the aspects of fishing may be modelled with the available data. Another question is also how can one estimate both fishing and natural mortality.

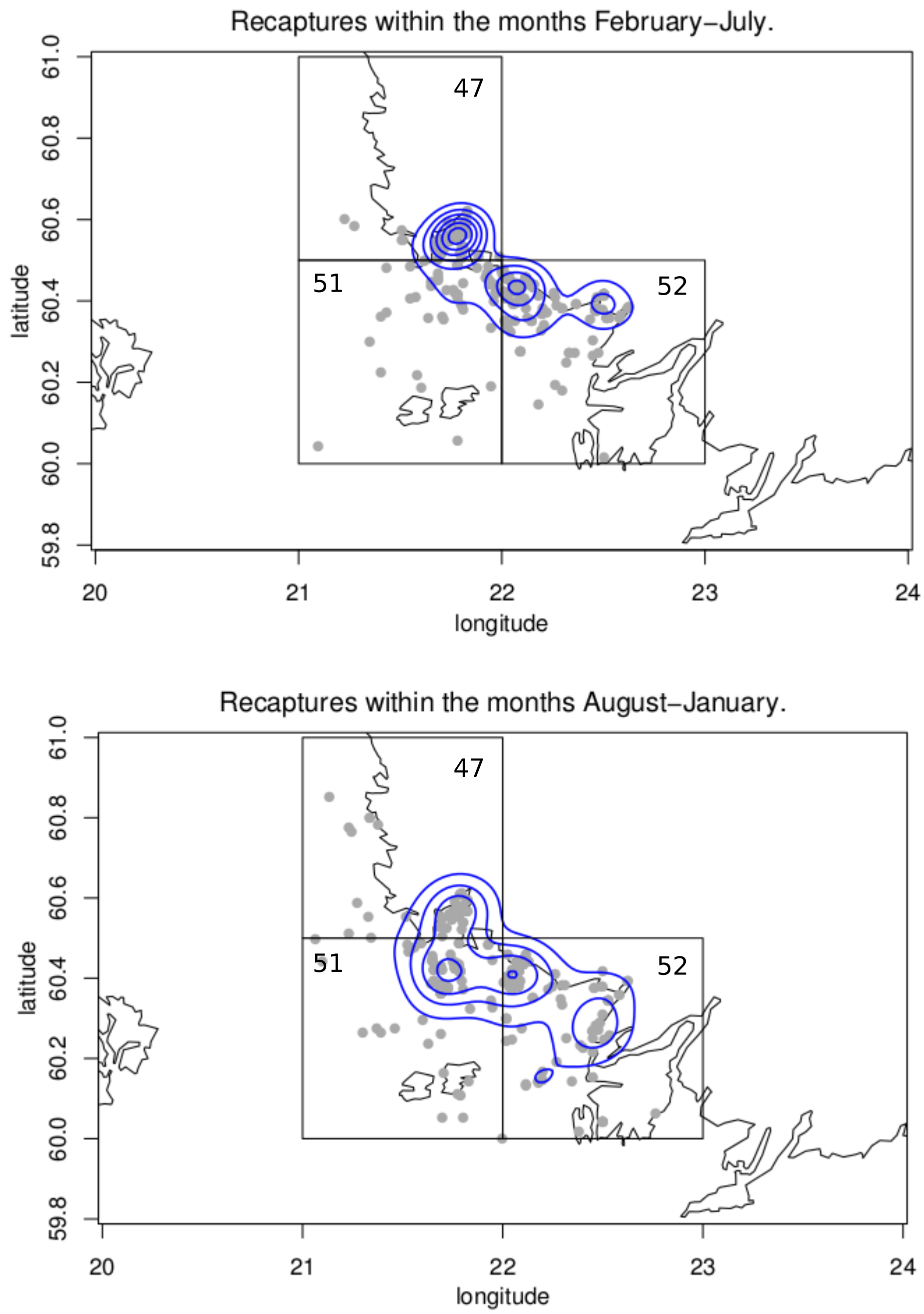


Figure 4: Density maps (coloured curved lines) of recapture locations in February-July and August-January. The study rectangles are shown as squares in the plot. The dots represent locations of the recapture pike perch. Some of the islands of the Archipelago Sea are not visible in the plot because of readability.

Table 2: The data observed, or reported professional and recreational recaptures by release and recapture year. In the cells below the main diagonal are empty because the fish can not be recaptured before the release.

Recaptures reported by professional fishermen.

	Rel.	1997	1998	1999	2000	2001	2002	2003-2005	2006	2007	2008	2009
1997	195	4	3	0	0	3	0	-	0	0	0	0
1998	85		4	0	0	0	0	-	0	0	0	0
1999	1146			64	17	4	0	-	0	0	0	0
2000	1000				33	20	1	-	0	0	0	0
2001	0					0	0	-	0	0	0	0
2002	0						0	-	0	0	0	0
2003	0							-	0	0	0	0
2004	0							-	0	0	0	0
2005	0							-	0	0	0	0
2006	1000								22	3	1	0
2007	496									16	2	0
2008	490										11	3

Recaptures reported by recreational fishermen

	1997	1998	1999	2000	2001	2002	2003	2004-2005	2006	2007	2008	2009	2010	2011	2012
1997	11	9	0	0	0	0	0	-	0	0	0	0	0	0	0
1998		16	2	2	0	0	0	-	0	0	0	0	0	0	0
1999			130	23	11	1	2	-	0	0	0	0	0	0	0
2000				46	8	0	1	-	0	1	0	0	0	0	0
2001					0	0	0	-	0	0	0	0	0	0	0
2002						0	0	-	0	0	0	0	0	0	0
2003								-	0	0	0	0	0	0	0
2004								-	0	0	0	0	0	0	0
2005									0	0	0	0	0	0	0
2006									50	11	3	0	1	0	1
2007										23	5	0	0	0	0
2008											10	8	3	2	0

3 Bayesian modelling of mark-recapture data

There are multiple reasons to use Bayesian approach in solving this kind of problems. The main reason is that significant proportion of the information comes outside of the measured data. Specifically it means that we want to incorporate expert understanding with the biological parameters, e.g. natural mortality or catchability, in the model. In addition to that, combining information from multiple data sources is natural using Bayesian methods. In this case the professional and recreational effort data and the mark-recapture data origin from different sources. Also, the key interest here is that how uncertain we actually are about the model variables in the light of data and additional information? Bayesian computation and sensitivity analyses give us tools to study the true uncertainties.

Although the data of this work arise from a mark-recapture experiment, the problem specification differs significantly from Petersen model. Reason to this is that catch data are not available. Instead of having second sample of marked and unmarked animals, only marked animals are now in the available data. The interest is on modelling yearly mortality, so this work can be seen as a relative to survival analysis having discrete time steps (Kalbfleisch and Prentice, 2002).

In this section an open population model is presented which can be used to estimate total mortality. The model will be developed according to data and phenomena of fishing and tagging experiments. Crucial things effecting these phenomena will be taken into account. Section 3.1 defines an open population model, which is developed further in Section 3.2. In Section 3.3 prior distributions are build for the developed model. We will reparametrize the model, include the effort data in the modelling and take into account the effect of missing data and missing variables. Finally, possibilities of modelling additional variation of the recapture data are discussed. Notation of this chapter is given in Table 3.

3.1 Cormack-Jolly-Seber model as a starting point

The following model can be viewed as a starting point for modelling of fish mortality. The section is based on the reasoning in Brooks et al. (2000). Data used in the original paper is collected on birds (European dippers, L. *Cinclus cinclus*). The described model suits both data on resightings and recaptures, so the model can be used in fishery applications as well.

The time resolution used is one year, and indexing of the years starts from one instead of the actual year itself. Let us denote the release years as $i = 1, \ldots, I$ and recapture years $j = 2, \ldots, J$, $I < J$. The count of released animals in the year i is denoted by R_i and release-recapture data matrix $\mathbf{M} = [m_{ij}]$, where each row $\mathbf{m}_i$ holds information on numbers of animals released in the year i and the jth column gives numbers of animals caught in the year j. Therefore, cell m_{ij} holds the number of those animals who were released in the year i and captured in the year j. Note, that cells on the diagonal and below are zero because animals cannot be captured before they are released. For example,

Table 3: The notation used in Chapter 3

Symbol	Meaning
	General notation
$i = 1, \ldots, I$	release years
$j = 1, \ldots, J$	recapture years
$f = 1, \ldots, C$	fishing fleets aka. groups of fishermen
$\mathbf{M}$	release-recapture matrix
$\mathbf{m}_i$	row of $\mathbf{M}$ holding data from release i
m_{ij}	cell of release-recapture matrix
R_i	count of released tags at year i
	Notation of Cormack-Jolly-Seber model
ϕ_k	survival probability for year k
p_k	capture probability used in CJS-model for year k
	Notation of fish mortality model
$E_{f,k}$	fishing effort of fleet f for year k
q_f	tag catch probability of fleet f
M	instantaneous natural mortality rate
$F_{f,k}$	instantaneous fishing mortality rate of fleet f year k
$Z_{f,k}$	instantaneous total mortality rate of fleet f year k
$a(i,k)$	age group a depending on release year i and current year k
$p^{\text{obs}}_{f,k,a}$	probability to observe a tag in data given that tag was in population at the end of previous year
$p^{\text{stay}}_{k,a}$	probability that tag remains in the population given that it was in population at the end of previous year
$p_{\text{retain},a}$	probability that tag retains (does not shed) in fish
$p_{\text{report},f}$	probability that tag is reported given that it was captured by fleet f
$p_{i \to j,f}$	probability of tag history: released at year i and reported at year j by fleet f

if one had three release years and J recapture years, data matrix and release counts would be following:

$$\mathbf{M} = \begin{pmatrix} 0 & m_{12} & m_{13} & m_{14} & \dots & m_{1J} \\ 0 & 0 & m_{23} & m_{24} & \dots & m_{2J} \\ 0 & 0 & 0 & m_{34} & \dots & m_{3J} \end{pmatrix}, \quad R = \begin{pmatrix} R_1 \\ R_2 \\ R_3 \end{pmatrix}. \tag{2}$$

Note that later in the developed fish mortality model the indexing of the years is different such that the diagonal holds the recaptures of the release years.

Let p_j stand for the probability of capturing a particular animal in the year j and ϕ_j for probability of a particular animal surviving the year j given that the animal is alive at the end of the previous year $j-1$. We assume that these probabilities do not vary between the animals.

The likelihood

$$L(\boldsymbol{\phi}, \mathbf{p}, R, \mathbf{M}) \propto \Delta(\boldsymbol{\phi}, \mathbf{p}) \prod_{i=1}^{I} \prod_{j=i+1}^{J} \left(\phi_i p_j \prod_{k=i+1}^{j-1} \phi_k (1 - p_k) \right)^{m_{\mathrm{ij}}} \tag{3}$$

is a multinomial, where $\Delta(\boldsymbol{\phi}, \mathbf{p}) = \prod_{i=1}^{I} \chi_i^{\nu_i}$ stands for the probability of animals being never recaptured after the release year and $\nu_i = R_i - \sum_{j=i+1}^{J} m_{ij}$ is the number of those animals. The term χ_i is a probability that an animal is not subsequently captured given that it was living at the end of year i. Note that χ_i depends on both of the survival probabilities $\phi_i, \dots, \phi_{J-1}$ and capture probabilities $p_i, \dots, p_J$. In (3), the animal has to survive the first year (thus term ϕ_i) but it cannot be captured. After that, the survival of the animal is a product over the years after the release year i and before the recapture year j, so the product term $\prod_{k=i+1}^{j-1} \phi_k (1 - p_k)$. Here, the animal survives if it does not die (term ϕ_k) or become recaptured (term $1 - p_k$). In addition, the capture probability p_j of the capture year j is needed to fulfill the probability from the release to the recapture. Note also that the likelihood contributed by each release i is multinomial. Thus, CJS-model assumes that each release has multinomial observations. An extension allowing overdispersion is given at the end of Section 3.2.

In order to sample from the posterior distribution, we will derive conditional distributions called *full conditional posteriors*. These full conditionals may then be used in the Gibbs sampling algorithm. The theory of Gibbs sampling is omitted here, but we refer the reader to Gelman et al. (2004) and Robert and Casella (2004). Let us first define independent beta priors

$$\begin{aligned} \phi_l &\sim \mathrm{Beta}(\alpha, \beta), \quad l = 1, \dots, J-1, \\ p_l &\sim \mathrm{Beta}(a, b), \quad l = 2, \dots, J. \end{aligned}$$

Now, the posterior full conditionals for ϕ_l are up to the scaling factor

$$\begin{aligned} \pi(\phi_l | \boldsymbol{\phi}_{(l)}, \mathbf{p}, \mathbf{R}, \mathbf{m}) \propto &\quad \phi_l^{\alpha-1} (1 - \phi_l)^{\beta - 1} \Delta(\boldsymbol{\phi}, \mathbf{p}) \phi_l^r \\ \propto &\quad \Delta(\boldsymbol{\phi}, \mathbf{p}) f_{\mathrm{beta}} \left(\phi_l; \alpha + r, \beta \right), \\ &\quad l = 1, \dots, J-1, \end{aligned}$$

where $r = \sum_{i=1}^{l*} \sum_{j=l+1}^{J} m_{ij}$ and $l* = \min(l, I)$. Here $f_{\text{beta}}(x; a, b)$ is a probability density function of a beta distribution for x with parameters a and b. We denote by $\boldsymbol{\phi}_{(l)}$ a vector of $\boldsymbol{\phi}$ omitting ϕ_l. The notation of $\mathbf{p}_{(l)}$ is analogous. Similarly, the posterior full conditionals for p_l are

$$\pi(p_l|\boldsymbol{\phi}, \mathbf{p}_{(l)}, \mathbf{R}, \mathbf{m}) \propto \quad \Delta(\boldsymbol{\phi}, \mathbf{p}) f_{\text{beta}}(p_l; a + r, b), \\ l = 2, \ldots, J.$$

The full conditionals may now be used in the Markov Chain Monte Carlo (MCMC) computation to sample from the posterior.

