A DAILY TAG RETURN MODEL FOR LOBSTER FISHERIES

by

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(A joint CSIRO and UTAS PhD program in quantitative marine science)

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February, 2012
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ABSTRACT

A daily tag return model was developed to estimate fishing and natural mortality, tag reporting rate and catchability with application to lobster fisheries. Tag return data is usually collected with knowledge of the exact date of recapture. By modelling tags individually, each tag contributes information on fishing and natural mortality, catchability and tag reporting rate to the likelihood. Providing sufficient tags are maintained in the fishery to enable recaptures to occur during the fishing season, finer resolution of parameters is possible.

Model performance was tested by simulation of different times of release and recapture as well as a range of different seasonal fishing patterns typically found in lobster fisheries. Precision and accuracy of estimates were improved when there was a contrast in fishing effort throughout the season or a seasonal closure within the year. The timing of tag release was not found to affect model performance.

Evaluation of the model was undertaken by comparison of estimates from a previous study using an identical dataset. Total mortality estimates were equivalent between models although separation of fishing and natural mortality differed between models. Small improvements in the precision of estimates were obtained for the model that incorporated exact times of tag release and recapture.

The daily model enabled finer time scale estimates of parameters and this was explored in the estimate of within season catchability. Penalised spline smoothing was applied to estimate catchability, resulting in a curve that captured the timing of biological events such as moulting and mating.

Higher fishing mortality estimates were obtained when the fishing fleet was separated into groups based on their reliability at returning tags. This suggests that fishing mortality estimates could be compromised when reporting rate is considered cosmopolitan across the entire fleet. However, the small number of reliable fishers and their fishing patterns, make interpretation of results problematic.

A cost-benefit analysis of the use of PIT tags compared to T-bar tags, the standard tag used in lobster fisheries, was undertaken. For a given cost the higher expenses associated with PIT tags and scanners resulted in fewer lobster being tagged compared to T-bar tags. The improved tag reporting rate from PIT tags resulted in improved precision and accuracy of mortality estimates using this technology unless the tag reporting rate for T-bar tags was substantially increased.
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Chapter 1

Introduction

1.1 Why Tag?

With increasing global demand for fish protein there has been increasing pressure on wild fish populations to sustain increased levels of production. This has led to 80% of the world’s fish stocks being classified as either fully exploited, overexploited or having already collapsed (Mora et al., 2009). Sustainable management of these resources requires accurate, high quality information with which fisheries managers and governments can determine appropriate harvest strategies (Beddington et al., 2007). The impact of stock collapse ranges from environmental degradation that may lead to regime shifts (Biggs et al., 2009), to the establishment of invasive species (Daskalov et al., 2007; Ling et al., 2009) and even to the socioeconomic dislocation of those people involved in harvesting and processing (Mason, 2002). Once a stock has collapsed as a result of over fishing, recovery often takes decades, if it occurs at all (Hutchings, 2000). It is therefore essential that managers have the best possible information available to manage fisheries sustainably in order to reduce the risk of over-exploitation. A key to ensuring sustainable management is to have accurate and reliable estimates of the resource.

In the terrestrial environment, animal abundance can usually be estimated easily and cheaply from direct observations (Seber, 1982). Estimating the abundance of marine populations is not as straightforward because obtaining direct observations is expensive, and the schooling behaviour of many species makes representative sampling difficult to achieve. With direct measurements of abundance being problematic to obtain, many fisheries are managed with relative measures of abundance, usually catch and effort data, under the assumption that

\[ C = NEq, \]

where \( C \) is catch, \( N \) is stock abundance, \( E \) is the fishing effort and \( q \) is catchability. This assumption forms the basis of most biomass dynamic models that are used to estimate exploitation rates in many fisheries (Hilborn and Walters, 1992). These models usually assume consistent pattern of catchability between fishing seasons. With many fisheries around the world, especially high value fisheries such as rock
lobster, moving to quota management, the link between catch and effort may change as fishers change their behaviour to maximise profit from their allocated quota rather than maximising catch. This often calls for the use of fishery independent methods of estimation such as direct surveys or tagging studies to better estimate abundance. An alternative method of estimating fisheries population parameters is the use of tagging models.

1.1.1 Tagging for Estimation of Demographic Parameters

While tagging studies are widely used in the marine environment to obtain movement and growth information, they are less frequently used to estimate abundance. Terrestrial tagging studies possess two considerable advantages compared with those undertaken in the marine environment. Firstly, it is usually easier to identify the target population, as barriers to movement are often more clear-cut. Secondly, tagging surveys are generally cheaper to undertake on land than at sea. Other issues, such as the unfamiliarity of fishery biologists with methods or software, may also contribute (Pine et al., 2003).

Originally used in fisheries to avoid perceived unreliability in catch and effort data, tagging studies provide a conceptually simple and powerful mechanism for providing estimates of parameters such as fishing mortality rates. The concept of tagging is straightforward; a captured animal is given a unique mark or tag and released back into the population. In the event of it being recaptured, the tag allows the identification of the individual. The tags used in studies designed to estimate mortality are generally small and cheap so that large numbers can be released. Recaptures are obtained either by researchers alone or with the cooperation of fishers who harvest tagged animals and return the tags to researchers. Other more sophisticated types of tags such as acoustic, satellite or archival tags can be used to collect more detailed information relating to the movement or behaviour of the animal. However, these applications are beyond the scope of this thesis.

Tagging models use an identifiable subset of a population to estimate population statistics. The origin of tagging is unknown but the basic principle has been in use for hundreds of years. The first recorded use of tagging experiments in fisheries was by Petersen in 1896, who marked members of a fish population and calculated the exploitation rate and total population of fish living in closed bodies of water, by comparing the ratio of marked to unmarked animals (Ricker, 1975). However, this method was not new. Graunt in 1662 used the same method to estimate the population of London following a plague, and Laplace in 1783 used the number of children born in 1803 as a marked sample to estimate the population of France (Ricker, 1975).

The Schnabel census (Schnabel, 1938) extended the method of Petersen to allow for multiple sampling times. Animals captured in every sampling event after the first, are inspected for tags, with those that do not have tags being tagged. All animals are then released and the population size is determined from the successive recapture events. Jolly (1965) and Seber (1965) generalised the Schnabel census to open populations allowing for deaths, recruitment, immigration and permanent
emigration, with animals entering or leaving the population only once. There are a number of review articles that discuss these and other capture-recapture models in greater detail (Seber, 1986; Pollock, 1991; Pine et al., 2003). Derivations of these methods are still widely used, especially for protected species of birds and mammals such as whales and seals (Cerchio, 1998; Baker, 2004). Since these models usually require tags to be recaptured by researchers, they are not considered further in this thesis. This thesis focuses on estimating fishing and natural mortality and catchability from studies where fishers are the primary source of tag returns. This is a common method for obtaining tag returns, and is very cost effective compared to studies where researchers alone recapture tags.

1.1.2 Brownie Models

The development of multi-year single recapture models permitted researchers to make use of tags returned by hunters or fishers who obtain them during the harvest of a population that includes tagged individuals (Seber, 1962, 1982; Brownie et al., 1985). This family of tag return models, hereafter referred to as Brownie models, differ from capture-recapture models where researchers alone recapture tags. Brownie models require that two or more cohorts of tags are released into a homogeneous population, with estimates of age and year specific survival derived from the ratio of recaptures between cohorts tagged in successive years.

While there are a number of alternate parameterisations of the basic model (Pollock et al., 1991; Hearn et al., 1998; Hoenig et al., 1998a), these all share a common complexity – in order for the model to be identifiable, the timing of releases must be carefully coordinated with the fishing season (Brownie et al., 1985). Pollock et al. (1991) partitioned total mortality into fishing and natural mortality by separately estimating tag reporting rate. Hearn et al. (1998) separated total mortality into fishing and natural mortality by tagging pre- and post-season. Hoenig et al. (1998a) showed that it was possible to estimate fishing and natural mortality by tagging only once a year with the inclusion of fishing effort data, but estimates of tag reporting rate were unreliable, requiring it to be estimated independently. A more detailed description of the Brownie model is given in Appendix A.

Brownie – Frusher and Hoenig

Frusher and Hoenig (2001a) applied a combination of aspects from Hoenig et al. (1998a) and Hearn et al. (1998), tagging three times a year and proportioning fishing effort over the season to estimate fishing and natural mortality, and tag reporting rate in a region of the Tasmanian lobster fishery. Estimates of fishing mortality and tag reporting rate had low relative standard errors. However, estimates of natural mortality approximated zero with large standard errors. Frusher and Hoenig (2003) used the same dataset and the exact effort data to estimate within season catchability together with natural mortality and tag reporting rate. Fishing mortality was then calculated using the relationship \( F = qE \), where \( F \) is fishing mortality, \( q \) catchability and \( E \) the fishing effort. The model estimates of fishing mortality and tag reporting rate were similar to Frusher and Hoenig (2001a), with natural
mortality being estimated at 0.12, and with minor reductions in the relative standard errors. The model produced three within season estimates of catchability that broadly corresponded to known seasonal fluctuations in catchability (Frusher and Hoenig, 2003).

1.1.3 Continuous Time Models

Continuous time models have two primary advantages over seasonal, Brownie-style models. Most obviously, they allow a finer time resolution than a Brownie style model. This has a hidden practical benefit in that it becomes possible to leverage more subtle differentials in fishing effort than the simple open/closed season paradigm required by the Brownie model. Secondly, these models do not aggregate over seasons, but model each tag individually, providing a more natural vehicle for modelling variability amongst tagged individuals.

Two continuous time models incorporating the exact times of release and recapture have been proposed (Lucas, 1975; Leigh et al., 2006). These models effectively parallel standard survival analysis (Kleinbaum and Klein, 2005). Lucas’ model estimates fishing and natural mortality, incorporating fishing effort information, when tag reporting rate is 100% and is an application of parametric survival theory, while Leigh’s model is an analogue of the Kaplan-Meier survival model (Kaplan and Meier, 1958).

As these models do not aggregate over seasons, but model each tag individually, they provide a more natural vehicle for modelling variability amongst tagged individuals. This allows for models of mortality that depend not only on the exact times of release or recapture, but also locations of release and recapture, size and other properties of the individual. By modelling individuals, it is possible to incorporate features of the individual and also details of how they are caught. This permits the separation of a fishery into multiple fleets, each with its own individual tag reporting rates. The flexibility of allowing for continuous releases allows tagging to be conducted all year round by researchers, observers or members of the fishing industry during normal fishing operations.

1.1.4 Tasmanian Rock Lobster Fishery

This thesis uses characteristics of the Tasmanian lobster fishery in the evaluation and development of a survival model for daily tag recovery data, in order to estimate fishing and natural mortality and catchability. The Tasmanian rock lobster fishery targets the southern rock lobster ($Jasus edwardsii$), using baited traps set on rocky reefs. Traps are required to conform to legislated maximum dimensions and must contain escape gaps that permit undersized lobsters to escape. Access is restricted to fishers who are licensed to use no more than 50 traps. There are separate size limits for males and females of 110mm and 105mm carapace length respectively that apply statewide (Ford, 2001). A season length of ten months for males and six months for females applies, with fishing commencing each year in November for both sexes and continuing until the end of April for females, and to the end of
August for males. Traps catch both sexes, with females caught during the male only season required to be immediately returned to the water. In addition, egg laden or “berried” females must be returned to the water at all times. There is no spatial management in the fishery, with fishers allowed to move freely between all areas open to commercial lobster fishing.

1.2 Aims of this Thesis

The original motivation for this thesis developed from the desire of Tasmanian lobster fishery scientists to determine if the additional information from the exact date tag recaptures provided increased precision and accuracy in mortality estimates. This thesis expands and extends the work of Burch (2002) that began the application of a continuous time survival model to tagging data from the Tasmanian lobster fishery. Increased attention has been given to the development of models that can be used in lobster fisheries where reliable effort information is available to estimate fishing and natural mortality and catchability.

1.2.1 Chapter 2: Development of the Survival Model

Chapter 2 introduces a survival model to estimate fishing and natural mortality and tag reporting rates from the exact date of tag recaptures and daily fishing effort. This model expands on the work of Lucas (1975) to incorporate tag reporting rates less than 100% and recaptures from multiple fishing fleets. A general development of the survival model is used to estimate fishing and natural mortality and tag reporting rate. Fishing mortality estimates are obtained from seasonal catchability estimates and daily effort data.

1.2.2 Chapter 3: Validation of the Model

By using simulated data, Chapter 3 investigates how the model performs with respect to the accuracy (lack of bias) and precision of the estimates of catchability, natural mortality and tag reporting rate, under different fishery management regimes, tagging strategies and mortality rates.

1.2.3 Chapter 4: Application of the Model to a Tasmanian Fishery

Chapter 4 applies the survival model developed in Chapter 2 to historical data from a local Tasmanian trap fishery for rock lobsters, and compares estimates of catchability, fishing and natural mortality and tag reporting rate with those obtained by Frusher and Hoenig (2001a) and Frusher and Hoenig (2003), who analysed the same data with Brownie models.
1.2.4 Chapter 5: Fine Time-Scale Catchability

Chapter 5 constrains the survival model with a penalised cubic spline to obtain estimates of fine time-scale catchability. Estimates of catchability are compared with those obtained by Ziegler et al. (2002a), who compared catch rates to an underwater visual census of an unexploited lobster population in a Tasmanian marine reserve. This chapter demonstrates that fine time-scale estimates of catchability can be obtained from tagging studies.

1.2.5 Chapter 6: PIT Tags and Trusted Fishers

Chapter 6 incorporates multiple fishing components with individual tag reporting rates into the survival model. Three components with high tag reporting rates are examined: hybrid passive integrated transponder (PIT) tags, “trusted” fishers and research fishing. Simulated data is used to test the benefits of hybrid PIT tags that have a tag reporting rate of 100% when scanned by a tag reader. The advantages of incorporating research fishing and “trusted” fishers are demonstrated by reanalysing the tagging study from Chapter 4. The benefits of having one component of the fishing fleet with a high tag reporting rate are demonstrated.

1.2.6 Chapter 7: Cost Benefit Analysis of Hybrid PIT and Conventional Tagging Scenarios

With the recent developments in tagging technologies such as PIT tags, there is a need to understand when the use of this technology is cost beneficial. PIT tags and the associated scanners/readers are substantially more expensive, but with high tag reporting rates, fewer tags are required, which reduces the days of vessel charter and “taggers” at sea. Chapter 7 presents a cost-benefit analysis, based on a fixed budget, to estimate initial conditions (i.e. tag reporting rates) where conventional or PIT tagging studies should be considered. Chapter 7 is presented with minor changes for continuity, but is otherwise as published:


The relative contributions of each co-author are outlined in the Statement of co-authorship in the preface to this thesis.

1.2.7 Chapter 8: Conclusions and Discussion

A brief overview of the general findings and conclusions of the thesis are provided in Chapter 8, along with a discussion of the implications of these findings to tagging studies using Brownie models and in fisheries other than lobster fisheries.
Chapter 2

Development of the Survival Model

2.1 Introduction

This chapter develops a continuous time survival model for fisheries tagging experiments, extending the work of Burch (2002). The model is similar to that proposed by Lucas (1975) who estimated fishing and natural mortality using the exact date of a tag recapture and daily effort data, assuming a tag reporting rate of 100%.

The survival approach is extremely flexible as it models individual rather than aggregate recaptures, allowing features of the tagged individuals to be incorporated as covariates in the model. An additional benefit of this approach is that tagging can be undertaken opportunistically rather than annually as required when using Brownie models. This chapter focuses on developing models that estimate fishing and natural mortality when the tag reporting rate is less than 100%. The foundations presented here are further extended to develop models with fine time scale resolution in Chapter 5, and to develop models for fisheries with multiple fleets in Chapter 6.

2.1.1 Survival Analysis

Survival analysis models the life of individuals or objects over a given period of time (McCullagh and Nelder, 1983; Klein and Moeschberger, 1997; Kleinbaum and Klein, 2005). Survival models have typically been used in medical studies to model patients’ survival time after treatment and in engineering and manufacturing to model the time to failure of key components. As survival models study the fate of the individual, they provide a convenient and flexible technique for analyzing individual tag recaptures to estimate fishing and natural mortality in a tagging study.

In survival analysis, individuals are followed through time until they expire or until the study ends. For those individuals who expire during the study period, the exact time of expiry is recorded. But for those individuals who survive the study, the exact time of expiry remains unknown. All that is known is that the individual survived, at least until the study ended. These observations are said to be “censored”.
To apply the methods of survival analysis to fisheries tagging experiments, effectively the tags themselves are viewed as the “individuals” in the study. Tags are “born” upon release, and “expire” upon recapture. Tags that are not recaptured during the course of the study are censored.

### 2.1.2 The Survival Function

In survival studies, the lifetime of an individual is represented by the survival function (McCullagh and Nelder, 1983; Klein and Moeschberger, 1997; Kleinbaum and Klein, 2005). The survival function $S(t)$ represents the probability that an individual alive at some initial time $s$ will still be alive at some later time $t$. Individuals are exposed to mortality represented by the mortality function $Z(t)$, the probability that an individual alive at time $t$ will die in a small time interval $\delta t$. Interest lies in the probability that an individual is still alive following this interval.

The probability an individual is alive at time $t + \delta t$ is

\[
\Pr(\text{Did not die in } (t, t + \delta t) \mid \text{was alive at } t) \times \Pr(\text{Was alive at } t).
\]

In terms of the survival and mortality functions, this can be represented by

\[
S(t + \delta t) = (1 - Z(t)\delta t)S(t)
\]

so that

\[
\frac{S(t + \delta t) - S(t)}{\delta t} = -Z(t)S(t).
\]

In the limit as $\delta t \to 0$

\[
\frac{dS}{dt} = -ZS.
\]

As $S(s) = 1$, this differential equation has solution

\[
S(t) = e^{-\int_s^t Z(t)dt}.
\]

### 2.2 Model Assumptions

Tagging studies make a number of assumptions relating to the tagged sample being representative of the target population as a whole. These assumptions can be separated into two general types, those relating to the mixing of newly tagged individuals with the rest of the population and those relating to the independence of recaptures (Brownie et al., 1985). The tagging studies considered in this thesis rely on fishers to return recaptured tags. Consequently, only legal-sized animals are considered. The model assumptions are stated below and then the appropriateness of each assumption is discussed with reference to lobster fisheries and in particular to the Tasmanian fishery and those in south eastern Australia.
2.2. MODEL ASSUMPTIONS

- The tagged sample is representative of the population.
- Recaptures are independent of one another.
- There is no emigration of the tagged sample, or alternately, any emigration can be estimated and adjusted for in the model.
- Fishing mortality is independent of the natural mortality.
- There is no tag loss or tag induced mortality, or alternately, any loss can be estimated and adjusted for in the model.

