ABSTRACT

KRACHEY, MATTHEW J. Hierarchical Bayesian Application to Instantaneous Rates Tag-Return Models. (Under the direction of Professor Kenneth H. Pollock).

Natural mortality has always been a challenging quantity to estimate in harvested populations. The most common approaches to estimation include a regression model based on life history parameters and more recently tag-return models. In recent years, Bayesian methods have been increasingly implemented in ecological models due to their ability to handle increased model complexity and auxiliary datasets. In this dissertation, I explore the implementation of Bayesian methods to analyze tag-return data focusing on natural mortality.

Chapter 1 is focused on the addition of two components to the tag-return model framework: random effects and auxiliary data. The random effects model is implemented in a Bayesian framework using a hierarchical prior on the instantaneous rate of harvest mortality. Auxiliary information on the instantaneous rate of natural mortality is provided through Hoenig’s equation relating lifespan to natural mortality, and also implemented through a hierarchical prior. A simulation study validates the performance of the model while an analysis of the classic Cayuga Lake trout dataset demonstrates its use. I show that random effects modeling can be implemented without much inflation of error, and the auxiliary data provides significant gain in precision and accuracy of natural mortality estimates.

Chapter 2 adds a change-point allowing for the estimation of two levels of natural mortality and the timing of the discrete-time shift in mortality. Analysis is focused on a Chesapeake Bay striped bass tagging dataset of fish tagged at six years of age and older from 1991-2002. Results show the ability to account for shift in timing. Contrasting with Jiang et al.’s study on the same striped bass dataset, the timing of the change-point was different between the two studies, likely because the Jiang study assumed a fixed tag-reporting probability of 0.43 whereas estimates seem to indicate it may be closer to 0.3. Mortality estimates were unreasonable, indicating that there may be additional complications to the dataset.

Chapter 3 introduces a change-point allowing for a shift in the tag-reporting probability while assuming a constant natural mortality rate. High reward tags are included in
a subset of the data time-series to improve estimation. A factorial simulation design was used to investigate the model performance with different reporting rate and high reward tag scenarios. Additionally, auxiliary simulation studies looked at the impact of high natural mortality, the timing of the shift in tag-reporting probability and reducing the study length to six years. In general, the model performed very well with little bias except in the case of no high-reward tags. The model performed surprisingly well in the shorter length study. The results suggest the importance of high reporting rates and/or auxiliary data sources such as high reward tags.
Hierarchical Bayesian Application to Instantaneous Rates Tag-Return Models

by
Matthew J. Krachey

A dissertation submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy

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APPROVED BY:

Dr. Kevin Gross
Dr. Sujit K. Ghosh
Dr. Kenneth H. Pollock
Dr. Joseph Hightower
Chair of Advisory Committee
Co-Chair of Advisory Committee
DEDICATION

To my mother Elsie, and my wife Liz, it’s been a long road.
BIOGRAPHY

Matthew James Krachey was born in Valparaiso, Indiana April 19, 1976 to Daniel and Elsie Krachey. He claims Arcata, California as his hometown. He received his BA in Creative Studies, emphasis in Biological Sciences from UC Santa Barbara in 1999. He received an MS in Statistics from NC State University in 2006. He is married to Elizabeth Catherine Krachey.
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Chapter 1

Use of auxiliary information about natural mortality for hierarchical Bayesian Brownie models

1.1 Introduction

The instantaneous rate of natural mortality rate has been one of the most challenging quantities to estimate for natural resource statisticians. The difficulty is partially due to the fact that natural mortalities are rarely seen, whereas those dying from hunting or fishing are directly observed. A few options have been used to estimate natural mortality. Demographic relationships, such as modeling natural mortality as a function of maximum longevity has been used to estimate natural mortality without carrying out a research study (20). Telemetry studies have also been used to provide direct estimates of natural mortality, though these studies may have problems such as emigration from study site, cost, equipment malfunction, and other complications (19).

Tag-return studies have been a popular choice for fisheries managers to assess the mortality rates of harvested populations at lower cost than telemetry studies. In these studies, annual cohorts of animals are tagged, and released into the population. As harvesters recover tagged animals their tags may be returned to managers. The pattern in the returns is then used to infer annual survival rates, using the Brownie models, for example (6; 44). The Brownie models have been extended to an instantaneous rates formulation that allows
natural and harvest mortality rates to be estimated separately (21).

In recent years, several developments have occurred in tag return models. One of these is the incorporation of hierarchical Bayesian modeling to tagging data (38; 3; 5). Another has been the addition of random effects models on annual survival estimates (8; 14; 38; 3). Finally, several approaches studies have investigated incorporating auxiliary data sources with tagging studies in order to estimate parameters (15; 34; 33; 35).

Hierarchical Bayesian models have been of increasing interest for ecologists (37; 28; 11; 10; 9). Advocates argue that these methods allow a unified framework to integrate multiple data sources, multiple scales, latent variables, sampling design, biological models, and therefore enhance parameter estimation (37; 10). Parameters such as natural mortality are notoriously difficult to estimate in the instantaneous rates formulation of the Brownie models. The additional flexibility provided by the Bayesian approach may prove to be helpful for estimation, especially, for example, for small data sets, cases where an a-priori estimate is available, or if increased complexity such as random effects are desired.

Random effects in annual survival rates have been increasingly applied in tagging studies (8; 14; 38). Random effects differ from fixed effects in that the estimates of survival are assumed to come from a statistical model themselves. For example, they can be assumed to come from a normal model, with mean equal to the mean survival with normal error (8). This approach has some advantages, including improved ability to forecast survival (25), improved estimation (8; 38), and the ability to incorporate covariates to survival estimates (3).

In this paper, developments in the instantaneous rates formulation are highlighted using the following structure: first, the instantaneous rates model will be introduced, with analysis of the important parameters and auxiliary data sources. Second, an overview of the instantaneous rates formulation will be developed under a Bayesian framework, including a random effects model. Third, hierarchical prior distributions will be developed, and applied to a subset of a dataset as well as an entire dataset to compare fit. Finally, a simulation study will be carried out in order to assess the performance of the models in greater detail. I conclude with a discussion of possible future research.
1.2 Methods

1.2.1 The Brownie models: Instantaneous Rates

The Brownie model carries the following assumptions:

1. There is no tag shedding
2. There is no tag-induced mortality
3. Tags are fully mixed by the onset of fishing
4. Fishing is assumed operate continuously throughout the year
5. Natural and harvest sources of mortality are additive
6. Returned tags are allocated to the correct release cohort and recovery year

To construct the Brownie likelihood function, first consider that $R_i$ individuals are released tagged in the year $i, i=1\ldots J$. Tag recoveries are aggregated by year, so that $x_{ij}$ are the number of tag returns from release year $i$ in the year $j, j=i, \ldots, J$. The probability of a recovery of $x_{ij}$ tags, $\pi_{ij}$ is defined as,

$$P_{ij} = \begin{cases} 
\prod_{k=i}^{j-1} S_k f_j & \text{if } j \neq i \\
 f_j & \text{otherwise}
\end{cases}$$

(see also Table 1.1)
Table 1.1: Generalized Brownie recovery probabilities

<table>
<thead>
<tr>
<th>No. tagged in year $i$</th>
<th>P(Recovery) in year $j$, (data)</th>
<th>Not Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R_1$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$f_1(x_{11})$</td>
<td>$S_1 f_2(x_{12})$</td>
</tr>
<tr>
<td></td>
<td>$R_2$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$f_2(x_{22})$</td>
<td>$S_2 f_3(x_{23})$</td>
</tr>
<tr>
<td></td>
<td>$R_3$</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$f_3(x_{33})$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$S_3 f_4(x_{34})$</td>
</tr>
</tbody>
</table>
where $S_i$ is the probability of survival from year $i$ to year $i + 1$ and $f_i$ is the probability of being harvested in year $i$. The instantaneous rates formulation defines $S_i = \exp(-M - F_i)$ and $f_i = \phi \lambda (1 - \exp(-M - F_i)) \frac{F_i}{M + F_i}$ where $M$ is the force of natural mortality and $F_i$ is the force of fishing mortality in year $i$, $\phi$ is the joint probability of surviving the immediate tagging and retaining the tag, and $\lambda$ is the tag-reporting probability. (21).

Let $P_{ij}, i, j = 1, 2, \ldots I$ be the cell probability of cell $ij$ as in Table 1.1. The Brownie model treats the each tagging year as a multinomial, thus the likelihood function $\Lambda$ is the joint multinomial,

$$\Lambda = \prod_{i=1}^{I} \left( \frac{R_i}{x_{ii}x_{ii+1}, \ldots, x_{ii}} \right) \prod_{j=i}^{J} \left[ P_{ij}^{x_{ij}} \right] P_{ij}^{R_i - \sum_{j=i}^{J} x_{ij}}$$

In the model development above, there are 3 fixed constant parameters over the course of the study ($\phi, \lambda, M$) and one that varies by year ($F_k$).

Bayesian approaches to statistics have advantages over frequentist approaches in the cases where prior information on the parameters is available. There has already been research on the four groups of parameters from the instantaneous rates model: the desired mortality parameters $F_i$ and $M$; and the nuisance parameters $\phi$ and $\lambda$. The instantaneous harvest mortality rates are possibly the easiest parameters in the set to estimate, as harvest mortality is directly observed through tag returns (31). Additional information or modeling of harvest mortality has been applied in a few ways. In pulse fisheries, research has investigated tagging fish before and after the harvest pulse to improve natural mortality rate estimates (17). Additionally, differential harvest rates can be estimated under the assumption that newly tagged fish may not have fully mixed with the rest of the population (26). Harvest mortality can also be modeled using effort information under the assumption that tags are equally catchable per-unit-effort (21).

The instantaneous rates formulation is largely interesting because it can estimate natural mortality rates. The estimation of natural mortality rates has long been a challenge (42). Several approaches have been undertaken to estimate $M$. Linear models have been applied to estimate the relationship between natural mortality and maximum longevity of a species (20). Recently, telemetry tagging studies have allowed the tracking of individuals to determine natural mortality rates directly (19; 35; 18; 43; 41; 4). Since estimating natural mortality is difficult, prior information in $M$ may drastically improve model performance
and flexibility.