3.2 Further development of the model

In the field of fisheries modelling, it is a practice to use instantaneous mortality rates rather than survival probabilities. Because we want to estimate these instantaneous rates, the CJS-model has to be modified to make this possible. Also, we need to model how data are observed. First, CJS-model assumes that tags cannot be lost. We will add a yearly tag loss probability to the model. Second, because tags are reported by volunteers gaining only a small revenue, returning of tags will affect our understanding the true fish mortality. We will add a tag reporting probability to the model. Estimation of these two new parameters may be questionable using only the data at our disposal. Parameter estimation is studied comprehensively in Chapter 4. Informative prior distributions for these variables are set to incorporate into the model all knowledge we have.

Further, the fishing effort data will be added to modelling. Fishing effort gives information about the variation of fishing intensity, so it makes sense to use the fishing effort data.

Model reparametrization

Let us for a moment consider such fish cohort that only mortality affects it, so the population size is decreasing. Now, one may describe the expected population growth (decay) using equation $\frac{dN}{dt} = -ZN$, where N is the number of fish in the cohort and $Z > 0$ is the instantaneous (total) mortality rate. Assuming that Z is constant between the times t and $t + 1$, so the solution of the differential equation is $N_{t+1} = e^{-Z} N_t$. The total mortality is composed of an instantaneous fishing mortality rate F and an instantaneous natural mortality rate M such that $Z = F + M$. The fishing mortality is a mortality component of the died fish caused by fishing. Natural mortality is the non-fishing mortality, which usually accounts mortality due to illnesses, high age and predation. In the later text, we will refer to these instantaneous rates as fishing mortality, natural mortality and total mortality. The total mortality Z_k of the year k is linked to the survival probability

$$\phi_k = P(\text{survive the year } k | \text{was alive at the end } k - 1) = e^{-Z_k}. \qquad (4)$$

Now, we can parametrize the model such that it incorporates tag shedding, fishing and natural mortalities, and tag reporting. We need probabilistic equations, which connect the fish survival and capture probabilities to these parameters. For now, let us leave out the effect of fish age and yearly variation from these equations and consider those later. Also, we start with an assumption that all the fishermen are similar, so there is only one fleet of fishermen in the model. The reader may follow the idea of the following paragraph from Figure 5.

First, let us denote the one-year tag shedding probability as p_{shed} and tag retaining probability as $p_{\text{retain}} = 1 - p_{\text{shed}}$. We may use the simplifying assumption that a tag can be lost only once in a year and in the beginning of a year. Now, if the tag is not shed, then probability that fish is alive after one year and has a tag attached to it is $\phi p_{\text{retain}} = e^{-Z} p_{\text{retain}}$, see (4). Now, the probability that a fish dies with a tag attached becomes $(1-\phi)p_{\text{retain}} = (1-e^{-Z})p_{\text{retain}}$ and the probability that a fish dies because of fishing given that the fish has died by any means is $P(\text{fish was killed by fishing}|\text{fish was killed}) = \frac{F}{Z}$. Then, the probability of death caused by fishing with a tag attached is $\frac{F}{Z}\left(1-e^{-Z}\right)p_{\text{retain}}$. Similarly, the probability to die naturally with a tag is $\frac{M}{Z}\left(1-e^{-Z}\right)p_{\text{retain}}$. Now, we need to have a probability of tag being reported given that a fisherman has captured a tagged fish. Let p_{report} stand for this probability and assume that the reporting probability does not vary between the fishermen. Given that fish has died by fishing, the probability of observing a tag in data becomes $\frac{F}{Z}\left(1-e^{-Z}\right)p_{\text{report}}p_{\text{retain}}$, which means that a fisherman reports the recaptured tag. The probability that a fish is captured with a tag, but not reported is $\frac{F}{Z}\left(1-e^{-Z}\right)(1-p_{\text{report}})p_{\text{retain}}$. Thus, adding a reporting probability only separates the event of capturing to two events. Now, the derived probabilities of mortality events are given in the equations (5)-(9)

$$
\begin{aligned}
&P(\text{captured and reported}) &&= \frac{F}{Z}\left(1-e^{-Z}\right)p_{\text{report}}p_{\text{retain}} && (5)\\
&P(\text{captured but unreported}) &&= \frac{F}{Z}\left(1-e^{-Z}\right)(1-p_{\text{report}})p_{\text{retain}} && (6)\\
&P(\text{uncaptured and survived}) &&= 1-\left(1-e^{-Z}\right) = e^{-Z}p_{\text{retain}} && (7)\\
&P(\text{uncaptured and died naturally}) &&= \frac{M}{Z}\left(1-e^{-Z}\right)p_{\text{retain}} && (8)\\
&P(\text{tag was shed}) &&= p_{\text{shed}} = 1-p_{\text{retain}}. && (9)
\end{aligned}
$$

These are multinomial probabilities of possible tag faiths during one year, if M and F are mortality rates for one years time period, and p_{retain} is a probability that a tag does not shed within one year. Also, other time resolutions may be used in connection of this parametrization, if the above-mentioned parameters are changed according to a time resolution used. By adding probabilities together, one may check that the sum of the five probabilities is one. In data, only events from equation (5) can be observed. Those fish which remain alive and are not captured may be observed in next year, see (7).

It is impossible to observe events from (6), (8) and (9) and it is impossible to

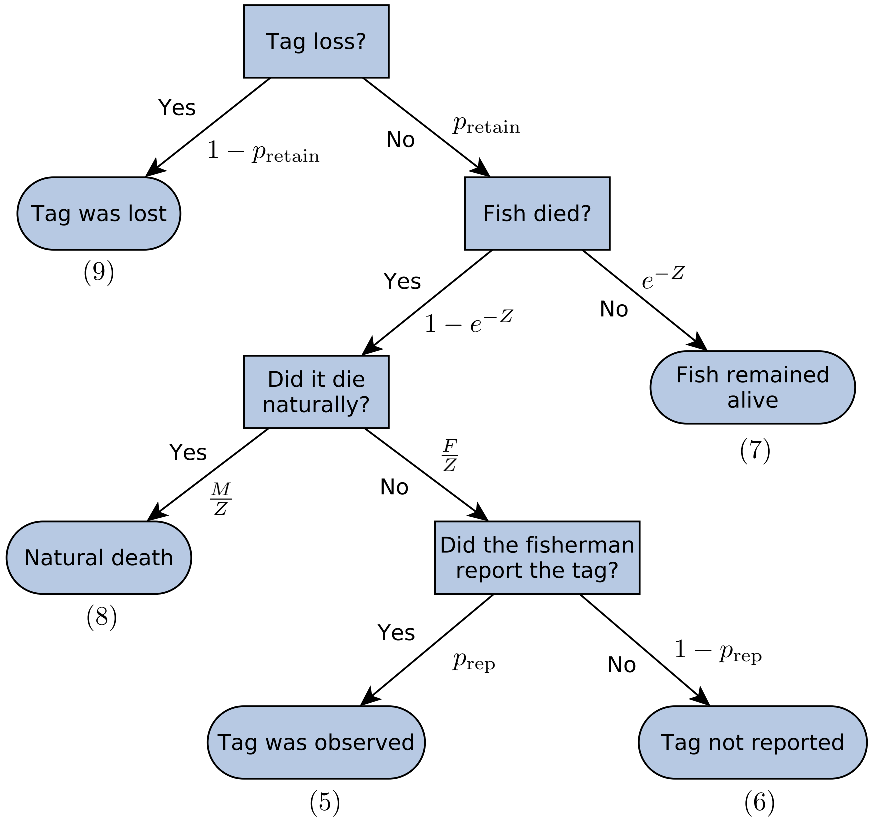


Figure 5: Probability graph of parametrization used in the model. Parametrization follows possible tag events within one time period (e.g. year). The rounded boxes are outcomes and the equation according to the outcome is referred below the box.

discriminate between these three using only mark-recapture data without double tagging. Single tagged mark-recapture data does not hold information about the reporting probability p_{report} and tag retaining p_{retain}, so additional information becomes crucial, which may come either from submodels with additional data or prior distributions.

Use of fishing efforts

Fishing effort may be linked to the model using its relation to fishing mortality $F_{f,k}$ for the fleet f in the year k

$$F_{f,k} = q_f E_{f,k}, \tag{10}$$

where q_f is the catch probability also known as the catchability coefficient of the fleet f having effort $E_{f,k}$. For example, if $E_{f,k}$ is fishing effort of gill nets and has the unit of effort in gear days, then q_f is a probability of catching one tagged fish using one net one fishing day.

Of course the assumption is rather simplifying in many ways. First, because q_f is a probability, it assumes that one can maximally capture only one fish per unit of effort. To get rid of this limiting assumption, we may allow q_f to have values larger than one. However, in many cases the yearly fishing effort is tens or hundreds of thousands per year and recapture counts yield F_f to be within the range from 0 to 2 with high probability. In this case, the assumption of q_f is not very restrictive because q_f tends to have a very small positive value.

We will also assume that the catch probability is constant over the whole study time period. This is equivalent to thinking that all the variability in the fishing mortality F_f origins the variation of fishing effort. However, we may allow q_f to be increasing over time, if there is a reason to believe that fishing methods have developed during the time period.

Multiple fishing fleets

Estimation of separate fishing mortalities is possible also in the case of multiple fleets. A fleet may consist of e.g. professional fishermen or even gear type, such as line gears. To use fleet-specific fishing mortality rates, the appropriate variable indicating the fleet is needed to tell via which fleet a recaptured tag has been collected. If that is available, then we may build a data matrix

$$\mathbf{M} = [\mathbf{M}_1, \mathbf{M}_2, \ldots, \mathbf{M}_c] \tag{11}$$

such that it is build from fleet specific data matrices $\mathbf{M}_f, f = 1, \ldots, C$. A fleet specific data matrix $\mathbf{M}_f$ holds recaptures from the fleet f over the whole study period. Row sums $\sum_{j=1}^{J} m_{f,ij}$ sum up to the count of recaptures reported by fleet f from the release i. Instead of using one single fishing mortality rate F and one natural mortality rate M, we will estimate separate fishing mortality rates $F_1, \ldots, F_C$ for each of the fleets and one natural mortality rate M. In that case, the instantaneous total mortality rate becomes $Z = \left(\sum_{f=1}^{C} F_f\right) + M$. We may also need to assume that tag reporting probability p_{report} varies between the fleets. In that case we have multiple tag reporting probabilities $p_{\text{report},f}$ for fleets $f = 1, \ldots, C$. Compared to the earlier parametrization in equations (5)-(9), the essential changes are that, in the multiple fleet case, (5) is replaced by set of C equations such that

$$P(\text{captured and reported by fleet } f) = \frac{F_f}{Z}\left(1 - e^{-Z}\right) p_{\text{report},f}\, p_{\text{retain}}.$$

Of course, (6) is similarly replaced by C equations

$$P(\text{captured but unreported by fleet } f) = \frac{F_f}{Z}\left(1 - e^{-Z}\right)(1 - p_{\text{report},f})p_{\text{retain}}.$$

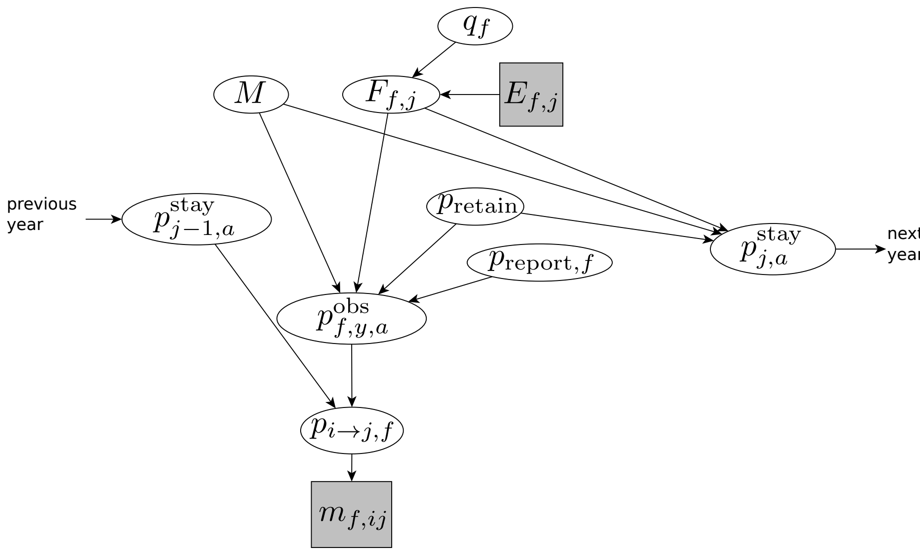


Figure 6: Directed acyclic graph describing the model.