2.2.1 Representative Sample

If the tagged sample is not representative of the population being studied, then any inferences drawn may be false. Two problems that result in the failure of this assumption are a lack of mixing of the newly tagged sample with the population and variable catchability among subgroups within the population (Burnham and Rexstad, 1993; Amstrup et al., 2005). Both violate the requirement that the probability of capture for tagged and untagged individuals at any given time is identical and each is discussed separately below.

The assumption of mixing requires that the tagged and untagged individuals become fully homogeneous by the time of future sampling, in this case the opening of the fishery. Detecting a lack of mixing in a population can be difficult. One way it can be assessed is to examine the frequency and distance of movement of tagged individuals in the population. If movement occurs, then it is likely the tagged and untagged populations will mix. If mixing does not occur, then inferences may still be valid if tagging is undertaken at random and fishing occurs at random. However, fishing seldom occurs at random. The levels of movement within lobster populations are known to vary greatly both between species and between geographically distinct populations of the same species. The spiny lobster *Panulirus argus* migrates long distances in the Gulf of Mexico (Gregory Jr and Labisky, 1986). In South Africa the rock lobster (*Palinurus gilchristi*) migrates up to several hundred kilometers (Groeneveld and Branch, 2002). Immature female and small male southern rock lobster (*Jasus edwardsii*) have been observed migrating along the south eastern coast of the South Island of New Zealand (McKoy, 1983). In South Australia, the same species is known to move from shallow to deep water (Linnane et al., 2005), while in Tasmania movements of more than a few kilometers are unusual (Gardner et al., 2003). A study of 32 lobsters tagged with acoustic tags in New Zealand found that 7 moved less than 100 meters, with the remaining 25 moving distances of up to 3.1 kilometers from the tagging site over a 12 month period (Kelly, 2001). While movement of southern rock lobster over large distances seems to vary with spatial location, it is likely that local movement does occur, suggesting that the assumption of mixing for this species is reasonable. However, it is unknown whether mixing occurs.

In Brownie models, incomplete mixing has been addressed by treating tag returns from the newly tagged cohort separately to those tagged in previous seasons (Hoenig
et al., 1998b). While this is a feasible option for the survival model, it has not been considered in this thesis.

Catchability of different subgroups in the population may vary for a number of reasons such as the fishing gear selecting for a particular size class, environmental changes such as water temperature or behavioural interactions among sexes and sizes. In the Tasmanian lobster fishery, changes in catchability have been shown to occur between genders and sizes, although there is little evidence of capture affecting the probability of recapture (Ziegler et al., 2002a,b). The effects of catchability varying with gender can be accounted for by modelling each gender separately and are addressed later in this chapter.

2.2.2 Independence of Recaptures

A lack of independence of recaptures for lobsters would likely be attributed to changes in catchability or selectivity. Detecting differences in catchability due to age is problematic since it is not possible to determine the age of lobsters as they shed their exoskeleton when they moult (Ehrhardt, 1990; Ju et al., 1999). In the Tasmanian fishery, the effects of size on catchability were studied by Ziegler et al. (2002b) with catchability found to generally increase with size. However, fishing mortality in the Tasmanian lobster fishery is high, with few lobsters above legal size remaining in the fishery for more than a few seasons. In the southern rock lobster it has been shown that selectivity can vary due to size, with large lobsters excluding small lobsters from entering traps in a marine reserve (Frusher and Hoenig, 2001b; Ihde et al., 2006). In the Tasmanian fishery, however, the proportion of large lobsters is small, with legal-sized biomass estimated at around 6% of virgin legal-sized biomass levels (Frusher and Hoenig, 2001a), so it is unlikely that enough large lobsters are present in the population to have a great effect on either the catchability or selectivity of lobsters. The impact of capture upon subsequent recapture for this species was also found to be small (Ziegler et al., 2002b). It is therefore likely that recaptures were independent of one another.

2.2.3 Emigration

If tagged lobsters were to emigrate from the study area it would appear as additional natural mortality. Movement of tagged southern rock lobster in Tasmanian waters has been discussed with relation to the mixing assumption above and been shown to be low (Gardner et al., 2003). It is therefore unlikely that any emigration of this species in Tasmanian waters occurs.

2.2.4 Independence of Fishing and Natural Mortality

For fishing and natural mortality to be independent of one another, the process of fishing must not affect the likelihood of an individual that is not harvested, dying from natural mortality. In fisheries where gill nets are used to harvest lobsters, increased predation of “netted” lobsters may occur. Lobster fisheries in south east-
ern Australia all use baited traps to harvest lobsters (Ford, 2001; Hobday and Punt, 2001; McGarvey and Gaertner, 1999). In Tasmanian waters, predation of lobsters in traps by octopus is known to occur at between 0.5% and 4% of the annual catch (Harrington et al., 2006). In South Australian waters, predation by seals and sea lions of lobsters in traps is also known to occur at low levels (Goldsworthy and Page, 2007). This violates the assumption of independence between fishing and natural mortality because lobsters in traps are exposed to additional predation mortality that would not otherwise occur. This additional mortality is then accounted for as an additional source of natural mortality that only occurs during the fishing season. Fortunately the rate of predation is low.

2.2.5 Tag Loss and Tag Induced Mortality

Tagging can be stressful for any animal, particularly if the tag is large in proportion to body size. Tag loss and tag induced mortality occur when tagged animals either shed their tags without dying, or die as a result of the tagging process. Both result in the tagged animal not being available for recapture during the course of the study.

Two processes of tag loss have been identified in the literature: initial tag shedding associated with the tagging and ongoing or chronic tag loss (Hoenig et al., 1998a). Tag loss is usually estimated from double tagging experiments (Wetherall, 1982; Fabrizio et al., 1999; Booth and Weyl, 2008). In southern rock lobster in captivity, tag loss using T-bar tags was estimated to be less than 3% and tag induced mortality less than 1% (Frusher and Hoenig, 2001a). However, in a marine reserve, a five year double tagging study estimated tag loss to be chronic and approximately 11% per year (Frusher et al., 2008).

Tag induced mortality is more difficult to estimate. Aquaria trials have been used to estimate tag induced mortality of the American lobster (Homarus americanus) in captivity (Comeau and Mallet, 2003). In the wild, a study comparing recaptures of lobsters tagged over successive years, estimated initial tag loss and tag induced mortality to vary with moult stage and to be 39% for males tagged post moult. However, estimates were confounded with lobsters moving, since sampling occurred at fixed locations (Frusher et al., 2008).

Tag loss and tag induced mortality, if estimated externally to the model, can be incorporated using the approach described in Section 2.4.4. Chapter 7 considers tagging scenarios incorporating initial tag loss and mortality using simulated data.

2.3 Model Development

This section develops a survival model based on parametric survival theory (Klein and Moeschberger, 1997; Kleinbaum and Klein, 2005) for fisheries tagging experiments. Firstly, the likelihood of recapture is determined in terms of the appropriate mortalities and reporting rates. Then models for these mortalities and reporting rates are considered.
2.3. MODEL DEVELOPMENT

2.3.1 Likelihood

Consider a sample of $N$ tagged individuals, where the $i^{th}$ individual is tagged at time $s_i$, and either recaptured at time $t_i$ or not recaptured before the end of the study at time $T$.

Decompose the total instantaneous mortality $Z_i(t)$ experienced by the $i^{th}$ individual into two components

$$Z_i(t) = F_i(t) + M_i(t),$$

the instantaneous fishing mortality $F_i(t)$ being the mortality due to fishing, and the natural mortality $M_i(t)$ being the mortality induced by all other sources. The survival of the individual is determined by the total instantaneous mortality $Z_i(t)$, but the likelihood an individual will be recaptured is determined by $F_i(t)$.

Typically, data is obtained from the return of tags by fishers. Ideally, all recaptured tags would be reported. However, for a variety of reasons, this is rarely the case. It may be that fishers are not entirely diligent in reporting, or it may be that fishers do not recognize every recapture, either through simple oversight, or because the tag has been shed before the tagged individual is recaptured. Define the tag reporting rate $\lambda_i(t)$ to be the probability that the recapture of the $i^{th}$ tagged individual is reported, given the individual has been recaptured at time $t$.

Assuming that the recaptures are independent, that is, the recapture of one individual does not impact on the recapture of any other, the total likelihood $L$ can be expressed as the product of contributions from each individual

$$L = \prod_{i=1}^{N} L_i(\lambda_i, F_i, M_i).$$

Therefore, to determine the total likelihood, it suffices to consider the contributions made by individual tags. This will be done in two stages. Firstly, the likelihood will be derived for the simpler case of complete reporting, and then the more complex incomplete reporting case will be considered.

Complete Reporting

First consider the contribution an individual makes to the total likelihood in the simple case where the tag reporting rate is 100% and there is no tag loss, so $\lambda \equiv 1$. For notational simplicity, as only a single individual is being considered, the subscripts on $F(t)$ and $M(t)$ will be suppressed.

Individuals tags can suffer one of two possible fates:

- either the tag is recaptured through fishing and returned to researchers, or
- the tag is not recaptured during the course of the study, and is censored.
The probability that the tag is recaptured in a small time interval \((t, t + \delta t)\) can be expressed as

\[
\text{Pr}(\text{Recaptured in } (t, t + \delta t)) = \text{Pr}(\text{Recaptured in } (t, t + \delta t) \mid \text{Was alive at } t) \times \text{Pr}(\text{Was alive at } t).
\]

The probability of recapture, given the individual is alive, is determined by the instantaneous fishing mortality

\[
\text{Pr}(\text{Recaptured in } (t, t + \delta t) \mid \text{Was alive at } t) = F(t)\delta t,
\]

while the probability that the individual was still alive at time \(t\) is given by the survival function derived in Section 2.1.2

\[
\text{Pr}(\text{Was alive at } t) = S(t) = \exp \left( - \int_{s}^{t} (F(\tau) + M(\tau)) d\tau \right).
\]

Therefore, for a non-censored tag, the probability of recapture is

\[
\Pr(\text{Recaptured in } (t, t + \delta t)) = \left[ F(t)\exp \left( - \int_{s}^{t} (F(\tau) + M(\tau)) d\tau \right) \right] \delta t. \quad (2.2)
\]

The alternative is that the tag is not recaptured before the study concludes at time \(T\), and the observation is censored. The probability that a tag released at time \(s\) is not recaptured during the course of the study is simply

\[
\text{Pr}(\text{Censored at } T) = 1 - \Pr(\text{Recaptured in } (s, T)) = 1 - \int_{s}^{T} F(t)\exp \left( - \int_{s}^{t} (F(\tau) + M(\tau)) d\tau \right) dt. \quad (2.3)
\]

It follows from Equations (2.2) and (2.3) that the contribution that the \(i^{th}\) individual makes to the likelihood is

\[
L_i(F, M) = \begin{cases} 
F(t_i)\exp \left( - \int_{s_i}^{t_i} (F(t) + M(t)) dt \right) & \text{if recaptured at } t_i \\
1 - \int_{s_i}^{T} F(t)\exp \left( - \int_{s_i}^{t} (F(\tau) + M(\tau)) d\tau \right) dt & \text{if censored at } T.
\end{cases}
\]

Returning to the entire sample, if individuals are indexed such that the first \(n\) individuals are recaptured and the remainder are censored, the total likelihood can be written

\[
L = \prod_{i=1}^{n} F_i(t_i)\exp \left( - \int_{s_i}^{t_i} (F_i(t) + M_i(t)) dt \right) \times \prod_{i=n+1}^{N} \left( 1 - \int_{s_i}^{T} F_i(t)\exp \left( - \int_{s_i}^{t} (F_i(\tau) + M_i(\tau)) d\tau \right) dt \right). \quad (2.4)
\]
Incomplete Reporting

Now consider the case of imperfect reporting, where $\lambda(t) < 1$.

The probability of observing a recapture within a small time interval $(t, t + \delta t)$ can be expressed as

$$\Pr(\text{Observe recapture in } (t, t + \delta t)) = \Pr(\text{Recapture observed } \mid \text{Recaptured in } (t, t + \delta t)) \times \Pr(\text{Recaptured in } (t, t + \delta t)).$$

Then again, the probability of recapture is given by Equation (2.2), while

$$\Pr(\text{Recapture observed } \mid \text{Recaptured in } (t, t + \delta t)) = \lambda(t)$$

so that

$$\Pr(\text{Observe recapture in } (t, t + \delta t)) = \lambda(t) F(t) \exp \left( - \int_s^t (F(\tau) + M(\tau)) d\tau \right) \delta t. \quad (2.5)$$

Similarly the alternative, that a tag released at time $s$ is not recovered before the study concludes at time $T$, is in this case

$$\Pr(\text{Censored at } T) = 1 - \Pr(\text{Observe a recapture in } [s, T]) = 1 - \int_s^T \lambda(t) F(t) \exp \left( - \int_s^t (F(\tau) + M(\tau)) d\tau \right) dt. \quad (2.6)$$

It follows from Equations (2.5) and (2.6) that the contribution an individual makes to the likelihood is

$$L_i(\lambda, F, M) = \begin{cases} 
\lambda(t_i) F(t_i) \exp \left( - \int_{s_i}^{t_i} (F(t) + M(t)) dt \right) & \text{if recaptured at } t_i \\
1 - \int_{s_i}^T \lambda(t) F(t) \exp \left( - \int_{s_i}^t (F(\tau) + M(\tau)) d\tau \right) dt & \text{if censored at } T.
\end{cases} \quad (2.7)$$

For the full sample, again assuming that the individuals are indexed such that the first $n$ individuals are recaptured and the remainder are censored, the total likelihood can be written in the form

$$L = \prod_{i=1}^n \lambda_i(t_i) F_i(t_i) \exp \left( - \int_{s_i}^{t_i} (F_i(t) + M_i(t)) dt \right) \times \prod_{i=n+1}^N \left( 1 - \int_{s_i}^T \lambda(t) F_i(t) \exp \left( - \int_{s_i}^t (F_i(\tau) + M_i(\tau)) d\tau \right) dt \right). \quad (2.8)$$
Note that this reduces to Equation 2.4 when $\lambda(t) \equiv 1$. Furthermore, note that $\lambda$ acts to reduce the action of fishing mortality $F$ where it pertains to reporting, but not where it pertains to survival – it is this that allows $F$ and $\lambda$ to be simultaneously estimated.

2.4 Parametrisation

The previous section developed expressions for the likelihood in terms of the reporting rate $\lambda(t)$, the fishing mortality $F(t)$ and natural mortality $M(t)$. The specification of the model is complete with the specification of models for these three key quantities. Moreover, as each individual makes a separate contribution to the total likelihood, it is possible to specify these three key quantities on an individual basis – that is, separate forms of $\lambda(t)$, $F(t)$ and $M(t)$ can be specified for any individual or group of individuals in the population. Thus $\lambda(t)$, $F(t)$ and $M(t)$ can be chosen to reflect features intrinsic to the individual, such as gender or age, or features related to the release or recapture, such as tag placement, or for fisheries with multiple fleets, the fleet that recaptures the individual. Models for multiple fleets will be explored further in Chapter 6.

While in principle an infinite variety of models can be formulated, in practice only a handful of forms will be of real interest. Some of these are discussed below.

2.4.1 Basic Models

The obvious, simple models allow for no individual variation and little or no time variation.

The most basic model is where reporting rate, fishing and natural mortality are all constant

$$
\lambda(t) = \lambda \\
F(t) = F \\
M(t) = M
$$

and the model has three parameters to be estimated, $\lambda$, $F$ and $M$. Where good estimates of reporting rate are available from other studies, the researcher may wish to specify $\lambda$ and only estimate $F$ and $M$.

The next most obvious model is where one or more of $\lambda(t)$, $F(t)$ and $M(t)$ are piecewise constant over time. So for example

$$
F(t) = \begin{cases} 
F_1 & t \in I_1 \\
F_2 & t \in I_2 \\
\vdots \\
F_m & t \in I_m 
\end{cases}
$$

where the intervals $I_1, \ldots, I_m$ form a finite disjoint cover of the study period, that is $I_i \cap I_j = \emptyset$ for $i \neq j$ and $\bigcup_{i=1}^m I_i$ contains the study period. These intervals might
correspond to years or seasons, in which case the $F_i$ would represent the fishing mortality in each year or season.

### 2.4.2 Gender

Since the survival model follows the life times of individuals, it is possible to incorporate characteristics of the individual separately. For males $m$ and females $f$, $F(t)$ can be represented as

$$F(t) = F_m(t) \quad \text{for males}$$

and

$$F(t) = F_f(t) \quad \text{for females.}$$

Similarly, the natural mortality function $M$ can also be represented as a function of gender $M_m(t)$ and $M_f(t)$ for females.

### 2.4.3 Fishing Effort

A major contributor to variability in fishing mortality is variability in fishing effort. In fisheries, the parameter that relates effort to fishing mortality is called the catchability. The survival model can be conditioned on fishing effort by assuming that $F(t)$ is directly proportional to effort $E(t)$ and catchability $q(t)$

$$F(t) = q(t)E(t). \quad (2.9)$$

This is the “strong” effort assumption of Hoenig et al. (1998a) and depends on reliable measures of effort.

In all southern Australian lobster fisheries, fishers are required to record their daily trap lifts (Ford, 2001). Only the number of individual lifts is recorded, not the amount of time a baited trap is in the water, so any one lift is not necessarily equal to any other. Typically though, fishers will set their traps in the evening and recover them the next morning. All traps are required to conform to legislated sizes for the outer dimensions, and the trap opening is required to have escape gaps. In this thesis, all trap lifts are assumed identical.

### 2.4.4 Tag Induced Mortality

Tag induced mortality may be modelled by allowing for a period of increased natural mortality following release. Therefore, if $\Delta$ is the duration of the period of increased mortality, the $i^{th}$ tagged individual experiences a natural mortality

$$M_i(t) = \begin{cases} M_0 + M_1 & t < s_i + \Delta \\ M_0 & \text{otherwise} \end{cases}$$
where $M_0$ and $M_1$ are parameters representing the baseline mortality and the additional tag induced mortality respectively, and they should not be confused with the individual mortality functions $M_i(t)$. The same approach can be used to incorporate tag loss into the model.

## 2.5 Estimation

The survival model is fully specified by the likelihood derived in Section 2.3, together with appropriately parametrised models for the reporting rate $\lambda(t)$, fishing mortality $F(t)$ and natural mortality $M(t)$. The parameters of these models for $\lambda(t)$, $F(t)$ and $M(t)$ are estimated by maximum likelihood.

This section outlines the basic principles of maximum likelihood estimation, and discusses some of the practicalities of the process.

### 2.5.1 Maximum Likelihood

The model parameters may be estimated by the method of maximum likelihood. Casella and Berger (2001) and Pawitan (2001) give thorough expositions of the theory; a basic outline is as follows.

Suppose the models for the reporting rate $\lambda(t)$, fishing mortality $F(t)$ and natural mortality $M(t)$ are parametrised in terms of a vector of parameters $\theta$. Then the likelihood is a function $L(\theta)$ of $\theta$, and the maximum likelihood estimate $\hat{\theta}$ of $\theta$ is that value of $\theta$ at which the likelihood is a maximum (Casella and Berger, 2001; Pawitan, 2001)

$$\hat{\theta} = \arg\max_{\theta} L(\theta).$$

In practice, it is often simpler to determine $\hat{\theta}$ by maximising the log likelihood – as the log function is monotonic, the likelihood and the log likelihood attain their maximum at the same point.