The two nuisance parameters, $\phi$ and $\lambda$ can have a large impact on parameter estimates. Most models assume that $\phi = 1$; however, tag retention rates can be estimated, for example with cage studies (13). Some approaches used auxiliary data to estimate tag-reporting rates include the use of high reward tags (33), planted tags (15) and fisheries observers (16). If the tag-reporting probability is underestimated, one would expect fewer tags to be reported than are observed by fishers which results in an overestimate of natural mortality. This relationship between the tag-reporting probability and natural mortality estimates has increased interest in tag-reporting probabilities.

The variety of different information sources on the tagging parameters listed above have had several studies investigating the augmenting of the likelihood structure in order to incorporate these models. While Bayesian approaches have been used in tagging studies, I am unaware of any that have investigated the use of hierarchical Bayes on the instantaneous rates formulation. The instantaneous rates formulation is very interesting since the parameters such as natural mortality can have estimates independent of the data (i.e. Hoenig’s equation (20)) which will be explored below.

1.2.2 Hierarchical Bayesian Models

The use of Bayesian statistics has been increasing in ecology (9; 37). Hierarchical Bayes is simply an extension of traditional Bayesian models where the prior distributions have some form of conditional dependency (10). Frequent criticisms of the Bayesian approach center around the difficulties in specifying prior distributions (37). The use of hierarchical Bayes allows for uncertainty in prior specification while allowing the prior distributions to have more structure than non-informative priors.

In this study, I use the Cayuga Lake lake trout ($Salvelinus namaycush$) dataset from Youngs and Robson (46). The dataset runs from 1960-1969, with a minimum of 360 tagged trout in a single year (1967) and a total of 7770 tagged individuals. A reporting rate of 0.18 has been used in multiple studies as a fixed, known quantity through a maximum likelihood estimate using the full dataset (21). Analysis will be based on the entire dataset, as well as a subset of the first six and first three years.
1.2.3 Random and fixed effects models

Here, the four models will be built based on different prior probability distribution specifications. These models will differ from those derived later in that prior information will not be used as hierarchical priors. All four models will use the same prior distributions on $M$,

$$[M] \sim -\log(beta(0.5, 0.5))$$

Note that this log transformation will be used frequently in this paper for the instantaneous natural and harvest mortality rates. This log transformation is used as the quantity $\exp^{-M}$ can be viewed as the annual survival from natural sources of mortality, which should be on the interval $(0,1)$. The beta distribution was selected since it is a very flexible model for data on the interval $(0,1)$. The log transformation would thus isolate $M$, as desired.

The tag reporting rate, $\lambda$ will parameterized under two scenarios, under a fixed, known reporting rate $\lambda = 0.18$, a value based on maximum likelihood estimates from the dataset (21). Additionally, $\lambda$ will also be allowed to vary under an non-informative prior, and therefore

$$[\lambda] = \begin{cases} 0.18 & \text{if } \lambda \text{ fixed,} \\ \sim beta(0.5, 0.5) & \text{if non-informative prior.} \end{cases}$$

The annual instantaneous rate of harvest mortality, $F_k$, will be derived in two scenarios, fixed and random effects,

$$[F_k|\alpha, \beta] \sim -\log(beta(\alpha, \beta))$$

$[\alpha], [\beta]$ are either assumed to be equal to 0.5 for the fixed effects formulation, or $[\alpha], [\beta]$ are assumed to be hyperparameters with uniform prior distributions on the interval $(0,3)$. That parameterization only approximates a classical random and fixed effects model from the Bayesian perspective (38).

The hyperparameter distributions, $[\alpha], [\beta]$ were selected to allow for a range of values, but be restrictive enough to allow WinBUGS to run the MCMC sampler. The formulation above provides four models, fixed and random effect on harvest mortalities,
with and without uncertainty on the tag reporting rates. These four models were applied to the full Cayuga Lake dataset.

1.2.4 Informative hierarchical priors

Natural mortality estimation is one of the goals of a tagging study, and the crucial dependency on estimates of the tag-reporting probability can influence estimates of $M$. In this section, informative priors will be developed for $\lambda$ and $M$. For simplicity, only the random effects prior formulation for $F_k$ will be considered from the models above. The focus of most tagging studies is to improve estimates of $M$. There have been several papers that have focused on improving estimates of $\lambda$ (33; 34; 15).

I used two prior distributions for the instantaneous rate of natural mortality, $M$. The first is the non-informative prior presented above,

$$[M] \sim -\log(\text{beta}(0.5, 0.5)).$$

Also, using Hoenig’s equation (20) to estimate natural mortality rates,

$$\log(M) = 1.44 - 0.92 \times \log(t_{\text{max}})$$

where $t_{\text{max}}$ is the maximum observed age for the stock. A search on FishBase (http://www.fishbase.org) for lake trout yielded an estimate of 50 years providing an $M$ estimate of approximately 0.115. Using this estimate as a mean for a hierarchical normal distribution, I get the hierarchical prior,

$$[M|\mu_M = 0.115] \sim N(\mu_M, \sigma^2)$$

The variance of this prior distribution was unknown, so a hierarchical uniform hyperprior on the interval (0,1) was put on $[\sigma^2]$. Note that this prior mean $M$ estimate is independent of the data collected from Cayuga Lake.

Youngs provided an estimate of $\lambda$ for this dataset of 0.18 using the dataset(21). I will apply the same prior probability structure on $\lambda$ as for $M$ using this mean $\mu_\lambda = 0.18$ with unknown $\sigma^2$ or beta(0.5,0.5) as a non-informative prior. Note that it is possible to have existing information in $\lambda$, from auxiliary studies.
1.2.5 Comparison of truncated and full dataset

I applied three different prior specifications to the full and truncated datasets to assess the fits of the model:

1. Non-hierarchical priors on both M and $\lambda$
2. Hierarchical prior on M
3. Hierarchical priors on both M and $\lambda$

This formulation was selected because the estimate used as the hierarchical prior mean for $\lambda$ was obtained using the dataset I am analyzing, so was not fully a priori. In contrast, the mean for M used only Hoenig’s equation, thus was independent of the dataset.

1.2.6 Simulation

A small simulation study was also conducted to test the model fit under a differing dataset size and under different prior information scenarios. The input parameter values are given in Table 1.2. The simulation ran hierarchical Bayesian model scenarios as on the dataset (no hierarchical priors, hierarchical M, and hierarchical M and $\lambda$). Two additional scenarios were added as well. First, a hierarchical $\lambda$ with non-informative M was provided to give symmetry to the other scenarios provided. Second, hierarchical M and $\lambda$ where an error of $\mu_\lambda = 0.3$ was given as the mean of the prior distribution on $\lambda$ to assess the sensitivity to this prior. The full dataset had 10 years of data, the model was run on the full dataset and a subset of the first 3 and 6 years of data as was analyzed with the true dataset.

Posterior means and standard errors were used to generate point estimates and measures of parameter variability. These estimates were generated using WinBUGS 1.4 (30). Additionally, WinBUGS was used to generate the Deviance Information Criterion (DIC) as a measure of model fit (39). Three chains were run with a burn-in of 10,000 iterations, with 90,000 iterations retained per chain.
1.3 Results

For the Cayuga Lake dataset, the random and fixed effects models for $F$ with $\lambda$ fixed and non-informative show interesting trends. First, both models have similar estimates of $\lambda$, with an estimate of about 0.01 different from the fixed value of 0.18 (Table 1.3). As shown in Figure 1.1, the marginal posterior distributions for $\lambda$ for the fixed and random effects model are virtually identical. However, there is a large disparity in the marginal posterior distributions of $M$ between the fixed and variable $\lambda$ groups, with much greater parameter uncertainty for the variable $\lambda$ scenarios (Figure 1.2). As shown in Table 1.3, this uncertainty translates to increased variability in estimates for all parameters. However, there is very little difference between the fixed and random effects models for $\lambda$ estimated in terms of DIC values or estimates. This trend also follows for the $\lambda$ fixed group. It is interesting to note the higher precision of the estimates for the random effects models on all parameters except the last few harvest mortality rates when $\lambda$ is allowed to vary, whereas there appears to be no trend in which has higher precision for the $\lambda = 0.18$ case, though the difference in precision is small.

The results of the hierarchical model depended on the amount of data used and the criterion to evaluate the fit (Table 1.4). When the full dataset was used, there appears to be little difference in the models comparing either DIC or the estimates of $\lambda$. This result is reassuring, as the non-informative model should approximate a maximum likelihood estimate, which has been available before. All three models show a $\lambda$ estimate of approximately 0.17, within a reasonable range of Young’s estimate of $\lambda=0.18$.

The three year data subset shows a divergence estimates and DIC (Table 1.4). The model with non-informative beta priors on both $M$ and $\lambda$ is overwhelmingly preferred by DIC, with the lowest DIC value by at least 26. In contrast, the hierarchical $M$ and $\lambda$ model had a DIC that was 35 greater than the best model. However, the hierarchical $M$ and $\lambda$ model had a $\lambda$ estimate of 0.181, similar to the estimates from the full dataset, while the non-informative beta $M$ and $\lambda$ model had an $\lambda$ estimate of 0.303. It thus appears that the addition of information on $\lambda$ does appear to have led to a significant improvement in parameter estimation for the three year dataset.

The six year data subset of the Cayuga Lake dataset appears to show a convergence of the different models. As shown in Table 1.4, the DIC for all three prior parameter all
appear to have converged to approximately 132. The model with non-informative priors on
M and λ seems to have slightly underestimated M and λ by posterior means, but these values
are reasonably close to those in the other two models. The cases with informed M showed
virtually identical estimates of M and λ, so that in this case the additional information on
λ appears to have little benefit for the six year dataset.