Likelihood function

Now, because both the data matrix and model parametrization have changed, we need to rewrite the likelihood according to data, compare with equation (3). Let us now denote

$$p^{\text{obs}}_{f,k,a} = \frac{F_{f,k}}{Z_k}\left(1 - e^{-Z_k}\right) p_{\text{report},f} p_{\text{retain},a}, \text{ where } F_{f,k} = q_f E_{f,k},$$

being the probability of observing a fish in the data set of fleet f at the year k in age a given that the fish was alive and had a tag attached at the end of the previous year. Also, denote

$$p^{\text{stay}}_{k,a} = e^{-Z_k} p_{\text{retain},a}$$

being the probability of tag staying available in the fish population for fishermen to capture when fish is in the age group a and the year is k. Note that the age group a is a function of release and recapture years $a(i,j) = \min(U, j-i+1)$ where U is the total number of age classes. Now, utilising the presented contributions (reparametrization, multiple fleets, reporting and retaining probabilities and the use of effort data) to the CJS-model in this chapter, the obtained likelihood is

$$L(\mathbf{M}|E_f, R, p_{\text{report},f}, p_{\text{retain}}, q_f, M) \propto \prod_{i=1}^{I} q_i^{R_i - \sum_{f=1}^{C}\sum_{j=1}^{J} m_{f,ij}} \prod_{f=1}^{C}\prod_{j=i}^{J} \left(p_{i\to j,f}\right)^{m_{\text{f,ij}}}, \tag{12}$$

where $q_i = \left(1 - \sum_{f=1}^{C} \sum_{j=1}^{J} p_{i\to j,f}\right)$ stands for probability of not observing a tag in the data matrix and $p_{i\to j,f}$ is a probability of such fish life history, that a fish is released in the year i and reported being captured with tag by fleet f. Therefore, we define

$$p_{i\to j,f} = \begin{cases} p^{\text{obs}}_{f,i,a(i,i)} & \text{where } j = i \\ p^{\text{obs}}_{f,j,a(i,j)} \prod_{k=i}^{j-1} p^{\text{stay}}_{k,a(i,k)} & \text{where } j > i. \end{cases}$$

The relationships between data and the variables are described in the directed acyclic graph in Figure 6.

Modelling with missing recapture data

If the fleet of the returned tag is not known, the missing data problem arises. With data in hand, we are heading a problem where recreational fleet is divided into two gear groups: lines and nets. In that case, quite often people do not report what gear was the tagged fish captured on, and so we do not know from which fleet the tag comes from. To solve this problem, we need to think what type of missing data is. We will assume that missingness is *Missingness At Random*, which means that probabilities for nonreporting of a gear type used are the same for both fleets (recreational lines and nets). This is done because it is not easy to know how missingness in this context behaves. Also, it is better to assume the type of missingness and try to use all the recaptures, even the ones which did not contain gear information. This reduces systematic errors on the posteriors of fishing mortality rates.

Modelling of missing effort data

Because of missing values in the effort data, we modelled the effort of fleet f using a state-space model

$$\begin{aligned} E_k &\sim \log\mathcal{N}(\mu_k,\, 1/\sigma_k^2) && (13)\\ \mu_k &\sim N(\mu_{k-1}, 1/\tilde{\sigma}^2) && (14)\\ \sigma_k^2 &= \log(\mathrm{CV}_k^2 + 1) && (15) \end{aligned}$$

and for these prior distributions were set

$$\begin{aligned} \mathrm{CV}_k &\sim \log\mathcal{N}(a, b) && (16)\\ 1/\tilde{\sigma}^2 &\sim \mathrm{Gamma}(0.01, 0.01) && (17) \end{aligned}$$

where a and b are prior parameters and σ_f^2 was fixed using its empirical estimate $\hat{\sigma}_f^2$. Here, the efforts E_k are log-normally distributed and may be observed or missing. The latent structure of expected values μ_k of efforts allows imputing the missing efforts using information about its neighbour values and variability between the neighbours. Note that instead of actual variance parameters, the distributions having parametrization via inverse variance parameters are used.

Unobserved variables

The tag reporting and tag shedding probabilities, p_{report} and p_{shed} are variables, which cannot be estimated using the mark-recapture data only. If applicable data sets are available, modelling of these variables using separate model (sub-model) is possible. If not, then we may impute these variables using prior distributions elicited from experts or based on earlier studies.

Adding overdispersion

Overdispersion of the observed count data, compared to the variance of multinomial distribution, may be modelled by adding variability to cell probabilities of the multinomial distribution. The use of Dirichlet distribution to increase variation is natural because Dirichlet distribution is conjugate of multinomial distributed observations. Note, that a vector valued variable $\mathbf{X} \sim \text{Dirichlet}(\boldsymbol{\theta})$ is a vector of probabilities such that the sum of its cell values is one.

Let us denote $\mathbf{p}_i = (p_{i\to 1,f=1}, \dots, p_{i\to J,f=1}, \dots, p_{i\to 1,f=3}, \dots, p_{i\to J,f=3})$ being the probability vector of observed recaptures from the release i computed from the values of q_f, M and $p_{\text{report},f}$ given effort data E_f. Now, we can add uncertainty, or ”random effects” using

$$(\mathbf{p}_i^{\text{samp}})^T \sim \text{Dirichlet}(\theta_{\text{OD}}\mathbf{p}_i) \tag{18}$$

$$\mathbf{m}_i{}^T \sim \text{Multinomial}\left((\mathbf{p}_i^{\text{samp}})^T\right) \tag{19}$$

where θ_{OD} defines how much overdispersion is allowed. The marginal expectations of the Dirichlet distribution are linked to $\mathbf{p}_i$. A row vector $\mathbf{m}_i$ is a row of release-recapture matrix $\mathbf{M}$ and $(\mathbf{p}_i^{\text{samp}})^T$ a probability vector sampled from the Dirichlet distribution.

As $\theta_{\text{OD}} \to \infty$ then overdispersion vanishes to zero. We have to assume that parameters of Dirichlet distribution are positive. We may also assume that each of the parameters is at least 1 so that the marginals of the Dirichlet distribution have non-zero modes. The former restriction leads to $\theta_{\text{OD}} p_{ij} > 1 \Rightarrow \theta_{\text{OD}} > \frac{1}{\min p_{ij}}$.

The overdispersion may be used with Bayesian computation if the prior distribution of θ_{OD} is set, e.g. $\theta_{\text{OD}} \sim \text{Uniform}(a, b)$ where $a > 0$ and $b > a$ is some value large enough. Implementation code of overdispersion is given in Appendix C.

3.3 Prior consideration

Now, the model is defined, and we can calculate the likelihood (12). Because of the missing data in effort data, the state-space model will be used simultaneously with tagging data model to impute the missing effort data. Simultaneous use of the models allows to update the missing efforts using both effort data and also tagging data. To provide all-embracing information about fish mortality using this model, the prior distributions for the model parameters are needed. When priors and likelihood with data are available, final posterior estimates can be computed. The model may be estimated using the MCMC computation, which gives a sample from the posterior distribution. From the sample, it is possible to draw plots, calculate e.g. mean, variance and quantile estimates.

Prior distributions needed for inference

Because we want to combine all the information available using this design, the informative prior distributions need to be set. If the goal were to estimate what information the tagging data alone gives about the mortality, then we would prefer using the uninformative or vague priors. We need prior distributions for model variables M, q_f, $p_{\text{report},f}$ and $p_{\text{retain},a}$.

A prior distribution for the natural mortality rate M was obtained from a modified version of a Bayesian meta-analysis model for biological parameters (Pulkkinen et al., 2011) that takes into account the correlations between the parameters. This provides a prior distribution

$$M \sim \log\mathcal{N}(\mu = -1.65, \tau = 5.2) \tag{20}$$

where τ is an inverse variance parameter of log-normal distribution.

The priors of catchability coefficients for the three fleets were defined using expected values of *harvest rates* of fleets H_1, H_2, H_3, which were estimates delivered by the experts. Here, the harvest rate H_f for the fleet f is a proportion of the population harvested within one year. Thus, using the idea of Michielsens et al. (2006) the catchability priors were set using the relation between the harvest rates and catchability coefficients such that

$$q_f = \frac{-\log(1 - H_f)}{E_{f,\text{init}}}, \tag{21}$$

where $E_{f,\text{init}}$ is an initial effort and H_f is the harvest rate such that

$$H_{1:3} \sim \text{Dirichlet}(\theta_{1:3}).$$

Here $\theta_{1:3}$ elicited from experts and $\theta_f/(\sum_k \theta_k) = E[H_f]$. The key point behind the use of harvest rates for formulation of catchability priors is that it defines one's prior belief such that the harvest rate induced by priors of catchabilities lies within range of $[0, 1]$. If independent prior distributions for all the catchability coefficients were set, then prior would allow harvest rate to be larger than one, which means that we are fishing more fish what exists in the population.

The initial effort should be e.g. previous effort before the beginning of the study period. In this case, such an effort has not been measured, so we decided to use average of the measured efforts as an initial effort. This decision may be criticized, but some value for the initial effort has to be given. Also, it is better to set an initial effort to have some value which is in accordance with the data, rather that fixing some arbitrary value, which might effect final results against the data.

For fleet-specific tag reporting probabilities the prior distributions elicited from experts are

$$
\begin{aligned}
p_{\text{report,prof}} &\sim \text{Beta}(3.013, 4.867) && (22)\\
p_{\text{report,recr net}} &\sim \text{Beta}(2.511, 1.846) && (23)\\
p_{\text{report,recr line}} &\sim \text{Beta}(4.346, 2.486). && (24)
\end{aligned}
$$

The experts were fishery biologists who have background in fish biology and ecology for at least two or three decades.

The prior distribution of tag shedding is based on the double tagging experiments of North-American Walleye (Kallemeyn, 1989) which is the closest relative species of pike perch. The double tagging data was reanalyzed using Bayesian methods, and the Beta-distributed posteriors were scaled by multiplying the posterior parameters by 0.5. This was done because the species and the environment are not the same, so the uncertainty of the pike perch tag shedding is larger than is in tag shedding of Walleyes. The tag shedding priors used were

$$
\begin{aligned}
p_{\text{retain},a=1} &\sim \text{Beta}(14.790, 72.210) && (25)\\
p_{\text{retain},a=2} &\sim \text{Beta}(28.536, 53.464) && (26)
\end{aligned}
$$

for the first age group being the pike perch spending their first year after the release, and the second age group being the rest.

Eliciting priors from experts

We elicited prior distributions for each of the three fleets' average reporting probabilities from three experts. From each of experts, three beta-distributions were elicited, and experts' opinions were pooled using the average over the elicited parameters

$$
\overline{\alpha} = \frac{1}{3}(\alpha_1 + \alpha_2 + \alpha_3) \qquad \overline{\beta} = \frac{1}{3}(\beta_1 + \beta_2 + \beta_3) \qquad (27)
$$

of the beta-distribution. This is what is called *simple mathematical aggregation* in O'Hagan et al. (2006), chapter 9.

The question pattern was carefully planned based on work of (O'Hagan et al., 2006, chapter 6). The mode, median and quantiles of 25 % and 75 % were asked from the experts. The beta-distribution was fitted to elicited quantiles using self-written R-code (R Core Team, 2013), and the elicited prior was plotted, showed and interpreted to experts by a statistician. If the experts found out that the distribution did not represent their belief, the quantiles were tuned to give satisfying distribution.

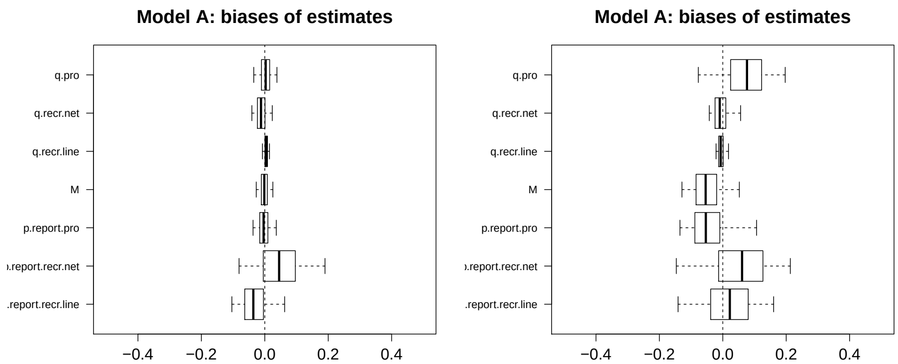
4 Simulation experiment

Four models, called A, B, C and "final model", are constructed and used in a simulation experiment in order to study the performance of suggested modelling. The main objective of this chapter is the estimation of parameters when tag shedding affects observed recapture counts. Implementing and estimation of the tag shedding is problematic because it effects posteriors of natural mortality. If the posterior of natural mortality is changed, so are the posteriors of other parameters, especially professional catchability and thus also professional fishing mortality. The available mark-recapture data do not contain information on tag shedding. Hence external knowledge is needed in the hierarchical modelling.

Let us now define the models A, B, C and final model. In the model A, no variables are fixed, but it is assumed that tags cannot be shed, which means that $p_{\mathrm{retain},a} = 1$ for all a. Model B is a complete model with freely varying yearly tag shedding probability, but assuming that the tag shedding probability is the same for all age groups: $p_{\mathrm{retain},i} = p_{\mathrm{retain},j}$ for all i and j. Model C uses a different approach: it includes tag shedding using similar parametrization used for the natural mortality rate. Final model is an extension of model C having all aspects of the true data.

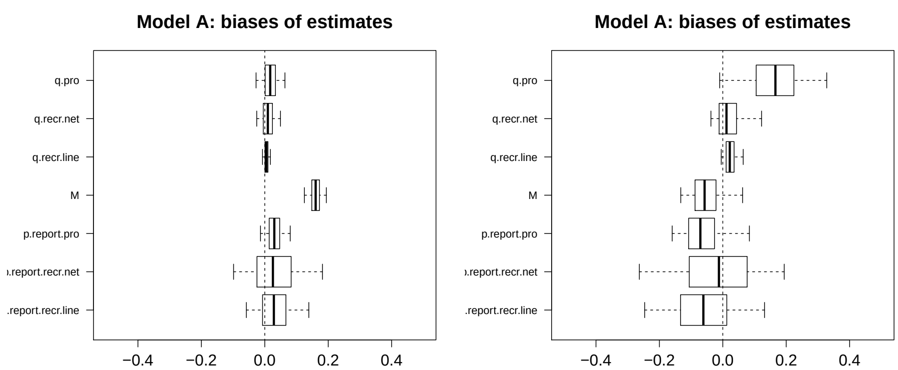
For each model, two data sets are simulated from the appropriate process. One of the two data sets will have yearly release count in the same scale compared with the true data, so $R_i = 1000$ for all i. Another data set is something which we could call highly informative, having extremely high release counts, $R_i = 100000$ for all i. This allows us to analyse the amount of uncertainty and systematic errors in the estimators, and also allows us to show how the model works for an informative data set. Also, it might be that the magnitude of systematic error is different having different release counts. An appropriate process is such a process where the assumptions of the model holds, but it still represents our understanding on the phenomena of tagging experiments.