Under mild regularity conditions, for large samples $\hat{\theta}$ is approximately Normally distributed about $\theta$

$$\hat{\theta} \sim N(\theta, V)$$

with a variance $V$ determined by the (observed) Fisher information

$$V = \left[ \frac{\partial^2 \log L}{\partial \theta^2} \right]^{-1}.$$

In turn, this allows approximate confidence intervals and Wald tests of hypotheses to be constructed for individual parameters.

### 2.5.2 Likelihood Ratio Tests

Given two competing models, A and B, such that B is nested within A (that is, B is a constrained form of A) then the fit of model B can be tested against the
fit of model A through a likelihood ratio test. If both models adequately describe
the observed data, but model A has \( p_A \) free parameters and model B has \( p_B < p_A \)
free parameters, then if \( L_A \) is the fitted likelihood for model A and \( L_B \) is the
fitted likelihood for model B, twice the log of the ratio of the fitted likelihoods is
approximately chi-square distributed with \( p_A - p_B \) degrees of freedom

\[
2 \log \frac{L_A}{L_B} \sim \chi^2_{p_A-p_B}.
\]

This allows a test of the hypothesis that A and B fit equally well against the alter-
native that A gives a better fit.

### 2.5.3 Akaike’s Information Criteria

Competing, non-nested models can be compared by Akaike’s Information Criteria
(Akaike, 1974; Pledger, 2000). For a model with \( p \) parameters and fitted likelihood
\( L \), the Akaike’s Information Criteria AIC is defined as

\[
\text{AIC} = -2 \log L + 2p.
\]

In essence, the AIC is a trade-off between goodness of fit (as measured by the
log likelihood) and model complexity (as measured by the number of parameters).
When comparing several models, the model with the lowest AIC is considered the
most parsimonious.

### 2.5.4 Profile Likelihood

For small sample sizes, confidence intervals based on the approximate normality of
the maximum likelihood estimator can perform poorly (Venzon and Moolgavkar,
1988). An alternative is to construct confidence intervals from likelihood ratio tests
based on profile likelihoods. Given a likelihood \( L(\theta) \) that is a function of a vector
of parameters \( \theta = (\theta_1, \theta_2, \ldots, \theta_m) \), the profile likelihood \( L(\theta_i) \) is the function

\[
L(\theta_i) = \max_{\theta_{-i}} L(\theta)
\]

where \( \theta_{-i} = (\theta_1, \ldots, \theta_{i-1}, \theta_{i+1}, \ldots, \theta_m) \) is the vector of parameters \( \theta \) with the \( i^{th} \)
component deleted. Then a \((1 - \alpha)100\%\) confidence interval \([a, b]\) for \( \theta_i \) can be ob-
tained by applying a likelihood ratio test to the profile likelihood \( L(\theta_i) \) to determine
endpoints \( a \) and \( b \) for which the models with \( \theta_i = a \) and \( \theta_i = b \) would be rejected at
significance level \( \alpha \).

Profile likelihood methods have previously been applied to both single release-
recapture (Cormack, 1992; Evans et al., 1996), multiple tagging and recapture mod-
els (Pledger, 2000; Gimenez et al., 2005).

### 2.5.5 Piecewise Approximation

The calculation of the likelihood is complicated by the two integral expressions in
Equation (2.8). While these integrals could be approximated by standard quadra-
ture methods, a more natural solution arises if two further restrictions are imposed on the model.

To simplify the calculation of the likelihood, assume that:

1. All releases occur at the beginning of the day and all recaptures occur at the end. Under this assumption, individuals experience the full mortality associated with every day they are at liberty.

2. The reporting rate $\lambda(t)$, fishing mortality $F(t)$ and natural mortality $M(t)$ experienced by any individual, are constant over any day. That is, these functions are piecewise constant with discontinuities at day boundaries.

These additional restrictions are not particularly onerous. In essence, they discretize time, limiting the time resolution of the model to a day.

With these two additional assumptions, it is natural to measure time in days, in which case $\lambda(t)$, $F(t)$, and $M(t)$ become piecewise constant with discontinuities at $t \in \mathbb{Z}$. For notational simplicity, for any piecewise constant function $Q(t)$, write $Q_k$ for the value of $Q$ on day $k$

$$Q_k = Q(t) \quad t \in [k, k+1).$$

So for a release time $s$ at the start of a day, and an arbitrary recapture time $t > s$

$$\int_s^t (F(\tau) + M(\tau))d\tau = \int_{[t]}^t (F_{[t]} + M_{[t]})d\tau + \sum_{k=s}^{[t]-1} \int_k^{k+1} (F_k + M_k)d\tau$$

$$= (F_{[t]} + M_{[t]})(t - [t]) + \sum_{k=s}^{[t]-1} (F_k + M_k)$$

where $[t]$ denotes the largest integer less than or equal to $t$.

Now consider the contribution an individual makes to the total likelihood. An individual released at the start of day $s$ and recaptured at the end of day $t$ experiences the mortality for both days $s$ and $t$, and so makes contribution

$$\lambda(t)F(t) \exp \left( - \int_s^{t+1} (F(\tau) + M(\tau))d\tau \right) = \lambda t F_t \exp \left( - \sum_{k=s}^{t} (F_k + M_k) \right).$$

Similarly, for a censored individual, if $T$ is the first day after the study period, an individual released at the start of day $s$ and not recaptured in the study period,
makes contribution

\[1 - \int_s^T \lambda(t) F(t) \exp \left( - \int_s^t (F(\tau) + M(\tau)) d\tau \right) \, dt = 1 - \sum_{j=s}^{T-1} \lambda_j F_j \exp \left( - \sum_{k=s}^{j-1} (F_k + M_k) \right) \int_j^{j+1} \exp \left( -(F_j + M_j)(t - j) \right) \, dt \]

\[= 1 - \sum_{j=s}^{T-1} \lambda_j F_j \exp \left( - \sum_{k=s}^{j-1} (F_k + M_k) \right) \int_j^{j+1} \exp \left( -(F_j + M_j)(t - j) \right) \, dt \]

\[= 1 + \sum_{j=s}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \exp \left( - \sum_{k=s}^{j-1} (F_k + M_k) \right) \left( \exp \left( -(F_j + M_j)(t - j) \right) \right) \bigg|_{j}^{j+1} \]

\[= 1 + \sum_{j=s}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \exp \left( - \sum_{k=s}^{j-1} (F_k + M_k) \right) \left( \exp \left( -(F_j + M_j)(t - j) \right) \right) \left( 1 - \exp(F_j + M_j) \right) \]

Note that the expression in the final line has been obtained from that in the previous line by including an additional term in the sum in the exponential that is then factored from the final term.

So the contribution that an individual released at time \(s_i\) makes to the total likelihood takes the form

\[L_i(\lambda, F, M) = \begin{cases} 
\lambda_i F_i \exp \left( - \sum_{k=s_i}^{t_i} (F_k + M_k) \right) & \text{if recaptured at } t_i \\
1 + \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j-1} (F_k + M_k) \right) \left( 1 - \exp(F_j + M_j) \right) & \text{if censored at } T 
\end{cases} \]

(2.10)

and the expression for the total likelihood follows immediately.

### 2.5.6 Numerical Minimisation

Unfortunately, maximising the likelihood is not an analytically tractable problem, even for the simplest of models, and it is necessary to adopt a numerical approach.

A quasi-Newton method (Dennis and Schnabel, 1983; Schnabel et al., 1985) in the R statistical package (R Development Core Team, 2010) was used to maximize the log of the likelihood. This requires both the log likelihood and its gradient. Expressions for the gradient of the log likelihood corresponding to Equation (2.10) are presented in Appendix B.

The parameters of the model are mortality rates and reporting rates. Mortalities are rates and so are constrained to be positive, while reporting rates are actually
proportions, and so are constrained to lie in the interval $[0, 1]$. While there exist numerical procedures for constrained optimization, typically it is more reliable to reparametrize the model in order to eliminate the constraints. For a parameter $\alpha$ corresponding to a rate, the model is reparametrised in terms of $\tilde{\alpha} = \log \alpha$, so that $\alpha = \exp \tilde{\alpha}$ is constrained to be positive. For a parameter $\beta$ corresponding to a proportion, the model is reparametrised in terms of its logit

$$\tilde{\alpha} = \text{logit} \alpha = \log \left( \frac{\alpha}{1 - \alpha} \right)$$

so that $\alpha = (1 + \exp(-\tilde{\alpha}))^{-1}$ is constrained to lie in the interval $[0, 1]$.

2.6 Summary

This chapter has developed a survival model to estimate fishing and natural mortality and tag reporting rates from the exact date of tag recaptures in fisheries tagging experiments. This approach has two principal advantages over aggregated Brownie style models. Firstly, tag reporting rate, fishing and natural mortality can be represented more freely. This allows both within and between season differences in these parameters to be modelled. Secondly, tagging can be undertaken at any time. It is not required that tags be released at the beginning of the fishing season. From an implementation perspective, this allows tagging to be undertaken when it is most cost effective to do so or when tag loss and tag induced mortality are low.

In the next chapter, simulation studies are used to investigate the performance of the model. Chapter 5 will build upon the foundations presented in this chapter to develop models with fine time scale resolution, while in Chapter 6 the model is extended to fisheries with multiple fleets.
Chapter 3

Validation of the Model

3.1 Introduction

All of the models in this thesis are fitted using the method of maximum likelihood estimation (Lindgren, 1976). While maximum likelihood estimators are asymptotically unbiased, for finite sample sizes this is not guaranteed to be the case. This chapter seeks to identify by use of simulation, how the survival model performs under a variety of conditions. As it is not feasible to consider all situations where the model may be applicable, and because it is likely that model performance will vary when applied to real data, a number of general scenarios are first used to identify the strengths and weaknesses of the model. Some more specific scenarios, using aspects of the Tasmanian, South Australian and Western Australian lobster fisheries, are then considered.

3.2 Methods and Assumptions Applied to All Models

All scenarios presented in this chapter presumed that the assumptions discussed in Section 2.2 hold. Specifically, tags mix upon release, recaptures are independent of one another and there is no tag loss or tag induced mortality. Additionally, to allow a year to be broken down into discreet seasons and for ease of implementation, a year was considered to have 365 days, with leap years ignored. In each case, tag releases were simulated from the survival model using known rates of fishing and natural mortality and tag reporting rate to generate tag recaptures. The model was then fitted to the simulated tag recapture data to estimate fishing, natural and total mortality.

3.3 Complete Reporting

In the ideal situation, there is no tag loss or tag induced mortality and all tags are reported. Brownie models require a closed season and tagging at the beginning and end of each fishing season in order to separate total mortality into its fishing
and natural components, unless there is sufficient contrast in fishing effort between seasons (Hoenig et al., 1998a). To determine whether the survival model can separate mortality into its two components without contrast in fishing effort between seasons, scenarios from the following three management regimes were considered:

- Continuous Fishing: fishing was constant for the entire year.
- Seasonal Fishing: fishing occurred in the first six months of the year and was closed for the remainder.
- Alternating Fishing: fishing alternated for one month on then one month off.

The use of the three management regimes sought to identify under what circumstances a closed season allows the separation of total mortality into its fishing and natural components. The continuous fishing regime had no closed season, while the seasonal and alternating fishing regimes both allowed fishing for six months, the only difference being that the seasonal regime had a single six month closure compared with the alternating regime that had six closures of one month each. For each management regime, a broad spectrum of fishing and natural mortalities are presented. In each scenario, 2000 tags were released on day one with tags collected for five seasons. Tag returns are simulated from the model for fishing mortalities $F$ of 0.3, 0.6, 0.9, 1.4, 1.8 and 2.3 and natural mortalities $M$ of 0.05, 0.1, 0.2 and 0.3. For all management regimes, fishing intensity was constant across the fishing season and there were no additional covariates such as gender. To permit comparison between scenarios with different fishing and natural mortalities, the results are presented as the standardised error, defined as

$$\frac{(x - \mu)}{\mu}$$

where $x$ was the estimated $F$, $M$ or $Z$ and $\mu$ was the true value used in the simulation. Standardised error is similar to the relative error

$$100\frac{(x - \mu)}{\mu}$$

presented, however, as a proportion rather than a percentage. Relative error has been used for the evaluation of model performance, using simulated data (Punt, 2003; Wilberg and Bence, 2006; Haltuch et al., 2009). Boxplots of the standardised errors for $F$, $M$ and $Z$ are presented from 1000 simulations for each of the six simulated fishing mortalities and four natural mortalities.

### 3.3.1 Results

There was little difference in the accuracy and precision of estimates of fishing, natural and total mortality between the three fishery management regimes (Figures 3.1 to 3.6). Estimates of fishing, natural and total mortality were also unbiased
for most of the scenarios tested. When fishing and natural mortality were low 
\((F = 0.3, M \leq 0.1)\), the alternating fishing regime consistently underestimates all 
mortality parameters by a small amount (Figure 3.1). Estimates of total mortality 
were more precise than estimates of fishing or natural mortality, except when fish-
ing mortality was low \((F = 0.3)\). The precision of the estimated natural mortality 
doubles as the simulated natural mortality increases from \(M = 0.05\) to \(M = 0.3\). 
There are slight improvements in the precision of estimated fishing mortality as the 
simulated fishing mortality increases from \(F = 0.3\) to \(F = 2.3\).

### 3.3.2 Discussion

Total mortality estimates were more precise than either the estimated fishing or 
natural mortalities, suggesting that \(F\) and \(M\) are negatively correlated. The lack 
of differences between the three management regimes suggests that fishing patterns 
have little influence on the accuracy or precision of mortality estimates when the 
tag reporting rate is 100\%. This is different from the way Brownie models obtain 
separate estimates of \(F\) and \(M\), with either a strong contrast in fishing effort (Hoenig 
et al., 1998a) or tagging at the beginning and end of the fishing season (Hearn et al., 
1998).
Figure 3.1: Box plots of standardised error from estimated $F$, $M$ and $Z$ under a range of natural mortalities ($M$) and a fishing mortality ($F$) of 0.3. Three scenarios are considered under a tag reporting rate of 100%: continuous fishing (white boxes), seasonal fishing (light grey boxes) and alternating fishing (dark grey boxes).
Figure 3.2: Box plots of standardised error from estimated $F$, $M$ and $Z$ under a range of natural mortalities ($M$) and a fishing mortality ($F$) of 0.6. Three scenarios are considered under a tag reporting rate of 100%: continuous fishing (white boxes), seasonal fishing (light grey boxes) and alternating fishing (dark grey boxes).
Figure 3.3: Box plots of standardised error from estimated $F$, $M$ and $Z$ under a range of natural mortalities ($M$) and a fishing mortality ($F$) of 0.9. Three scenarios are considered under a tag reporting rate of 100%: continuous fishing (white boxes), seasonal fishing (light grey boxes) and alternating fishing (dark grey boxes).
Figure 3.4: Box plots of standardised error from estimated $F$, $M$ and $Z$ under a range of natural mortalities ($M$) and a fishing mortality ($F$) of 1.4. Three scenarios are considered under a tag reporting rate of 100%: continuous fishing (white boxes), seasonal fishing (light grey boxes) and alternating fishing (dark grey boxes).
Figure 3.5: Box plots of standardised error from estimated $F$, $M$ and $Z$ under a range of natural mortalities ($M$) and a fishing mortality ($F$) of 1.8. Three scenarios are considered under a tag reporting rate of 100%: continuous fishing (white boxes), seasonal fishing (light grey boxes) and alternating fishing (dark grey boxes).
Figure 3.6: Box plots of standardised error from estimated $F$, $M$ and $Z$ under a range of natural mortalities ($M$) and a fishing mortality ($F$) of 2.3. Three scenarios are considered under a tag reporting rate of 100%: continuous fishing (white boxes), seasonal fishing (light grey boxes) and alternating fishing (dark grey boxes).
3.4 Tag Reporting Rate

Section 3.3 has shown that the survival model is generally unbiased, except perhaps when fishing and natural mortality are both low. When the tag reporting rate is 100%, the precision of mortality, particularly total mortality, is high. Tagging studies where reporting rate is 100% are unusual, however, and most estimates are less than 30%, so it is necessary to assess the performance of the survival model at estimating mortality, under different tag reporting rates.

Tag reporting rate has been estimated separately from the model in a number of ways: high reward tags (Nichols et al., 1991), tag seeding (Green et al., 1983) and observers (Hearn et al., 1999). Typically, reporting rate is confounded with fishing and natural mortality. It is difficult to distinguish the fate of a tag that has been recaptured but not returned, from a tag that could not be returned because the animal died or from a tagged animal that is alive but has not been recaptured. This section seeks to identify the conditions under which the model performs well and those where it does poorly when tag reporting rate is less than 100%. To restrict the simulation to a manageable number of scenarios, the Tasmanian lobster fishery is used as an example.

A three year tagging study was simulated with 1000 tags being released at the beginning of the first two seasons, and tag returns being collected for a third season. Season lengths of six months for females and ten months for males are simulated with constant fishing and natural mortalities of $F = 0.9$ and $M = 0.1$. This generally corresponds with the Tasmanian lobster fishery. A more complete overview of the fishery is described in Section 1.1.4. Twenty scenarios with tag reporting rates of between $\lambda = 0.05$ and 0.99 were tested, with 1000 simulations each. Estimates of fishing, natural and total mortality are presented as boxplots for each scenario.

3.4.1 Results

The results show that at low tag reporting rates, estimates of $F$ are biased low and $M$ are biased high. However, estimates of $Z$ appear unbiased for $\lambda > 0.1$ (Figure 3.7). Estimates of natural mortality are highly variable at low tag reporting rates, with $M$ often slightly overestimated until $\lambda$ is greater than 0.5. Similarly, estimates of fishing mortality tend to be minor underestimates when tag reporting rate is low.

3.4.2 Discussion

The survival model has difficulty separating total mortality into its fishing and natural components when tag reporting rates are very low ($\lambda < 0.2$). A similar feature has been observed for Brownie models when tagging is undertaken once per year, with tag reporting rate generally needing to be estimated externally to the model (Hearn et al., 2003). As observed in Section 3.3, fishing and natural mortality estimates are negatively correlated. However, total mortality is unbiased when tag reporting rate is above 0.1 and quite precise when $\lambda$ is greater than 0.3. From a
fisheries management perspective, having unbiased and relatively precise estimates of total mortality when the tag reporting rate is above 0.3, is probably sufficient.

