

Stock-recruit models for Fraser River Sockeye Salmon (*Oncorhynchus nerka*) escapement planning

by

Ann-Marie M. Huang

B.Sc., University of British Columbia, 1996

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Approval

Name: Ann-Marie M. Huang
Degree: Master of Resource Management
Project No.: 611
Title: *Stock-recruit models for Fraser River Sockeye Salmon (Oncorhynchus nerka) escapement planning*
Examining Committee: **Chair:** Lindsay Gardner
Master of Resource Management Candidate

Dr. Sean P. Cox
Senior Supervisor
Associate Professor

Michael J. Staley
Supervisor
Biologist, IAS Ltd.

Alan J. Cass
Supervisor
Biologist (retired), Fisheries and
Oceans Canada

Date Defended/Approved: December 02, 2014

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Abstract

The Larkin stock-recruit model has been used to evaluate long term escapement plans for Fraser Sockeye (*Oncorhynchus nerka*) since 2006. However, relatively few studies have examined how the Larkin model represents the long term behavior of Fraser Sockeye stocks in comparison to the Ricker stock-recruit model. I identify a representative cyclic Larkin-type, non-cyclic Ricker-type, and undetermined cyclic pattern stock using Deviance Information Criterion. I then compare the bias and precision of parameter estimates using the Ricker and Larkin models and the abundances projected in forward simulations using both models to a historical baseline. My results suggest that the use of stock-specific model forms may be warranted for some stocks and that evaluation of long term escapement plans should focus more on performance measures calculated on the first few generations of forward simulations.

Keywords: *Oncorhynchus nerka*; sockeye salmon; Larkin stock-recruit model; cyclic stocks; bias; escapement plan

to mark

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Chapter 1.

Introduction

The Fraser River system in British Columbia produces the most abundant run of sockeye salmon in Canada. Fraser River Sockeye Salmon (*Oncorhynchus nerka*), herein referred to as Fraser Sockeye, are mainly caught in the marine waters of British Columbia (BC) and Washington State and in-river fisheries in BC. Fraser Sockeye are caught in commercial and recreational fisheries on both sides of the border as well as in First Nations' food, social, and ceremonial fisheries in BC and tribal ceremonial and subsistence fisheries in Washington. The United States and Canada originally signed the Pacific Salmon Treaty (PST) in 1985.

In the PST, Fraser Sockeye are aggregated into four management groups for planning fisheries. These management groups are constructed based on the marine return timing of Fraser Sockeye. With the exception of the Early Stuart management group, which consists of one stock, the management groups are comprised of stocks that differ with respect to productivity, abundance, susceptibility to mortality associated with migration conditions, and whether they exhibit cyclic patterns in return abundance or not. Despite these differences, annual escapement goals are set at the management group level, with one Total Allowable Mortality (TAM) rule for each management group.

TAM rules define escapement goals for management groups at three levels of abundance: (1) at abundances below the lower fisheries reference point (L-FRP), the escapement goal is 70-90% of the abundance, depending on the management group, (2) at abundances above the upper fisheries reference point (U-FRP), the escapement goal is 35-40% of the abundance, and (3) at abundances between the L-FRP and U-FRP, the escapement goal is set at the L-FRP (Figure 1.1). TAM rules are chosen based on feedback from participants in the annual escapement planning process. The

participants evaluate performance measures that summarize the outcomes of different TAM rules on 19 Fraser Sockeye stocks that have long term stock-recruit datasets, herein referred to as “forecasted stocks”. The performance measures most frequently used for deliberations are probabilities associated with catch and escapement. For example, when applying a TAM rule to a management group, what is the probability of the escapement of a forecasted stock within the management group dropping below an abundance benchmark over the 48 year simulation period? The participants decide what their tolerance is for occurrences of low catch compared to low escapement. Thus, for each management group and harvest rule combination, participants in the escapement planning process must not only weigh the outcomes of catch and escapement for each forecasted stock within a management group, but how each TAM rule interacts with the other three TAM rules and all of the forecasted stocks within those groups (Pestal et al. 2008).

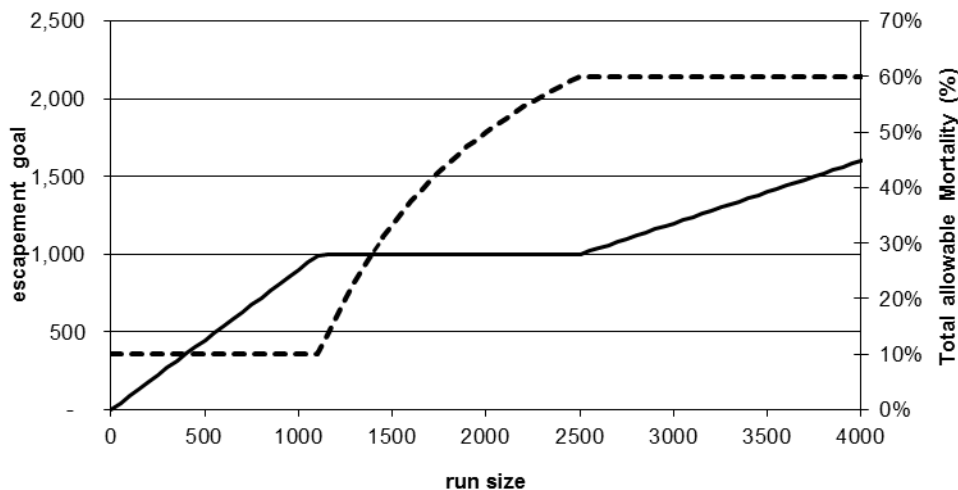


Figure 1.1. Schematic of hypothetical Total Allowable Mortality (TAM) rule (dotted black line) and resulting escapement goal (solid black line) defined by a lower fisheries reference point of 1000, an upper fisheries reference point of 2500, and a maximum TAM of 60%.