The simulation results for the ten-year study were consistent to these hierarchical
model results (Table 1.5). All four models were very close to the true parameter values and
had similar DIC values. However, the three-year subset showed a great deal of disparity
between the different models. Like in the real dataset the non-informative M and λ model
showed the lowest mean DIC value while the mean parameter estimates for M and λ have
the largest bias. While none of the models were able to get a great fit for this subset, the
informative models were the closest to the real values, however they also had the highest
DIC values.
Table 1.2: Parameter values for simulation study, where $\alpha, \beta$ are beta hyperparameters for the instantaneous harvest mortality rates, $F_k$

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$</td>
<td>0.11</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>0.66</td>
</tr>
<tr>
<td>$\beta$</td>
<td>1</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>0.18</td>
</tr>
</tbody>
</table>
Table 1.3: Comparison of the posterior means (standard errors in parentheses) of tag reporting rate $\lambda$, natural mortality rate $M$, year-specific harvest mortality rate $F_y$, random effects hyperparameters $\alpha$ and $\beta$, and DIC for fixed and random effects formulations of the Brownie models harvest mortality rates with a fixed tag reporting rate ($\lambda=0.18$) and tag reporting rate estimated with an uninformative beta prior for Cayuga Lake trout dataset.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\lambda = 0.18$</th>
<th>$\lambda \sim \beta(0.5, 0.5)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fixed Effects</td>
<td>Random Effects</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>0.121 (0.021)</td>
<td>0.122 (0.022)</td>
</tr>
<tr>
<td>$M$</td>
<td>0.560 (0.074)</td>
<td>0.555 (0.073)</td>
</tr>
<tr>
<td>$F_1$</td>
<td>0.671 (0.070)</td>
<td>0.664 (0.068)</td>
</tr>
<tr>
<td>$F_2$</td>
<td>0.381 (0.043)</td>
<td>0.379 (0.042)</td>
</tr>
<tr>
<td>$F_3$</td>
<td>0.602 (0.053)</td>
<td>0.599 (0.056)</td>
</tr>
<tr>
<td>$F_4$</td>
<td>0.382 (0.043)</td>
<td>0.382 (0.041)</td>
</tr>
<tr>
<td>$F_5$</td>
<td>0.607 (0.067)</td>
<td>0.609 (0.069)</td>
</tr>
<tr>
<td>$F_6$</td>
<td>0.301 (0.041)</td>
<td>0.305 (0.045)</td>
</tr>
<tr>
<td>$F_7$</td>
<td>0.351 (0.051)</td>
<td>0.353 (0.052)</td>
</tr>
<tr>
<td>$F_8$</td>
<td>0.147 (0.029)</td>
<td>0.151 (0.028)</td>
</tr>
<tr>
<td>$F_9$</td>
<td>0.174 (0.029)</td>
<td>0.179 (0.031)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>2.520 (0.418)</td>
<td></td>
</tr>
<tr>
<td>$\beta$</td>
<td>1.628 (0.458)</td>
<td></td>
</tr>
<tr>
<td>DIC</td>
<td>264.507 (4.651)</td>
<td>264.880 (4.817)</td>
</tr>
</tbody>
</table>
Figure 1.1: The posterior densities for the tag reporting rate, $\lambda$, for the fixed and random effects models with variable $\lambda$. 
Figure 1.2: The posterior densities for the instantaneous rate of natural mortality, $M$, for the four fixed and random effects models.
Table 1.4: Comparison of posterior means for the instantaneous rate of natural mortality, $M$, the tag-reporting probability, $\lambda$, and DIC for the instantaneous rates Brownie models for Cayuga Lake dataset. Three prior specifications were used: a non-informative beta distribution on $\lambda$ and the natural mortality rate, $M$; an informative hierarchical normal prior on $M$ with mean 0.11 and non-informative beta distribution on $\lambda$, and the informative normal prior on $M$ and an informative normal prior on $\lambda$ with mean 0.18. The Cayuga dataset was analyzed whole, as well as subsets of the first three and six years of the dataset.

<table>
<thead>
<tr>
<th>Model</th>
<th>$M$</th>
<th>$\lambda$</th>
<th>DIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3 Years</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-informative $M$ and $\lambda$</td>
<td>0.277 (0.230)</td>
<td>0.303 (0.222)</td>
<td>11.221 (2.880)</td>
</tr>
<tr>
<td>Non-informative $\lambda$, informative $M$</td>
<td>0.229 (0.172)</td>
<td>0.245 (0.154)</td>
<td>35.973 (2.708)</td>
</tr>
<tr>
<td>Informative $M$ and $\lambda$</td>
<td>0.191 (0.122)</td>
<td>0.200 (0.061)</td>
<td>45.998 (2.824)</td>
</tr>
<tr>
<td></td>
<td>6 Years</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-informative $M$ and $\lambda$</td>
<td>0.063 (0.076)</td>
<td>0.169 (0.033)</td>
<td>131.634 (3.735)</td>
</tr>
<tr>
<td>Non-informative $\lambda$, informative $M$</td>
<td>0.104 (0.071)</td>
<td>0.183 (0.046)</td>
<td>132.169 (3.685)</td>
</tr>
<tr>
<td>Informative $M$ and $\lambda$</td>
<td>0.102 (0.058)</td>
<td>0.180 (0.025)</td>
<td>132.719 (3.857)</td>
</tr>
<tr>
<td></td>
<td>Full Dataset</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-informative $M$ and $\lambda$</td>
<td>0.079 (0.079)</td>
<td>0.169 (0.037)</td>
<td>263.942 (4.563)</td>
</tr>
<tr>
<td>Non-informative $\lambda$, informative $M$</td>
<td>0.116 (0.066)</td>
<td>0.180 (0.029)</td>
<td>264.815 (4.575)</td>
</tr>
<tr>
<td>Informative $M$ and $\lambda$</td>
<td>0.116 (0.058)</td>
<td>0.179 (0.026)</td>
<td>265.396 (4.873)</td>
</tr>
</tbody>
</table>
Table 1.5: Results from 50 simulations for tagging study, where $M=0.11$, $\lambda=0.18$. For the instantaneous rates models, four prior specifications were used: a non-informative beta distribution on $\lambda$ and the natural mortality rate, $M$; an informative hierarchical normal prior on $M$ with mean 0.11 and non-informative beta distribution on $\lambda$, and the informative normal prior on $M$ and an informative normal prior on $\lambda$ with mean 0.18, and the informative normal prior on $M$ and a mis-specified normal distribution on $\lambda$ with mean 0.30.

<table>
<thead>
<tr>
<th>Prior specifications</th>
<th>3 Years of Data</th>
<th>10 Years of Data</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{M}$</td>
<td>$\hat{\lambda}$</td>
</tr>
<tr>
<td>Noninform $\lambda$, Noninform $M$</td>
<td>0.387</td>
<td>0.287</td>
</tr>
<tr>
<td>Noninform $\lambda$, Hierarchical $M$</td>
<td>0.279</td>
<td>0.248</td>
</tr>
<tr>
<td>Hierarchical $\lambda$, Hierarchical $M$</td>
<td>0.238</td>
<td>0.217</td>
</tr>
<tr>
<td>Hierarchical $\lambda$ with error, Hierarchical $M$</td>
<td>0.295</td>
<td>0.237</td>
</tr>
</tbody>
</table>
1.4 Discussion

There has been a debate over the introduction of subjectivity through the implementation of prior distributions (28). Bayesian methods allow one examine the impacts of a variety of priors on the inference of a problem. Here I investigated several scenarios, and showed that given an adequately long time-series of data there is relatively little difference according to DIC regardless of the prior specification made for the entire dataset. Additionally, I showed that informative priors, assuming that the specification is reasonable, not necessarily fully correct, can improve estimation for very small datasets. The improvement in estimation for small datasets may be very important since it is likely that managers would want some information from the tagging study prior to a ten-year period.

In assessing the appropriate prior specification, an appropriate criterion would be desirable to reduce the subjectivity in model selection. Unfortunately, the simulation study showed that DIC may fail to select the model that is closest to the truth. This failure may be due to a difficulty in estimating $\sigma$, resulting in inflated deviance of the model, increasing DIC. Through the posterior analysis of several prior specifications, one may have a more robust inference to the problem being analyzed (28). Here I observed that increasing precision in the $\lambda$ estimates results in more precise estimate of natural mortality. The precision may be overstated if uncertainty in the estimate for $\lambda$ is not represented in the model.

In this paper, it has been shown that there is relatively little loss when using random effects to estimate annual harvest mortality rates under the instantaneous rates formulation. As I have shown, the Bayesian approach to the instantaneous rates formulation is essentially as simple as applying fixed effects. In classical statistics, maximum-likelihood estimators typically fail to provide estimates of random effects, and methods such as empirical Bayes are applied to formulate these estimates (8). In contrast, the same general approach to estimating any parameter from within the Bayesian approach can be applied to estimating random effects.

Hierarchical Bayesian methods may prove to be a powerful approach in a variety of scenarios. Here models using simple auxiliary data or parameter estimates using the existing data were used to increase the precision of estimates. Certainly, the hierarchical Bayes approach allows additional studies to be included through the use of parameter estimates.
from these studies to be included as prior mean and variance. Additionally, auxiliary data can be used as an additional level in the hierarchy and parameter estimates can be made using the data jointly and simultaneously (10).

The use of additional datasets in tag-return studies is likely to be an area of increasing interest. Estimates of natural mortality appear to be exceptionally difficult to obtain. One approach for improving these estimates has been to improve precision of the other parameters, which in turn increases the precision of natural mortality (21). For example, the correlative nature of the natural mortality and reporting rates may suggest that improved estimates of the reporting rate could be beneficial to natural mortality rate estimates. Additionally, natural mortality can be directly estimated using telemetry studies (35; 19).