Figure 3.7: Box plots of estimated fishing ($F$), natural ($M$) and total ($Z$) mortalities for tag reporting rates between $\lambda = 0.05$ and 0.99. True values of $F = 0.9$, $M = 0.1$ and $Z = 1.0$ are shown by dashed lines.
Brownie models estimate mortality by comparing aggregated recaptures over successive fishing seasons. Technically, tagging must be undertaken on the same day each year. However, in fisheries where catch rates are low, tagging events occur over several days and releases are aggregated into a single day (Frusher and Hoenig, 2001a). An advantage of the survival model, compared with Brownie models, is the flexibility to release tags whenever the opportunity arises. It may be advantageous from a logistical point of view to do all the tagging for one or more seasons at once, or tag in periods of high catch rates to maximise the number of fish tagged per day. To investigate the subtleties of how the timing of releases affects the precision and accuracy of estimates of fishing and natural mortality, five scenarios with different release patterns were considered.

The five scenarios tested were again based on the dynamics of the Tasmanian lobster fishery (Section 1.1.4). A five year tagging study was simulated with season lengths of six months for females and ten months for males, with the fishing season for both genders opening on the same day. Constant fishing and natural mortalities, the same for both genders of $F = 0.9$ and $M = 0.1$ and a tag reporting rate of $\lambda = 0.5$, were used. A total of 2000 tags were released during the study under five different tagging patterns. In each case, equal numbers of males and females were tagged. The five tested scenarios were:

- **Scenario 1**: 500 tags were released at the beginning of each season for the first four seasons.
- **Scenario 2**: 500 tags were released at the end of each male season for the first four seasons.
- **Scenario 3**: 500 tags were released at the end of each female season for the first four seasons.
- **Scenario 4**: 250 tags were released at the beginning of the season and at the end of the male season for the first four seasons.
- **Scenario 5**: 1000 tags were released at the beginning of years one and three.

In the first three scenarios, 500 tags were released at the specified time during the season, every year for four years. In Scenario 4, 250 tags were released at the beginning of the fishing season, and 250 tags after the closure of the male season, every year for four years. Scenario 5 released 1000 tags at the beginning of years one and three. The level of fishing effort was constant over the fishing season, with exploitation rates varying between males and females due to the differing length of the fishing season. All models assume that natural mortality is the same for males and females. Each of the scenarios was tested with 1000 simulations and estimated $F$, $M$ and $Z$ are presented using boxplots.
3.5.1 Results

The estimated total mortality was unbiased for all scenarios without any major differences in precision between the five scenarios (Figure 3.8). Estimates of fishing and natural mortality are slightly negatively correlated, with $F$ prone to minor underestimation and $M$ to overestimation. The most precise and accurate estimates of $F$, $M$ and $Z$ were obtained from scenario 3 where 500 tags were released at the end of the first four female fishing seasons. The least precise estimates of $F$, $M$ and $Z$ were obtained from scenario 2 where 500 tags were released at the end of the first four male seasons.

Figure 3.8: Box plots of estimated fishing ($F$), natural ($M$) and total ($Z$) mortalities from five scenarios with different release patterns.
3.5.2 Discussion

To separate total mortality into its two components, Brownie models require tagging to be undertaken at the beginning and end of each fishing season (Hearn et al., 1998). This is not the case for the survival model. The lack of major differences between the five release patterns, demonstrates that tagging need only be undertaken to maintain the number of tags in the population. There were subtle differences between the scenarios. It is unclear why scenario 3 produced the most accurate and precise estimates of $F$, $M$ and $Z$. Tagging at the end of the female fishing season allows six months when females are only exposed to natural mortality but males are exposed to both fishing and natural mortality. It is possible that this contrast, when one gender is open to fishing and the other is closed, allows slightly more accurate separation of the total mortality into its fishing and natural components.

3.6 Australian Lobster Fisheries

The results from Section 3.5 suggested that tagging at different times of the year affected the precision of mortality estimates for a fishery with different season lengths for the two genders. Not all Australian lobster fisheries have this characteristic. In order to determine if a seasonal closure for one gender affects the precision of mortality estimates, the following four scenarios were considered:

- Scenario 6M: A seasonal closure of six months for males and six months for females.
- Scenario 4M: A seasonal closure of four months for males and six months for females.
- Scenario 2M: A seasonal closure of two months for males and six months for females.
- Scenario 0M: No seasonal closure for males, with fishing occurring continuously, and a six month closed season for females.

Scenario 6M represented a fishery where the fishing season is the same length for both genders. The six month season is similar to the South Australian and Western Australian lobster fisheries where the fishing season lasts for seven months (McGarvey and Gaertner, 1999; Srisurichan et al., 2005). Both the Tasmanian and Victorian lobster fisheries have season lengths of six months for females and ten months for males (Ford, 2001; Hobday and Punt, 2001). This was represented by scenario 2M. The remaining two scenarios (4M and 0M) represented hypothetical lobster fisheries that were similar to those in Tasmania and Victoria, in that fishing continued for males after it had stopped for females.

A three year tagging study was simulated with 500 males and 500 females being tagged and released at the beginning of the first two fishing seasons and recaptures accepted for a further year. All four scenarios were simulated with fishing and
natural mortalities of $F = 0.9$ and $M = 0.1$ that were constant over the course of the study and did not vary with gender. Fishing for both genders commenced on the same day. Four tag reporting rates that were also constant and did not vary during the study, were tested. They were $\lambda = 0.2$, 0.4, 0.6 and 0.8. A total of 1000 simulations were undertaken with estimated $F$, $M$ and $Z$ for each scenario being presented as boxplots.

3.6.1 Results

Scenario 6M had unbiased and precise estimates of total mortality (Figure 3.9). Estimates of total mortality from model 0M were also unbiased, although not as precise as scenario 6M. For scenario 2M, total mortality estimates were slightly biased when tag reporting rate was 0.4 or below, and for scenario 4M total mortality estimates were slightly biased when $\lambda$ was 0.6 or below. The accuracy and precision of all estimates improved as tag reporting rate increased. Scenario 0M had unbiased and the most precise estimates of fishing and natural mortality of all the scenarios at all tag reporting rates. The accuracy (lack of bias) and precision of fishing and natural mortality estimates decreased with the increasing length of the seasonal closure for males (scenarios 2M, 4M and 6M). Estimates of $F$ and $M$ from scenario 4M were biased when $\lambda$ was less than 0.8, while estimates of $F$ and $M$ from scenario 6M were biased for all $\lambda$’s tested.

3.6.2 Discussion

The increasing precision of fishing and natural mortality estimates associated with the increasing length of the male fishing season, suggests that the model benefits from the length of time females are exposed to natural mortality alone, while males are exposed to both fishing and natural mortality. This increased precision is observed not just in estimates of $F$ and $M$ but also in estimates of $Z$. It is not clear why scenario 6M, the management regime with a six month closure for both genders, produced the most accurate and precise estimates of total mortality, when estimates of fishing and natural mortality were biased and less precise than those of the other scenarios. The bias observed in estimates of $F$ and $M$ could be explained by the different closed seasons for males and females, allowing the model to more accurately separate total mortality into its fishing and natural components. This, however, does not explain why estimates of total mortality from scenario 6M were more accurate and precise than those of the other three scenarios.
Figure 3.9: Boxplots of estimated fishing ($F$), natural ($M$) and total ($Z$) mortalities for tag reporting rates of $\lambda = 0.2$, 0.4, 0.6 and 0.8 under four fishery management scenarios. All scenarios had a six month closure for females, while the fishing season length for males varied between the scenarios. Scenario 6M (white boxes) had a six month closure for both genders; scenario 4M (light grey boxes) had a four month closure for males; scenario 2M (grey boxes) had a two month closure for males and scenario 0M (dark grey boxes) did not have a male closure.
3.7 Conclusions and Discussion

When the tag reporting rate was 100%, the model produced unbiased estimates of fishing, natural and total mortality under the three fishery management regimes tested: \(0.3 \leq F \leq 2.3\) and \(0.05 \leq M \leq 0.3\). The lack of differences between the continuous fishing, alternating fishing and seasonal fishing management regimes suggests that when tag reporting rate is 100%, the precision and accuracy of mortality estimates is not dependent on seasonal fishing patterns. This is an improvement compared with Brownie models that require some contrast in fishing effort to estimate fishing and natural mortality tagging once per season (Hoenig et al., 1998a).

As tag reporting rate decreased below 80%, estimates of fishing and natural mortality were slightly biased for most scenarios tested. In this situation, \(F\) was generally underestimated and \(M\) overestimated. However, \(Z\) was unbiased. It appears that the model has difficulty distinguishing between fishing and natural mortality, as did Frusher and Hoenig (2001a) using Brownie models.

For a two gender management regime based on the Tasmanian lobster fishery, there was little difference between the five release patterns tested. The best performing release pattern was to release tags at the end of each female fishing season. Model performance improves as the difference between the season lengths for males and females increases. As tag reporting rate increased above 0.6, the level of bias in estimates of \(F\) and \(M\) reduced substantially for the two gender management regimes, but is still present under the single gender regime. This supports the hypothesis that the model obtains additional leverage in separating total mortality into its fishing and natural components from the period when the fishery is open for one gender only.
Chapter 4

Application of the Model to a Tasmanian Fishery

4.1 Introduction

This chapter applies the survival model (Chapter 2) to reanalyse tag recovery data previously analysed with Brownie models, so as to estimate fishing and natural mortality and tag reporting rate (Frusher and Hoenig, 2001a, 2003). The survival model is shown to be a viable replacement for Brownie style models in fisheries tagging studies, having the additional benefit of added flexibility. Three parameterisations of catchability are tested: constant over the study, varying between, but not within, fishing seasons and varying within, but not between, fishing seasons. All models are fitted with constant natural mortality and tag reporting rates over the period of the study. Both gender specific and non-gender specific catchabilities and natural mortalities are tested. Brownie models require that tags in each cohort are released on a single day. This is not feasible when catch rates are low. Frusher and Hoenig (2003) used the midpoint of each tagging survey as the release date in their models. To test if the aggregation of release times influences mortality estimates, a survival model with aggregated release dates and one with the exact date of release, are fitted with the catchability periods used by Frusher and Hoenig (2003).

4.1.1 Background

Between May 1992 and May 1995, fisheries scientists at the Tasmanian Aquaculture and Fisheries Institute undertook a tagging experiment on rock lobster in north-west Tasmania, in order to obtain growth and movement information (Frusher and Hoenig, 2001a). It was later realised that this data could be used to estimate fishing and natural mortality with Brownie models. The tagging study was undertaken on commercial fishing grounds off the west coast of King Island, that is located to the north west of the Tasmanian mainland (Figure 4.1). A total of ten survey voyages, lasting between 11 and 13 days, were conducted from a commercial vessel between May 1992 and May 1995 (Table 4.1). Weather permitting, between 42 and 84 traps
with the escape gaps closed, were set each day of the survey to capture lobsters for tagging. All captured lobsters, including those undersized, were tagged ventrally in the tail, using individually numbered T-bar tags (Hallprint Pty. Ltd, Victor Harbor, South Australia, 5211, Australia). Lobsters had their carapace length and gender recorded, before being released at the location of capture.

As only legal sized lobsters contribute to fishing mortality, all lobsters below the size limit, were excluded for the purposes of this analysis. While it is possible to incorporate undersized lobsters into the model, estimates of mortality may be biased because fishers may be less likely to check undersized lobsters for tags, and undersized lobsters may not be fully selected by the fishing gear.

Over the ten survey voyages, almost five thousand legal-sized lobsters of both genders were tagged, with approximately fifteen hundred being tagged each year. The number of lobsters tagged varied with the time of year, due to changes in catch rates, with approximately twice as many lobsters tagged in February or September as opposed to May (Table 4.2). Many of these tagged lobsters were subsequently recovered by fishers during the course of their normal fishing operations.
Recaptured tags were solicited from fishers in three ways: (1) notices requesting tags to be returned were sent to all fishers and all known processors of rock lobster on King Island; (2) the tagging project was advertised in the fishing industry magazine (*Fishing Today*) and (3) regular oral presentations were given at Tasmanian Rock Lobster Fishermen’s Association meetings. In addition to this, as an incentive for fishers to return the tags, a lottery was established. For every correctly completed tag returned, the fisher received one entry in the lottery.

Information on the recapture of tagged lobsters was returned to researchers voluntarily by fishers when they submitted the mandatory log of their catch details. A total of 1020 lobsters were recaptured and their tags returned to researchers from the beginning of the study on the 5th of May 1992 until the 31st of August 1997. By this date, tag returns had fallen to very low levels (Table 4.2). All tags that were not returned during this period were censored on the 1st of September 1997 to be consistent with Frusher and Hoenig (2003). Tagged lobsters were primarily recaptured in the location of release (Frusher and Hoenig, 2001a).

### The Tasmanian Fishery

At the time that the study was undertaken, the Tasmanian lobster fishery was managed with a combination of seasonal closures and effort controls (Ford, 2001). During the study, effort was reduced due to concerns about over-fishing of the resource. This resulted in minor changes to the opening date of the fishing season and the total effort between years. The fishing effort at King Island during the period of the study varied seasonally from highs in summer that were around twice the levels of the lows in autumn (Figure 4.2). The fishery has since moved to an individual transferable quota system (Ford, 2001). A more detailed description of the Tasmanian fishery is given in Section 1.1.4.
4.1. INTRODUCTION

Recaptures

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Table 4.2: Aggregated tagging and recapture details from male and female legal-sized lobsters from May 1992 to the census date of the 1st of September 1997. Only males may be retained by fishers between May and September.
4.1. INTRODUCTION

4.1.2 Previous Research

This dataset has been analysed on two previous occasions to estimate yearly fishing mortality, natural mortality and tag reporting rate, using a combination of aspects from Hoenig et al. (1998a) and Hearn et al. (1998). Firstly, Frusher and Hoenig (2001a) adopted the “weak effort” assumption (Hoenig et al., 1998a) to apportioned effort within the duration of each fishing season. As tagging was undertaken at the beginning and end of the fishing season, it was possible to separate total mortality into fishing and natural components, using the method proposed by Hearn et al. (1998). Their most parsimonious model produced reasonable estimates of annual fishing mortalities and tag reporting rate with low standard errors. However, estimates of natural mortality approximated zero with high standard errors. Secondly, Frusher and Hoenig (2003) reanalysed the data using the “strong effort” assumption $F = qE$, to partition fishing mortality directly by catchability $q$ and fishing effort $E$ (Hoenig et al., 1998a). The timing of tagging surveys allowed for the estimation of three periods of constant catchability over the fishing season, one for each sampling period. A constant natural mortality and tag reporting rate were assumed equal between seasons. As the model support between gender-specific and non-gender-spe-
specific catchabilities was only 1.5 likelihood units, the more parsimonious non-gender specific model was selected. Annual fishing mortalities were calculated using

\[ F_{\text{year}} = q_a E_a + q_b E_b + q_c E_c, \]

where \( a \) was the November to February period, \( b \) February to May and \( c \) May to September. Estimates of annual fishing mortalities and tag reporting rate were similar to Frusher and Hoenig (2001a), with natural mortality being estimated at \( M = 0.12 \), and with minor reductions in the relative standard errors. The model produced three within season estimates of \( q \) which broadly corresponded to catchability variability known for the fishery (Frusher and Hoenig, 2003).

### 4.2 Methods and Models

The survival model (Chapter 2) was used to estimate annual fishing mortalities, constant natural mortality and tag reporting rate from the tag return data obtained at King Island and analysed by Frusher and Hoenig (2001a, 2003). Similar to Frusher and Hoenig (2003), natural mortality \( (M) \) and the tag reporting rate \( (\lambda) \) were assumed not to vary during the study so as to reduce the number of parameters being estimated. While natural mortality may vary within a fishing season, due to factors such as molting and mating, allowing \( M \) to vary within or between years would over-parameterise the models. Three general parameterisations of catchability were considered: constant models where \( q \) was constant over the entire study period, seasonal models where \( q \) was allowed to vary between fishing seasons and sub-seasonal models where \( q \) was allowed to vary within, but not between, fishing seasons. Both gender specific and non-gender specific models were considered for \( q \) and \( M \). Annual fishing mortalities were then calculated from catchability and effort, using equation 2.9.

#### 4.2.1 Model Assumptions

The assumptions of the model relate to randomness in the tagging and recapture process, with all tags equally likely to be recaptured. A full description of the assumptions made by the model and how they relate to south eastern Australian lobster fisheries is presented in Section 2.2.

#### 4.2.2 Proposed Models

The fitted models fell into three broad categories based on how catchability was parameterised. All models were fitted with a single tag reporting rate \( \lambda \) that was constant over the study. The models are described in detail below.
4.2. METHODS AND MODELS

Constant Models (C)

These models were defined such that all parameters were constant for the duration of the entire study. Four constant models were fitted, allowing for both gender specific and gender non-specific catchabilities and natural mortalities. The fitted models were:

- Model C1: A single tag reporting rate (1 $\lambda$), a gender non-specific catchability (1 $q$) and natural mortality (1 $M$) (3 parameters).
- Model C2: A single tag reporting rate (1 $\lambda$), two gender specific catchabilities (2 $q$) and a non-gender specific natural mortality (1 $M$) (4 parameters).
- Model C3: A single tag reporting rate (1 $\lambda$), a gender non-specific catchability (1 $q$) and two gender specific natural mortalities (2 $M$) (4 parameters).
- Model C4: A single tag reporting rate (1 $\lambda$), two gender specific catchabilities (2 $q$) and natural mortalities (2 $M$) (5 parameters).

Seasonal Models (S)

Four seasonal models were fitted that permitted catchability to vary between, although not within, the six fishing seasons from 1991/92 to 1996/97. The seasonal models were fitted with both gender specific and gender non-specific catchabilities and natural mortalities. The tag reporting rate and the natural mortality, either gender specific or gender non-specific, were assumed constant over the study. Because tagging in the 1991/92 fishing season did not occur until after the female fishing season closed in May, the first fishing season, 1991/92, was incomplete. The estimate of fishing mortality in the 1991/92 season applied to males only, from the 6th of May until the 31st of August. The fitted models were:

- Model S1: A single tag reporting rate (1 $\lambda$), one gender non-specific catchability per year (6 $q$) and a gender non-specific natural mortality (1 $M$) (8 parameters).
- Model S2: A single tag reporting rate (1 $\lambda$), one gender non-specific catchability per year (6 $q$) and two gender specific natural mortalities (2 $M$) (9 parameters).
- Model S3: A single tag reporting rate (1 $\lambda$), two gender specific catchabilities per year (12 $q$) and a gender non-specific natural mortality (1 $M$) (14 parameters).
- Model S4: A single tag reporting rate (1 $\lambda$), two gender specific catchabilities per year (12 $q$) and two gender specific natural mortalities (2 $M$) (15 parameters).
Sub-seasonal Models (U)

These models were defined as allowing catchability to vary within, but not between, fishing seasons. Four groups of within season catchability were considered. They were:

- Two periods of catchability, the first period starting with the opening of the fishing season in November and running to the closing of the female season at the end of April. The second period began on the 1st of May and ended with the closure of the male only part of the fishing season on the 31st of August.