While the process for setting escapement goals is complicated, the model that the process relies on for performance measures is not. The escapement plan evaluation model uses a Larkin stock-recruit model to represent the range of future adult recruits to the fishery that will result from the parental spawning stock in response to different TAM

rules over a 48 year period. The model simulations are summarized into performance measures for the escapement planning process.

Historically, the Ricker model has been used for run size forecasts and evaluation of escapement plans for Fraser Sockeye (Cass et al. 2004, Cass et al. 2006). However, since a recommendation was made to use the Larkin model for evaluating escapement plans due to its ability to include interactions between cycle lines in a 2006 workshop on population dynamics (DFO 2006), the Larkin model has played a growing role in both of these products. Unlike the Ricker model, for which there have been numerous papers evaluating potential biases and effects of priors on estimating stock-recruit parameters and management parameters such as the stock size that maximizes sustainable yield (S_{msy}) (e.g., Walters and Staley 1987, Adkison and Peterman 1995, Rivot et al. 2001, Su and Peterman 2012), relatively few studies evaluate potential biases in the Larkin model (e.g., Collie and Walters 1987). To my knowledge, no studies evaluate the effects of Larkin model priors on estimating stock-recruit parameters or long term projections of run size. Several studies evaluate the ability of both the Ricker and Larkin models to forecast short term run size (Cass et al. 2006, Grant et al. 2010), and to evaluate alternate harvest strategies if historical deviations from the stock-recruit models were known (Martell et al. 2008, Marsden et al. 2009), but only Collie and Walters (1987) and Myers et al. (1998) used the Larkin model for longer term forward simulations. Myers et al. simulated a hypothetical stock for 100 years to compare the abundance patterns created by a Larkin model to the patterns created by a Ricker model subjected to stochastic events and found them to be comparable. Collie and Walters' simulations focussed on evaluating the effects of different harvest strategies on the Late Shuswap stocks over 50 years. The Late Shuswap stocks are the largest contributor to the total abundance of Fraser Sockeye and cycle in a distinct pattern of one dominant cycle line followed by a sub-dominant line, that is on average less than 20% of the dominant cycle run size, and then two off-cycle lines that average less than 1% of the dominant cycle run size. Not all Fraser Sockeye stocks exhibit cyclic behavior.

Fishing plans are dependent on the interaction between the in-season estimated run size and the TAM rules. There are costs associated with over or under estimating a spawning escapement goal. In the short term, the immediate costs are fewer fish

reaching the spawning grounds if the goal is underestimated, or lost harvest opportunities in the case of overestimation. In the longer term, both scenarios will lead to fewer fish recruited to the fishery than the theoretical optimum. In the escapement planning process, an annual TAM rule is chosen partially based on the outcomes of simulations that apply TAM rules 48 years into the future. A stock modelled with the Larkin model has lower potential productivity than the same stock modelled with the Ricker model (Marsden et al. 2009) and a higher harvest rate that maximizes sustainable yield (Martell et al. 2008). Applying these findings by Martell et al. (2008) and Marsden et al. (2009) to escapement planning means that using the Larkin stock-recruit model as opposed to the Ricker model will result in lower long term catches, but stocks that are capable of withstanding higher total mortalities. Therefore, it is important to know whether there are biases associated with estimating Larkin parameters and what the implications are of using different stock-recruit models when evaluating long term escapement plans for Fraser Sockeye.

In this paper, I evaluate (1) biases associated with estimating stock-recruit parameters for non-cyclic stocks with the Larkin model and cyclic stocks with the Ricker model, and (2) the potential implications of using different model forms and priors on the probabilities of catch and escapement calculated for the escapement planning process. Specifically:

1. are the Larkin parameters that describe the interaction between cycle lines caused by biases in parameter estimation for non-cyclic stocks? which model has the least bias and uncertainty associated with it when estimating stock-recruit parameters from all stock types?
2. how does the choice of Larkin model form and priors that are used to model the interactions between cycle lines affect the performance measures used to evaluate TAM rules?

The first part of my project extends a portion of the work of Collie and Walters (1987). I assess whether the parameters that describe the interaction between cycle lines are due to bias from using the Larkin model to estimate stock-recruit parameters for stocks other than the highly cyclic Late Shuswap stock. This is needed because the Larkin model is being used to model all Fraser Sockeye stocks in the escapement plan model, not only the cyclic ones. The second part of my project evaluates how changing

model forms or priors could potentially affect the catch and escapement performance measures used in the escapement planning process to choose between TAM rules.

1.1. A brief overview of Fraser Sockeye biology

For a detailed life history of Pacific salmon, I refer the reader to Groot & Margolis (1991). Below, I focus only on Sockeye salmon life history characteristics that are directly relevant to this project.

1.1.1. Life history

Fraser Sockeye are semelparous salmonids that mostly return to spawn in their fourth year of life after spending two years in the ocean. Some populations have a large five year old component (Pitt and Birkenhead) or are immediate ocean migrants that spend two to three years in the ocean environment (Harrison); however, these stocks are the exceptions that make up a small percentage of the annual return in most years. Fraser Sockeye adults are intercepted in fisheries along the coast of Alaska, British Columbia (BC) and Washington while en-route to their natal streams. The Alaskan catch of Fraser Sockeye is typically low and occurs during fisheries directed on northern salmon stocks weeks in advance of fisheries on Fraser Sockeye in BC and Washington waters. The in-season estimates of run size do not take into account the Alaskan catch since information on how much of their sockeye catch was Fraser-bound is unavailable until after the fishing season. Escapement goals for Fraser Sockeye are applied only to the management of fisheries in BC and Washington.