The performance of estimation is studied visually using bias plots where each variable has a boxplot of bias. Bias is the deviance of the estimator from the value used in simulation. If the deviance is 0, then we say that estimation is unbiased. The aim here is to find such bias plots for which the median of the shifted posteriors is close to zero for all the most significant parameters. The most important parameters for the objective of this thesis are fleet specific catchability coefficients and natural mortality. Tag reporting probabilities are secondary because those may be treated as nuisance parameters, and will not be applied in the forthcoming study.



Simulation of $R_i = 100000$ released fish. Simulation of $R_i = 1000$ released fish.

Figure 7: Simulation experiment for model A, assuming $p_{\text{shed}} = 0$ when the true tag shed rate is the same. Catchability coefficients q are multiplied by 10^6 to make plot readable. The variable names in bias plots are replaced with the ones used in programming: q.pro stands for the q_{pro}, q.recr.net $q_{\text{recr net}}$, q.recr.line $q_{\text{recr line}}$, p.report.pro $p_{\text{rep,pro}}$, p.report.recr.net $p_{\text{rep,recr net}}$ and p.report.recr.line $p_{\text{rep,recr line}}$.



Simulation of $R_i = 100000$ released fish. Simulation of $R_i = 1000$ released fish.

Figure 8: Simulation experiment for model A, assuming $p_{\text{shed}} = 0$ when the true tag shed rate is $p_{\text{shed}} = 0.18$. Catchability coefficients q are multiplied by 10^6 to make plot readable.

4.1 Simulated data

The simulated data will not have any missing values in the effort data. This is to cut down the length and complexity of the simulation experiment. Missing values are allowed in the gear reporting data in the final model.

The true values used in simulations are $p_{\text{report,pro}} = 0.55$, $p_{\text{report,recr lines}} = 0.8$ (0.75 for model B), $p_{\text{report,recr nets}} = 0.75$, $M = 0.2$, $q_{\text{prof}} = 5.5 \times 10^{-7}$, $q_{\text{recr nets}} = 2.0 \times 10^{-7}$, $q_{\text{recr lines}} = 1.0 \times 10^{-7}$. For the final model, the tag shedding probabilities were 0.18 and 0.34 for the first year in the water and other years, respectively. In the bias plots, Figures 7, 8, 9, 10 and 11, the catchabilities are multiplied by ratio 10^6 in order to ease readability of plots.

The priors used in the simulation experiment were the same as the ones used in the modelling of the actual data, see Table 6. For the models A, B and C tag shedding prior of "pshed[1]" was used and for the "final model", the priors for both age groups (given in Table 6) were set. Prior distributions of natural mortality, reporting rates and tag shedding are informative, but priors of catchability coefficients are semi-informative.

4.2 Interpretation of simulation experiment results

In the model A, where the assumption of no tag shedding holds, the estimation works very well for all parameters, see Figure 7. Introducing tag shedding, the bias in the natural mortality M is visible in Figure 8a. Bias of M also causes some minor upward bias to other variables.

For the model B, we simulated data using tag shedding probability 0.18 and tested different assumptions in the model used in the estimation. We tried: fixing the tag shedding to the known true value (Figure 9a), using informative prior on the tag shedding (Figure 9b) and fixing the tag shedding to the zero (Figure 9c). Out of these three attempts, the first one gives very poor posteriors the second one seems to be the best though still having significant bias in M, and the third one is almost as good as the second one.

In the experiment of Figure 9b, the tag shedding rate becomes estimated close to zero, so the model is very close to the model in the experiment of Figure 8. The bias plots of the two models are very similar.

In the model C, the tag shedding was parametrized as an additional natural mortality rate. To write this formally,

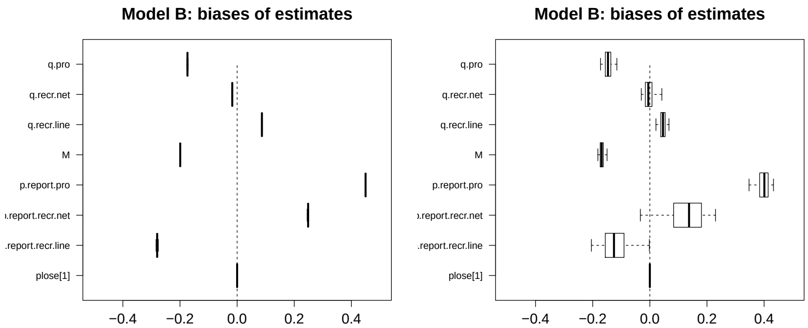
$$
\begin{aligned}
p_{\text{shed}} &\sim \text{Beta}(a_{\text{shed}}, b_{\text{shed}}) && (28)\\
M &\sim \log N(\mu_M, \tau_M) && (29)\\
M_{\text{tagshed}} &= -\log(1 - p_{\text{shed}}) && (30)\\
M_{\text{bind}} &= M + M_{\text{tagshed}}, && (31)
\end{aligned}
$$

where p_{shed} is probability of tag shedding and M is instantaneous natural mortality rate. All the information for the tag shedding probability comes via its prior in (28). Binded natural mortality M_{bind} is the natural mortality seen in the data including the tag shedding and natural mortality, and M is the true natural mortality causing fish to die. Here, M_{bind} is now used in the model parameterization instead of M in equations (5)-(9). This parametrization is perhaps rather more experimentally than theoretically argumented.

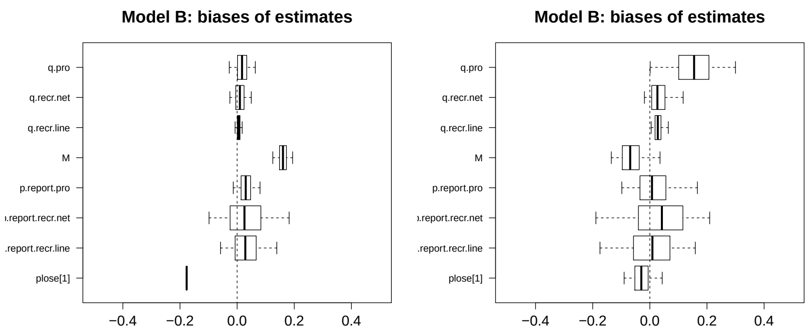
Now, we are heading an issue that two natural mortality rates might be confounded. However, one decided to try how would this approach work. It was found out that if the release counts are 1000 per year, one still has bias and that bias takes place in the professional catchability coefficient. If we use extremely high release counts, then the bias approaches towards the natural mortality rate. So, this model seems not to be any better than the best among the earlier models since our total mortality estimates become biased.

The final model contains all aspects of the model used in the next chapter except that, for this case, we assumed that no missing effort values exists. Compared with the model C, the gear nonreporting of recreational fleets was added and so was tag shedding having two age groups instead of one. This can be seen as a very realistic model for fish mortality. The model seems to be almost unbiased for the catchabilities and natural mortality in the case of 1000 released fish per year, see Figure 11b. However results with 100000 released fish gives a bit larger biases, but still the biases are rather small compared with the ones of models A, B and C.

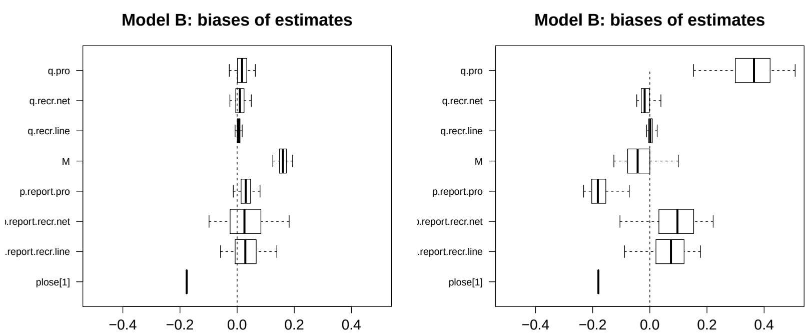
All in all, models A, B and C did not give very good results in the sense that the posteriors of interesting parameters have systematic errors, but one truly realistic model with very small systematic errors for the important variables was found. If some other models are used, the biasedness of those models must be studied using simulation experiments similar as the one represented in this chapter. If the results of the model seem to be biased, it might be possible to use ad-hoc methods to reduce the existing bias. This means shifting the posteriors by using the amount of the bias studied. However, this is risky since the simulation studies do not show how the bias develops depending on the model variables. For some case, this might be better than straightforwardly applying the estimated posteriors.



(a) Tag shed rate was fixed to the known true value in the estimation.



(b) Tag shed rate was not fixed but informative prior was used.



(c) Tag shed rate was fixed to $p_{\text{shed}} = 0$.

Figure 9: Simulation experiment for model B, having different assumption in the estimation, while true tag shed rate is $p_{\text{shed}} = 0.18$. Catchability coefficients q are multiplied by 10^6 to make plot readable. Plots on the left hand side have $R_i = 100000$ simulated released fish and on the right hand side $R_i = 1000$.

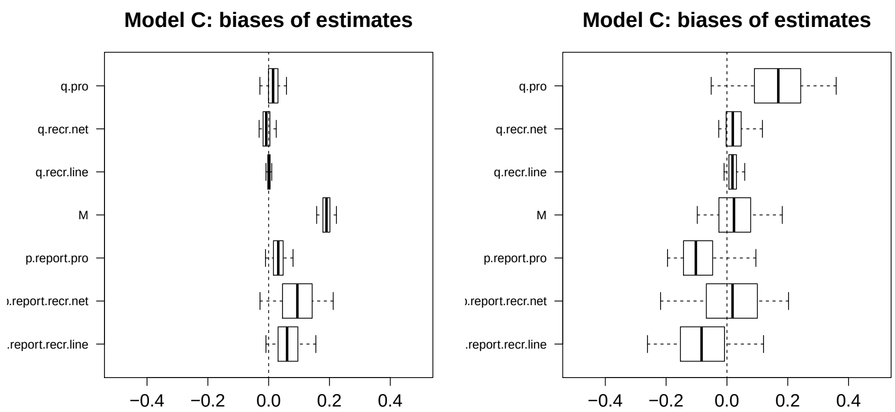
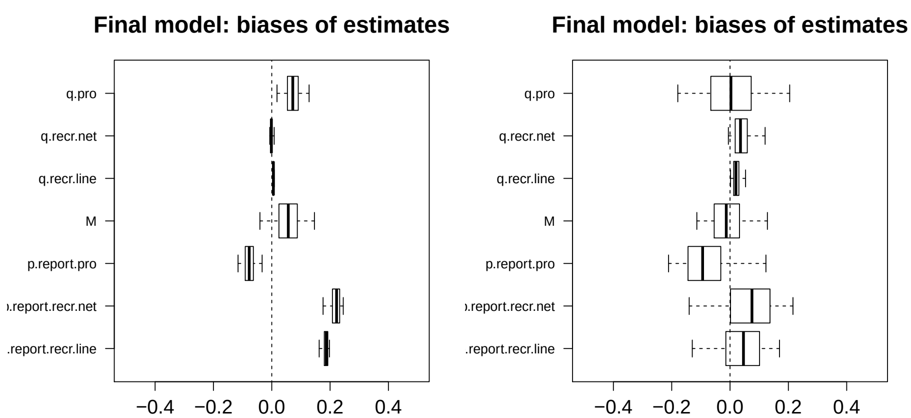


Figure 10: Tag shed rate was included as additional natural mortality rate through $M_{\text{tagshed}} = -\log(1 - p_{\text{shed}})$.



Simulation of $R_i = 100000$ released fish. Simulation of $R_i = 1000$ released fish.

Figure 11: Simulation experiment for final model, where the tag shedding probabilities are age group specific. Catchability coefficients q are multiplied by 10^6 to make plot readable.

5 Results

This chapter represents the final results in the form of marginal posteriors and their interpretations. In addition, model comparisons, model validation and sensitivity analysis are included into this chapter. First, differences between the modelling with the true data compared to simulation experiments in the previous chapter are discussed.

We intend to compare four models resembling the final model of the previous chapter. The models differ from each other in tag reporting probabilities and overdispersion. More precisely, having either one common or two separate recreational tag reporting probabilities, and the ones either having or not having the overdispersion compared to the multinomial distribution. Overdispersion was described in detail in Section 3.2.

5.1 Modelling of real data

In the real data, as similar observational data sets in general, data often have to be modified. From the data applied in this work, we did remove some of the professional reported recaptures. The reason was that some of the professional fishermen tend to report tags in bunches of tens, and these people do not usually report the recapture date. This unreporting could be modelled as interval censoring, but it is problematic in the case of multinomial model when data consist of cell counts. Practically these only tell us that the fish were captured by professionals, but almost no information about when the fish was captured exists. This is very problematic because we do not even know which year the fish was captured. Imputation of these values would be possible, but it would not give much additional information for the final results. Imputation would be quite difficult having model basing on the multinomial observations.

It is commonly known that tag shedding in the waters is usually different during the first year compared to the rest of the years (e.g. Cadigan, Brattey, 2006).

5.1.1 Model comparisons

The deviance information criterion (DIC) version proposed by Spiegelhalter et al. (2002) was used in the model comparison.

Four models are compared. Let us call them models 1, 2, 3 and 4 so that these cannot be confused with models in the previous chapter. Model 1 has the same reporting rate for recreational fishing fleets and no overdispersion. Model 2 is similar to model 1 but allows overdispersion. Models 3 and 4 have separate recreational fleet reporting rates. Model 4 has overdispersion while model 3 has not.

Referring to table 4, models 1 and 3 seem to give the lowest DIC values, 935.8 and 936.0, respectively. The difference of the values is just 0.2, so we can not distinguish the two. These two models describe the data equally well. This conclusion based on the idea that likelihood ratios of the models describing

Table 4: Deviance information criterion (DIC) and effective number of parameters (pD) values given by JAGS for the four models. Models without overdispersion (1 and 3) are supported the most but certain conclusions about the distinguishing the models cannot be drawn.