- Three periods of catchability, with the first running from the opening of the fishing season in November until the 31st of January. The second ran from the 1st of February to the closure of the female season on the 30th of April and the third ran from the 1st of May until the closure of the male only part of the fishing season on the 31st of August.

- Five periods of catchability, being the months November and December, January and February, March and April, May and June, and July and August, with September and October closed to fishing.

- A monthly catchability with ten periods, September and October being closed to fishing.

For the first three groups, both gender specific and gender non-specific models were fitted. No gender term was considered for the monthly catchability model so as not to over-parameterise the model. All sub-seasonal models assumed a single tag reporting rate and a single natural mortality for both genders that were constant over the study. The fitted models were:

- Model U1: A single tag reporting rate ($\lambda$), a single natural mortality ($M$) and two periods of catchability ($q$) that were gender non-specific (4 parameters).

- Model U2: A single tag reporting rate ($\lambda$), a single natural mortality ($M$) and two periods of gender specific catchability, with the female season closed in the second period (3 $q$, 5 parameters).

- Model U3: A single tag reporting rate ($\lambda$), a single natural mortality ($M$) and three periods of catchability ($q$) that were gender non-specific (5 parameters).

- Model U4: A single tag reporting rate ($\lambda$), a single natural mortality ($M$) and three periods of gender specific catchability, with the female season closed in the third period (5 $q$, 7 parameters).

- Model U5: A single tag reporting rate ($\lambda$), a single natural mortality ($M$) and five periods of catchability ($q$) that were gender non-specific (7 parameters).
• Model U6: A single tag reporting rate (1 $\lambda$), a single natural mortality (1 $M$) and five periods of gender specific catchability, with the female season closed in the fourth and fifth periods (8 $q$, 10 parameters).

• Model U7: A single tag reporting rate (1 $\lambda$), a single natural mortality (1 $M$) and ten periods of monthly catchability (10 $q$) that were gender non-specific (12 parameters).

• Model U8: A single tag reporting rate (1 $\lambda$), a single natural mortality (1 $M$) and monthly periods of catchability (16 $q$) that were gender specific (18 parameters).

• Model U9: A single tag reporting rate (1 $\lambda$), a single natural mortality (1 $M$) and ten periods of monthly catchability including an additional additive term, delta, with an indicator function to show if the observation is from a male (11 $q$, 13 parameters).

**Frusher and Hoenig (2003) Models (B)**

In addition to the models described above, two additional sub-seasonal models and the optimal Brownie model from Frusher and Hoenig (2003), were fitted to allow direct comparison between the survival model and the Brownie model. Two sub-seasonal models were fitted with three periods of gender non-specific catchability identical to those used by Frusher and Hoenig (2003). The optimal model of Frusher and Hoenig (2003) assumed three periods of gender non-specific constant catchability over the fishing season, one for each sampling period: November to February, February to May and May to September, as well as constant natural mortality and a constant tag reporting rate. The catchability periods varied slightly to those in models U3 and U4, due to the dates of tagging, with the period from February to May finishing on the 10th of May.

Brownie models assume that all tags are released on a single day. Catch rates in this study made it infeasible to tag a sufficient number of lobsters in a single day, and the tagging surveys took between 11 and 13 days (Table 4.1). The models fitted by Frusher and Hoenig (2003) aggregated the release times for each tagging survey to the mid point of the survey dates, in order to give a single date of release.

Due to the correction of minor errors in the tagging database, it was not possible to reproduce the exact data used by Frusher and Hoenig (2003) with the exact date of recapture information. However, the differences are minor. When model B1 (model 3x-Ce-yA Frusher and Hoenig (2003)) was implemented in the R statistical package (R Development Core Team, 2010), checked using the computer program SURVIV, which is currently incorporated into the program MARK (White and Burnham, 1999) and rerun using the updated dataset, minor differences in estimates from the two fitting processes were consistent with the use of different implementations of numerical optimisation and the results from the R implementation presented.

---

1Model suggested by an examiner.

2Model suggested by an examiner.
4.3. RESULTS

The models using the same catchability periods from Frusher and Hoenig (2003) were:

- Model B1: The equivalent of model 3x-Ce-yA (Frusher and Hoenig, 2003), with a single tag reporting rate ($1 \lambda$), a single natural mortality ($M$) and three periods of gender non-specific catchabilities ($3 q$) (5 parameters).
- Model B2: The survival model fitted to the aggregated release times and exact recapture time, with a single tag reporting rate ($1 \lambda$), a single natural mortality ($M$) and three gender non-specific catchabilities ($3 q$, 5 parameters).
- Model B3: The survival model fitted to the exact release and recapture times, with a single tag reporting rate ($1 \lambda$), a single natural mortality ($M$) and three gender non-specific catchabilities ($3 q$, 5 parameters).

4.2.3 Evaluation of Candidate Models

All models except B1 and B2 (those with aggregated tag release times) were compared for fit using AIC (Section 2.5.1; Burnham and Anderson, 2002), the model with the lowest AIC being the optimal model. Models B1 and B2 were fitted to different data. B1 was fitted to aggregated release and recapture data, while B2 was fitted to aggregated release and exact date of recapture data. For this reason they could not be compared with each other, nor with the models that use the exact date of release and recapture.

Due to concerns about the non-normality in the data, profile likelihood methods (Section 2.5.1) were used to estimate standard errors for all models.

4.3 Results

Estimates of annual fishing mortalities, natural mortality and tag reporting rate are presented for the best fitting constant, seasonal and subseasonal models. Instantaneous fishing mortalities were annualised, providing separate estimates for males and females due to the difference in the length of the fishing season, regardless of whether gender specific catchabilities were included in the model or not.

Constant, Seasonal and Subseasonal Models

All seasonal (S) models were better supported in terms of lowest AIC than the constant (C) models (Table 4.3). Except for model U2, all subseasonal (U) models were better supported than the seasonal models. Models U7 and U9 were equally well supported in terms of AIC; a likelihood ratio test ($p=0.21$) provided no evidence to prefer the model U9 against the more parsimonious model U7, the model with ten monthly gender non-specific catchability parameters, a single natural mortality and tag reporting rate. The best fitting constant catchability model was C3 that had gender non-specific catchability and gender specific natural mortality. The
seasonal models with greatest support were S3 and S4, both of which had gender specific catchabilities. All parameter estimates from these models were unbounded, so model S2 was determined to be the optimal seasonal model.

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</table>

Table 4.3: Model summary information for constant models (C1-C4), seasonal models (S1-S4), subseasonal models (U1-U9) and models using the same catchability periods as Frusher and Hoenig (2003) (B1-B3). * indicates that estimates of $M$ were unbounded. ** indicates estimates of all parameters were unbounded. *** indicates the model was fitted to a unique data set and is not directly comparable with other models.

For males, estimates of annual fishing mortalities from model C3 and S2, were higher than those from model U7, between 0.87 and 1.31 compared with 0.71 to 0.84 (Figure 4.3). The 95% confidence intervals for $F$ from the seasonal model S2, increased greatly in the 1995/96 and 1996/97 fishing seasons. Estimates of natural mortality from models C3 and S2, were approximately zero, while for model U7, $M$ was 0.22. Estimates of $M$ from all models were unbounded. Similar trends in annual fishing mortalities were present for females, with $F$ higher for models C3 and S2, compared with model U7 (Figure 4.4). Estimates of annual fishing mortalities ranged from 0.63 to 0.85 for model C3, 0.56 to 0.92 for model S2 and 0.47 to 0.66 for model U7. Natural mortality estimates were 0.07 for models C3 and S2, and 0.22 for model U7, as it was parameterised to be identical to males. Tag reporting rate estimates were 0.22 for models C3 and S2, and 0.28 for model U7.

Catchability estimated from model U7 rapidly declined from the peak at the opening of the fishing season in November (Figure 4.5). Catchability was lowest in April
before increasing in May after the closure of the female season. It was stable between May and July before increasing again in August, the last month of the male fishing season. A local peak in catchability was observed in March. The width of the 95% confidence intervals suggests that the differences in the magnitudes of monthly catchability estimates should be interpreted cautiously.

![Figure 4.3](image-url)  
Figure 4.3: Estimates of annual fishing mortalities ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models C3, S2 and U7 for females. Model C3 (white bars) is the optimal constant model; model S2 (light grey bars) is the only seasonal model that estimated standard errors and model U7 (dark grey bars) is the optimal subseasonal model. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates which were unbounded.
4.3. RESULTS

Figure 4.4: Estimates of annual fishing mortality ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models C3, S2 and U7 for females. Model C3 (white bars) is the optimal constant model; model S2 (light grey bars) is the only seasonal model that estimated standard errors and model U7 (dark grey bars) is the optimal subseasonal model. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates for models S2 and U7 which were unbounded.
4.3. RESULTS

Frusher and Hoenig Models

For males, estimates of annual fishing mortalities from model B1, the optimal model from Frusher and Hoenig (2003), were lower than those from models B2 and B3 in all years (Figures 4.6). Estimates of $F$ were between 0.81 and 0.96 for model B1, compared with 0.97 to 1.15 for model B2, and 0.98 to 0.16 for model B3. There were only slight differences ($< 1\%$) in estimates of $F$ from models B2 and B3 in any given year. Similar trends between models were present in female fishing mortality estimates (Figure 4.7). Annual female fishing mortality estimates were from 0.55 to 0.73 for model B1, 0.66 to 0.88 for model B2 and 0.67 to 0.88 for model B3. The natural mortality estimate from model B1 was 0.16, while $M$ from model B2 and B3 were approximately zero. All three models gave similar estimates of the tag reporting rate $\lambda$, 0.25 for model B1 and 0.21 for models B2 and B3.

All three models had similar patterns in the estimates of catchability, with $q$ being highest in the November to February period and lowest in the February to May period, before increasing slightly in the May to September period. The 95% confidence intervals for all three models overlapped, indicating no statistical difference between the models, although the spread of the 95% confidence intervals decreased

Figure 4.5: Estimates of monthly catchability ($q$) from the optimal sub-seasonal model U7. Models are presented with 95% confidence intervals (bars). No estimates were available for September or October, as those months were closed to fishing.
from model B1 to model B2 and then to model B3 for all estimates (Figure 4.8).

Yearly fishing mortality estimates for males were similar to those of Frusher and Hoenig (2003). Trends between models were consistent, with $F$ increasing between the 1992/93 and 1993/94 fishing seasons, then declining slightly over the following three seasons. However, the 95% confidence intervals for all estimates overlapped (Figure 4.6). As with the catchability estimates, the 95% confidence intervals for all three models overlapped, with minor improvements in precision from models B1 to B2 to B3. Estimates of fishing mortality for females for models B1, B2 and B3, were lower and had similar trends to those for males (Figures 4.6 and 4.7). This is consistent with the shorter fishing season, six months for females as opposed to ten months for males.

Figure 4.6: Estimates of annual fishing mortality ($F$), the overall natural mortality ($M$) and tag reporting rate ($\lambda$) for the models B1, B2 and B3 for males. Model B1 (white bars) is the optimal model from Frusher and Hoenig (2003), model B2 (light grey bars) is the exact time of recapture with aggregated release times, and model B3 (dark grey bars) is the exact time of release and recapture model. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates for models B2 and B3, where estimates were approximately zero and the confidence intervals were unbounded.
Figure 4.7: Estimates of annual fishing mortality ($F$), the overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models B1, B2 and B3 for females. Model B1 (white bars) is the optimal model from Frusher and Hoenig (2003), model B2 (light grey bars) is the exact time of recapture with aggregated release times, and model B3 (dark grey bars) is the exact time of release and recapture model. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates for models B2 and B3, where estimates were approximately zero and the confidence intervals were unbounded.
4.4 Discussion

The sub-seasonal models, where catchability was permitted to vary within the fishing season, fitted better in terms of lower AIC than either the constant or seasonal models (Table 4.3). Of the sub-seasonal models, those with more catchability periods generally fitted better than those without, suggesting that catchability changes over short periods during the fishing season. It was unclear whether models fitted with separate gender specific catchability were preferred, compared with those that had equivalent catchability for both males and females. The best supported model, (excluding model B1), was model U7 that estimated monthly catchabilities and a single natural mortality and tag reporting rate. It has been shown that there are seasonal fluctuations in the catchability of rock lobsters in the Tasmanian fishery, due to factors such as mating and moulting (Ziegler et al., 2002a). This may explain why models U7, U8 and U9, models with monthly catchability, were preferred.

While model B1 had the lowest AIC value by a considerable amount, it is not
possible to compare it with the other models because the data is not the same. That is, recaptures are pooled. Estimates of catchability, natural mortality and tag reporting rate from models B1, B2 and B3 were not significantly different from one another. Model B3, incorporating the exact time of release and recapture, had a greater level of precision of the estimates than models B1 and B2. Estimates of natural mortality for models B2 and B3 were very low, approximately 0.03, with very high standard errors. In contrast, model B1 from Frusher and Hoenig (2003), estimates $M$ to be 0.16 and the 95% CI to be within [0,0.43].

Natural mortality has historically been a difficult parameter to estimate in fisheries, and for lobster fisheries is thought to be low (Frusher et al., 1997). It is unclear whether the estimates from model B1 or those from models B2 and B3, are correct. In terms of the total instantaneous mortality $Z = F + M$, all three models gave similar estimates of around 1.05 to 1.15, depending on the year. Thus it is likely that the differences between $F$ and $M$ between model B1 and models B2 and B3, are due to the partitioning of total mortality into fishing and natural mortality. From a management perspective, knowledge of relative changes in $Z$ is the important factor when determining fishery harvest strategies. In many stock assessment models, $M$ is not estimated but held fixed because it is too difficult to estimate (Quinn and Deriso, 1999; Hilborn and Walters, 1992). Any variability in $M$ between years is instead incorporated into estimates of $F$. Thus the failure of the model to correctly partition may not be an issue from a fisheries management perspective.

The results indicate that environmental drivers are likely to be the major factors affecting catchability, although gender is also likely to contribute. Of the environmental factors that impact catchability, Ziegler et al. (2003) found temperature to be most important. With the increasing impact in Tasmanian waters of the strength and duration of the East Australia current in recent years (Hill et al., 2008; Thompson et al., 2009), changes in historical catchability patterns in the lobster fishery are increasingly likely, with the survival model being a method of detecting any change.

An alternative theory suggested by an examiner is that individual variability in catchability, common in bird banding studies (Burnham and Rexstad, 1993), may account for the high catchability estimates in November. In this case, a highly catchable group of lobsters are removed at the beginning of the fishing season.

Estimates of mortality and reporting rate are broadly consistent with those obtained by Frusher and Hoenig (2001a) and Frusher and Hoenig (2003), using Brownie models, and are consistent with mortality estimates obtained from stock assessment models (Punt and Kennedy, 1997). This strongly suggests that the model is correctly determining mortality in the application to this dataset.

The benefits of the survival model when compared to Brownie models, are the ability to accommodate changes in catchability over the fishing season and its flexibility for the design of tagging studies. Changes in fishing patterns, such as a change in the time of peak market demand, can be detected and incorporated into the model, whereas a seasonal model may be unable to identify the reason for the associated change in mortality. The use of the exact date of release eliminates the need to conduct tagging studies at specific times. As lobsters can be tagged at any time of the year, tagging can be conducted in conjunction with other research, thereby
saving money. Additionally, trained fishers as volunteers are able to tag lobsters opportunistically. For fishers, when one gender is closed to fishing (e.g. females) but still encountered by the fishing gear, these legal-sized animals can be tagged upon release.
Chapter 5

Estimating Fine Time-Scale Catchability

5.1 Introduction

This chapter develops a penalised smoothing model to estimate within season variability in catchability. The model is applied to the King Island tagging study (Chapter 4) in order to estimate fine time-scale catchability of southern rock lobster in northwest Tasmania, to explore the potential for daily recaptures and to provide a more continuous representation of catchability. Estimates of catchability were compared to those obtained by Ziegler et al. (2002a) from comparisons between underwater diving and trap surveys in a marine reserve in south eastern Tasmania.

Most fisheries stock assessments seek to relate fishing effort and catch to abundance, since this is the most prevalent, and often the only data available (Hilborn and Walters, 1992). Catchability is an important parameter in this process, relating catch to abundance (Ricker, 1975; Hilborn and Walters, 1992), and is defined as

\[ q_t = \frac{C_t}{E_t N_t} \]

where \( q_t \) is the catchability, \( C_t \) and \( E_t \) are the catch and fishing effort for time period \( t \), and \( N_t \) is the population size.

Present methods of estimating catchability are either expensive or unreliable and lack temporal resolution, which has resulted in catchability being estimated as a nuisance parameter in stock assessments (Walters et al., 1993; Punt and Kennedy, 1997). Inaccurate estimates of catchability can lead to false assessments of stock size which can have detrimental effects on the management of the fishery. If catchability varies within a fishing season, then a resultant change in catch for the same effort would give a false appearance of a change in abundance. While there is evidence that the catchability of fished species varies seasonally, catchability is normally estimated as a single parameter that is held constant over a fishing season (Arreguín-Sánchez, 1996). If within season variability of catchability can be estimated, then those
estimates can be used to validate and inform the stock assessment models (Punt and Kennedy, 1997).

Tagging models offer a method of estimating catchability within a fishing season. The model proposed by Hoenig et al. (1998a) and applied to the King Island data by Frusher and Hoenig (2003), divided the fishing year into three periods of constant catchability, determined by the dates of tagging surveys. \( F \) was then estimated using the relationship \( F = qE \). The survival model does not require tagging to be undertaken at specific times (Chapter 3), but instead allows flexibility of representation of \( q \), with model estimates derived from the daily recaptures and effort data.

The models presented in Chapter 4 gave improved fit when catchability was permitted to vary within a fishing season, with the best fitting model U7 having catchability estimated over monthly periods (Figure 4.5). Based on the same dataset, Frusher and Hoenig (2003) showed an improved fit of tag return data using a strong effort model which allowed catchability to vary within a year. Frusher and Hoenig’s model assumed periods of constant catchability between survey times, while model U7 assumed monthly catchability to be constant between fishing seasons.

### 5.1.1 Biological Variation of the Southern Rock Lobster

In lobster fisheries, catchability is known to vary with a large number of factors, including size, gender, moult status, behavioural interactions, trap design, temperature and habitat (Tremblay et al., 2006). The southern rock lobster (*Jasus edwardsii*) in particular, shows evidence of catchability varying with changes in water temperature, moultng and mating times (Frusher and Hoenig, 2003; Ziegler et al., 2002a). Ziegler et al. (2002a,b) estimated catchability in the southern rock lobster by comparing catch rates from baited traps, with visual estimates of lobster density from dive surveys. These took place in a marine reserve in south eastern Tasmania, over a 14 month period. Catchability was found to decline in winter and increase in early summer, with the magnitude of the fluctuations being smaller for females than for males. There was an effect due to size, with large lobsters having greater catchability than small lobsters (Ziegler et al., 2002b).