1.1.2. Cyclic Dominance

Several populations of Fraser Sockeye exhibit “cyclic dominance” – a repeating four year pattern of high and low abundance cohorts, the most obvious example being the Late Shuswap pattern mentioned earlier. Cycles are not unchangeable. Prior to the Hells Gate slides of 1913-14, the Fraser Sockeye stocks cycled simultaneously, with one large, dominant cycle followed by three small off-cycle years (Larkin 1971, Gilhousen 1992). Following the 1913-14 Hells Gate slides, the dominant cohorts of cyclic stocks re-

established themselves on different years. In the years since, there have been further changes to the cyclic pattern of some stocks. As an example, since the start of the run size dataset in 1952, the 2001 cycle line has been the dominant line for Early Stuart. However, the low productivity affecting the 2005 brood year resulted in much lower than cycle average returns for Early Stuart in 2009, and the subsequent improvement in productivity exhibited by most stocks returning in 2010 also applied to Early Stuart. As a result, the preliminary estimate of the 2014 Early Stuart run appears to be greater than the preliminary 2013 run size, which may indicate the start of a shift in the cyclic pattern for this stock. (data from Pacific Salmon Commission, M. Lapointe pers. comm.).

Cass & Wood (1994) identified eight strongly cyclic stocks (lower Adams, lower Shuswap, Quesnel, Early Stuart, Late Stuart, Gates, Portage, and Seymour), six inconsistently cyclic stocks (Chilko, Stellako, Nadina, Bowron, Raft, and Cultus), and three non-cyclic stocks (Weaver, Birkenhead, Upper Pitt). The stocks with the most prominent cyclic pattern are also stocks with the highest percentage of four year old fish in the age structure and tend to be in the upper watershed, where the spawning and rearing conditions are more stable (Collie and Walters 1987). The biological cause for cycles is unknown. Researchers have proposed different causal mechanisms, including: predation during the freshwater life history stage (Ward and Larkin 1964, Guill et al. 2013), fishing pressure (Walters and Staley 1987, Martell et al. 2008), and age composition (Levy and Wood 1992, Walters and Woody 1992). Others have eliminated fisheries (Cass and Wood 1994) and age composition (Walters and Woodey 1992) as the sole causal mechanism for cyclic patterns. Some have concluded that cycles are not inherent, but caused by external events (Myers et al. 1997 and 1998). And others still that density dependence is the only plausible explanation (Ricker 1997).

1.2. Stock-recruit models

Fraser Sockeye stock-recruit models are mathematical representations of the biological relationship between the number of successful spawners in a brood year and the number of adults returning 4-5 years later. Fisheries planning relies heavily on the stock-recruit models used to provide forecasts of run size and to evaluate TAM rules. The models used for forecasting are stock-specific and can incorporate near-term

information such as estimates of juvenile abundance, recent productivity trends, and environmental data (e.g., sea surface temperature or sea surface salinity). There is currently only one stock-recruit model used to evaluate TAM rules, but this has changed over time. Initially, the density dependent Ricker model, which assumes that the juvenile mortality rate increases as the number of eggs increases (Hilborn and Walters 1992), was used to represent all stocks. Following that, two Ricker stock-recruit models were used for cyclic stocks – one to represent the dominant and sub-dominant cycles and the second to represent the off-cycles (Cass et al. 2004). Since 2006, all stocks are represented with the Larkin model, which assumes delayed-density dependence, where the juvenile mortality rate not only depends on the number of eggs laid in that particular year, but also in the four previous years (Pestal et al. 2011). Both Ricker and Larkin models are included in the suite of models used for forecasting run size. However, the priors that describe the between cycle line interactions differ between the escapement plan evaluation model and the run size forecast model. The escapement plan model only allows for negative interactions between cycle line interactions whereas the run size forecast models allow for both positive and negative interactions (Grant et al. 2010, Pestal et al. 2011). I compare the effect of using different Larkin model priors in my project.

1.2.1. Identifying “Ricker” versus “Larkin” stocks

The first part of my analysis on using the Deviance Information Criterion (DIC) to identify stock-specific model forms was completed earlier and subsequently included into a broader review of the escapement plan model. It was reviewed by the Pacific Scientific Advice Review Committee (PSARC) and published as part of Pestal et al. (2011). Part of the original recommendation by Pestal et al. was to use the stock-specific model forms determined by the DIC in the escapement plan model. The PSARC process recommended the continued use of the Larkin model for all stocks. The rationale was that although there was evidence that the Ricker model or Larkin models with fewer lag β terms was the most parsimonious model for some stocks, in those cases, the lag β coefficients should be close to zero and wouldn't exert much influence over the stocks during the forward simulations. The Larkin lag β coefficients describe the between cycle line interactions. No tests were conducted to validate this recommendation following the

meeting. It wasn't recognized until after the meeting that the Larkin lag β coefficients for the stocks identified as Ricker-type were the highest out of all of the different types of stocks. As part of this project, I evaluate two versions of the Larkin model: (1) with constrained lag β coefficients, and (2) with unconstrained lag β coefficients. I expect to find that for the Ricker-type stocks, the parameters for the model with the unconstrained lag β coefficients will be closer to zero than the constrained parameters. When simulating forward, I expect to find that the Larkin with the unconstrained lag β coefficients will provide run size trajectories more similar to the Ricker model trajectories than the constrained Larkin model trajectories.

Abundance patterns of Fraser Sockeye stocks can be assigned to four cyclic behaviours: (1) Ricker-types that are not cyclic, (2) Larkin-types that are persistently cyclic, (3) Undetermined with respect to persistent cyclic patterns, and (4) Miscellaneous, which do not have a full stock-recruit dataset and are neither modelled in the escapement plan, nor have run sizes forecast with a stock-recruit model. Of the total Fraser Sockeye return from 1952-2011, the Miscellaneous stocks make up approximately 1% of the total return, although that percentage has increased over time and can be much larger in individual years. On average, the Ricker-type stocks make up 5% of the total return of forecasted stocks but approximately 10% of one cycle line. The Larkin and Undetermined stocks contributed 59% and 36% of the total return on average, respectively. Therefore, it is important to be able to represent the stock dynamics of the first three types in forward simulations. (data from Pacific Salmon Commission, M. Lapointe, pers.comm.)