Model	pD	DIC
Model 1	36.7	935.8
Model 2	184.7	940.4
Model 3	36.1	936.0
Model 4	187.6	943.6

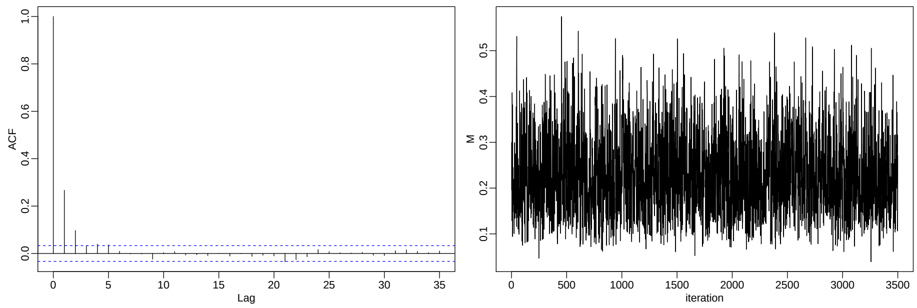
two hypotheses H_0 and H_1 is $\exp((\mathrm{DIC}_0 - \mathrm{DIC}_1)/2)$ (Lunn et al., 2012) so for models 1 and 3 it yields a likelihood ratio of 1.10. Comparing the models 1 and 3 to other two models, the smallest likelihood ratio is between models 3 and 2: 9.49. Thus, the assumption of model 1 is 1.1 times more likely than model 3, and these two models are at least 9.49 times as probable than other two models. Data does not support overdispersion.

5.1.2 Diagnostics and model checking

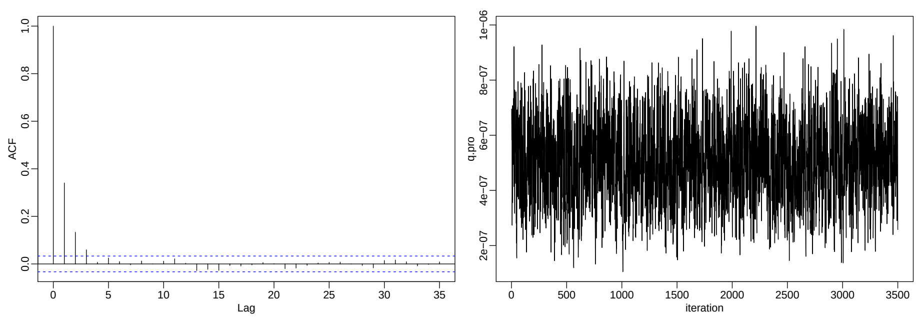
All models were fitted using MCMC methodology implemented in JAGS. The convergence of MCMC chains were inspected visually using autocorrelation plots and chain plots. Some of the autocorrelations and chains for Model 1 are plotted in Figure 12. In addition, also Brook-Gelman-Rubin convergence diagnostics $\hat{R}$ were used. The chain has converged if $\hat{R} < 1.05$, but in the final runs we aimed at having $\hat{R}$ less than 1.01. The Brooks-Gelman-Rubin convergence diagnostic values are given in Table 5.

The fit to data was inspected using posterior predictive values plotted with respect to actual observations. Observations are counts, so the use of residual plots were avoided. The data matrix consists of (count of years) $\times$ (count of fleets + 1) $\times$ (count of releases) cells, so in total $16 \times 4 \times 7 = 448$ count values. Presenting such a vast number of values is not reasonable in the thesis, but can be visually inspected when plotted as a multipage image. Predictive values of a single release year, the year 1997 are given in Figure 13. The release years 1997 fit to data is typical to this data. Some of the years give better fits than the others. The worst fit is in the professional recaptures from the release year 1999 and the recapture 1999, being 80 reported recaptures as we were expecting reported recaptures to lie in a range of $[27, 53]$ (95 % credible interval). In total 96.6 % of the observed values lie within 95 % credible interval. This indicates a good fit to data.

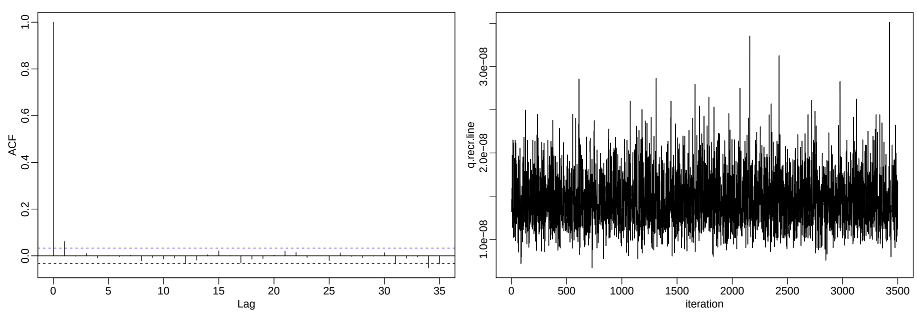
Also, correlation of samples of posterior estimates may indicate how the model fits to data or reveal issues in the model formulation. For example, if two variables have a negative correlation close to -1, it indicates that perhaps



(a) Autocorrelation and chain of M.



(b) Autocorrelation and chain of q.pro.



(c) Autocorrelation and chain of q.recr.line.

Figure 12: Autocorrelation and chain plot of natural mortality M, professional catchability q.pro and recreational lines catchability q.recr.line.

Table 5: Brooks-Gelman-Rubin $\hat{R}$ convergence diagnostics show that Markov chain has converged ($\hat{R} < 1.05$). Variable n.eff shows the effective number of sampled observations from posterior distribution.

Variable	$\hat{R}$	n.eff
M	1.002	2300
Mtagshed	1.002	1600
p.report.pro	1.009	730
p.report.recr.line	1.001	3400
pshed	1.001	6000
q.pro	1.009	770
q.recr.line	1.002	2100
q.recr.net	1.001	5000
scale	1.001	6000
tau.process.line	1.001	6000
tau.process.net	1.001	6000

only the sum of the two variables is estimable. On the other hand, high positive correlation would reveal that the two variables are linked to each other. Bivariate posterior plots of Model 1 are given in Figure 14. The plot describes negative correlation between the professional catchability and natural mortality and nonlinear relations between the catchability coefficients and reporting rates the fleets. Negative correlation of the first-mentioned may be understood as following: if professional reporting rate goes to zero, then all the mortality caused by professional fleet becomes estimated in the natural mortality rate because no information about the professional recaptures. Thus, the source of correlation may be because low reporting rate. Nonlinear relations of fleet-specific catchabilities and reporting rates can be understood by reminding that expected recaptures of a particular year and fleet is proportional to nonlinear function of catchability coefficient and reporting rate $E(m_{f,ij}) \propto (1 - exp(-q_f E_f) p_{\text{report},f}$ causing a nonlinear relation between the two variables. Even though now we perhaps have an intuitive understanding about the causes of posterior correlations and relations, this does not guarantee that the problems in the estimation could not occur. That is why the simulation study of Chapter 4 is important.

According to experts, the estimated posterior probability distributions are reasonable. For the Model 2, which have separate tag reporting probabilities for recreational line and net fishing fleets, the experts commented that the two reporting probabilities should be close to each other. This is supported by the knowledge that many of the recreational fishermen tend to use both net and line fishing methods, so much of persons are the same (Moilanen, 2004, p. 16). The order of the catchabilities is as expected, so the professionals have the highest catch probability per unit of effort, and next comes the recreational nets and last recreational lines. Experts were not capable of telling the magnitude between the fleet-specific catch probabilities, but they said that the professional catch probability could be much higher than the others. The argument of this is that professionals use drift nets to gain knowledge about the most intense movement routes of pike perch.

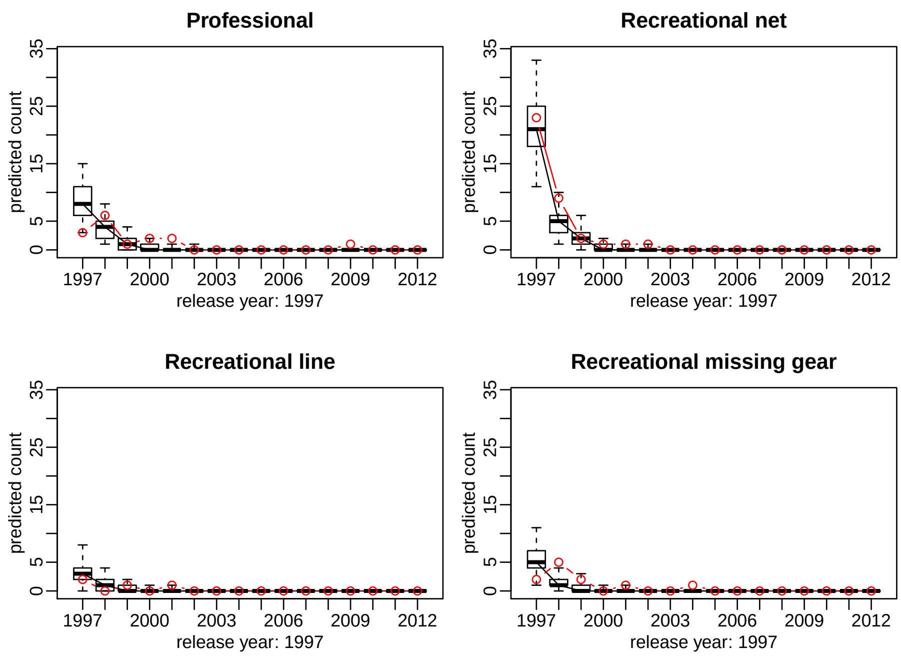


Figure 13: Predictive values alongside observed values for the release 1997.

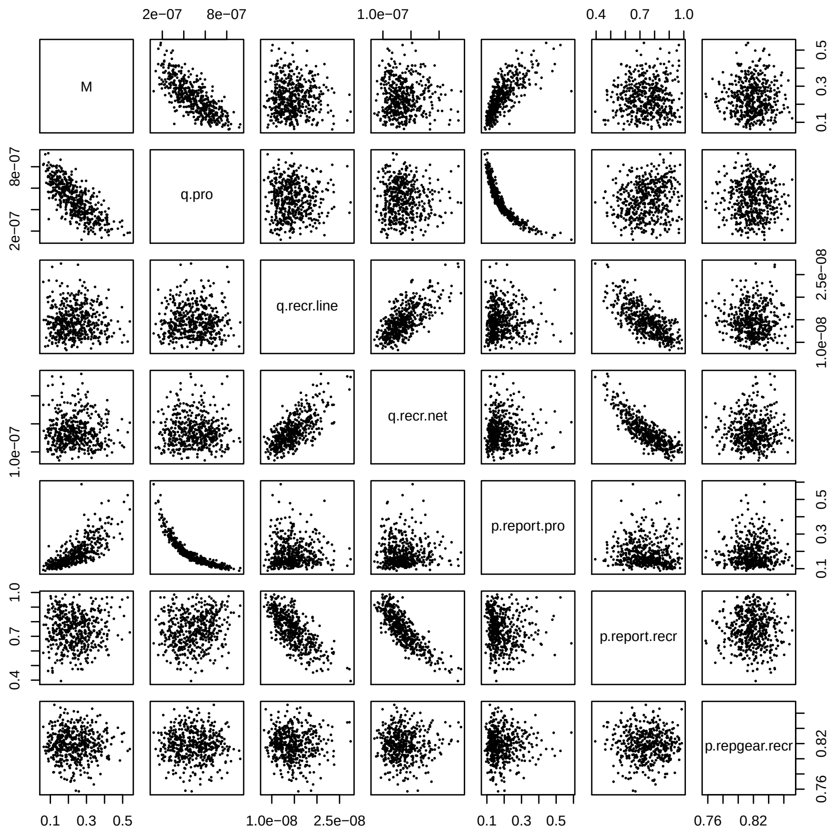


Figure 14: Pairwise plots of 500 samples from posterior distribution. Negative correlation between the natural mortality M and professional fishing mortality is visible. Also, reporting rates are nonlinearly related to catchability coefficients.

5.2 Posterior distributions and interpretations

The final posterior distributions are described in Figures 15-17. The black lines of plots are posteriors and dotted red lines are priors. In the following text, interpretations are given in high detail.

Figure 15 shows instantaneous fishing mortality rates by fleets and the instantaneous total mortality rate. Most of the fishing mortality is induced by professional fishing. The fishing mortalities of the two recreational fleets for the years 1997 and 1999 seem to be quite different compared to their previous and following years. The reason to this is: the recapture counts for those fleets are very high, and the fishing effort of the mentioned years is missing, which has been stochastically imputed using the posterior predictive distribution. In the light of knowledge we have and, given the model, the estimates of these are the best possible.

Figure 16 gives posterior distributions of instantaneous natural mortality rate and fleet-specific catch probabilities. Independent prior distributions were used to produce these catchability estimates. One should be careful when interpreting the catch probabilities: those can not be compared if the unit of effort is different, as it is in between the professional and recreational efforts. The interpretation of catch probability is the following: probability of capturing a single tagged fish using one unit of effort (e.g. one day of fishing). Although the prior distribution of natural mortality could seem to be quite restricting, the informative prior distribution is justified by having a lot of information about the variable from earlier studies.

Figure 17 describes the fleet-specific reporting probabilities: the probability of reporting a tagged fish, given that the fish with a tag was captured by the fleet. The recreational gear reporting rate describes a probability of reporting the gear used to capture the fish given that the fisherman was recreational fisher. We do not have professional gear reporting in the model because all the professional gear-specific fleets were treated as one combined fleet in the modelling.

To interpretate these fishing and natural mortality estimates, the most natural way to do it is to transform the mean estimates to probability scale. Cumulative probability plot of mortality causes is presented in Figure 18.