Timing of catchability in the southern rock lobster is known to be associated with the biological events of mating and moultng, and to fluctuate over the course of the fishing season (Ziegler et al., 2003). Peak catchability was observed in December, and is thought to be associated with compensatory feeding after the male moult. The low catchability in April, and the subsequent local peak observed in late May, are thought to correspond to the female moult and mating (Ziegler et al., 2002a). Estimates were obtained in a marine reserve that had been unfished for more than 30 years, with the population structure containing many large lobsters that are not present in fished regions of Tasmania.
5.2 Smoothing

There are many methods for smoothing (Simonoff, 1998). Two common approaches are basis smoothing and penalty smoothing, and these will form the basis of the techniques developed in this chapter.

5.2.1 Basis Smoothing

In basis smoothing, the function to be fitted $g$ is represented in terms of a set of complete basis functions $\phi_k$

$$g(x) = \sum_{k=0}^{\infty} a_k \phi_k(x),$$

and $g$ is smoothed by truncating this expansion after $N$ terms

$$g(x) = \sum_{k=0}^{N} a_k \phi_k(x).$$

The expansion coefficients $a_n$ are chosen to minimise some measure $L(g, y)$ of lack of fit to data $y$. The level of smoothing is determined by the number $N$ of terms retained in the series, and the nature of the smoothing is determined by the choice of basis functions $\{\phi_k(x)\}$.

A common choice of basis functions $\{\phi_k(x)\}$ is the Fourier basis

$$\phi_k(x) = \begin{cases} \cos(kx/2) & k \text{ even} \\ \sin((k+1)x/2) & k \text{ odd} \end{cases}.$$ 

One disadvantage of basis smoothing is that the level of smoothing is discretised—choosing $N = n$ may oversmooth, but choosing $N = n + 1$ may not smooth enough.

5.2.2 Penalty Smoothing

In penalty smoothing (Reinsch, 1967; Wegman and Wright, 1983), $g$ is fitted by minimising the cost functional

$$J_\alpha(g) = L(g, y) + \alpha R(g)$$

where $L$ is a measure of lack of fit to the data $y$, $\alpha$ a smoothing parameter, and $R$ is a roughness penalty—a measure of the “roughness” of $g$. In essence, goodness of fit is traded off against the smoothness of $g$. The smoothing parameter $\alpha$ determines the degree to which any improvement in fit is penalised for a lack of smoothness.

So the level of smoothing is determined by $\alpha$, and the nature of the smoothing is determined by the choice of roughness penalty $R$. This has two advantages: it allows finer control over the level of smoothing than in the basis approach, and often the
nature of the smoothing imposed by a given choice of roughness penalty is more intuitive than the smoothing imposed by a choice of basis functions.

In practice, \( J_\alpha(g) \) is minimised by first determining the functional form of the optimal \( g \), and then solving a secondary problem to minimize \( J_\alpha(g) \).

As an example, consider the standard problem of fitting a smooth curve \( y = g(x) \) to a set of observations \( \{(x_1, y_1), (x_2, y_2), \ldots, (x_n, y_n)\} \) on an interval \([a, b] \). It is common to choose

\[
J_\alpha(g) = \sum_{i=1}^{n} (y_i - g(x_i))^2 + \alpha \int_a^b g''(x)^2 dx.
\]

The first term is a standard sum of squares measure of fit, and the second is a roughness penalty that penalises curvature in \( g \).

If \( g_0 \) minimizes \( J_\alpha(g) \), then for any small perturbation \( g_0 + \epsilon g_1 \), it must be the case that

\[
\left. \frac{dJ_\alpha(g_0 + \epsilon g_1)}{d\epsilon} \right|_{\epsilon=0} = 0.
\]

That is, for any \( g_1 \)

\[
0 = \frac{dJ_\alpha(g_0 + \epsilon g_1)}{d\epsilon} \bigg|_{\epsilon=0} = 2 \sum_{i=1}^{n} (y_i - g_0(x_i))g_1(x) + 2\alpha \int_a^b g''_0(x)g''_1(x) dx.
\]

Assuming \( g''_0 = 0 \) and \( g'''_0 = 0 \) at \( x = a \) and \( x = b \) and integrating by parts twice, this expression reduces to

\[
0 = \sum_{i=1}^{n} (y_i - g_0(x_i))g_1(x) + \int_a^b g'''_0(x)g''_1(x) dx
\]

where \( \delta(x) \) is the Dirac delta function. As this must be true for arbitrary \( g_1 \), it must be the case that the expression in the square brackets vanishes. This implies the fourth derivative of \( g \) is identically zero except at the \( x_i \), from which it is readily deduced that \( g_0 \) must take the form of a cubic spline with knots at the \( x_i \).

Knowing \( g \) takes the form of a cubic spline, it is then simple to set up a secondary problem to determine the precise \( g \) that minimises \( J_\alpha(g) \) for the data at hand.

Unfortunately, a similar approach is not feasible for the tagging model developed in Chapter 2. For the tagging problem, \( g \) might represent fishing mortality, catchability, or natural mortality, \( L(g, y) \) would be the negative log likelihood, and the roughness penalty \( R(g) \) could be chosen as above. However, this leads to a complex integro-differential equation for \( g \), and even for simple problems, the functional form of \( g \) is not so readily deduced.
5.2.3 Hybrid Approach

To retain the advantages of penalty smoothing while obviating the need to deduce functional form of the function to be smoothed, a hybrid approach is adopted for the tagging problem.

The function to be smoothed is represented as a truncated expansion

\[ g(x) = \sum_{k=0}^{N} a_k \phi_k(x), \]

but the expansion coefficients \( a_k \) are determined by minimising the cost functional

\[ J_\alpha(g) = L(g, y) + \alpha R(g) \]

by purely numerical means.

5.2.4 Selecting \( \alpha \) and Cross-Validation

Smoothing is a trade off between bias and variance. As the level of smoothing increases, bias increases, while the variance drops. To determine a suitable level of smoothing, a compromise is needed. Cross-validation provides an objective method for selecting \( \alpha \). Cross-validation estimates each observation from a curve fitted to the remainder of the data, and a measure of goodness of fit is determined based on these fitted values. The optimal \( \alpha \) is then chosen by maximising this measure of goodness of fit. While this is appealing, cross-validation tends to under-smooth in practice (Simonoff, 1998).

Unfortunately, the model defined above does not allow cross-validation for two reasons. Firstly, it is not clear how the censored observations should be re-estimated from the remainder of the data and secondly, it is too computationally expensive to recalculate the fit for every observation. The value of \( \alpha \) must therefore be determined subjectively by inspecting the plots of catchability with different levels of smoothing, and by trying to correlate periods of changing catchability with known biological processes.

5.3 Application to King Island Data

To test the penalised smoothing method described in Section 5.2, it was applied to the tagging data from King Island (Chapter 4) to estimate within season catchability of lobster in the study region.

5.3.1 Fourier Representation of Catchability

The fishing mortality \( F(t) \) was represented in terms of daily fishing effort \( E(t) \) and a smooth, periodic catchability \( q(t) \)
5.4. RESULTS

\[ F(t) = q(t)E(t). \]

Catchability was then represented as a truncated Fourier series

\[ q(t) = c_0 + \sum_{i=1}^{n} (c_i \cos(2i\pi t) + s_i \sin(2i\pi t)), \quad (5.1) \]

where \( c_i \) and \( s_i \) are the constants associated with the sine and cosine terms in the Fourier series. In this case, 20 terms were used to represent \( q \) and separate \( q \)s were fitted for males and females. Catchability was constrained to be identical between the fishing seasons, and the leap year in 1996 was ignored. Natural mortality and tag reporting were held constant over the course of the study.

5.4 Results

Figure 5.1 displays relative catchability curves for males and females during the fishing season for increasing levels of the smoothing parameter \( \alpha \). Models with \( \alpha \) of 0.5 and 1 appear to be over-smoothed, with little change in catchability, apart from a decline at the beginning of the season. The model with \( \alpha \) of 0.01 showed signs of under-smoothing. Catchability for males is extremely high at the beginning of the fishing season and falls away rapidly in the first month of fishing, while there are four subsequent peaks in catchability, more than would be explained by mating and moulting.

The catchability curves for males and females are generally similar, with the main differences being at the opening and the closure of the fishery for females. Catchability for males was greater than for females at the beginning of the fishing season in November. From February to April, male and female catchability follow similar trends. After April, female catchability is slightly lower than male catchability. This difference increases until the sampling of females ceases in May.

Smooth estimates of catchability in the same species were obtained by Ziegler et al. (2002a) by comparing trapping and dive surveys in a marine reserve in southern Tasmania (Figure 5.2, dotted line). The daily catchability estimates obtained with the \( \alpha = 0.25 \) and gender specific catchability, show that for both genders catchability was highest at the beginning of the fishing season in November, while Ziegler et al. (2002a) found gender non-specific catchability was highest in late December. The spline smoothing model shows smaller peaks in catchability in late February, in early March for both genders and a peak in May for males only.
5.4. RESULTS

Figure 5.1: Relative catchability for males (solid lines) and females (dashed lines) obtained from four different levels of the smoothing parameter $\alpha$. 
5.5 Discussion

Without an objective method to determine the magnitude of the smoothing parameter \( \alpha \), it is problematic. The model with \( \alpha \) of 0.25 appears to provide the most reasonable representation of catchability, with a more modest peak in \( q \) at the beginning of the season for males, and three subsequent peaks that could be explained by mating and two moultng events. However, it is unknown if this is correct.

There was general overall similarity between the catchability estimates of this study and those obtained by Ziegler et al. (2002a). Differences of one month between the two estimates could be accounted for by location, population structure or interannual variability. Ziegler sampled a population that had been protected from fishing for three decades and thus consisted of a large biomass of very large (>135mm female and >150mm male) lobsters. His sampling was undertaken several years after surveys conducted off King Island (Chapter 4) and in south eastern Tasmania where water temperatures are much lower.

Figure 5.2: Smoothed estimates of catchability for males (solid line) and females (dashed line) with smoothing parameter \( \alpha = 0.25 \). Estimates of gender non-specific catchability from Ziegler et al. (2002a) (dotted line) are shown for comparison.
The Tasmanian lobster fishery is unusual among Australian lobster fisheries because of large differences in growth rates, maximum size and population density between the north and south of the state. Sea surface temperatures in northern Tasmanian waters are between 2 and 4 degrees warmer than those in the south west of the state. Population densities are much greater in the south, compared with the north. In the north of the state, male lobsters just above the legal size limit, moult twice yearly in September/October and in February. They grow over four times faster than those in the south (Ziegler et al., 2003), which moult once a year in September/October. The onset of sexual maturity varies from between 112 mm carapace length in the northwest to 59 mm in the south west (Gardner et al., 2006). Mating in the northwest occurs in May after the female moult in April. In southern Tasmania, mating occurs in June, with females mouling in May. Water temperature, mating and mouling are all known to affect the catchability of lobsters in general (Tremblay et al., 2006), and Tasmanian southern rock lobsters in particular (Ziegler et al., 2002a,b).

Comparing catch rates from trapping with observations from underwater diving surveys in a marine reserve in south eastern Tasmania, Ziegler et al. (2002a) identified changes to be associated with gender and water temperature. Ziegler found that catchability generally declined from a peak in December to a low in September the following year. In addition, Ziegler et al. (2002b) found that catchability varies with size, not gender. The low period of catchability in April is most likely associated with the female moult and mating, and the low in September is likely associated with the male moult in September. Each of these events was associated with a compensatory increase in catchability after the event, presumably because of increased feeding immediately afterwards.

The results from the spline model in a fished area in north west Tasmania, identified that catchability declined from a peak for both males and females in November to a low at the end of April for females, after which the female season is closed and estimates are no longer available. The low in catchability in June is associated with males. Catchability curves for both genders generally follow the same trends. There is a low point in catchability for both genders at the end of January, presumably associated with the second male moult. In April, the catchability curves for males and females separate, with female catchability declining until estimates stop with the closure of the female fishing season. This is probably due to the female moult that is followed by mating. This could also explain the peak of male catchability in May.

While this analysis cannot directly associate the changes in catchability with any of these biological factors, because the exact times of mating and mouling in that area are not known, the first two peaks in catchability do generally correspond with the times of lobster mating and mouling in Tasmania (Figure 5.2). Estimates obtained by Ziegler et al. (2002a), are highest in December, fall away to a low in April then peak again in late May. While there are differences in the estimates obtained by Ziegler et al. (2002a) and those from the penalised smoothing model, there are also several similarities. Both show highs in catchability in early summer that moderate into winter, with one or more short peaks that last about a month.

Differences with Ziegler et al. (2002a) could be attributed to differences in water
temperature and moulting and mating times between northwestern and southeastern Tasmania. The additional peak seen in male catchability in late February from the spline model, could be explained by male lobsters in the north moulting a second time each season, while those in the south moulting only once. Ziegler et al. (2002a) estimated catchability by comparing dive and trap surveys in a marine reserve in southern Tasmania that had been protected from fishing for more than 30 years, while the penalised smoothing model was fitted to data from a fished population in the north west of the state. With the marine reserve containing many large individuals, some of the differences in catchability compared with the penalised smoothing model, may be explained by behavioural differences in fished and unfished populations, because the catchability of the southern rock lobster is known to vary by size (Ziegler et al., 2002b).

The catchability estimates appear reasonable compared to known biological variation, with \( q \) known to be affected by mating and moulting, which could explain the peaks. Catchability is highest when the fishing season opens in November and falls away over the fishing season, before increasing again towards the close of fishing in September. One benefit of this method is that it does not require expensive diving surveys. In addition, estimates may be obtained from areas that are unsuitable for diving and over large spatial scales where diving surveys are impractical. While tagging studies may not necessarily be cheaper than dive surveys to estimate catchability, they can be used in areas where diving is not possible, such as in deep water. With the model only requiring that the number of tags in the population is maintained, additional cost benefits may be realised by fishers tagging some lobsters during the course of their normal operations, such as tagging females after the closure of the female fishery in May each year.

If the primary aim of a tagging study is to estimate fishing and natural mortality, then catchability estimates are essentially a bonus. Brownie style tagging studies only permit crude seasonal estimates of catchability (Frusher and Hoenig, 2003). The ability to estimate fine time-scale catchability within a fishing season, without further surveys, is a distinct advantage over Brownie models. Frusher and Hoenig (2003) used the same dataset to estimate constant catchability for three periods, finding that catchability was highest from November to February, lowest from February to May and increased from May to September. These estimates are broadly consistent with those obtained in the penalised smoothing model.

Stock assessment models often assume catchability to be constant over the course of a fishing season. In recent years, there has been an increase in the strength and duration of the East Australia Current bringing warm water to the north and east coasts of Tasmania during spring and summer (Hill et al., 2008). There has also been an increase in the frequency and strength of the Bonney Upwelling in summer that brings cold water to the east coast of South Australia (Kampf et al., 2004). Changes in catchability resulting from changes in water temperature, may be misinterpreted as changes in abundance, with potential impact on the sustainability and profitability of the fisheries. This method of estimating catchability could be used as a check of the assumptions of catchability used in the stock assessment models, particularly if there are changes to historic fishing patterns that may mask changes in biomass.


Chapter 6

Improving Reporting Rate: PIT Tags, Trusted Fishers and Research Fishing

6.1 Introduction

The survival model has been shown with simulation to be a viable alternative to using Brownie style models to estimate fishing and natural mortality in tagging studies (Chapter 3). Estimates of fishing mortality obtained from an historical dataset were broadly consistent with those obtained using Brownie models (Chapter 4; Frusher and Hoenig, 2001a, 2003). The model has the additional benefit of being able to estimate fine time-scale catchability (Chapter 5).

Tag reporting rate is crucial to the precision of fishing and natural mortality estimates, with precision increasing as reporting rate increases or if the reporting rate is known (Chapter 3; Frusher and Hoenig, 2001c). When tag reporting rate is underestimated, mortality must be overestimated to account for the number of tag recaptures. Conversely, when tag reporting rate is overestimated, mortality is underestimated. In the past, increasing tag reporting rate has relied on persuading or encouraging fishers to return more tags, such as the use of high reward tags (Pollock et al., 2001). Other studies have estimated the tag reporting rate using tag seeding, port surveys or by placing observers onboard vessels (Green et al., 1983; Pollock et al., 1991; Hearn et al., 1999).

The use of observers in fisheries tagging experiments is often prohibited by the cost of observer programs. Three methods of increasing tag reporting rate that are analogous to observers are hybrid passive integrated transponder (PIT) tags, trusted fishers and research fishing.

In Australian lobster fisheries, the most commonly used conventional tag is the T-bar tag (Figure 6.1). The tag is usually attached ventrally in the first abdominal segment. These tags are relatively robust and cheap but rely on the fisher to report tagged fish. An alternative approach to increasing tag reporting rate that has received limited attention, is to supplement or replace traditional tags in tagging studies with passive integrated transponder (PIT) tags and the associated scanners (Pengilly and Watson, 1994; Gibbons and Andrews, 2004). A PIT tag is an elec-
6.1. INTRODUCTION

Electronic microchip encased in bio-compatible glass or plastic 10 millimetres long and 2 millimetres in diameter (Figure 6.1). PIT tags are injected into the body cavity or muscle tissue of the fish. Tags are read with the use of a scanner that generates a magnetic field, activating the tag that then transmits its number (Gibbons and Andrews, 2004). PIT tags have been used on a range of fisheries in the past decade for estimation of survival in migrant salmonid smolts (Skalski et al., 1998), investigating the effects of tagging on growth, moulting and survival of freshwater crayfish (Bubb et al., 2002), and also the population dynamics in a rare species of percid (Labonne and Gaudin, 2005). A number of detection devices are in use, including scanners in conveyor belts (Pengilly and Watson, 1994) and hand-held devices (Bubb et al., 2002).

![Figure 6.1: A passive integrated transponder (PIT) tag with a food-safe coating (top), standard T-bar tag (middle) and T-bar tag incorporating a PIT tag without a food-safe coating.](image)

Injecting PIT tags into the tail muscle of Tasmanian lobsters (*Jasus edwardsii*) that have a high likelihood of being destined for human consumption, was determined to be a choking hazard. Trials of injecting PIT tags into the body cavity, where the likelihood of human consumption is much lower, determined tag induced mortality to be high (Frusher et al., 2009). A solution to the high rates of tag mortality associated with internal PIT tags, was to incorporate the PIT into a conventional T-bar. These hybrid PIT tags (Hallprint Pty Ltd, Victor Harbor, South Australia, 5211) have the PIT incorporated into a conventional T-bar tag that can be reported by vessels that have a tag scanner onboard, as well as by those that do not. The hybrid PIT tag has similar dimensions to conventional T-bar tags, so it is reasonable to assume that it has similar levels of tag shedding and mortality (Figure 6.1). Hybrid tags have the benefit of automated data collection for vessels equipped with scanners.
They also allow tags to be identified, even when the external number is no longer readable, due to wear and tear. In addition, if it is assumed that the behaviour of fishers with tag scanners on their vessels is no different from the behaviour of those without scanners on their vessels, the tag reporting rate for the remainder of the fleet can be estimated in the same manner as “high reward” tags (Pollock et al., 2001). As the new tag incorporates the PIT tag, and has basically the same dimensions as the conventional tag, it is assumed that any tag loss or tag induced mortality would be equivalent to estimates for the conventional T-bar (Frusher et al., 2008). A full description of the technical specifications of PIT tags, hybrid PIT tags and the associated tag scanners, is given in Frusher et al. (2009).