1.2.2. Potential implications of using the “wrong” model

Forward simulations of the Quesnel stock using the Ricker model with a fixed annual exploitation rate of 30% lead to the disappearance of the cyclic pattern in approximately five generations, with the annual return similar to the dominant cycle line (Pestal et al. 2011). The same simulations using the Larkin model result in a continuation of cycles over a 48 year period (Pestal et al. 2011).

Starting from different assumptions about what is possible in the long term results in different strategies to optimize potential long term yield from the system by an “omniscient manager” (Martell et al. 2008). Martell et al.’s omniscient manager was given perfect knowledge of stock-recruit anomalies for the 1948-1998 brood years and programmed to find the pattern of annual harvest rates that would maximize catch over the entire time period. For a Ricker-simulated system, Martell et al.’s omniscient manager gave up catch in years of low spawners to maximize returns in later years. In the case of a Larkin-simulated system, the omniscient manager manages fisheries to a lower optimum escapement and generates lower total harvest than the Ricker simulation, a result of the Larkin S_{msy} being lower than the Ricker S_{msy} (Martell et al.). They note that if a Larkin system was managed to policies based on Ricker S_{msy} , the higher Ricker S_{msy} would mean substantial losses in the harvest of the Fraser Sockeye stocks they evaluated. The opposite case of managing a Ricker system based on Larkin S_{msy} based policies would presumably result in lower than optimal escapement and end with losses in long term yield, as well. It is important to note that unlike their estimates of S_{msy} , Martell et al.’s estimates of optimal exploitation rates were much more similar both between stocks and across models.

With the available dataset beginning well after the start of industrial fisheries, it is difficult, if not impossible to determine what optimal stock sizes could be, or whether the delayed density-dependence of the Larkin model or density-dependence of the Ricker model better represents Fraser Sockeye stocks (Martell et al. 2008). In the absence of a method to theoretically resolve density-dependent dynamics, several researchers have suggested finding empirical evidence by experimentally increasing spawning escapement on off-cycle years to differentiate between the two hypotheses represented by the Ricker and Larkin models (Collie and Walters 1987, Martell et al. 2008). The main concern that has prevented the full implementation of an experimental testing policy appears to be economic, as the testing would require severely restricting exploitation rates in the two off-cycle years (Walters and Martell 2004, Martell et al. 2008). This would not only restrict the harvest of the stock or stocks being tested, but fisheries on any co-migrating stocks or species. Some modified experiments to increase escapement have been attempted in the past, but not in a manner that was useful for quantitatively analyzing the population dynamics (Walters and Martell 2004).

1.2.3. Estimation of stock-recruit model parameters

While the evaluation of management policies such as harvest or escapement strategies on Fraser Sockeye has often used the Ricker and Larkin models to represent population dynamics, the methods used to estimate the parameters of these models has changed over time. The estimation of stock-recruit parameters has moved increasingly from maximum likelihood methods (e.g., Collie and Walters 1987) to Bayesian methods (e.g., Schnute et al. 2000, Cass et al. 2004). The use of state-space models to separately estimate the effects of process and measurement errors has become more prevalent in recent years for salmonids, although not specifically for Fraser Sockeye (e.g., Schnute and Kronlund 2002, Su and Peterman 2012). The use of state-space models for this project was not considered, as: (1) having a separate estimate of process or measurement errors would be useful for forward simulations only if the magnitude and direction of future process or measurement errors were known, and (2) Su and Peterman (2012) recommended the use of the traditional Bayesian stock-recruit methods, such as the one I am using in this paper, over state-space methods for stocks with Ricker α values less than 4 when it is important to have good quality estimates of α (e.g., when management is based on a harvest rate). I found that only six of the forecasted stocks have Ricker α values higher than 3 included in the 95% probability interval. None include a Ricker α value higher than 4 in the 95% probability interval.

1.3. Summary

Historically, the Ricker stock-recruit model has been used to represent Fraser Sockeye population dynamics and response to harvesting. After a workshop on the population dynamics of Fraser Sockeye in 2006 (DFO 2006), models that inform fisheries management decisions have shifted towards using the Larkin stock-recruit model. While the Ricker model has been rigorously tested in simulations, the Larkin model has not. In this project, I assess whether parameters that describe the interaction between cycle lines are generated by biases caused by using the Larkin model to estimate parameters for non-cyclic stocks or stocks that are not persistently cyclic, and if using the Ricker model for these stocks would result in less biased parameter estimates than the Larkin model. I then compare the effects of using different model forms and

priors on long term forward simulations to the historical range of abundances. Finally, I discuss the potential implications of my results on the current methods used to evaluate long term escapement plans for Fraser Sockeye.

Chapter 2. Methods

This chapter begins with my data sources, followed by a description of the stock-recruit models used in this paper along with parameter estimation methods, and then describes the three main components of my analysis: model selection, assessing bias when estimating stock-recruit parameters with Ricker and Larkin models, and comparing the run size trajectories of different models in forward simulations.

2.1. Data sources

The 2013 Fraser Sockeye run size forecast data was used for all stock-recruit analyses in this paper, unless otherwise noted (S. Grant, pers.comm.). This dataset contains the four and five year old recruits beginning in the 1948 brood year for the forecasted stocks with longer datasets. The last brood year for all stocks is 2006. Jacks (precocious three year old males) are not included. The spawner units are effective female spawners (EFS), and recruits are adults estimated to have returned four and five years after the brood year, with the exception of Harrison sockeye, which return as three and four year old sub-1 adults. The historical adult run size data from 1952 – 2011 was obtained from the Pacific Salmon Commission (M. Lapointe, pers. comm.).