Estimating natural mortality rates is likely to continue to be an area of research in fisheries science. In this study, I have shown that the relatively "free" prior mean estimate provided by the Hoenig equation may be very beneficial to improving estimates of M under an instantaneous rates formulation. Including both this information on natural mortality and adding uncertainty in the estimate is not easily reconciled in classical statistics. As further methods of estimating M are developed, inclusion of these estimates are likely to be readily incorporated into the hierarchical Bayesian formulation as presented here. With the development of WinBUGS software, I feel that managers now have the tools to incorporate these additional data sources, improve mortality estimates, and provide better information of the stock status into management plans.
Chapter 2

A Bayesian multiple change-point model for tag return data

2.1 Introduction

The estimation of natural mortality rates in fish stocks is both one of the most fundamental and difficult to estimate quantities in fisheries population dynamics (42). Here natural mortality is defined as death from any cause other than human harvest (i.e. fishing or hunting). Natural mortality is hard to estimate, in part, because natural deaths are rarely directly observed (6). Several methods have been proposed to improve estimates of natural mortality (20; 19), and new statistical methods, namely hierarchical Bayesian models, may provide the flexibility to incorporate these ideas within a single framework (37; 10).

Hierarchical Bayesian models are defined as Bayesian statistical model where the prior information is decomposed into conditional probability distributions (36). This approach is desirable as it can provide inference for very complex relationships (9; 10). These models may incorporate both biological and sampling information which may allow more inference of the ecological dynamics (37). For example, in the first chapter of this proposal, I demonstrated how this framework allows for simple inclusion of auxiliary data to improve parameter estimates. Bayesian approaches also provide an integrated framework for model selection (36) and model averaging (22).

Multimodel inference and model selection have been an increasing area of interest
for statisticians (7; 40; 22; 29). Common current approaches include the use of the Akaike Information Criterion (AIC) (7; 1) in classical statistics, and for Bayesians a choice of the Bayesian Information Criterion (BIC) (22; 45) and the Deviance Information Criterion (DIC) (40). These information criterion methods all have different ways of balancing models that have very good model fit while penalizing those with more parameters.

Model averaging has gotten a great deal of recent interest from both classical (7; 1) and Bayesian statisticians (22; 29; 45). Noting the sources provided, there is a large degree of synergy between model averaging and model selection. Model averaging allows the uncertainty in determining the appropriate model to be incorporated into model estimates by providing a weighted average of the included models according to some criteria. In classical statistics, AIC weights are advocated as a method to select the model weights (7; 1), likewise DIC or BIC weights for Bayesians (40; 22). In cases where there is a high degree of model uncertainty, model averaging approaches may be appropriate. In this paper, I will describe a framework where model uncertainty is incorporated through model averaging using a tag-return study.

The Brownie tag-return models have long been used to analyze tagging data (6; 33; 34; 15; 35). Extensions to these models have allowed a constant natural mortality rate and annual harvest mortality rates to be estimated (21). This research is focused on incorporating auxiliary data into tagging models. Commonly, the Brownie models assume a constant natural mortality rate. In the case of a tagging study for Chesapeake Bay striped bass, an outbreak of the disease mycobacteriosis may have caused a shift in natural mortality rates, a violation of most tagging models (23; 24). The uncertainty in the timing of the outbreak makes this an interesting scenario to explore model selection and model averaging issues.

In this paper, I will develop a Bayesian discrete change-point model for estimating the timing of a shift in natural mortality. I will show that the posterior probability distribution on the change-point parallels a weighting parameter from model averaging. Thus this model will integrate model averaging and model selection from within the base hierarchical Bayesian framework. I will contrast this framework to scenarios with only one level of natural mortality, and models where the change-point is predetermined using the Chesapeake Bay striped bass dataset.
2.2 Methods

In this section, the dataset and the five models that were used to analyze this dataset will be developed. After describing the dataset, I will develop the Brownie instantaneous rates models (6; 21; 23) with fixed and random effects in the instantaneous harvest mortality rates using hierarchical Bayes. Next, a model will be developed using the random effects formulation incorporating two natural mortality rates, where the shift in natural mortality will occur in a year determined from previous modeling efforts. Finally, a discrete change-point model will be developed to estimate the year that the mortality shift occurred, using both fixed and random effects formulations in harvest mortality.

2.2.1 Dataset

In this paper we considered the Chesapeake Bay striped bass tagging dataset between 1991 and 2002 (23). Fish were tagged at all ages above 2 years. The age at full selectivity is believed to be at age 6, so all fish tagged at age 6 and above were lumped into a single "adult" age class for this paper. This subset results in a total of 12,847 tagged individuals, with an annual minimum of 448 tagged fish released in a single year. An outbreak of mycobacteriosis occurred during this time series. The estimated time of the mortality shift occurred between 1998 and 1999 (23).

2.2.2 Single natural mortality model

Here, we will build four models based on different prior probability distribution specifications. These models will differ from those derived later in that prior information will not be used as hierarchical priors. All four models will use the same prior distributions on M,

\[ M \sim -\log(\text{beta}(0.5, 0.5)) \]

Note that this log transformation will be used frequently in this paper for the instantaneous natural and harvest mortality rates. This log transformation is used as the quantity \( \exp^{-M} \) can be viewed as the annual survival from natural sources of mortality, which should be on the interval (0,1). The beta distribution was selected since it is a very
flexible model for data on the interval (0,1). The log transformation would thus isolate M, as desired.

We will take advantage of the prior information on the tag-reporting probability, \( \lambda \) with a hierarchical prior specification. As noted above, a previous survey independent of this dataset estimated a tag-reporting probability of 0.43 based on a survey by the Delaware Division of Fish and Wildlife (23). Since this value is used in stock assessments, we will apply it in a hierarchical normal prior with unknown variance,

\[
[\lambda] \sim N(0.43, \sigma^2), \sigma^2 \sim \text{unif}(0, 1)
\]

Inverse gamma priors were considered, but resulted in frequent model fitting errors with WinBUGS.

The annual instantaneous rate of harvest mortality, \( F_k \), will be derived in two scenarios, fixed and random effects,

\[
[F_k|\alpha, \beta] \sim -\log(\text{beta}(\alpha, \beta))
\]

\([\alpha], [\beta]\) are either assumed to be equal to 0.5 for the fixed effects formulation, or \([\alpha], [\beta]\) are assumed to be hyperparameters with uniform prior distributions on the interval (0,3). That parameterization only approximates a classical random and fixed effects model from the Bayesian perspective (38).

The hyperparameter distributions, \([\alpha], [\beta]\) were selected to allow for a range of values, but be restrictive enough to allow WinBUGS to run the MCMC sampler. The formulation above provides four models, fixed and random effect on harvest mortalities, with and without uncertainty on the tag reporting rates. These four models were applied to the full Chesapeake Bay dataset.

In this scenario, the instantaneous natural mortality rate, M was modeled as the transformed non-informative beta as above,

\[
[M] \sim -\log(\text{beta}(0.5, 0.5)).
\]
2.2.3 Mortality shift change-point model

In order to account for the shift in natural mortality caused by the outbreak of mycobacteriosis, a discrete change-point model will be applied. In this model, the same prior distributions were applied to the instantaneous rate of harvest mortality as well as the tag-return probability above. For the mortality shift change-point model, a discrete categorical distribution for the change-point for year, $\tau_Y$ was generated such that

$$P(\tau_Y = k) = p_k, \sum_k p_k = 1, k = 1, 2, \ldots, I,$$

where $k$ represents a specific year. Then

$$[exp(-M_q)|\tau_Y] \sim beta(0.5, 0.5), \text{where } q=1 \text{ if } j \leq \tau_Y, \text{ 2 otherwise}$$

A discrete uniform prior was used for $\tau_Y$.

I allowed a second prior specification to occur on $M$ using the work from Chapter 1. Using FishBase (http://www.fishbase.org), I found a maximum age estimate for striped bass of 30 years. Applying Hoenig’s equation,

$$\log(M) = 1.44 - 0.92 \times \log(t_{\text{max}}),$$

yields an estimate of $M$ of 0.185. Then,

$$[M_1|k < \tau_Y] \sim N(0.185, \sigma^2)\sigma^2 \sim \text{unif}(0, 1)$$

$$[M_2|k \geq \tau_Y] \sim -\log(beta(0.5, 0.5))$$

Change-point and model averaging

The mortality change-point parameter can be viewed as a single parameter within the model as I have presented here. An alternative viewpoint of this formulation is to consider the case where the true year of the change-point, $K^*$, is modeled using change-point formulation. Then the change-point parameter, $\tau_k = P(K^* = k)$, that is, probability of any specific year is the true year. Then, this model can be viewed as $i=I$ models, each with a different set mortality shift year $k$. Then,
\[ E(M, F, \lambda, \tau_k | X, R) = \sum_k E(M, F, \lambda | k, X, R) P(K^* = k) = \sum_k E(M, F, \lambda | k, X, R) \tau_k \]

where \( E(x, y - z) \) is the posterior marginal means of \( x \) and \( y \) given \( z \). Here, we see this model as a model averaging process using the weights of \( P(K^* = k) = \tau_k \).

### 2.2.4 Estimation

For this study posterior mean and posterior standard errors were used to provide point-estimates and estimates of precision, respectively. WinBUGS 1.4 was used to provide these estimates (30). Three chains were run with a burn-in of 10,000 iterations, with 90,000 iterations retained per chain.

### 2.3 Results

These results were not expected for a few reasons. First, the selected shift year is different than the estimated from previous studies (Table 2.1) (23). The first year of the switch, with \( \tau_Y = 10 \) corresponds to 2000, one year later than that of the previous study, though there is approximately 24% posterior probability that the change-point occurs in 1999 (Table 2.2)(23). Direct comparison with the Jiang (23) model is not possible, as our models add complexity in different places. However, the reporting rate found in this study is lower than that of the prior estimate, between 0.27 and 0.318 versus the prior mean of 0.43. The marginal posterior density on \( \lambda \) shows a strong selection for a mean around 0.3, regardless of whether a single natural mortality model or change-point model are selected (Figure 2.1) or if the shift in mortality is fixed at 1999 or 2000 (Figure 2.2).