If tag scanners are appropriately placed in the fishing operation so that each animal has to pass within the detection range, then it is possible to have a 100% PIT tag reporting rate. As lobsters are individually handled at various stages during the capture process, scanners can be designed to be associated with these ‘natural’ bottlenecks, such as the holding tank on a fishing vessel (Figure 6.2). This enables fishers to undertake their normal activity on board their vessels with minimal interference. The tag reporting rate of vessels equipped with PIT scanners can either be fixed at 100% or estimated within the model.

Figure 6.2: PIT tag scanner mounted over the holding tank of a fishing vessel in the Tasmanian lobster fishery.

In any fishery, there are some individuals who are more reliable than others at returning tags and providing information to researchers. Trusted fishers are a group of fishers that are deemed by fisheries’ scientists to have a high level of tag reporting.
Three approaches for incorporating the tag reporting rate of trusted fishers into the model were tested. Tags returned by trusted fishers can be assumed to have a reporting rate of 100%. The reporting rate for the trusted component can be estimated freely in the model, or the reporting rate of the trusted component can be constrained to be higher than that of the remainder of the fleet.

In the Tasmanian lobster fishery, tagging surveys have been undertaken from chartered commercial fishing vessels using commercial fishing gear, to capture lobsters for tagging (Frusher and Hoenig, 2001a; Frusher et al., 2008). In the course of obtaining lobsters for tagging, tagged lobsters from previous survey voyages are often resighted. The tag numbers of these resighted lobsters are recorded then they are released along with the newly tagged individuals. Assuming no individual heterogeneity in the probability of recapture, and making appropriate allowances in the model for tagging mortality and age related tag loss these re-releases may be treated as newly tagged individuals. Tagging mortality and tag loss associated with re-releases can be either identical to newly tagged lobsters, or a more complex model could be adopted. Section 2.4.4 describes how tagging mortality and tag loss can be incorporated into the model. In this study, both tagging mortality and tag loss were assumed to be zero. Since researchers check all lobsters that are captured for tags, it was assumed that they had a tag reporting rate of 100%.

This chapter investigates the use of hybrid PIT tags, trusted fishers and research fishing to improve the precision and accuracy of mortality estimates in the Tasmanian lobster fishery. The performance of hybrid PIT tags is evaluated using simulation. Trusted fishers and research fishing are evaluated using historical data from the tagging study analysed in Chapter 4.

6.2 Methods and Models

Since the model focuses on individuals, not only can features of the individual be incorporated into the model, but the model can be easily extended to account for differences in how an individual has been recaptured. This allows tag returns from different components of the fishery to be treated separately, each with their own fishing effort and tag reporting rate.

6.2.1 Model Development—Multiple Fleets

This section extends the model derived in Chapter 2 to allow for multiple fishing components. These different fishing components might correspond to different fleets, different vessels, or even to the use of different forms of fishing gear, and with each component are associated a separate fishing mortality and reporting rate. The derivation of the model follows that of Chapter 2, except that the survival of an individual depends on fishing mortality from all components, but the probability of recapture depends only on the fishing mortality of the component that recaptured the tag.

Suppose the fishery consists of $M$ components, and let $f_{ic}(t)$ be the fishing mortality
to which individual \( i \) is exposed as a result of fishing by component \( c \) at time \( t \). Similarly, let \( \lambda_{ic}(t) \) denote the reporting rate for individual \( i \) were it to be recaptured by fishing component \( c \) at time \( t \). The total fishing mortality to which individual \( i \) is exposed is

\[
F_i(t) = \sum_{c=1}^{M} f_{ic}(t)
\]

and for convenience, define

\[
R_i(t) = \sum_{c=1}^{M} \lambda_{ic}(t)f_{ic}(t).
\]

The probability that tag \( i \) is recaptured by fishing component \( c \) in the interval \((t, t + \delta t)\), given it was released at time \( s_i < t \) is

\[
\Pr(\text{Recapture observed by } c \text{ in } (t, t + \delta t)) = \Pr(\text{Observed by } c \text{ in } (t, t + \delta t) \mid \text{Recaptured by } c \text{ in } (t, t + \delta t)) \times \Pr(\text{Recaptured by } c \text{ in } (t, t + \delta t) \mid \text{Was alive at } t) \times \Pr(\text{Was alive at } t),
\]

or equivalently

\[
\Pr(\text{Recapture observed by } c \text{ in } (t, t + \delta t)) = \left[ \lambda_{ic}(t)f_{ic}(t) \exp \left( - \int_{s_i}^{t} (F_i(t) + M_i(t))dt \right) \right] \delta t.
\]

(6.1)

Note that the probability of recapture depends only on the component specific mortality, but the survival to time \( t \) depends on all components of mortality.

A censored individual is not observed by any fishing component

\[
\Pr(\text{Censored at } T) = 1 - \Pr(\text{Observe a recapture in } [s, T])
\]

\[
= 1 - \int_{s}^{T} R_i(t) \exp \left( - \int_{s}^{t} (F_i(\tau) + M_i(\tau))d\tau \right) dt.
\]

(6.2)

Again it is assumed that recaptures are independent, so the total likelihood can again be expressed as a product of contributions from individual tags. From Equations 6.1 and 6.2, each tagged individual makes a contribution to the likelihood of the form

\[
L_i = \begin{cases} 
\lambda_{ic}(t_i)f_{ic}(t_i) \exp \left( - \int_{s_i}^{t_i} (F_i(t) + M_i(t))dt \right) & \text{if recaptured by component } c \text{ at } t_i \\
1 - \int_{s_i}^{T} R_i(t) \exp \left( - \int_{s_i}^{t} (F_i(\tau) + M_i(\tau))d\tau \right) dt & \text{if censored at } T
\end{cases}
\]

As in Chapter 2, if it is assumed that individuals are indexed, such that the first \( n \) individuals are recaptured and the remainder are censored, the total likelihood can
be written in the form
\[
L = \prod_{i=1}^{n} \lambda_i(t_i) f_i(t_i) \exp \left( - \int_{s_i}^{t_i} (F_i(t) + M_i(t)) dt \right) 
\times \prod_{i=n+1}^{N} \left( 1 - \int_{s_i}^{T} R_i(t) \exp \left( - \int_{s_i}^{t} (F_i(\tau) + M_i(\tau)) d\tau \right) dt \right) \tag{6.3}
\]
where
\[
f_i(t) = f_{ic(i)}(t) \\
\lambda_i(t) = \lambda_{ic(i)}(t)
\]
and \(c(i)\) is the index of the component that actually recaptured tag \(i\).

Given this expression for the likelihood, the model is complete with specification of models for the component specific fishing mortalities \(f_{ic}(t)\), reporting rates \(\lambda_{ic}(t)\) and the individual natural mortality \(M_i(t)\).

Estimators can again be obtained by the method of maximum likelihood as described in Section 2.5.

There are three ways that multiple components can be dealt with from a modelling perspective. Firstly, each component can be estimated separately; secondly, the reporting rate of one or more components can be fixed at one, and finally, a condition can be added that forces one or more components to be greater than the other components.

### 6.2.2 Piecewise Approximation

As in Chapter 2, the evaluation of the likelihood can be simplified by imposing the additional restraints described in Section 2.5.5.

For notational simplicity, consider only a single individual, and suppress the subscripts that distinguish individuals. As in Section 2.5.5, assume that

1. All releases occur at the beginning of the day and all recaptures occur at the end.
2. The reporting rates \(\lambda_c(t)\), fishing mortalities \(f_c(t)\) associated with each fishing component and the natural mortality \(M(t)\) experienced by any individual, are constant over any day.

Again, measure time in days, so that \(\lambda_c(t), f_c(t), M(t)\) and hence \(R(t)\) become piecewise constant with discontinuities at \(t \in \mathbb{Z}\). For notational simplicity, for any piecewise constant function \(Q(t)\), write \(Q_k\) for the value of \(Q\) on day \(k\), so that
\[
Q_k = Q(t) \quad t \in [k, k+1) \\
Q_{ck} = Q_k(t) \quad t \in [k, k+1).
\]
Comparing Equation 2.7 and Equation 6.3, it is readily shown that with the above assumptions, the contribution 6.3 that a tagged individual makes to the total likelihood, can be written

\[
L_i = \begin{cases} 
\lambda_{ct} f_{ct} \exp \left( - \sum_{k=s_i}^{t_i} (F_k + M_k) \right) & \text{if recaptured at } t_i \\
1 + \sum_{j=s_i}^{T-1} \frac{R_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \right) \left( 1 - \exp(F_j + M_j) \right) & \text{if censored at } T
\end{cases}
\]

in analogy with Equation 6.4, and the expression for the total likelihood follows immediately.

### 6.3 Testing the Multiple Fishing Component Model

To test the performance of the model in fisheries where multiple fleets are present, three scenarios were investigated. The performance of hybrid PIT tag technology was demonstrated using simulation. The King Island tagging data (Chapter 4) was also reanalysed to incorporate a single trusted fishing component and then two trusted components with a research fishing component.

#### 6.3.1 Hybrid PIT Tags

Simulation was used to determine the proportion of the fleet that should be equipped with tag scanners in a hybrid PIT tagging experiment. The characteristics of the Tasmanian lobster fishery (Section 1.1.4) were again used. Three year tagging studies were simulated with season lengths of six months for females and ten months for males, and with the fishing season for both genders opening on the same day. At the beginning of the first two seasons, 500 males and 500 females were released with hybrid PIT tags. Constant fishing and natural mortalities, the same for both genders of \( F = 0.9 \) and \( M = 0.1 \), were used. Three scenarios were tested with 30, 20 and 10% of the fishing fleet equipped with tag scanners. A tag reporting rate of 100% was assumed for vessels with tag scanners, and reporting rates for the remainder of the fishing fleet of 0, 20, 40, 60 and 80% were tested. A total of 1000 simulations were undertaken for each scenario considered.

- Scenario PIT 1: 10% of the fishing fleet was equipped with PIT scanners.
- Scenario PIT 2: 20% of the fishing fleet was equipped with PIT scanners.
- Scenario PIT 3: 30% of the fishing fleet was equipped with PIT scanners.
6.4. RESULTS

6.3.2 Trusted Fishers and Research Fishing

To assess the performance of trusted fishers, the King Island data from Chapter 4 was again used. This study had two reliable fishers whom fisheries’ scientists considered would report 100% of tags. The tag reporting rates of these trusted fishers were modelled in two ways. Firstly, the tag returns of both fishers were combined to create two components: trusted fishers and the remainder of the fleet. The optimal constant, seasonal and subseasonal models from Chapter 4 were fitted. These are the two component models. Secondly, the two trusted fishers were considered individually and research recaptures were included. This created four components, two trusted fishers, research fishing and the remainder of the fleet. The optimal constant, seasonal and subseasonal models from Chapter 4 were then fitted. For all models, the tag reporting rates of the trusted fishers and research components were freely estimated and not constrained to be greater than the $\lambda$ for the remainder of the fleet.

6.4 Results

6.4.1 Hybrid PIT Tags

There was little discernible difference among the hybrid PIT tag scenarios, either as the proportion of the fleet equipped with tag scanners, or as the tag reporting rate of the remainder of the fleet increased (Figure 6.3). Estimates of $F$, $M$ and $Z$ were all unbiased and the level of precision was high. This suggests that there is no benefit having more than 10% of the fleet equipped with tag scanners.
Figure 6.3: Estimated fishing (F), natural (M) and total (Z) mortality from hybrid PIT tagging scenarios where 10% (white boxes), 20% (light grey boxes) and 30% (dark grey boxes) of the fleet are equipped with tag scanners. Tag reporting rates (λ) of the proportion of the fleet not equipped with scanners of 0, 20, 40, 60 and 80%, were simulated.
6.4. RESULTS

6.4.2 Trusted Fishers and Research Fishing

Constant Models

For all two and four component models, the tag reporting rates of the trusted fishers and research components were estimated to be 100%, so only the $\lambda$ for the remainder of the fleet are presented. The constant models assumed that catchability, natural mortality and tag reporting rate were constant over the length of the study, with yearly differences in $F$ determined by the daily fishing effort in that season. For both males and females, the constant models (Figures 6.4 and 6.5) show little difference in estimates of $F$ between the three models, with $F$ being slightly higher in the two and four component models. Natural mortality estimates for both the two and four component models were approximately zero, and the confidence intervals were unbounded. The tag reporting rate of the remainder of the fishing fleet was estimated to be approximately 9%, compared with 21% for the one component model.

Figure 6.4: Estimates of yearly fishing mortality ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) of males for models with constant fishing mortality over the entire study. Model C3 (white bars) is the optimal one component constant catchability model from Chapter 4; model 2C3 (light grey bars) is the two component equivalent of model C3 and model 4C3 (dark grey bars) is the optimal four component equivalent of model C3. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates where estimates were approximately zero and the confidence intervals were unbounded.
Figure 6.5: Estimates of yearly fishing mortality (\(F\)), overall natural mortality (\(M\)) and tag reporting rate (\(\lambda\)) of females for models with constant fishing mortality over the entire study. Model C3 (white bars) is the optimal one component constant catchability model from Chapter 4; model 2C3 (light grey bars) is the optimal two component equivalent of model C3 and model 4C3 (dark grey bars) is the optimal four component equivalent model of C3. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates for models 2C3 and 4C3 where estimates were approximately zero and the confidence intervals were unbounded.
6.4. RESULTS

Seasonal Models

The seasonal models assumed that natural mortality and tag reporting rate were constant over the length of the study. Catchability did not vary with gender, and was estimated separately for each fishing season. While there were small differences between estimates of fishing mortality in the first four full years of the study, estimates of $F$ in 1996/97 from the two and four component models, diverged markedly from those of the one component model (Figures 6.6 and 6.7). Fishing mortality estimates for both males and females from the two and four component models in the final year of the study, were more than three times greater than those from the single component model. For males, all of the models estimated natural mortality to be approximately zero, with confidence intervals that were unbounded. Estimates of natural mortality for females were also zero for the two and four component models. The tag reporting rate of the remainder of the fleet was approximately 9% for the two and four component models, compared with 21% for the one component model.

![Parameter estimates with 95% CIs](image)

Figure 6.6: Estimates of yearly fishing mortality ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models S2, 2S2 and 4S2 for males. Model S2 (white bars) is the optimal one component constant catchability model from Chapter 4; model 2S2 (light grey bars) is the optimal two component equivalent of model S2 and model 4S2 (dark grey bars) is the optimal four component equivalent of model S2. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates where estimates were approximately zero with confidence intervals that were unbounded.
Figure 6.7: Estimates of yearly fishing mortality ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models S2, 2S2 and 4S2 for females. Model S2 (white bars) is the optimal one component constant catchability model from Chapter 4; model 2S2 (light grey bars) is the optimal two component equivalent of model S2 and model 4S2 (dark grey bars) is the optimal four component equivalent of model S2. Models are presented with 95% confidence intervals (bars), except for natural mortality estimates that were approximately zero with confidence intervals that were unbounded.
Subseasonal Models

The subseasonal models assumed that natural mortality and tag reporting rate were constant over the length of the study, and that catchability was separated into 10 estimated monthly components that did not vary between seasons or gender. Differences in $F$ between seasons were accounted for by differences in fishing effort. For males, estimates of $F$ from the two and four component models were around 1.25 and 1.5 times greater respectively than those of the single component model (Figure 6.8). For females, estimates of $F$ were similar for both the two and four component models and generally around 30% greater than those from the single component model (Figure 6.9). Estimates of $M$ from the two and four component models were approximately zero, while the tag reporting rate from the remainder of the fleet was approximately 9%, compared with 21% from the single component model.

Figure 6.8: Estimates of yearly fishing mortality ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models U7, 2U7 and 4U7 for males. Model U7 (white bars) is the optimal one component constant catchability model from Chapter 4; model 2U7 (light grey bars) is the optimal two component equivalent of model U7 and model 4U7 (dark grey bars) is the optimal four component equivalent of model U7. Models are presented with 95% confidence intervals (bars), except for natural mortality where estimates were approximately zero and confidence intervals unbounded.
Figure 6.9: Estimates of yearly fishing mortality ($F$), overall natural mortality ($M$) and tag reporting rate ($\lambda$) for models U7, 2U7 and 4U7 for females. Model U7 (white bars) is the optimal one component constant catchability model from Chapter 4; model 2U7 (light grey bars) is the optimal two component equivalent of model U7 and model 4U7 (dark grey bars) is the optimal four component equivalent of model U7. Models are presented with 95% confidence intervals (bars), except for natural mortality where estimates were approximately zero and confidence intervals unbounded.

### 6.5 Discussion

The lack of any discernible difference between the three hybrid PIT tag scenarios, suggests that only a small proportion of the fishing fleet needs to be equipped with tag scanners. In addition, because the precision and accuracy of mortality estimates are not dependent on the tag reporting rate of the portion of the fleet without tag scanners, there is no benefit from it returning tags. Estimates of mortality from hybrid PIT tags were independent of the tag reporting rate of the remainder of the fleet, suggesting that the conventional portion of the hybrid tag does not contribute to improving the precision and accuracy of fishing and natural mortality estimates. Internal PIT tags were not used in the Tasmanian study because of high rates of tag induced mortality in aquaria trials when inserted into the body cavity (Frusher et al., 2009). If the mortality rate could be reduced, for example by implanting the PIT tag in the muscle tissue of the tail, it is possible that tag loss and tag induced
mortality could be minimised, as there would be no external components.

Estimates of fishing mortality obtained from the constant models were similar between the single, two and four component variants, suggesting that the model can distinguish between tag reporting rate and mortality. The estimate of tag reporting rate of around 9% for the remainder of the fleet from the two and four component models, appears reasonable, since it was less than the tag reporting rate estimated by Frusher and Hoenig (2003) of 23% obtained using Brownie models, and by the survival models fitted in Chapter 4 of around 21%. Estimates of natural mortality from the two and four component models were not improved, with \( M \) being approximately zero, with unbounded confidence intervals. It was unsurprising that this occurred because the extra information from the additional model components was already present in the models from Chapter 4, but averaged over the entire fleet.

For the seasonal models, estimates of fishing mortality appear to be reasonable, except for the 1996-97 fishing season where the fishing mortality for the two and four component models was clearly far too high. One possible explanation for this was that there were only a small number of tags remaining in the population because of the high exploitation rate, as the tagging program had finished in May 1995. It is also possible that the assumption that tag reporting rate was constant over the time period of the study, was not valid. It has been reported that the enthusiasm for reporting tags can fall over time. This has been observed in studies into exploited bird populations (Nichols et al., 1991) and in lobsters (Frusher and Hoenig, 2001a). Estimates of natural mortality from the two and four component models were approximately zero, with confidence intervals that were unbounded. This again highlights the difficulty of the model to partition total mortality into its separate fishing and natural components, as seen in Chapter 4.