2.2. Stock-recruit models

2.2.1. Ricker, Larkin, and Larkin variants

The Larkin model was originally proposed as an alternate method of simulating the delayed density dependence that was assumed to result in cyclic dominance without using complicated life history models. The linearized model form used in this analysis is the same as the one used for the evaluation of spawning escapement goals, estimating

annual abundance forecasts of Fraser Sockeye, and in the sensitivity analysis for Wild Salmon Policy abundance benchmarks (Pestal et al. 2011, Grant et al. 2010, Holt 2009) (eq.1). Sequentially dropping the lag β coefficients of β_1 , β_2 , and β_3 , results in eight different model variations of the Larkin, with the variation without any lag β coefficients being the Ricker model (eq. 8):

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_1 S_{t-5} - \beta_2 S_{t-6} - \beta_3 S_{t-7} + \varepsilon_t \quad \text{Larkin (1)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_1 S_{t-5} - \beta_2 S_{t-6} + \varepsilon_t \quad \text{Larkin 1\&2 (2)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_1 S_{t-5} - \beta_3 S_{t-7} + \varepsilon_t \quad \text{Larkin 1\&3 (3)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_2 S_{t-6} - \beta_3 S_{t-7} + \varepsilon_t \quad \text{Larkin 2\&3 (4)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_1 S_{t-5} + \varepsilon_t \quad \text{Larkin 1 (5)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_2 S_{t-6} + \varepsilon_t \quad \text{Larkin 2 (6)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} - \beta_3 S_{t-7} + \varepsilon_t \quad \text{Larkin 3 (7)}$$

$$\ln(R_t/S_{t-4}) = \alpha - \beta_0 S_{t-4} + \varepsilon_t \quad \text{Ricker (8)}$$

Where R is the recruits in year t , S is the effective female spawners from the brood year t , α is the productivity parameter, α/β_0 describes the capacity of the system for the Ricker equation, β_1 , β_2 , and β_3 are the Larkin parameters that describe the between-cycle delayed-density interaction, and ε is the annual process error in recruitment. I will refer to β_1 , β_2 , and β_3 as “lag β coefficients”.

In the Ricker model, the biological assumption is that the mortality is proportional to the initial number of eggs deposited (Hilborn and Walters 1992). The Larkin model was originally described as a simple method to imitate cyclic patterns observed in Late Shuswap Sockeye (Larkin 1971). The biological assumptions listed by Larkin were that the cyclic patterns were due to predator-prey interactions, with juvenile salmon as the prey, and that the abundance of predators was related to the “initial abundances of prey in any year and the 3 preceding years” (p. 1501).

2.2.2. Parameter estimation

Bayesian estimation techniques are routinely used for Fraser Sockeye management models. Currently, Bayesian methods are used to generate run size forecasts, in-season run size estimates, in-season estimates of predicted loss rates, and assessments of long term escapement plans. I based my parameter estimation methods on those used for the escapement plan model in Pestal et al. (2011), which is a variation of Cass et al. (2004).

Bayesian methods summary

For all Bayesian estimation procedures in this paper, unless otherwise noted, an initial burn-in of 10,000 was conducted, after which every 7th set of parameters was sampled, resulting in the final number of Markov Chain Monte Carlo (MCMC) sample sets. For the initial parameter estimation, 20,000 MCMC sample sets of parameters were generated. For DIC goodness of fit estimates and Bayes step() function probabilities, 5,000 MCMC samples per model per stock were used, and for the simulation-estimation procedure, 1,000 MCMC samples per simulation were drawn for each of the 100 simulations resulting in a total of 100,000 MCMC samples. The burn in and thin values were decided after visually inspecting posterior density graphs, autocorrelation plots, and BGR plots of the three representative stocks for constraints imposed by priors, autocorrelation, and convergence issues, respectively. Estimation of stock-recruit parameters was conducted using WinBUGS version 1.4.3, which uses a Gibbs sampler to approximate the posterior probability density function. WinBUGS was used as both a standalone program and called from the R platform using the R2WinBUGS package.

Bayesian priors

The base case priors are the same as the priors used for the escapement plan evaluation model (i.e., as described in Pestal et al. 2011).

α – priors

The α -parameter prior is normal with mean=0 and variance =1000 (equivalent of a standard deviation of ~31.6 recruits per effective female spawner). This prior for α was used in all analyses.

β – priors

The β_0 prior is lognormal with mean = $1/\ln(S_{\max})$ and variance = 1, where S_{\max} is the highest effective female spawners ever recorded. The prior is censored so that if it is re-described as $1/C$ with C being a lognormal distribution with a mean of $\ln(S_{\max})$ and a variance of 1, then C cannot be larger than 3 times S_{\max} . This β_0 prior was used for all analyses.

In the base case, the prior for the lag β coefficients are bounded-uniform distributions between zero and 100. Alternate priors for the lag β coefficients are described in Section 2.4.3.

2.3. Model selection

The following section (2.3.1) on model selection using Deviance Information Criterion (DIC) methods was completed with the 1948-2004 dataset earlier in my project. The methods and results were subsequently incorporated into a general review of the Fraser Sockeye escapement plan methods scheduled for 2010. A paper was written describing the structure of the escapement plan model and included a section on DIC methods and recommendations. The paper was reviewed by the Pacific Scientific Advice Review Committee (PSARC) in 2010 and published as Pestal et al. 2011. The results shown in this project use the 1948-2006 dataset, consistent with the rest of my analyses.