According to the final estimates, the yearly average total mortality of tagged Archipelago pike perch is relatively high, as high as 43.2-55.0 % while the posterior standard deviances are in the range of 4.5-5.6 %. It must be emphasized, that the estimate is sensible to the assumptions made: fish are at least two years old (as were the released fish), and the estimated rate is the average over the ages of fish (no age-specific mortality rates were estimated). The estimate mostly represents the mortality of 2-4 years old pike perch, which are about 31-60 cm long.

Also, one wants to make clear that it can not be interpreted whether or not the fishing intensity is too high or low. The risk of population collapse depends not only on mortality, but also fecundity and environmental factors. As far as I have understood, the biologists say that the Archipelago is relatively eutrophicated, which means that there is a lot of nutrition available for pike perch. Also, pike perch reproduction is currently high. Those facts support the idea that even this high mortality might not be too much. In the further work ecologists could be able to produce estimates about suitable fishing intensity levels and give regulation recommendations.

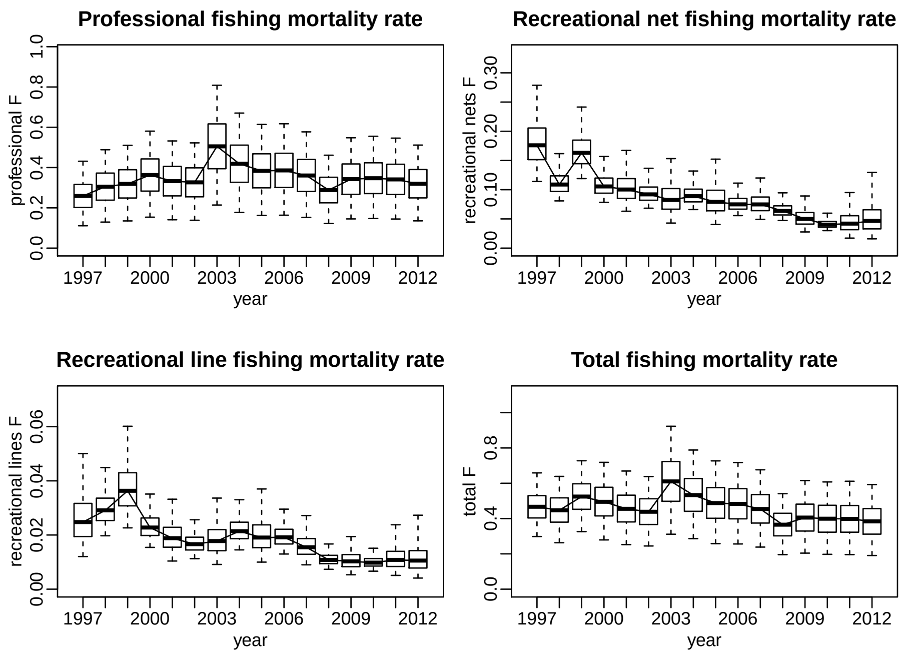


Figure 15: Yearly instantaneous fishing mortality rates by fleets and instantaneous total fishing mortality rate.

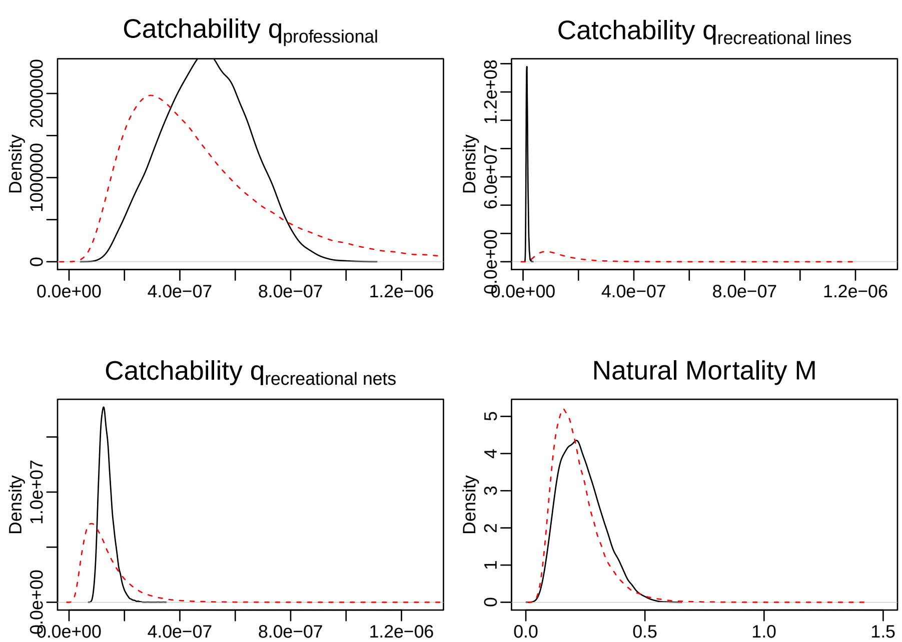


Figure 16: Posteriors of catchabilities and natural mortality rate (black line) and priors (dotted red line).

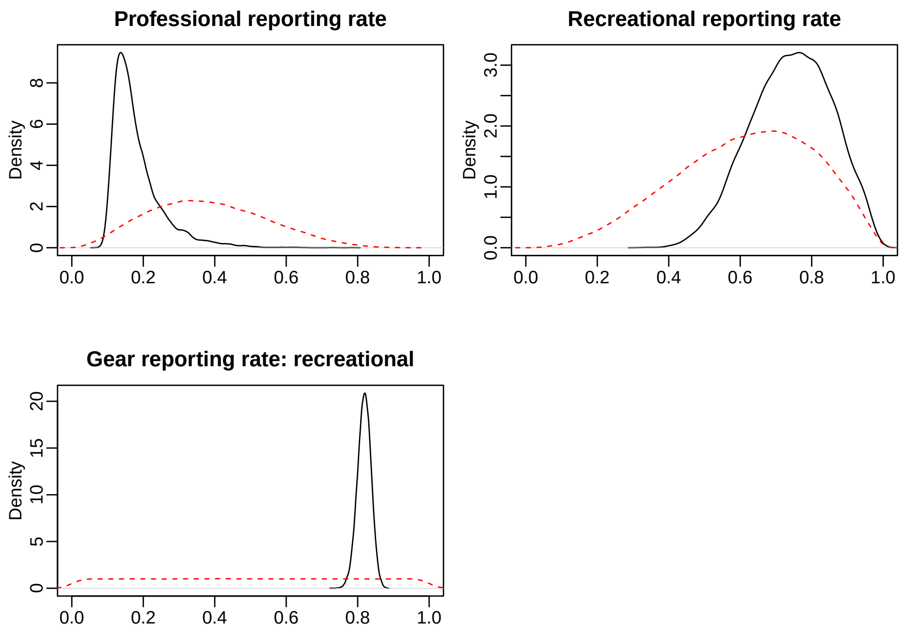


Figure 17: Posteriors (black line) and priors (dotted red line) of professional and recreational tag reporting probabilities and recreational gear reporting probability.

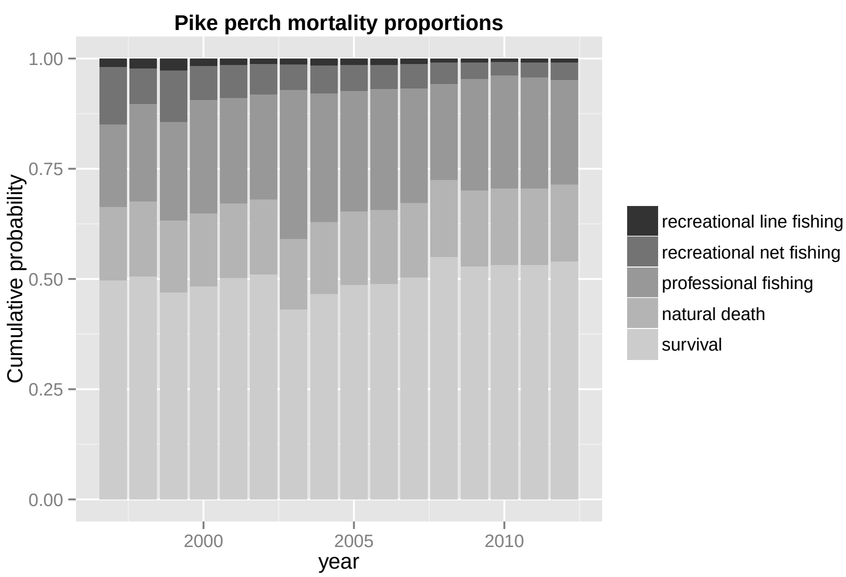


Figure 18: Posteriors means (point estimate) of the mortality reasons by year.

5.3 Sensitivity analysis

The idea of sensitivity analysis is to show, which variables are sensitive to the used prior distributions and what is the effect of used priors. It is also possible to study sensitivity to data values and model assumptions, but here we have a look at the effect of the prior distributions only.

It was stated earlier in Chapter 4 that the estimation works well if there is no tag shedding. However we do have tag shedding included into a model causing some bias. We intend to study the sensitivity of Model 1, which is the final model we have. Model 1 implements tag shedding as an additional natural mortality component, see (28)-(31) in Chapter 4. It was assumed that the reporting rates of the two recreational fleets are equal, so we have only two reporting rates. Posteriors of Model 1 were described and interpreted in Section 5.2.

Sensitivities to prior distributions of catch probabilities $q_{\text{prof}}, q_{\text{recr net}}, q_{\text{recr line}}$, tag shedding probabilities p_{shed}, natural mortality rate M and reporting probabilities $p_{\text{report,prof}}, p_{\text{report,recr}}$ are studied. One will define alternative prior distributions (alterprior for short) for all the variables whose sensitivity is to be studied. The two posteriors produced using the actual prior and the alterprior of the variable in question will be compared. If these posteriors are similar then we say that the estimation using this model and this data is not sensitive, or is insensitive, to prior distributions used. Similarity is studied using overlapping posterior density plots. The priors and alternative priors of the variables are presented in Table 6. The plots related to this section (four pages) are in Appendix A.

Table 6: Priors and alternative priors for the variables inspected.

Variable	Prior	Alternative prior
M	$\log\mathcal{N}(\mu=-1.65, \tau=5.2)$	$\log\mathcal{N}(\mu=-0.65, \tau=5.2)$
p.report.pro	$\text{Beta}(a=3.01, b=4.87)$	$\text{Beta}(a=5.12, b=2.76)$
p.report.recr	$\text{Beta}(a=3.43, b=2.17)$	$\text{Beta}(a=4.48, b=1.12)$
pshed[1]	$\text{Beta}(a=14.79, b=72.21)$	$\text{Beta}(a=3.70, b=83.30)$
pshed[2]	$\text{Beta}(a=28.536, b=53.46)$	$\text{Beta}(a=7.13, b=74.87)$
q.pro	$\log\mathcal{N}(\mu=-14.7, \tau=3)$	$\log\mathcal{N}(\mu=-12.7, \tau=3)$
q.recr.line	$\log\mathcal{N}(\mu=-16, \tau=3)$	$\log\mathcal{N}(\mu=-14, \tau=3)$
q.recr.net	$\log\mathcal{N}(\mu=-16, \tau=3)$	$\log\mathcal{N}(\mu=-14, \tau=3)$

Results of sensitivity analysis

The use of alterpriors for both reporting probabilities yields slightly higher (about 0.1) recreational reporting posteriors than does the actual priors, see Figure 19. For the professional reporting probability, the posterior mean is slid upwards, but posterior mode remain similar as when using the actual prior. The posterior of natural mortality is increased. Change in priors of reporting rates causes lower professional catchability posteriors, but distributions of two recreational fleets are not much influenced. Due to only small changes in posteriors of catchabilities, the posteriors of fishing mortality rates remains on similar levels compared to the actual results.

The results seem to be the most sensitive to priors of catchability coefficients, see Figure 20. The model was run changing priors for all three catchabilities together upwards. The priors were formulated as log-normal distribution in both cases, and only the mean parameter μ is changed while inverse variance parameter $\tau = 1/\sigma^2$ remained the same. Our alternative prior knowledge causes opposite changes to posteriors of natural mortality and professional catchability as does the alterprior of reporting rates in the previous paragraph. Posterior catchability of recreational nets is lifted up and the recreational reporting rate goes down. Influences to recreational catchability and gear reporting are minor. Although the alterprior nearly doubles the fishing mortalities of both recreational fleets, the absolute affect to total fishing mortality rate is not very large. This is due to recreational fishing mortality rates having smaller absolute values than professionals.

Alterpriors of tag shedding probabilities have very high upward impact on the posterior of professional catchability coefficient, see Figure 21. Other catchabilities are not much influenced and the change in natural mortality posterior is small. Recreational reporting rate becomes lifted upwards, and posterior of professional reporting becomes highly skewed to the right even though the posterior mode remains rather similar. The large change in professional catchability posterior is crucial; if we believe in lower tag shedding then we should believe that professionals are capturing much larger amount of fish.

Alterprior of natural mortality rate influences the posteriors of natural mortality upwards, and professional catchability downwards, see Figure 22. Also, professional reporting rate is increased to 0.2 (doubled). Reporting rate or catchabilities of recreational fleets are not influenced. Posteriors of total fishing mortality are almost halved for some years, due to such massive change in professional catchability. However, upward change of natural mortality is about the same size: close to 0.5. So, the total mortality rate (natural plus fishing) is very robust to priors even in this case.

To put this all together, the most of the variables of interest are sensitive to prior distributions set. Priors used are informative by nature, and the data give only relatively weak information about the fish mortality. Some of the variables are more sensitive to priors than others. Especially professional catchability and natural mortality seemed to be quite sensitive to prior distributions. Catchabilities of recreational lines and recreational nets fleets were less variable to changes in prior distributions than other variables. The total mortality is less sensitive than marginal distributions to changes of priors. Reason to this is a negative correlation between the natural mortality and professional catchability. The sensitivity analysis implies that carefully produced and scientifically argumented prior distributions are important in this type of problems, were the information coming from the data is weak.