The shift of \( \lambda \) from the prior mean has some cascading consequences in the estimates of natural mortality. The estimates of \( M \) with variable reporting rate are approximately 0.014 for \( M_1 \) (corresponding to an annual mortality rate of approximately 4%) and 0.5 for \( M_2 \) (annual mortality of approximately 40%). When contrasted with a fixed reporting rate at 0.43, the estimates are 0.2 for \( M_1 \) (18% annual mortality) and 0.6 for \( M_2 \) (45% annual mortality).

The selected model had little change in weight whether the year was 1999 or 2000 (Table 2.1). With the fixed change-point scenarios there is virtually no difference in DIC.
between these models or the variable change-point models. The set change-point for 1999 shows a higher posterior mean for \( M_1 \) and lower \( M_2 \) than shown for the set change-point in 2000. The 1999 set change-point also showed a higher posterior mean on \( \lambda \) than that of the 2000 set change-point. It is also interesting to note that the posterior means for the variable change-point models all fell between the values from the two set change-point models while the estimates from the single M models were largely outside of this interval.

The estimates of \( \lambda \) also have a strong influence on the selected change-point year (Table 2.2). With the reporting rates we see approximately 76% of the weight on the change-point in 2000. With a fixed reporting rate at the previous estimate of 0.43, we see a switch to favoring a change-point in 1999, with approximately 55% of the weight. The parameter posterior means with a fixed reporting rate of 0.43 also show significant difference from the variable reporting rate estimates (Table 2.3). Of interest, the estimates of \( M_k \) are different between the two, with the fixed reporting rate estimates being higher than the variable reporting rate model. This difference is a bit distressing, as for the set \( \lambda \) scenario, \( M_1 =0.15 \) is very close to the prior mean of 0.2, however, the estimate of \( M_2 =0.6 \) seems to be a quite high annual mortality of approximately 45%. For the variable \( \lambda \) scenarios, the annual mortality from \( M_1 \) is approximately 1% which seems way too low, though \( M_2 \) would be approximately 39% which does seem more reasonable. It is also interesting to note in Table 2.3 the harvest mortality estimates are all higher in the variable case.

Incorporating an informative prior onto \( M_1 \) shows only a moderate shift in estimates of \( M_1 \) and \( M_2 \) (Table 2.4). There appears to thus be a strong signal pulling the estimates of \( M_1 \) towards zero. An additional series of models were run with the informative hierarchical priors on M and without mortality shifts for the first seven, eight, nine and ten years of data. Since the change-point was estimated to occur between nine and ten, and chapter 1 showed reasonable ability to estimate the parameters with only six years of data, this was deemed to be a reasonable approach to see what the estimates of M and would be in the absence of the change-point. The results (Table 2.5) show relative stable M and estimates through the first nine years of the study, however, at the tenth year of data there is a dramatic shift in M and.
Table 2.1: Comparison of posterior means and DIC from single M fixed and random effects models, fixed effects models with fixed change-points set at 1999 and 2000, and variable change-point fixed and random effects models. Standard deviation in parentheses, except for DIC which has standard deviation of the deviance in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Fixed Effect</th>
<th>Random Effect</th>
<th>Fixed Effect</th>
<th>Fixed Effect</th>
<th>Fixed Effect</th>
<th>Random Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \lambda )</td>
<td>0.276(0.021)</td>
<td>0.274(0.013)</td>
<td>0.324(0.045)</td>
<td>0.301(0.028)</td>
<td>0.318(0.043)</td>
<td>0.308(0.034)</td>
</tr>
<tr>
<td>( M_1 )</td>
<td>0.016(0.027)</td>
<td>0.013(0.019)</td>
<td>0.041(0.047)</td>
<td>0.027(0.034)</td>
<td>0.042(0.047)</td>
<td>0.03(0.038)</td>
</tr>
<tr>
<td>( M_2 )</td>
<td>0.383(0.043)</td>
<td>0.387(0.042)</td>
<td>0.355(0.055)</td>
<td>0.371(0.048)</td>
<td>0.356(0.054)</td>
<td>0.366(0.049)</td>
</tr>
<tr>
<td>( F_1 )</td>
<td>0.511(0.044)</td>
<td>0.514(0.042)</td>
<td>0.471(0.063)</td>
<td>0.496(0.051)</td>
<td>0.477(0.062)</td>
<td>0.489(0.056)</td>
</tr>
<tr>
<td>( F_2 )</td>
<td>0.433(0.037)</td>
<td>0.436(0.033)</td>
<td>0.393(0.053)</td>
<td>0.416(0.042)</td>
<td>0.398(0.052)</td>
<td>0.411(0.045)</td>
</tr>
<tr>
<td>( F_3 )</td>
<td>0.415(0.034)</td>
<td>0.419(0.029)</td>
<td>0.375(0.047)</td>
<td>0.398(0.038)</td>
<td>0.382(0.048)</td>
<td>0.39(0.04)</td>
</tr>
<tr>
<td>( F_4 )</td>
<td>0.521(0.039)</td>
<td>0.526(0.036)</td>
<td>0.458(0.057)</td>
<td>0.493(0.044)</td>
<td>0.471(0.057)</td>
<td>0.484(0.051)</td>
</tr>
<tr>
<td>( F_5 )</td>
<td>0.508(0.037)</td>
<td>0.51(0.033)</td>
<td>0.427(0.054)</td>
<td>0.473(0.045)</td>
<td>0.448(0.056)</td>
<td>0.46(0.049)</td>
</tr>
<tr>
<td>( F_6 )</td>
<td>0.569(0.045)</td>
<td>0.572(0.039)</td>
<td>0.444(0.058)</td>
<td>0.509(0.05)</td>
<td>0.476(0.067)</td>
<td>0.489(0.059)</td>
</tr>
<tr>
<td>( F_7 )</td>
<td>0.669(0.062)</td>
<td>0.67(0.055)</td>
<td>0.455(0.065)</td>
<td>0.553(0.061)</td>
<td>0.511(0.085)</td>
<td>0.526(0.073)</td>
</tr>
<tr>
<td>( F_8 )</td>
<td>0.701(0.079)</td>
<td>0.704(0.068)</td>
<td>0.483(0.07)</td>
<td>0.516(0.066)</td>
<td>0.49(0.073)</td>
<td>0.504(0.068)</td>
</tr>
<tr>
<td>( F_9 )</td>
<td>0.58(0.071)</td>
<td>0.585(0.063)</td>
<td>0.496(0.07)</td>
<td>0.498(0.057)</td>
<td>0.484(0.067)</td>
<td>0.498(0.06)</td>
</tr>
<tr>
<td>( F_{10} )</td>
<td>0.424(0.051)</td>
<td>0.431(0.048)</td>
<td>0.486(0.07)</td>
<td>0.533(0.063)</td>
<td>0.504(0.075)</td>
<td>0.52(0.068)</td>
</tr>
<tr>
<td>( F_{11} )</td>
<td>0.26(0.028)</td>
<td>0.265(0.026)</td>
<td>0.367(0.053)</td>
<td>0.429(0.055)</td>
<td>0.401(0.065)</td>
<td>0.413(0.061)</td>
</tr>
<tr>
<td>( \alpha )</td>
<td>3.486(0.432)</td>
<td>3.519(0.418)</td>
<td>3.537(0.423)</td>
<td>2.635(0.327)</td>
<td>2.023(0.459)</td>
<td>2.023(0.459)</td>
</tr>
<tr>
<td>( \beta )</td>
<td>2.68(0.574)</td>
<td>2.435(0.589)</td>
<td>2.635(0.6)</td>
<td>2.023(0.459)</td>
<td>2.023(0.459)</td>
<td>2.023(0.459)</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>9(0)</td>
<td>10(0)</td>
<td>9.703(0.457)</td>
<td>9.725(0.451)</td>
<td>9.725(0.451)</td>
<td>9.725(0.451)</td>
</tr>
</tbody>
</table>

DIC: 574.699(5.194) 575.054(5.254) 504.168(5.612) 503.764(5.487) 505.28(5.582) 506.479(5.785)
2.4 Discussion

In recent years, the variety of data sources that have been incorporated into tagging studies to improve estimation and inference, for example, joining mark-recapture, tag-return and tag-resighting without recovery (2) and recapture and release (24). In some ways adding auxiliary data sources is problematic since the resulting statistical models are more complicated. However, as more data sources become available, it is possible that estimation and inference will improve.

The major difficulty in tag-return studies, outside of assumption violations, has been the estimation of natural mortality and tag-reporting probabilities (42; 33; 34). Raising model flexibility and data sources may be a vital source to improve model fit. This is especially true, in my opinion, of the tag reporting rate as tag-return studies can be established to estimate tag-reporting rates annually (16; 33; 34). The tag-reporting probability typically is considered to be a fixed quantity over the course of the study, however, it is possible that participants may lose interest in a program over time, or events like a disease outbreak may increase participation. Since reporting rates seemed to have a large impact on inference, resources should be used for improving these estimates.

In terms of the models shown here, there were a few factors that made model selection difficult. First, \( \lambda \) appeared to have a strong effect on the estimates of which model was appropriate. Second, there were strong shifts in the estimates of natural mortality that were somewhat distressing as the estimates seemed to be unrealistic. Third, the Brownie model assumption that the shift in mortality occurs at the start of the selected year is likely to be violated. A transition period is likely between the two natural mortality rates, though the difficulties in estimating natural mortality makes it unlikely that additional parameters on natural mortality can be estimated without very informed prior information.

Previous attempts to model this data looked at the ability to incorporate tag and release data with the catch data with a shift in natural mortality (23). The Jiang et al. study allowed for separate natural mortality rates on young and adult fish. One difficulty in their approach was that the year of the shift in natural mortality was estimated assuming that the reporting rate was fixed at 0.43, and they found the mortality shift occurring in 1999, one year earlier than the best estimate here. The authors did allow the reporting rate to vary, and in that case the reporting rate was estimated at 0.321(0.081) with \( M_1=0.001 \).
and $M_2=0.491$ which is very close to the estimates presented here (23). It is thus likely that under variable reporting rate that Jiang’s model and the model presented here would yield similar parameter estimates.