2.3.1. Deviance Information Criterion

I calculated the Deviance Information Criterion (DIC) estimates to find the most parsimonious Larkin model form for each stock based on the series of models given above (eq. 1-8). The DIC was calculated in WinBUGS as a measure of relative support

for the eight model forms for each of the 19 forecasted stock groups, excluding Cultus, which has a large hatchery and captive brood component. To compare between model forms, I used the method in the DIC documentation which states that models with the smallest DIC has the most support, and that models with differences in DIC values of less than 5 are not substantially different. While (Spiegelhalter et al. 2002) suggest that Burnham and Anderson's (2002) "within 2 AIC values" rule of thumb could also work for DIC values, they also noted that Monte Carlo error could have an effect on DIC values.

When the DIC analysis published in Pestal et al. (2011) was reviewed at PSARC in 2010, the PSARC advice was to use the Larkin for all stocks instead of a stock-specific model form, as the "extra" lag β terms would not contribute much to how the model simulates into the future because the coefficients would be close to zero. However, instead of being close to zero, the lag β coefficients of the stocks that are classified as Ricker-type have the largest median lag β coefficients out of all forecasted stocks. This counterintuitive result comes from priors that constrain the lag β coefficients to positive values. This only allows for negative between-cycle effects (Martell et al. 2008). As part of the sensitivity analysis, I examine the effects of using the lag β priors used for forecasting annual run size as described by Grant et al. (2010). The forecast priors allow for negative coefficients and therefore, median values closer to zero.

2.3.2. Using the step() function to assess lag β coefficient terms

In addition to the DIC assessment of model fit, I assessed the probability of including each lag β coefficient using the step() function within WinBUGS. The step function assigns a value of 1 when the parameter in a single MCMC draw is ≥ 0 and a value of 0 when it is < 0 . Thus, the mean of the step() function term is the probability that a given parameter is positive. The closer the mean is to 1, the more likely that the parameter value is positive. The closer the mean is to 0, the more likely that the parameter value is a negative value. A mean near 0.5 indicates parameter value is likely near zero.

In WinBUGS, the parameters for the full Larkin model (three lag β s) were estimated using wide, normal priors (mean=0, variance = 100,000) for the lag β

coefficients to determine which direction (positive or negative) the parameter estimates would be using the step function. Lag β coefficients with probabilities higher than 80% or lower than 20% were taken to be an indication that the parameter was unlikely to be near zero. When evaluating lag β coefficients with the step() function, the thin had to be increased to 15 to avoid autocorrelation effects in some of the parameters. A total of 5000 MCMC samples were used for this part of the analysis. The results were used to identify a potential stock-specific model form for the Undetermined-type stock, since the DIC did not exclude any model forms.

2.3.3. Selection of hypothetical representative stocks

I grouped the forecasted stocks into three types using the results from the DIC evaluation of model forms: Ricker-type, where the possible models included the Ricker, but not the Larkin; Larkin-type where the possible models included the Larkin but not the Ricker, and the Undetermined-type, where neither the Ricker nor Larkin models were excluded. From each of these types, I selected the following three stocks to represent them: Bowron as an example of a Ricker-type non-cyclic stock, Late Shuswap as a Larkin-type cyclic stock, and Late Stuart as an example of a stock that is “equally likely” to be modelled by any of the Larkin variants (including Ricker) and therefore undetermined as to whether it is a persistently cyclic stock or not. Some criteria that assisted with choosing these representative stocks were: long stock-recruit datasets (back to 1948 brood year for Late Shuswap and Bowron and 1949 for Late Stuart); no recent active human intervention in the population (e.g., spawning channels, hatchery supplementation, transplants); and an age structure which is “typical” of Fraser Sockeye (i.e., mainly 4 year old returns, approximately 10% 5 year olds). As an added benefit, all three of these stocks have similar α values.

To determine the Larkin parameter set to represent each of these three stocks, I used a method described by Catherine Michielsens (pers. com.): using the 20,000 MCMC outputs from the parameter estimation on the historical dataset for the three representative stocks, determine the median alpha value and retain all of the estimates that have the median alpha value plus or minus a small increment (0.01). From the remaining set of MCMC outputs, retain the parameter sets with the 30th to 70th

percentile estimates of the β_0 parameter. For the remaining three β values, the 25th to 75th percentile estimates were retained, narrowing down the 20,000 MCMC estimates down to approximately 2-3 dozen. From this final “shortlist”, the parameter set that most closely resembled the median values for each parameter from the original 20,000 at the nearest hundredth was chosen to represent the stock for the remainder of the project, again working from the alpha to β_0 to the lag β coefficients. The Ricker representative parameter set was determined in a similar fashion, but the increment for the alpha parameter was 0.005. The median of each parameter as well as the representative parameter set is shown in Table 3.1. Priority was given to the α parameter based on the observation that it is more important to know the productivity parameter for harvest policies based on exploitation rates (Su and Peterman 2012).

2.4. Assessing bias in parameter estimation

This section describes the methods for evaluating whether the Larkin parameters that describe the interaction between cycle lines are caused by biases in parameter estimation for the three representative stocks selected in the last section. The bias associated with estimating parameters for the three types of stocks with both the Ricker and Larkin model will be assessed.

2.4.1. Simulation & estimation model

Data was simulated for 48 years, which is the length of the forward simulations used for escapement planning, using the same equation as the escapement plan evaluation model (eq. 9). Equation 9 is the non-linear form of the Larkin model previously shown (eq. 1).

$$R_t = S_{t-4} * \exp(\alpha - \beta_0 S_{t-4} - \beta_1 S_{t-5} - \beta_2 S_{t-6} - \beta_3 S_{t-7}) * \exp(\epsilon_t) \quad (9)$$

Each stock was initiated with a spawning stock based on the median effective female spawners of each cycle line (i.e., S_{t-4} in eq. 9). For the Larkin model, the average of the previous three cycle lines was used as the spawning stock for the very first year

(i.e., S_{t-5} to S_{t-7} in eq 9). Refer to Table 3.16 for the initial effective female spawner values.