Estimates of fishing mortality from the subseasonal models showed poor correlation between the single, two and four component variants for males, although confidence intervals did overlap in most years. The correlation of estimates of \( F \) between the three model variants for females, was much better. Estimates from the two and four component model variants were similar and around 30% greater than the single component model. As with the seasonal models, estimates of \( M \) were zero for the two and four component variants, and \( \lambda \) for the remainder of the fleet was around 9%.

All models estimated \( F \) to be high, with \( M \) either zero or close to it. Estimating natural mortality in a mature fishery is difficult when there is not any data available on the unfished population (Hilborn and Walters, 1992). It is probable that the model failed to distinguish between the separate components of the total mortality. From a fisheries management perspective, this is not a handicap as it is the total mortality \( Z \) that determines the viability of exploited populations.

While the use of internal PIT tags was not directly assessed by this study, some general conclusions can be inferred from the use of trusted fishers that are essentially the same in modelling terms. PIT tags, either hybrid or internal, offer a method of increasing the tag reporting rate in the fishery. Increasing the reporting rate has been shown to be more effective than increasing the number of tags that are released (Chapter 3; Frusher and Hoenig, 2001c). They offer the potential to provide a more
cost effective way of increasing the reporting rate of a component of the fishery, and of allowing reliable estimates of fishing and natural mortality. They can often be deployed in situations where it is not possible to use observers, such as on small vessels or in remote areas.

The problem of estimating and increasing tag reporting rate is present in all tagging studies where tags are returned by commercial or recreational fishers (Miranda et al., 2002). Trusted fishers, research fishing and PIT tags are all methods of increasing tag reporting rate that do not rely on observer programs. While the use of hybrid PIT tags in the Tasmania fishery was not successful, due to failure of the scanners (Frusher et al., 2008), the development of robust scanners should be possible with the application of sufficient resources.
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Chapter 7 Cost benefit analysis of Hybrid PIT and conventional tagging scenarios

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CHAPTER 8

Final Conclusions

8.1 Model Performance

The survival model has been shown to produce unbiased estimates of fishing and natural mortality when at least one component of the fishery had a tag reporting rate of 100%. When fishing is continuous, the survival model is able to separate fishing and natural mortality from total mortality, when the tag reporting rate is 100%. At lower tag reporting rates, model performance improved when there were separate season lengths for each gender. The magnitude of the improvement increased with the increasing difference of season lengths for males and females.

8.2 Comparison with Brownie

Continuous time models have two primary advantages over a seasonal, Brownie-style model. Most obviously, they allow a finer time resolution than a Brownie style model. This has a hidden practical benefit, in that it becomes possible to leverage more subtle differentials in fishing effort than with the simple open/closed season paradigm required by the Brownie model. Secondly, these models do not aggregate releases and recaptures over seasons, but model each tag individually, providing a more natural vehicle for modelling variability amongst tagged individuals. This allows for models of mortality that depend not only on the exact times of release or recapture, but also on locations of release and recapture, size of individuals, etc. A disadvantage of Brownie style models is that they require tagging to be undertaken multiple times each fishing season, over at least two seasons, either to obtain within season estimates of total mortality, or to separate total mortality into its fishing and natural components.

When designing the tagging surveys for use with the survival model, tags only need to be released to maintain the number of tags in the population. This has the advantage of being able to tag when conditions are the most favourable. In the case of rock lobster, tagging could be conducted when catchability is highest, thereby allowing a greater number of individuals to be tagged in a fixed amount of time.
In addition, females could be tagged when the female season is closed and ad hoc tagging by fishers and observers could be incorporated into the model.

In fisheries for short lived species such as squid, a tagging study could be undertaken using a survival model where there are not multiple years of data available to apply a Brownie model. Unlike Brownie models, it is possible to obtain an estimate of total mortality during the fishing season from a single season tagging study. However, it may not be possible to separate the total mortality into its fishing and natural components.

### 8.3 Tag Reporting Rate

Tag reporting rate is crucial in obtaining accurate estimates of mortality. Unfortunately, increasing the tag reporting rate of fishers, by increasing their participation and awareness, can be difficult. Chapter 6 used trusted fishers to show the benefits of having one component of the fishing fleet with a tag reporting rate of 100%. Similarly, hybrid PIT tags have the potential to provide one component of the fishing fleet with perfect reporting. The benefits of hybrid PIT tags, compared with conventional T-bar tags, were shown in Chapter 7. For Australian lobster fisheries, it is more cost effective to use hybrid PIT tags, unless tag reporting rate is high. Current PIT tag scanners are not robust enough for deployment at sea. However, as technology improves, PIT tags offer a cost effective method of estimating fisheries parameters, a situation that is relatively uncommon in fisheries.

It was shown in Chapter 3 that, while the model can fail to accurately estimate fishing and natural mortality, estimates of the total mortality are generally more accurate. From a fisheries management perspective, total mortality is often sufficient for implementing appropriate harvest strategies, as natural mortality is often considered constant across fishing seasons. In most fisheries assessment models, $M$ is usually unknown and fixed at an arbitrary value considered appropriate for the species. For lobster fisheries $M = 0.1$ is often used. As estimates of $F$ and $M$ from the survival model can be negatively correlated, with $F$ overestimated and $M$ underestimated and visa versa, total mortality $Z$ is more precisely estimated and thus potentially more valid.

### 8.4 Variable Catchability

It is usual in fisheries assessment models for catchability to be considered a nuisance or scaling parameter. Changes in catchability between seasons may appear as changes in underlying biomass. The smoothing methods presented in Chapter 5 offer the ability to estimate catchability from tag recapture and effort data. Climate change has the potential to impact on catchability in rock lobster stocks, due to the positive relationship between water temperature and catchability (Ziegler et al., 2003). Changes in catchability can affect catch rates that may be misinterpreted as changes in biomass, leading to inappropriate management decisions. More accurate methods of determining catchability or estimating relative changes in $q$ are required.
The survival model is one method of providing this information.

8.5 Further Work

Recent research has suggested that initial tag loss and tag induced mortality for lobsters may be higher than originally thought, and may vary within a season, due to the timing of tagging and the proximity of the next moult (Frusher et al., 2008). The sensitivity of the model to low tag reporting rates, suggests that it may not perform well under scenarios of high initial tagging mortality. However, the flexibility of the model allows the straightforward incorporation of initial tagging mortality, if it is known. Sensitivity testing of various combinations of tag loss and tag induced mortality, are required. Importantly, it will be necessary to understand the sensitivity of parameter estimates from tagging models that have multiple tagging events within the fishing season.

The model was conditioned on effort because in Australian lobster fisheries, effort is considered reliable. An alternative would be to condition fishing mortality on catch. In many fisheries, landed catch is more reliably measured than effort is. Estimates from tagging models could be incorporated into stock assessment models in a similar way to Tuck et al. (2003).

8.6 Final Conclusions

With the majority of the world’s fisheries either fully exploited or over exploited, tagging experiments offer the ability to obtain direct estimates of mortality, without the need for a long time series of observation. The survival model has been shown to reliably estimate fishing and natural mortality and catchability from tag return data. Total mortality can be separated into its fishing and natural components from one tagging event, with subsequent tag releases only required to maintain the number of tags in the population. While estimates of $F$ and $M$ are biased at low tag reporting rates ($\lambda < 0.5$), estimates of total mortality are unbiased when the reporting rate is above 0.1.

The survival model’s flexibility to parameterise catchability into periods of arbitrary length, allows for a more realistic representation of the dynamics of the fished population and consequently, more accurate estimates of mortality. Fine time-scale catchability can be estimated without the expense of comparing diving and trapping surveys.

Model performance is greatly improved when one component of the fishery has a tag reporting rate of 100%. PIT tagging technology has the potential to provide a cost effective method of increasing tag reporting rate in one component of a fishery. When using hybrid PIT tags, there was no benefit in collecting tag returns from the proportion of the fleet not equipped with scanners, suggesting that internal PIT tags would perform equally well. For a required level of precision, a smaller number of PIT tags need to be released, compared with conventional tags. When the full cost of a tagging study in Australian lobster fisheries was considered, hybrid PIT
tags were more cost-effective than conventional tags, unless the tag reporting rate of the remainder of the fleet was high. Implanting internal PIT tags in tissue could potentially minimise tag loss and tag induced mortality. Although the up-front cost of scanners is expensive, once the problems of working in a marine environment are solved and scanners are reliable, the future of tagging with PIT tags looks very promising.
Appendix A

Brownie Models

While Brownie models (Brownie et al., 1985) were originally developed to estimate survival in exploited bird populations, they are equally applicable to fisheries. Tags are returned to researchers by hunters or fishers during the course of harvesting. Estimates of survival are obtained by comparing the ratio of tag recaptures from cohorts tagged in successive years.

A.1 Development of the Brownie Model

Consider a capture-recapture study with an exploited animal population where tag recoveries from dead animals are observed. One cohort, or group of $N$ subjects, is tagged every year, for three years and tag returns are accepted for an additional year. Tags are recaptured in the $i^{th}$ season and returned to researchers at the rate of

$$f_i = \frac{R_i}{n_iS_i}$$  \hspace{1cm} (A.1)

where $R_i$ is the number of tags recovered, $n_i$ the number of tags remaining in the population, $S_i$ the survival rate and $f_i$ is the tag recovery rate incorporating any tag loss and tag induced mortality.

For $N_i$ animals released in year $i$, the observed recaptures $r_{ij}$ are the number of tags recaptured and returned to researchers that were released in year $i$ and recaptured in year $j$. The expected and observed tag recoveries by year of recapture and tagging cohort are then constructed from the number of animals tagged and recaptured by year (Table A.1).

Estimates of the recovery rate $f$ and the survival rate $S$, can be obtained for a particular year from the observed recoveries $r_{ij}$ and the sample size $N_i$ from table A.1. So for example, $f_1$ can be estimated as
Table A.1: The expected and observed tag recoveries from a multi-year tagging study where tags are released for three seasons and tag recoveries are accepted for an additional season under the Brownie model.

\[ \hat{f}_1 = \frac{r_{11}}{N_1}, \]

while \( S_1 \) can be estimated from

\[ \hat{S}_1 = \frac{N_2r_{12}}{N_1r_{22}} \text{ or } \frac{N_2r_{13}}{N_1r_{23}} \text{ or } \frac{N_2r_{14}}{N_1r_{24}}. \]

### A.1.1 Expected Values

For the general case of tagging cohorts \( N_i \) over \( i \) years, and collecting recoveries \( r_{ij} \) of the \( i^{th} \) cohort in the \( j^{th} \) year then

\[ E[r_{ij}] = \begin{cases} N_if_j, & i = j \\ N_i \prod_{h=i}^{j-1} S_hf_j, & j > i \end{cases} \]

(A.2)

where \( S_h \) is the annual survival rate for the \( h^{th} \) year, and \( f_j \) is the tag recovery rate for the \( j^{th} \) year.

### A.1.2 Likelihood Function

Assuming that tag recoveries are Poisson independent, the likelihood can be expressed as a product of the individual marginal densities. The likelihood is then developed from the expected values in equation A.2. Treating \( E(r_{ij}) \) to be \( N_iP_{ij} \), the likelihood \( l \) is proportional to

\[ \prod_{i=1}^{l} \left( \prod_{j=1}^{J} P_{ij}^{r_{ij}} \right) P_i^{J_i - \sum_j r_{ij}} \]

(A.3)
where $P_{i,J^*}$ is the probability that a tag from cohort $i$ is not recovered before the end of the study in year $J$.

\[ P_{i,J^*} = 1 - \sum_{j=i}^{J} P_{ij}. \]

Once the likelihood $l$ has been developed, maximum likelihood estimation (Lindgren, 1976) can be directly applied to equation A.3 to obtain estimators for $f$ and $S$. The total mortality can then be calculated from the survival as $Z = 1 - S$.

### A.1.3 Model Assumptions

Brownie models are subject to the same group of assumptions as the survival model. See Section 2.2 for details.
APPENDIX B

Derivation of the Gradient

The likelihoods for the models derived in Chapters 2 and 6 must be maximized numerically. As described in Section 2.5, a quasi-Newton method is used, but this requires expression for both the log likelihood and its gradient. This appendix presents expressions for the required gradients.

B.1 Likelihood

The models presented in chapters 2 and 6 both assume that recoveries are independent, so the total likelihood can be expressed as a product of contributions from individual tags

\[ L = \prod_{i=1}^{N} L_i. \]

Correspondingly, the log likelihood

\[ \log L = \sum_{i=1}^{N} \log L_i \]

and the \( h \text{th} \) component of the gradient

\[ \frac{\partial \log L}{\partial \theta_h} = \sum_{i=1}^{N} \frac{\partial \log L_i}{\partial \theta_h} \]

can be also expressed as a sum of contributions from individual tags. So to determine expressions for the log likelihood and its gradient, it is sufficient to consider the contribution made by a single individual.

B.2 Single Component Fishery

Chapter 2 derived a model for a single component fishery. In Section 2.5.5, it was shown that under some reasonable assumptions, the contribution that an individual
makes to the total likelihood can be written in the form

\[
L_i = \begin{cases} 
\lambda_t F_t \exp \left( - \sum_{k=s_i}^{t_i} (F_k + M_k) \right) & \text{if recovered at } t_i \\
1 + \sum_{j=s_i}^{T-1} \lambda_j F_j \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \right) \left( 1 - \exp(F_j + M_j) \right) & \text{if censored at } T
\end{cases}
\]

### B.2.1 Recovered Tags

A recovered tag contributes a factor

\[
L_i = \lambda_t F_t \exp \left( - \sum_{k=s_i}^{t_i} (F_k + M_k) \right)
\]

to the likelihood, so that

\[
\log L_i = \log \lambda_t + \log F_t - \sum_{k=s_i}^{t_i} (F_k + M_k)
\]

and hence

\[
\frac{\partial \log L_i}{\partial \theta_h} = \frac{\lambda_t'}{\lambda_t} + \frac{F_t'}{F_t} - \sum_{k=s_i}^{t_i} (F_k' + M_k'),
\]

where primes denote derivatives with respect to \( \theta_h \).

### B.2.2 Censored Tags

A censored tag contributes a factor

\[
L_i = 1 + \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \right) \left( 1 - \exp(F_j + M_j) \right)
\]

to the likelihood, so that

\[
\log L_i = \log \left( 1 + \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \right) \left( 1 - \exp(F_j + M_j) \right) \right)
\]

\[
= \log \left( 1 + \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \right) - \exp \left( - \sum_{k=s_i}^{j-1} (F_k + M_k) \right) \right)
\]

\[
= \log \left( 1 + \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \left( \exp(-S_j) - \exp(-S_{j-1}) \right) \right)
\]
where
\[ S_i = \sum_{k=s_i}^i F_k + M_k. \]

The contribution to the \( h \)th component of the gradient is then
\[
\frac{\partial \log L_i}{\partial \theta_h} = L_i^{-1} \sum_{j=s_i}^{T-1} \left( \frac{\lambda_j F_j + \lambda_j F'_j}{F_j + M_j} - \frac{\lambda_j F_j (F'_j + M'_j)}{(F_j + M_j)^2} \right) \left( \exp (-S_j) - \exp (-S_{j-1}) \right)
- L_i^{-1} \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_j + M_j} \left( S'_j \exp (-S_j) - S'_{j-1} \exp (-S_{j-1}) \right)
\]

where
\[ S'_i = \sum_{k=s_i}^i F'_k + M'_k. \]

and again primes denote derivatives with respect to \( \theta_h \).

### B.3 Multiple Component Fishery

Chapter 6 extended the model of Chapter 2 to allow for multiple component fisheries. In Section 6.2.2, it was shown that under some simple assumptions, the contribution that an individual makes to the total likelihood can be written in the form

\[
L_i = \begin{cases} \\
\lambda_{ct_i} f_{ct_i} \exp \left( - \sum_{k=s_i}^{t_i} (F_k + M_k) \right) & \text{if recovered at } t_i \\
1 + \sum_{j=s_i}^{T-1} \frac{R_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \right) \left( 1 - \exp(F_j + M_j) \right) & \text{if censored at } T \\
\end{cases}
\]

where
\[
F_i(t) = \sum_{c=1}^M f_{ic}(t)
\]
\[
R_i(t) = \sum_{c=1}^M \lambda_{ic}(t) f_{ic}(t).
\]

#### B.3.1 Recovered Tags

A tag recovered by fishing component \( c \) contributes a factor
\[
L_i = \lambda_{ct_i} f_{ct_i} \exp \left( - \sum_{k=s_i}^{t_i} (F_k + M_k) \right)
\]
to the likelihood. So

$$\log L_i = \log \lambda_{ct_i} + \log f_{ct_i} - \sum_{k=s_i}^{t_i} (F_k + M_k)$$

and the contribution to the gradient is

$$\frac{\partial \log L_i}{\partial \theta_h} = \frac{\lambda'_{ct_i}}{\lambda_{ct_i}} + \frac{f'_{ct_i}}{f_{ct_i}} - \sum_{k=s_i}^{t_i} (F'_k + M'_k).$$

where primes denote derivatives with respect to $\theta_h$.

### B.3.2 Censored Tags

A censored tag contributes a factor

$$L_i = 1 + \sum_{j=s_i}^{T-1} \frac{R_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \left( 1 - \exp(F_j + M_j) \right) \right)$$

to the likelihood. So the contribution to the log likelihood is

$$\log L_i = \log \left( 1 + \sum_{j=s_i}^{T-1} \frac{R_j}{F_j + M_j} \exp \left( - \sum_{k=s_i}^{j} (F_k + M_k) \left( 1 - \exp(F_j + M_j) \right) \right) \right)$$

$$= \log \left( 1 + \sum_{j=s_i}^{T-1} \frac{R_j}{F_j + M_j} \left( \exp(-S_j) - \exp(-S_{j-1}) \right) \right)$$

where

$$S_i = \sum_{k=s_i}^{i} F_k + M_k.$$ 

In this case, the contribution to the derivative of the log likelihood is

$$\frac{\partial \log L_i}{\partial \beta} = L_i^{-1} \sum_{j=s_i}^{T-1} \left( \frac{\lambda'_j F_j + \lambda_j F'_j}{F_j + M_j} - \frac{\lambda_j F_j (F'_j + M'_j)}{(F_j + M_j)^2} \right) \left( \exp(-S_j) - \exp(-S_{j-1}) \right)$$

$$- L_i^{-1} \sum_{j=s_i}^{T-1} \frac{\lambda_j F_j}{F_i + M_j} \left( S'_j \exp(-S_j) - S'_{j-1} \exp(-S_{j-1}) \right).$$
BIBLIOGRAPHY