The results of this model leaves several questions about the biology of striped bass over this time-series. First, the rapid shift in natural mortality from the single M model with 10 years of data is suspicious (Table 2.5). The stability of estimates for the years 7-9 and sharp shift in year 10 may suggest additional violations of the model assumptions. It is possible that as media attention focused the mycobacteriosis outbreak had an impact in fisher tag-return rates, thus confounding the shift in natural mortality rates at tag-reporting probabilities. Second, the previous estimate of tag-reporting probability (0.43) does appear to be too high in all cases examined here, and even by previous authors (23). This may suggest a need to implement high-reward studies every year, as has been previously suggested for all tag-return studies (33). There is, as of yet, no substantial research into the possibility of a shift in tag-reporting probabilities, and it is clear that should such a trend occur, it would be problematic to the estimation of mortality rates.

In this paper, especially evidenced from the posterior distributions on the change-point year, a considerable degree of uncertainty in determining the "true" model has been presented. This degree of uncertainty is naturally integrated in the formulation provided here. Model averaging has been increasingly applied in ecological settings (22; 45). Model averaging could have extensive application to fisheries management where competing models offered by different interest groups and the data would allow all of the models to have an influence in management regimes, but the data would sort the impact of each.

As noted, there were some problems getting rational estimates of mortality rates in this model. There are problems with the tag-reporting probability estimates, and this study shows that the auxiliary estimate of a 43% return rate is way too optimistic. In spite of the fact that the parameter estimates may be too extreme, this model flexibility has allowed for additional insight into the tagging study that would not be possible with a conventional model. Additionally, the results suggest that a violation of the models occurred, perhaps a shift in tag-reporting probability. In the next chapter, I will look at the impact of variable tag-reporting probabilities on the Brownie models.
Table 2.2: Comparison of the posterior weights for the fixed and random effects change-point models, and the fixed effects model with a set reporting rate, $\lambda=0.43$.

<table>
<thead>
<tr>
<th>Model</th>
<th>Proportion $\tau_Y = 1999$</th>
<th>Proportion $\tau_Y = 2000$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed effects, hierarchical $\lambda$</td>
<td>0.240</td>
<td>0.760</td>
</tr>
<tr>
<td>Random effects, hierarchical $\lambda$</td>
<td>0.234</td>
<td>0.776</td>
</tr>
<tr>
<td>Fixed effects, $\lambda = 0.43$</td>
<td>0.55</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Table 2.3: Comparison of fixed effects change-point models with varying certainty on $\lambda = 0.43$

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\lambda$ hierarchical prior</th>
<th>$\lambda=0.43$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda$</td>
<td>0.318</td>
<td></td>
</tr>
<tr>
<td>$M_1$</td>
<td>0.042</td>
<td>0.155</td>
</tr>
<tr>
<td>$M_2$</td>
<td>0.493</td>
<td>0.601</td>
</tr>
<tr>
<td>$F_{1991}$</td>
<td>0.356</td>
<td>0.259</td>
</tr>
<tr>
<td>$F_{1992}$</td>
<td>0.477</td>
<td>0.348</td>
</tr>
<tr>
<td>$F_{1993}$</td>
<td>0.398</td>
<td>0.291</td>
</tr>
<tr>
<td>$F_{1994}$</td>
<td>0.382</td>
<td>0.285</td>
</tr>
<tr>
<td>$F_{1995}$</td>
<td>0.471</td>
<td>0.348</td>
</tr>
<tr>
<td>$F_{1996}$</td>
<td>0.448</td>
<td>0.325</td>
</tr>
<tr>
<td>$F_{1997}$</td>
<td>0.476</td>
<td>0.342</td>
</tr>
<tr>
<td>$F_{1998}$</td>
<td>0.511</td>
<td>0.354</td>
</tr>
<tr>
<td>$F_{1999}$</td>
<td>0.490</td>
<td>0.351</td>
</tr>
<tr>
<td>$F_{2000}$</td>
<td>0.484</td>
<td>0.356</td>
</tr>
<tr>
<td>$F_{2001}$</td>
<td>0.504</td>
<td>0.364</td>
</tr>
<tr>
<td>$F_{2002}$</td>
<td>0.401</td>
<td>0.287</td>
</tr>
<tr>
<td>$\tau_Y$</td>
<td>9.703</td>
<td>9.422</td>
</tr>
<tr>
<td>DIC</td>
<td>505.280</td>
<td>505.251</td>
</tr>
</tbody>
</table>
Figure 2.1: The posterior densities for the tag reporting rate, $\lambda$, for the fixed and random effects models with variable $\lambda$. 
Figure 2.2: The posterior densities for the tag reporting rate, $\lambda$, for the fixed and random effects models with variable $\lambda$. 
Table 2.4: Comparison of posterior means and DIC from change-point models with informed normal priors on natural mortality. The mean of these distributions is 0.185 based on Hoenig’s equation. The results on the left come from a model using an informed normal prior on $\lambda = 0.43$. Results on the right use a non-informative beta prior on $\lambda$. Data shown as posterior mean (MCMC standard deviation).

<table>
<thead>
<tr>
<th></th>
<th>Informed $\lambda$</th>
<th>Non-informed $\lambda$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_1$</td>
<td>0.072 (0.056)</td>
<td>0.059 (0.055)</td>
</tr>
<tr>
<td>$M_2$</td>
<td>0.523 (0.088)</td>
<td>0.513 (0.09)</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>0.343 (0.055)</td>
<td>0.333 (0.062)</td>
</tr>
<tr>
<td>$F_{1991}$</td>
<td>0.331 (0.058)</td>
<td>0.342 (0.06)</td>
</tr>
<tr>
<td>$F_{1992}$</td>
<td>0.444 (0.069)</td>
<td>0.458 (0.069)</td>
</tr>
<tr>
<td>$F_{1993}$</td>
<td>0.372 (0.058)</td>
<td>0.383 (0.058)</td>
</tr>
<tr>
<td>$F_{1994}$</td>
<td>0.357 (0.052)</td>
<td>0.368 (0.054)</td>
</tr>
<tr>
<td>$F_{1995}$</td>
<td>0.443 (0.066)</td>
<td>0.455 (0.065)</td>
</tr>
<tr>
<td>$F_{1996}$</td>
<td>0.419 (0.064)</td>
<td>0.431 (0.064)</td>
</tr>
<tr>
<td>$F_{1997}$</td>
<td>0.446 (0.072)</td>
<td>0.459 (0.073)</td>
</tr>
<tr>
<td>$F_{1998}$</td>
<td>0.478 (0.089)</td>
<td>0.494 (0.088)</td>
</tr>
<tr>
<td>$F_{1999}$</td>
<td>0.457 (0.08)</td>
<td>0.471 (0.08)</td>
</tr>
<tr>
<td>$F_{2000}$</td>
<td>0.449 (0.072)</td>
<td>0.463 (0.072)</td>
</tr>
<tr>
<td>$F_{2001}$</td>
<td>0.47 (0.083)</td>
<td>0.486 (0.08)</td>
</tr>
<tr>
<td>$F_{2002}$</td>
<td>0.374 (0.067)</td>
<td>0.388 (0.069)</td>
</tr>
<tr>
<td>$\tau$</td>
<td>9.702 (0.458)</td>
<td>9.712 (0.453)</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>2.639 (0.311)</td>
<td>2.642 (0.299)</td>
</tr>
<tr>
<td>$\beta$</td>
<td>1.894 (0.466)</td>
<td>1.942 (0.487)</td>
</tr>
<tr>
<td>DIC</td>
<td>506.315 (5.602)</td>
<td>506.89 (5.777)</td>
</tr>
</tbody>
</table>

Table 2.5: Comparison of single M models with varying lengths of data sets. All models were used the informed hierarchical M and prior distributions. Data shown as posterior mean (MCMC standard deviation).

<table>
<thead>
<tr>
<th></th>
<th>Length of data series</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7 Years</td>
</tr>
<tr>
<td>$M$</td>
<td>0.122(0.065)</td>
</tr>
<tr>
<td>Deviance</td>
<td>177.103(4.232)</td>
</tr>
</tbody>
</table>
Chapter 3

Effect of variable tag-reporting probability on instantaneous rates tag-return model estimates of natural mortality

3.1 Introduction

Fisheries managers need demographic information of target stocks in order to project population dynamics (44). One of the most important quantities of interest is the magnitude of natural mortality (21). Since managers cannot directly influence natural mortality, obtaining accurate estimates of the magnitude of natural mortality can help dictate an appropriate harvest rate(21). Natural mortalities are rarely observed, thus estimating this parameter with little direct information requires targeted studies.

Tag-return studies are a common method for obtaining estimates of mortality rates in an exploited population (44; 21; 34). In these studies a fixed number of tagged animals are released systematically (here annually). When tagged individuals are recovered dead by resource participants, the tag may be returned to managers. The instantaneous rates Brownie models allow for the estimation of natural and harvest mortality, annual instantaneous rates of harvest mortality, and a constant tag-reporting probability (21; 34).
The tag-reporting probability is defined as the probability a tag is returned to managers given that it was recovered.

The tag-reporting probability is a nuisance parameter that can create difficulties in estimating mortality rates. In particular, natural mortality rates and tag-reporting probability are correlated in the most common tagging models (33; 34; 16). Additionally, the assumptions of constant tag-reporting probability and constant natural mortality may be violated (23). Violation of the constant tag-reporting probability may occur for several reasons: changing interest in the tagging study, changes in management that may affect recoveries by specific groups of fishermen, and changes in public perception in the fishery (the conclusion of a reward study, for example). Violation of the assumption of a fixed tag-reporting probability may impact other desired estimates, especially natural mortality estimates.