6 Discussion

The objective of this master's thesis was to produce posterior probability distributions of instantaneous natural mortality and fleet-specific instantaneous fishing mortality rates using mark-recapture tagging data and fishing effort data. The idea was to produce estimates using all the relevant information excluding information given by total catch data. The work also aimed at producing the gear-specific catchability coefficients. In addition, we intended to study the sensitivities of the final results to prior distributions set.

The objectives set were accomplished, and we were able to estimate posterior distributions of fleet-specific catchabilities and tag reporting rates, and also the instantaneous natural mortality rate was estimated. Unfortunately, one did not manage to accomplish one of the aims: estimating the gear-specific catchabilities. The aim was relieved due to insufficient size of data. One had to split the data to multiple fleets because of differences between fleets in the reporting probabilities. If the rather small data set are yet once again splitted to many subgroups and gear-specific catchabilities are estimated, the uncertainties would have been very high. Also, we did not want to surpass the time limits set to this work. To put this altogether, one managed to produce posterior probability distributions, which could be applied in the subsequent work of the ECOKNOWS project.

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A Sensitivity plots

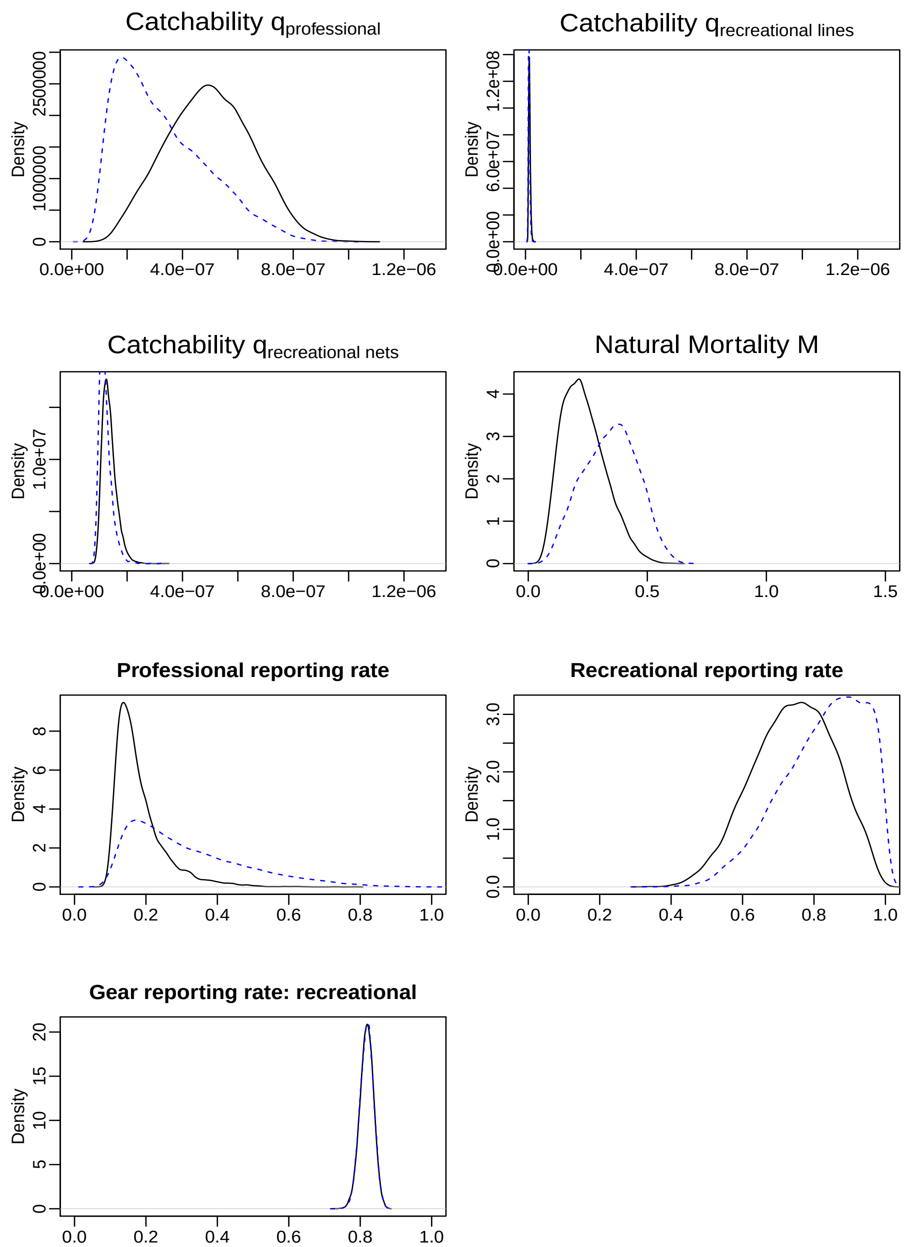

Figure 19: Sensitivity to reporting rate priors: Catchability, reporting rates and natural mortality posteriors of alternative priors (dotted blue line) and actual prior (black line). Plot visualized sensitivity to prior of reporting probabilities.

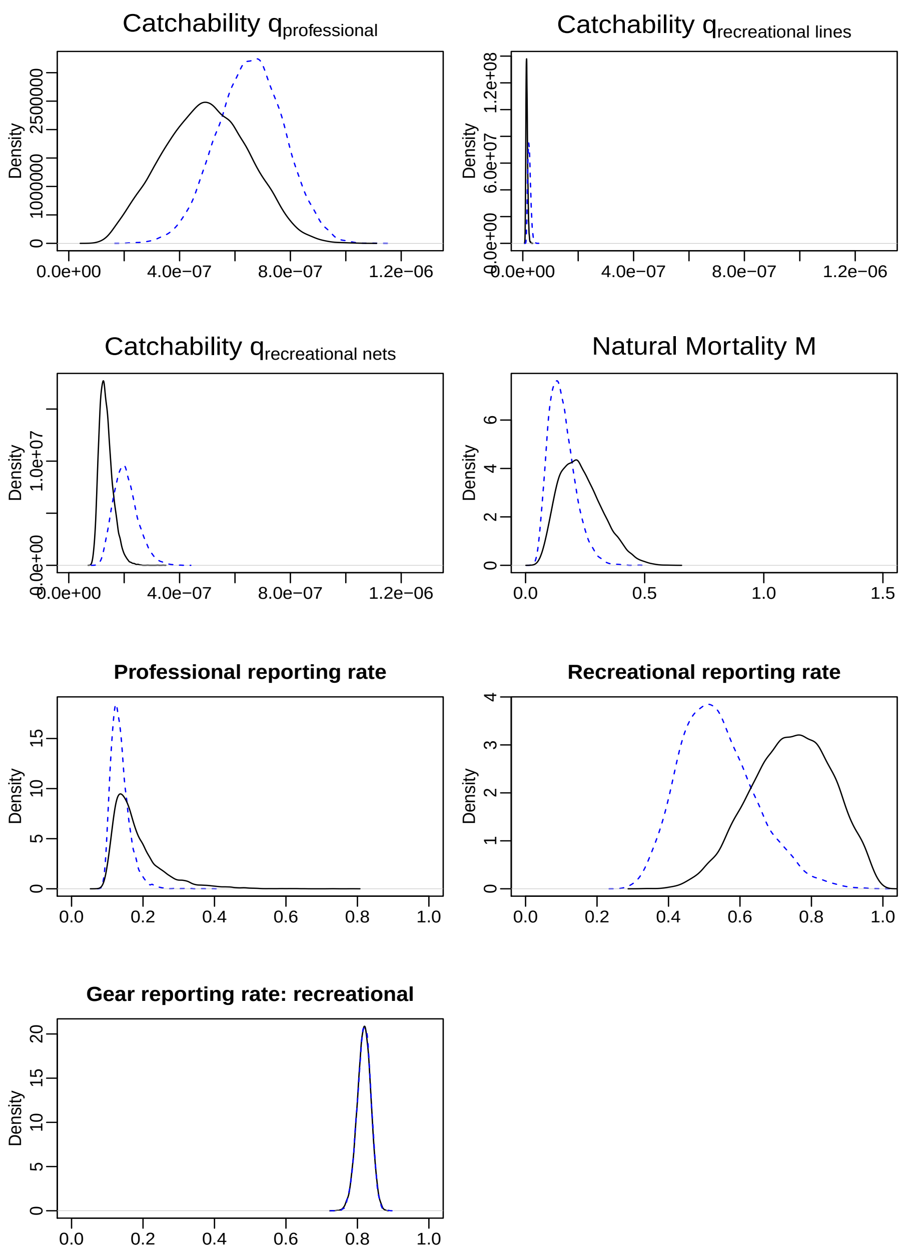

Figure 20: Sensitivity to catchability priors: Catchability, reporting rates and natural mortality posteriors of alternative priors (dotted blue line) and actual prior (black line). Plot visualized sensitivity to prior of catchabilities.

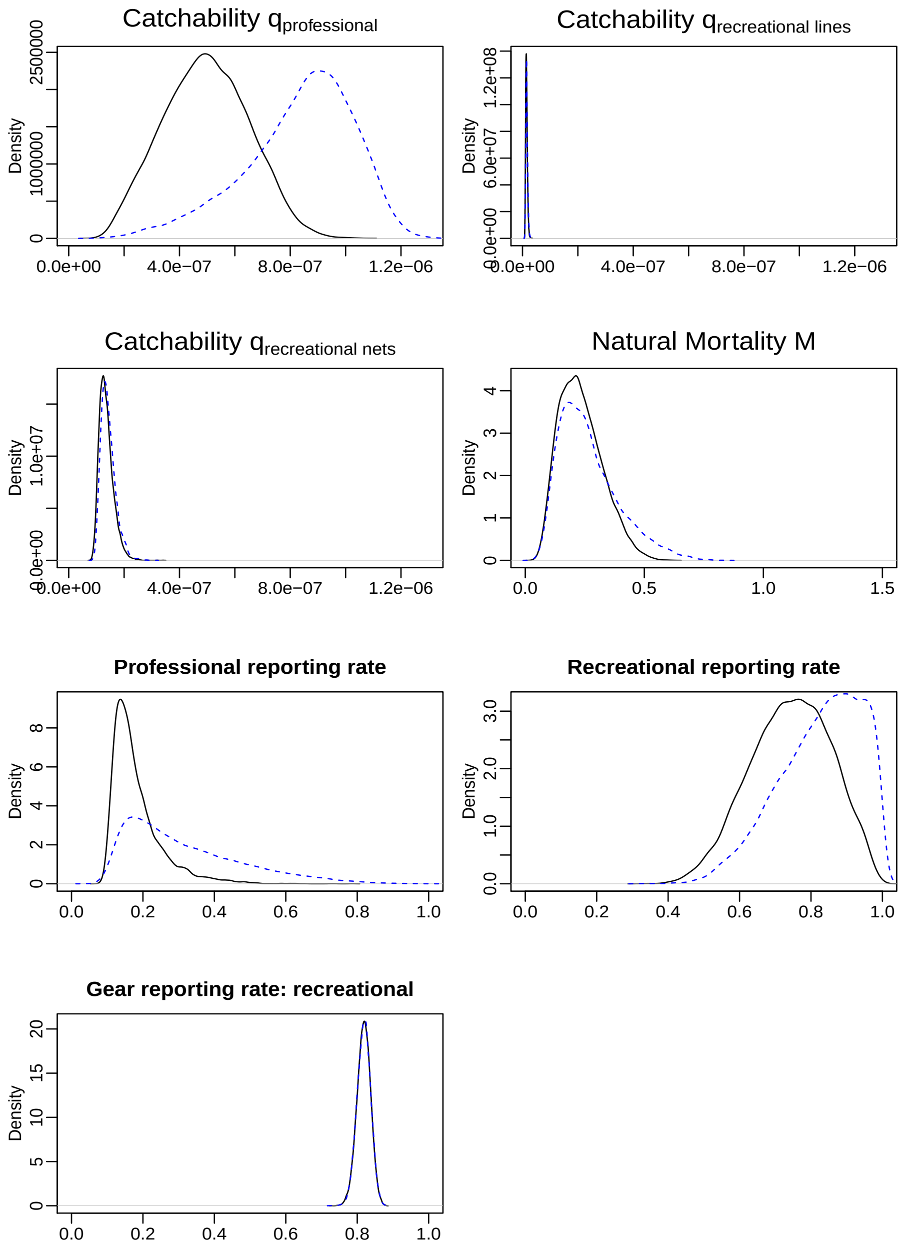

Figure 21: Sensitivity to tag shedding priors: Catchability, reporting rates and natural mortality posteriors of alternative priors (dotted blue line) and actual prior (black line). Plot visualized sensitivity to prior of catchabilities.