When assessing the bias associated with estimating parameters, the 48 year simulation was repeated 100 times each using the Ricker and Larkin models. At the end of 48 years, the stock-recruit parameters were estimated by both the Ricker and the Larkin models using the Bayesian estimation method resulting in 1,000 MCMC estimates, which is the same number of estimates used as inputs into the Fraser Sockeye escapement planning model. For comparing trends in abundance over time, the 48 year simulation was repeated 1,000 times each using the Ricker and Larkin models.

Discarding “problematic” simulations

Simulating with the normal priors on the lag β coefficients generated the occasional simulation that ended up with “Inf”s and “NA”s in the projected run. For the bias assessment, the dataset was manually assessed and the same 23 simulations were removed for all three stocks in order to get 100 simulations that no longer contained the above, as well as of simulations that had more than one instance of a run size rounding to zero. This latter situation was present for both the base case and the normal prior scenarios.

Total mortality

For the purpose of this evaluation, all sources of mortality from the time that a fish is considered recruited into the fishery to the time of spawning was combined into a single value. This encompasses three sources of mortality that are estimated separately for the stocks each year, as well as other sources that are not. The three types of mortality that are estimated each year are: the catch (i.e., exploitation rate), the en-route mortality (an estimate of the mortality between a hydroacoustics assessment site in the lower part of the Fraser River and assessment sites on the spawning grounds), and the pre-spawn mortality (an estimate of the number of fish which die after reaching the spawning grounds, but prior to successfully spawning). Sources of mortality for which there are no estimates include the mortality that occurs during the marine migration prior to the lower reaches of the Fraser River, mortality associated with fish that die after

encounters with or avoidance of fishing gear, and non-human predation. All of these sources of mortality (estimated and unestimated) are combined into one value for the purpose of this paper.

A total mortality rate for each year is drawn from a beta distribution that approximates the total mortality rate for different time periods. When choosing a base case total mortality scenario, a number of factors were considered. The escapement goal for abundances larger than the upper fisheries reference point had been 40% of the run size of the management group since the current escapement plan began in 2006. In 2014, however, that percentage dropped to 35% for three out of four of the management groups in anticipation of very high returns, increasing the allowable mortality from 60% to 65%. The average pre-spawn mortality (PSM) rate is 10% (median = 8%) from 1938-2013 (K. Benner, pers. comm.). The allowable mortality of 60-65% combined with the average long term PSM of 10% results in an average potential total mortality of 70-75%. However, differences between management groups in en-route mortality rates and relative abundances can result in one group with an allowable exploitation rate of close to 60% co-migrating with another group with an allowable exploitation rate of 10%. This results in one or more management group acting as a harvest constraint during mixed stock fisheries so that the maximum allowable exploitation rate for all management groups may not be reached. Approximately 12% of potential catch is lost due to managing fisheries to management groups with different allowable exploitation rates (Martell et al. 2008). The 8 generations from 1980-2011 was chosen to be the base case scenario for total mortality, as it corresponds to half of the full dataset and results in an average total mortality of 66%, which is in keeping with some amount of inaccessible harvest (Table 3.1). The total mortality rate from the historical dataset was calculated as in equation 10.

$$M_t = \frac{R_t - 2 \times S_t}{R_t} \quad (10)$$

where: M is the total mortality rate in year t , R is the number of recruits, S is the number of effective female spawners and is multiplied by two to approximate the total number of successful adult spawners, male and female. A beta distribution was fit to the

total mortality rates using the `fitdist()` function in R, which is a maximum likelihood method.

Age composition & sex ratio

An age composition of 90% 4 year olds and 10% 5 year old fish was applied to the recruits generated from each brood year. This is a generalization of Fraser sockeye age compositions (Pestal et al. 2011).

A 50% male:female ratio was applied to generate the number of females on the spawning grounds. Use of a 50:50 ratio is consistent with the assumption made by DFO Stock Assessment programs when they are unable to access systems by ground to confirm the sex ratio and there are no nearby populations that can be used as a proxy (e.g., isolated systems assessed solely by overflights) (K. Benner, pers. comm.). Pre-spawn mortality in this model is incorporated into the total mortality.

2.4.2. Performance measures

The mean percentage error (MPE) and mean absolute percentage error (MAPE) were calculated from the estimated median parameter estimates from the 1,000 MCMC samples.

MPE gives an indication of bias, and MAPE the range of uncertainty. The MPE will indicate whether the overall directional bias is to overestimate or underestimate, but suffers from a shortfall in the instances where large overestimates are balanced by large underestimates. The MAPE corrects for this by taking the absolute value of the errors and giving an indication of the overall uncertainty associated with the model. The percent error performance measures as opposed to the mean raw error (MRE) or mean absolute error (MAE) were used as MPE & MAPE are not scale dependent and so can compare across stocks and parameters to find a model that performs well for all stocks. (Haeseker et al. 2005 & 2008)

Squared evaluators (e.g., root mean squared error) are strongly influenced by outliers and are not appropriate to use for the purpose of this paper because in the

escapement plan evaluation, probabilities of outcomes are evaluated based on the entire range of parameter values. When considering the escapement plan options, participants in the process evaluate performance measures in the form of “the probability of the abundance of stock X going below Y number of fish”. Outliers won’t cause issues as long as they are not biased – and if they are, will be picked up by percent error evaluators. (Haeseker et al. 2005 & 2008)

The MPE and MAPE were calculated for each parameter individually, as well as for the α and β_0 parameters combined for both Ricker and Larkin models (see next section). These evaluation metrics were calculated for each simulation. The summary statistics are calculated from all of the simulations for each simulation-estimation combination (e.g. Ricker simulated data and Larkin estimated parameters) for each stock type.

$$MPE = \frac{1}{n} \sum_{i=1}^n \frac{(\hat{R}_i - R)}{R} \times 100 \quad \text{mean percentage error (11)}$$

where R = actual parameter value, \hat{R}_i = estimated parameter value in simulation i , and n = number of simulations times number of MCMC samples.