Relaxing the assumption of a constant tag-reporting probability without having the help of auxiliary data means there may not be enough information to provide reliable estimates. There are several methods for obtaining auxiliary information about the tag-reporting probability. One of the most popular are high reward tag studies (33; 34). In a high reward tag study, a subset of the tagged animals are released with high reward tags. It is necessary that these high reward tags are easily distinguished from normal tags. When a high reward tag is returned, the individual returning the tag receives a reward. The assumption that makes these studies attractive is that the reward is sufficient to ensure that anyone recovering a tag will be sure to return it. Then, for this subset of tags, I can treat the data as an instantaneous rates Brownie with a perfect tag-reporting probability. The information from this study can then be used to infer the differences in the rates of recovery between the two tag types in order to estimate the tag-reporting probability for the common tags.

Changing the tag-reporting probability can be easily conceptualized as a simple shift in the tag-reporting probability after a given change-point in time. However, the exact timing of this change-point may be uncertain. In this paper, the impacts of a shift in tag-reporting probabilities will be investigated using a simulation study. The timing of the shift of tag-reporting probability will be assumed to be uncertain. Parameters will be estimated using Bayesian inference with non-informative prior distributions. The simulation will contrast the ability of the standard fixed change-point models and a change-point model
to estimate natural mortality given a variety of models. Auxiliary data will be provided through high reward tagging studies.

3.2 Bayesian Instantaneous Rates Models

3.2.1 A reparameterization of the standard Brownie model

This section provides an alternative parameterization to the standard Brownie model commonly used in the instantaneous rates tag-return literature (21; 33; 34). This new formulation allows for a Bayesian estimation approach while avoiding parameter constraints, which will be clarified below.

Suppose \( R_i \) animals are tagged and released into the population in year \( i \), and prior to harvest these animals are perfectly mixed into the population. As harvest occurs in year \( j \), \( x_{ij} \) tags released in year \( i \) are returned to managers with the assumption that tags are returned in the year of capture. Let \( \pi_{i,j} \) be the probability that a tag from an animal released in year \( i \) is recovered and returned in year \( j \). Then the likelihood of a release cohort \( i \) is,

\[
\vec{X}_i | R_i, \Pi_i \sim \text{Multinomial}(R_i, \vec{\Pi}_i)
\]

where \( \vec{X}_i \) is the vector of tag recoveries from release year \( i \), \( \vec{\Pi}_i \) is the vector of recovery probabilities for the release cohort \( i \). This model is thus a joint multinomial, the model likelihood is defined as

\[
\Lambda = \prod_{i=1}^{I} \left( \prod_{j=i}^{J} \frac{R_i}{x_{ii}x_{ii+1}, \ldots, x_{ij}} \prod_{j=i}^{J} \pi_{ij}^{-R_i - \sum_{j=i}^{J} x_{ij}} \right)
\]

In order to generate this multinomial model, the probability structure for the probability of recovering a tag in year \( j \) released in year \( i \),

\[
\pi_{i,j} = \begin{cases} 
h_j(1 - S_j) & \text{if } i = j \\ 
h_j(1 - S_j) \prod_{k=i}^{j-1} S_k & \text{if } i \neq j 
\end{cases}
\]

where \( h_j \) is the probability that a dead animal was killed in year \( j \) due to harvest and the tag returned, and \( S_j \) is the probability of surviving from year \( j-1 \) to year \( j \), \( 0 \leq h_j, S_j \leq 1 \).
The probability of a tag released in year \( i \) not being returned through the course of the study, \( \pi_{i,J+1} \), is defined as

\[
\pi_{i,J+1} = \prod_{k=i}^{J} (S_k) + \sum_{m=i}^{J} \left( (1-h_m)(1-S_m) \prod_{n=i}^{m-1} S_n \right)
\]

Note that \( \sum_{k=i}^{J+1} \pi_{i,k} = 1 \) for any \( 0 \leq S_k, h_k \leq 1 \). The more standard parameterization defines \( \pi_{i,J+1} = 1 - \sum_{k=i}^{J} \pi_{i,k} \), which may be negative depending on the given values of \( S_k \) and \( f_k \). In this case, employing a Bayesian estimation strategy via Markov chain Monte Carlo samples from the posterior distribution of \( \pi_{i,J+1} \) may often be negative, which will slow the sampling algorithm. Therefore, this unconstrained parameterization is used in order to speed up convergence.

The instantaneous rates formulation allows the separation of natural and harvest mortality. Here I define,

\[
h_j = \lambda \phi \frac{F_j}{M + F_j}
\]

\[
S_j = \exp(-M - F_j)
\]

where \( \lambda \) called the “tag-reporting probability” is the probability that a tag recovered from a harvested individual is returned to managers \( 0 \leq \lambda \leq 1 \), \( \phi \) is the probability that a tagged individual survives initial tagging and the tag is not shed, \( M \) is the instantaneous rate of natural mortality \( (0 \leq M \leq \infty) \) and \( F_j \) is the instantaneous rate of harvest mortality \( (0 \leq F_j \leq \infty) \). Here \( \phi = 1 \), but this assumption is not necessary.

### 3.2.2 A Change-Point Model for Tag-Reporting Probability

The assumption of a constant tag-reporting probability(\( \lambda \)) from the previous section is now relaxed. Instead I introduce the “change-point model”, whereby one time-dependent shift in the tag-return probability with uncertain timing of the shift is included. More specifically, define \( \lambda_1 \) and \( \lambda_2 \) as two tag-reporting probabilities occurring before or after time \( \tau \), respectively. The only difference between the standard model and the change-point model appears in the definition of \( h_j \); namely,

\[
h_j = \begin{cases} 
\lambda_1 \frac{F_j}{M + F_j} & \text{if } j < \tau \\
\lambda_2 \frac{F_j}{M + F_j} & \text{if } j \geq \tau 
\end{cases}
\]
where $\tau$ is the change-point variable describing the timing in the change in tag-reporting probability, $P(\tau = j) = p_j, \sum_{k=1}^{J} p_k = 1$.

### 3.2.3 High reward tags

In addition to traditional tags, various auxiliary studies may be employed to provide additional information which can help estimate key parameters (33; 34; 21; 32; 15; 19). For a particular analysis I will include data from both a high reward tag study and a traditional tagging study. The standard and change-point models are valid for traditional tagging studies. However, the model is slightly altered for high reward tag data, because the reward for returning a tag is assumed to be large enough that all recovered high reward tags are returned. Hence, the standard model developed above may still be employed, with the assumption that $\lambda = 1$. Thus, the type of tag will dictate the likelihood employed.

### 3.2.4 Prior probability distribution

Having specified the model in section 3.2, prior probability distributions must be specified for each of the parameters in the model. Let

$$\exp(-M) \sim \text{beta}(0.5, 0.5)$$
$$\exp(-F_j) \sim \text{beta}(0.5, 0.5)$$
$$\lambda_l \sim \text{beta}(0.5, 0.5)$$
$$p_l = 1/J$$

where $j=1, \ldots, J, l=1$ if using the standard Brownie model, $l=1,2$ otherwise. Priors were set on the quantities $\exp(-M)$ and $\exp(-F_j)$ since they are defined on the interval $(0,1)$, and it was reasoned that more people would be able to describe prior information on mortality as a probability instead of an instantaneous rate. Beta(0.5,0.5) was chosen as priors as it is the Jeffrey’s prior (36).

### 3.2.5 Simulation

In order to investigate the ability of these models to estimate parameters, particularly $M$, given a shift in tag-reporting probability, a small factorial design was developed.
For the factorial study, two different factors were varied, the number of years of high reward tags released and the magnitude of the tag-return probability. Three reward tag scenarios are considered in order to investigate the impact of the quantity of reward tags on estimation: (i) 100 high reward tags released in the first three years only, (ii) 100 high reward tags released in the first year only, and (iii) no high reward tags released. Additionally, there were two tag-return probability scenarios, (a) $\lambda = [0.7, 0.5]$ with the change-point $\tau = 6$, and (b) $\lambda = [0.5, 0.3]$ with the change-point $\tau = 6$. For these scenarios $M = -\log(0.9)$, corresponding to 90% survival from natural causes of mortality.

In addition to the factorial study run above, three additional cases were investigated. First, to make sure that the change-point was able to detect a shift in tag-reporting probability that wasn’t in the middle of the time-series, a scenario was generated with $\lambda = [0.7, 0.5]$ with the shift occurring after year 3 (called the “Early Shift” scenario). Here, $M = -\log(0.9)$. Additionally, to investigate a scenario with higher natural mortality rates, a scenario with $M = -\log(0.7)$, $\lambda = [0.7, 0.5]$ with the shift after year 5 (called the “High Mortality” scenario). Finally, to test the ability to detect the shift in tag-reporting probability in a shorter time series, a six-year time series was run, with $\lambda = [0.7, 0.5]$ with the change-point $\tau = 4$ (called the “short” scenario. Again, $M = -\log(0.9)$. All of these scenarios used 3 years of high reward tag releases as above.

For each scenario, 100 simulations were run, both the standard and change-point Brownie models were fit. All scenarios had 1000 normal tags associated with each release year. $F = -\log([0.5,0.7,0.5,0.7,0.5,0.7,0.5,0.7,0.5,0.7])$ in all cases except the truncated scenario, where the first six elements were used. For each model, posterior means and “MCMC standard error” were used as point and precision, respectively. The Gelman-Rubin statistic was used to confirm convergence, and additional analyses with the likelihoods set to zero were used to confirm that the sampler would return the prior distributions; also to confirm posterior convergence. All models were run using WinBUGS 1.4 software (30). For each model, three chains were run, and 5,000 samples were returned from each chain for estimation. Burn-in varied from 20,000 to 30,000 for the standard model and 60,000-70,000 for the change-point model. The high burn-ins were used for the two lower information scenarios (no high reward tags, high mortality) out of precaution to ensure convergence.
3.3 Results

Tables 3.1-3.2 provide the results to these simulation studies. There appears to be a substantial impact of a shift in tag-return probability on the ability of the standard instantaneous rates Brownie models to estimate the instantaneous rate of natural mortality (see Table 3.1). For the factorial study, increasing the number of high reward tags improves estimates of \( M \) for both models in terms of bias and precision. One year and zero years of high reward tagging studies resulted in very poor fit of the standard model, including extreme difficulty in estimating the tag-reporting rate for the higher tag-reporting probability scenario. This result is somewhat counter-intuitive, as one would expect with more data, one would have better estimates.