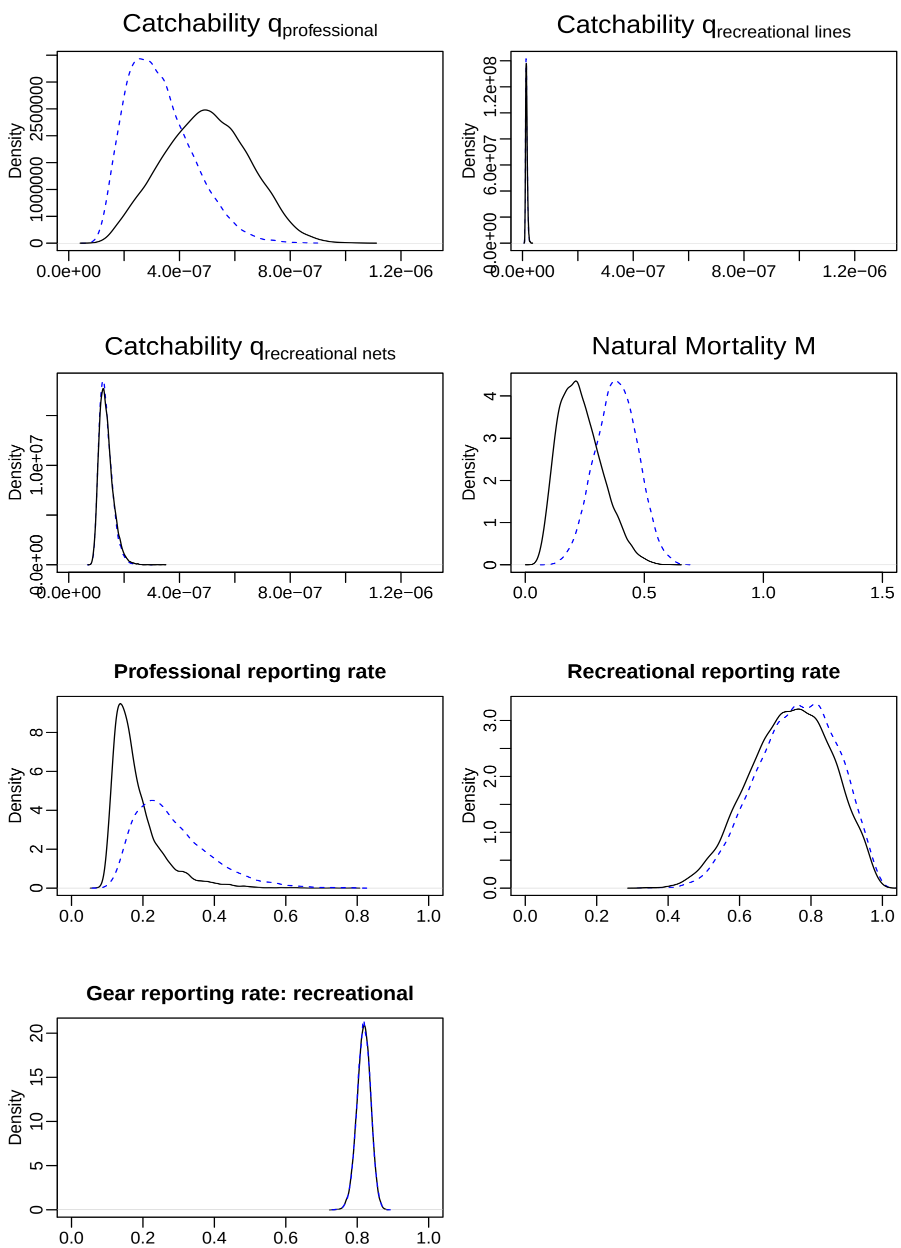

Figure 22: Sensitivity to natural mortality priors: Catchability, reporting rates and natural mortality posteriors of alternative priors (dotted blue line) and actual prior (black line). Plot visualized sensitivity to prior of natural mortality.

B Backgrounds of mark-recapture

The Petersen method is an early version of mark-recapture methods. It assumes that marked subpopulation of animals in the release phase is a random sample from the whole population of interest, called as the "first sample". The second sample refers to the recapture stage. The same assumption of a random sample also holds in the recapture phase.

Assumptions of Petersen method are:

(i) The population is closed, so that N is constant.

(ii) All animals have the same probability of being caught in the first sample.

(iii) Tagging does not affect the catchability of an animal.

(iv) The second sample is a simple random sample.

(v) Animals do not lose their marks in the time between the two samples.

(vi) All marks are reported on recovery in the second sample.

Petersen estimator $\hat{N}$ is an estimator of the true population size N. Let us denote the number of animals in the first sample as n_1, in the second sample as n_2, and the number of the tagged animals in second sample as m_2. See Table 1. Then under the assumptions (i)-(vi) ratios between the samples $\frac{m_2}{n_2} \approx \frac{n_1}{\hat{N}}$ are expected to be the same. Therefore Petersen estimator is

$$\hat{N} = \frac{n_1 n_2}{m_2}. \tag{32}$$

The estimator (1) can be largely biased in small samples, so one might want to use a modified estimator

$$N^* = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1. \tag{33}$$

When $n_1 + n_2 \geq N$ the modified estimator is unbiased and if $n_1 + n_2 < N$ then bias is reasonably small.

The asymptotic variance of Petersen estimator (1) is

$$\mathrm{Var}(\hat{N}) = \frac{n_1 n_2 (n_1 - m_2)(n_2 - m_2)}{m_2^3} \tag{34}$$

(Bishop et al., 1975, p. 233). Approximately unbiased estimator of variance of modified Petersen estimator (33) is

$$V^* = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)}. \tag{35}$$

Both variance estimates (34) and (35) are approximately the same when sample sizes are large.

Petersen estimate can be still used, when natural mortality takes place. The same equations still hold, if mortality is a random sample or if marked and unmarked animals have the same survival probability ϕ. This can be seen from the equation

$$E\left[\frac{m_2}{n_2}|n_1\right] \approx \frac{\phi n_1}{\phi N} = \frac{n_1}{N}.$$

C JAGS code

Following JAGS-code consist of data section and model section. In data section the data is modified and in the model section the model is defined. The model section begins by defining of a state-space model in rows 24-51, which imputed the missing effort values. Rows 53-87 define the prior distributions of the parameters to be estimated. Next, in rows 89-104 the parametrization described in Section 3.2 is implemented. The code of the rows 106-135 calculates the probabilities of fish life-histories (probabilities related to data matrix). This is where our model highly relies on the work of Brooks et al., 2000. In the end, rows 137-145 implements the multinomial likelihood and predictive values of the model.

Variables m.prof.net, m.recr.net, m.recr.line and m.recr.mis are given in the data as matrices having dimensions 12×16. In addition E.recr.net, E.recr.line and E.prof are vectors which could have missing values typed in as NA.

```
1  # data section begins
2  data {
3      for(i in 1:7) {
4        # professional net gears
5        m[years.index[i],1:16]  <-
             m.prof.net[years.index[i],1:16]
6        # recreational net gears
7        m[years.index[i],17:32] <-
             m.recr.net[years.index[i],1:16]
8        # recreational line gears
9        m[years.index[i],33:48] <-
             m.recr.line[years.index[i],1:16]
10       # recreational line+net gears with unreported gear
             type
11       m[years.index[i],49:64] <-
             m.recr.mis[years.index[i],1:16]
12
13         m[years.index[i],65]    <- r[years.index[i]] -
               sum(m[years.index[i],1:(4*16)])
14     }
15     for(ii in 5:9) {
16       for(j in 1:49) {
17         m[ii,j] <- 0
18       }
19     }
```

```
} #data section ends

model {

  # Observation model for recreational fishing effort:
  for(t in 2:16) { #loop over the years
    E.recr.net[t] ~ dlnorm(mu.net[t],tau.obs.net[t])
    E.recr.line[t] ~ dlnorm(mu.line[t],tau.obs.line[t])
  }

  E.recr.net[1] ~ dlnorm(14.57059,8)
  E.recr.line[1] ~ dlnorm(14.67791,6)
  mu.net[1] <- 14.57059
  mu.line[1] <- 14.67791
  for(t in 2:16) {
    mu.net[t] ~ dnorm(mu.net[t-1],tau.process.net)
    mu.line[t] ~ dnorm(mu.line[t-1],tau.process.line)
  }
  tau.process.net ~ dgamma(0.01,0.01)
  tau.process.line ~ dgamma(0.01,0.01)

  #priors
  for(i in 1:16) {
    cv.recr.net[i] ~ dlnorm(-2.12,5)
    tau.obs.net[i] <- 1/log(pow(cv.recr.net[i],2)+1.00001)
        # added 0.00001 to avoid division by zero

    cv.recr.line[i] ~ dlnorm(-2.12,5)
    tau.obs.line[i] <- 1/log(pow(cv.recr.line[i],2)+1.00001)
  }

  #lets impute one missing professional effort
  E.prof[1] ~ dlnorm(13.33226,1/0.01689149)

# Fish parameters:  semi-informative priors
#-----------------
  # natural mortality
  M ~ dlnorm(-1.65,5.2)
  Mtagshed[1] <- M-log(1-pshed[1]) #Mtagshed holds all the
      visible tag shedding
  Mtagshed[2] <- M-log(1-pshed[2])

  # tag shedding
  pshed[1] ~ dbeta(14.79, 72.21)
  pshed[2] ~ dbeta(28.536, 53.464)

  # catchability coefficients
  q.recr.line ~ dlnorm(-16, 3)
  q.recr.net  ~ dlnorm(-16, 3)
  q.pro       ~ dlnorm(-14.7, 3)
```

```
  for(i in 1:16) { #loop over the recapture years
    F.recr.line[i] <- q.recr.line * E.recr.line[i]
    F.recr.net[i]  <- q.recr.net  * E.recr.net[i]
    F.pro[i]       <- q.pro       * E.prof[i]
  }

  # total mortality
  for(t in 1:16) {
    F.total[t] <- F.pro[t] + F.recr.line[t] + F.recr.net[t]
    Z[t,1] <- F.total[t]+Mtagshed[1] # age group 1
    Z[t,2] <- F.total[t]+Mtagshed[2] # age group 2
  }

  #reporting rates
  p.report.recr  ~ dbeta(3.428241, 2.1662)
  p.report.pro   ~ dbeta(3.012988, 4.866686)

  #reporting rate of gear information given that capture is
      reported
  p.repgear.recr ~ dbeta(1,1)

#----------------------
# Code similar to Brooks' begins
#----------------------

  # Possible fish event during a year:
  for(agegr in 1:2) {
    for(t in 1:16){
      #probability of fish staying alive for a one year
      p.survive[t,agegr] <- exp(-Z[t,agegr])
      #probabilities of actually observing in the data
          frame by fleets
      p.observe.pro[t,agegr] <- (F.pro[t]/Z[t,agegr]) *
          (1-exp(-Z[t,agegr])) * p.report.pro
      p.observe.recr.line[t,agegr] <-
          (F.recr.line[t]/Z[t,agegr]) * (1-exp(-Z[t,agegr]))
          * p.report.recr * p.repgear.recr
      p.observe.recr.net[t,agegr]  <-
          (F.recr.net[t]/Z[t,agegr]) * (1-exp(-Z[t,agegr]))
          * p.report.recr * p.repgear.recr
      p.observe.recr.mis[t,agegr]  <-
          (F.recr.line[t]/Z[t,agegr]) * (1-exp(-Z[t,agegr]))
          * p.report.recr * (1-p.repgear.recr) +
          (F.recr.net[t]/Z[t,agegr]) * (1-exp(-Z[t,agegr]))
          * p.report.recr * (1-p.repgear.recr)
    }
  }

  # Calculate the cell probabilities
```

```
  for(i in 1:16){
    p[i,i] <- p.observe.pro[i,1]
    p[i,i+16] <- p.observe.recr.net[i,1]
    p[i,i+16+16] <- p.observe.recr.line[i,1]
    p[i,i+16+16+16] <- p.observe.recr.mis[i,1]
    prod_surv[i,i] <- p.survive[i,1]

    for(j in (i+1):16){ #loop over recapture years
      prod_surv[i,j]  <- p.survive[j,2]      * prod_surv[i,j-1]
      p[i, j]          <- p.observe.pro[j,2]  * prod_surv[i,j-1]
      p[i, j+16]       <- p.observe.recr.net[j,2]  * prod_surv[i,j-1]
      p[i, j+16+16]    <- p.observe.recr.line[j,2] * prod_surv[i,j-1]
      p[i, j+16+16+16]<- p.observe.recr.mis[j,2]  * prod_surv[i,j-1]
    }

  # Probability of animal never being seen again
  p[i, nj] <- 1 - sum(p[i, 1:(nj-1)])        # this should be checked by writing equations of not observing an animal in j-i+1 years
}


  for(i in 2:16) {
    # Zero probabilities in lower triangles of table
    for(j in 1:(i-1)){
      p[i, j] <- 0
      p[i, j+16] <- 0
      p[i, j+16+16] <- 0
      p[i, j+16+16+16] <- 0
    }
  }

  # Define the likelihood
  for(i in 1:7){
    m[years.index[i], 1:(4*16+1)] ~ dmulti(p[years.index[i], 1:(4*16+1)], r[years.index[i]]);
  }

  # Try some predictive values
  for(i in 1:7){
    m.pred[i, 1:(4*16+1)] ~ dmulti(p[years.index[i], 1:(4*16+1)], r[years.index[i]]);
  }

```

```
147 }
```

Overdispersion may be implemented by replacing lines 144-152 by

```
144 # Define the likelihood
145 theta.od ~ dunif(2.01,10000)
146 for(i in 1:7){
147   psamp[i, 1:(4*16+1)] ~ ddirch(theta.od *
        p[years.index[i],]+0.1)
148   m[years.index[i], 1:(4*16+1)] ~ dmulti(psamp[i, ],
        r[years.index[i]]);
149 }
150
151 # Try some predictive values
152 for(i in 1:7){
153   psamp.pred[i, 1:(4*16+1)] ~ ddirch(theta.od *
        p[years.index[i],]+0.1)
154   m.pred[i, 1:(4*16+1)] ~ dmulti(psamp.pred[i, ],
        r[years.index[i]]);
155 }
```

Catchability priors may be set by using alternative approach replacing lines 60-67 by

```
60
61   # catchability prior via harvest rates
62   theta[1] <- 5.833 #prof
63   theta[2] <- 3.417 #recr net
64   theta[3] <- 3.417 #recr line
65   H[1:3] ~ ddirich(theta[1:3])
66   scale ~ dbeta(1,1) # this parameter can be interpreted as
        proportion of fishing from the living population
67
68   # catchability coefficients
69   q.recr.line <- -log(1-H[3]*scale)/E.recr.line.init
70   q.recr.net  <- -log(1-H[2]*scale)/E.recr.net.init
71   q.pro       <- -log(1-H[1]*scale)/E.pro.init
```

where E.recr.line.init, E.recr.net.init and E.pro.init are initial fishing efforts given in the data.