In contrast to the standard model, the change-point model performed very well for the factorial study, also shown in Table 3.1. For the three years and one year of high reward tag data, with posterior means of \( M \) between 0.104 and 0.109 compared to a true value of 0.105, the model did very well at estimating natural mortality. Also, as expected, precision of the model estimates improved with increased years of high reward tag releases. With a lack of high reward tags, the change-point model did show biased estimates of natural mortality, but no worse than the standard model did with three years of high reward tags. In all cases, the estimates of tag-reporting probability and change-point were very reasonable, with only the change-point showing some slight bias for the three and one year of high reward tag scenarios. Reducing the tag-reporting rate had very little impact on the precision of the parameter estimates.

The results were similar across the additional scenarios shown in Table 3.2. The change-point model showed very precise estimates of \( M \) (\( \hat{M} = 0.355 \) compared to \( M = 0.357 \)) and \( \lambda_1 \) (\( \hat{\lambda}_1 \approx \lambda_1 = 0.7 \)) for the scenario of increased natural mortality whereas the standard model showed a much more substantial bias in the estimate of \( M \). To assess if the change-point model was doing well simply because \( \tau \) was the exact middle of the time-series, the model shifting \( \tau \) to year 4 showed identical performance to the cases above with estimates of \( \tau = 4.2 \), and very precise estimates of the target parameters, with \( \hat{M} = 0.111 \), \( \hat{\lambda}_1 = 0.705 \) and \( \hat{\lambda}_2 = 0.505 \). The standard model was exceptionally biased in this case (\( \hat{M} = 0.425 \), \( M = 0.105 \)),
Table 3.1: Summary of the results of the 100 simulations of the factorial study. Estimates are the posterior means, and SE is the MCMC standard error. $M = 0.105$ and $\tau = 6$

<table>
<thead>
<tr>
<th>Model</th>
<th>Reward</th>
<th>$\lambda$</th>
<th>$M(SE)$</th>
<th>$\lambda_1(SE)$</th>
<th>$\lambda_2(SE)$</th>
<th>$\tau(SE)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard 3 Yr</td>
<td>0.7,0.5</td>
<td>0.131(0.016)</td>
<td>0.685(0.024)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CP 3 Yr</td>
<td>0.7,0.5</td>
<td>0.104(0.014)</td>
<td>0.716(0.022)</td>
<td>0.515(0.025)</td>
<td>6.12(0.293)</td>
<td></td>
</tr>
<tr>
<td>Standard 3 Yr</td>
<td>0.5,0.3</td>
<td>0.129(0.016)</td>
<td>0.481(0.018)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CP 3 Yr</td>
<td>0.5,0.3</td>
<td>0.107(0.014)</td>
<td>0.501(0.018)</td>
<td>0.296(0.019)</td>
<td>6.19(0.253)</td>
<td></td>
</tr>
<tr>
<td>Standard 1 Yr</td>
<td>0.7,0.5</td>
<td>0.272(0.022)</td>
<td>0.951(0.049)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CP 1 Yr</td>
<td>0.7,0.5</td>
<td>0.109(0.024)</td>
<td>0.709(0.034)</td>
<td>0.499(0.032)</td>
<td>6.195(0.338)</td>
<td></td>
</tr>
<tr>
<td>Standard 1 Yr</td>
<td>0.5,0.3</td>
<td>0.185(0.03)</td>
<td>0.541(0.038)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CP 1 Yr</td>
<td>0.5,0.3</td>
<td>0.108(0.024)</td>
<td>0.503(0.026)</td>
<td>0.3(0.023)</td>
<td>6.206(0.313)</td>
<td></td>
</tr>
<tr>
<td>Standard 0 Yr</td>
<td>0.7,0.5</td>
<td>0.275(0.02)</td>
<td>0.958(0.045)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CP 0 Yr</td>
<td>0.7,0.5</td>
<td>0.128(0.062)</td>
<td>0.751(0.098)</td>
<td>0.534(0.077)</td>
<td>6.24(0.448)</td>
<td></td>
</tr>
<tr>
<td>Standard 0 Yr</td>
<td>0.5,0.3</td>
<td>0.359(0.034)</td>
<td>0.882(0.089)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>CP 0 Yr</td>
<td>0.5,0.3</td>
<td>0.131(0.083)</td>
<td>0.555(0.111)</td>
<td>0.333(0.079)</td>
<td>6.235(0.519)</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.2: Summary of the results of the 100 simulations of the auxiliary scenarios investigating a high natural mortality, early change-point and short study. Estimates are the posterior means, and SE is the MCMC standard error. $M = 0.105$ with the exception of the high mortality scenario, $\tau = 4$ with the exception of the high mortality scenario where $\tau = 6$

<table>
<thead>
<tr>
<th>Model</th>
<th>Scenario</th>
<th>$M(SE)$</th>
<th>$\lambda_1(SE)$</th>
<th>$\lambda_2(SE)$</th>
<th>$\tau(SE)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard</td>
<td>M=0.357</td>
<td>0.402(0.026)</td>
<td>0.712(0.038)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CP</td>
<td>M=0.357</td>
<td>0.355(0.026)</td>
<td>0.7(0.038)</td>
<td>0.491(0.041)</td>
<td>6.182(0.5)</td>
</tr>
<tr>
<td>Standard</td>
<td>$\tau = 4$</td>
<td>0.425(0.026)</td>
<td>0.673(0.038)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CP</td>
<td>$\tau = 4$</td>
<td>0.111(0.024)</td>
<td>0.705(0.038)</td>
<td>0.505(0.028)</td>
<td>4.178(0.32)</td>
</tr>
<tr>
<td>Standard</td>
<td>6 Yr Study</td>
<td>0.096(0.018)</td>
<td>0.657(0.023)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CP</td>
<td>6 Yr Study</td>
<td>0.108(0.018)</td>
<td>0.695(0.073)</td>
<td>0.511(0.060)</td>
<td>4.066(0.69)</td>
</tr>
</tbody>
</table>

which may question whether the standard model can provide reasonable estimates if the change-point isn’t in the middle of the time series. Both the standard and change-point models performed remarkably well for the 6 year tagging study, with reasonable estimates of M in both cases, though the change-point model did show slightly less bias. This may be due to the fact that there were only six years of standard tags, but three-years of high reward tags, so a more substantial fraction of the tagging data came from the high reward tags.
3.4 Discussion

The change-point model framework shown here appears to be able to estimate natural mortality given a shift in tag-reporting rate with reward tag studies under a change-point model. The traditional fixed $\lambda$ instantaneous rates Brownie model appeared to have very biased estimates of natural mortality in virtually every scenario with the exception of the shorter survey. For the shorter survey, the reward tags would have provided a greater relative contribution to the likelihood, resulting in better information.

These results suggest greater investment into tag-return studies may be necessary in order to obtain reliable estimates of natural mortality. Clearly, additional information in the form of high reward studies enhanced estimates, especially in the case of a truncated data series. If managers are interested in a single, fixed estimate of natural mortality, it may be better to reduce the length of the traditional tagging study while concurrently utilizing longer high reward tagging study. Ideally, a high reward tagging study should run the length of the standard tagging study (33). In fact, these results seem to argue that unless the system is deemed to be ideal (i.e. constant natural mortality, constant tag-reporting probability), when no auxiliary data such as a high reward tag study is available, the resulting parameter estimates generated from a tagging study should be under considerable scrutiny.

There are several alternatives to reward tagging studies as ways to improve information on parameters. Tag-reporting rates can benefit from other auxiliary studies such as planted tags (15) and observers (16). Natural mortality estimates can benefit from telemetry studies (35; 19) and multiple annual tagging events (17). Reducing uncertainty in one parameter will improve estimates of other parameters (Chapter 1). Thus managers may have many options to improve the information in tagging studies, and the results here suggest they add as much information as is feasible. High reward tag studies seem advantageous compared to alternative methods for auxiliary information in the sense that the modeling framework is identical to a traditional tagging study, the parameters are under the identical processes and time-scales as a traditional tagging study. These studies would require less additional work relative to other alternatives.

Reward tag studies carry the strong assumption that tag-return behavior is not effected by the study (33; 34). This assumption may be violated as enthusiasm in return tags
may change if there is no longer a strong monetary incentive. The change-point framework may allow a relaxation of this assumption by allowing a separate reporting rate at the conclusion of the reward study, hopefully encouraging more managers to use high reward tags in their studies.

There has been a long debate on the application of Bayesian methods (for recent debate see (12; 27)). One of the most frequent complaints about Bayesian statistical methodology is computationally intensive. There is certainly truth to this argument, however, no individual model-scenario took longer than two hours of processing time. In the course of analyzing a real dataset, a maximum of a day to analyze several models for a 10 year data study seems very reasonable. As processing power gets faster and cheaper, and numerical algorithms and software improve, the complaints about the processing time will become more trivial. The alternative formulation of the Brownie model probability structure formulated here greatly reduced the processing time versus other models investigated (i.e. Chapter 2), and as such I recommend using this formulation in the future.

In light of the computer intensive nature of Bayesian methods, it is important to ask if these methods provide enough benefits to justify either managers learning the methods or investing in hiring statisticians to do the analysis. I can’t claim to be unbiased in this argument, but it appears to me that the Bayesian methods make it easier to ask biological questions and provide inference (10; 12). As research continues on improving sampling methods, model selection, and estimation, the methodology will only improve. It’s important that two major barriers to wider acceptance of the method be reduced; Bayesian methods need to be taught in ecology programs, and software needs to become available that allows specific models to be easily investigated. Until these two steps occur, I feel that this type of modeling approach will largely have a niche amongst quantitative ecologists, but may lack the wider support I feel it warrants.
Bibliography