$$MAPE = \frac{1}{n} \sum_{i=1}^n \frac{|\hat{R}_i - R|}{R} \times 100 \quad \text{mean absolute percentage error (12)}$$

Combined α and β_0 MPE and MAPE

The estimates of α , β_0 , and the lag β coefficients from each MCMC estimate are not independent of each other, as they are sampled from the joint posterior probability density function as a parameter set. Therefore, they should not only be compared individually against the “true” parameters, but be viewed together as a parameter set – that is, as a particular combination of α , β_0 , and lag β coefficients. As the β coefficients can differ from the α coefficient by an order of magnitude or more, the relative or proportional estimates of error (e.g., MPE & MAPE) will be more informative when

comparing bias and precision across the simulated stocks than absolute or raw estimates of error (e.g., mean raw error, mean absolute error). Since the Ricker model only estimates the α and β_0 parameters, only the combined α and β_0 MPE and MAPE was calculated as a method for comparing across all four simulation-estimation scenarios.

combined α and β_0 mean percentage error:

$$MPE(combined) = \frac{1}{n} \sum_{i=1}^n \left[\frac{\frac{(\hat{\alpha}_{(i)} - \alpha)}{\alpha} + \frac{(\hat{\beta}_{0(i)} - \beta_0)}{\beta_0}}{2} \right] \times 100 \quad (12)$$

where: $\hat{\alpha}$ = paired estimates of the α and β_0 parameters in a single MCMC sample

combined α and β_0 mean absolute percentage error:

$$MAPE(combined) = \frac{1}{n} \sum_{i=1}^n \left[\frac{\frac{|\hat{\alpha}_{(i)} - \alpha|}{\alpha} + \frac{|\hat{\beta}_{0(i)} - \beta_0|}{\beta_0}}{2} \right] \times 100 \quad (13)$$

2.4.3. Sensitivity analyses

Alternate lag β priors

While the escapement plan evaluation model uses the bounded-uniform priors for the lag β coefficients (Pestal et al. 2011), the run size forecast model for Fraser Sockeye uses normal priors for all Larkin β coefficients with a mean of zero and a

variance of 1000 (standard deviation ~ 31.6), which allows for negative β coefficients (Grant et al. 2010).

As a sensitivity analysis, I used normal priors for the Larkin lag β coefficients, consistent with the priors used in the run size forecast models and inferred by the PSARC recommendation to use the Larkin form for all stocks. Although Rivot et al. (2001) tested the use of normal priors for the β_0 term, I rejected this scenario as being impractical to implement, after performing a preliminary check on the Ricker α and β_0 estimates using normal priors for both parameters. The β_0 estimate results in a $\ln(R/S)$ vs EFS relationship for Scotch Creek Sockeye with a positive slope, implying that there is no upper capacity constraint, at least in the case of the Ricker model.

2.5. Population trajectories with different models

The methods in this section were used to assess the effect of alternate stock-recruit model forms and an alternate prior for the Larkin model on 48 year population trajectories.

2.5.1. Simulation model

The simulation model was the same as described for the previous analysis on assessing bias, with the exception of the discarding of problematic simulations. For this part of the analysis, an algorithm discarded simulations that had any of the following: NAs, run sizes larger than 200 million, and any instances of a run size rounding to zero fish. The 48 year simulation was repeated 1,000 times using the Ricker and Larkin models for each scenario.

2.5.2. Simulation scenarios

Alternative total mortality scenarios

The base case total mortality scenario was based on the years 1980-2011. Additional total mortality scenarios, based on the the entire available “long term” dataset

(1952-2011) and the last three generations in the “recent” dataset (2000-2011) were used to compare forward simulations.

Alternative priors and model forms

The base case model was the Larkin model with three lag β coefficients with bounded-uniform priors. The alternate prior examined was the Larkin model with three lag β coefficients with normal priors described at the beginning of section 2.4.3. The Ricker model (eq. 8) was an alternate model used for all stock types. In addition, for the Undetermined-type stock, I selected the Larkin model form with the first two lag β coefficients (eq. 2), using the information from the WinBUGS step() function. I kept the priors for the lag β coefficients to bounded-uniform priors, as in the base case.

2.5.3. Performance measures

Summary statistics on the projected run sizes from the first and last third of the 48 year simulations were compared to the historical run size range from the base case total mortality years (1980-2011). I do not expect past run sizes to represent future run sizes, however, using historical information provides a consistent measure to compare scenarios with, while providing perspective about a range of past run sizes.

Chapter 3. Results

In this section, I begin by describing the total mortality scenarios used for simulating population trajectories. Second, the results from the model selection methods are shown for all forecasted stocks (excluding Cultus). The remainder of the results are shown for the three representative stocks only. The third set of results show the bias and precision associated with estimating parameters with the Larkin and Ricker models. The fourth section examines the population trajectories for the representative stocks when simulated with the Larkin and Ricker models. Lastly, results from performing sensitivity analyses on alternate total mortality scenarios, Larkin lag β priors, a stock-specific model form for the Undetermined-type stock only, and recent historical initial effective female spawners are shown.

3.1. Total mortality estimates

The summary statistics of the beta distribution used to fit the total mortality scenarios were checked against the actual data and are both shown in Table 3.1. The median total mortality of the long term scenario is only 5% larger than the base case, but the recent mortality scenario is 12% less than the base case (Table 3.1).

Table 3.1. Summary statistics of total mortality scenarios. Modelled distribution is shown in the first row of each scenario with summary statistics from the historical data shown in italics.

scenario	start year	p25	median	mean	p75
long term	1952	63%	72%	71%	81%
		<i>64%</i>	<i>76%</i>	<i>71%</i>	<i>81%</i>
half (base case)	1980	56%	67%	66%	77%
		<i>58%</i>	<i>70%</i>	<i>66%</i>	<i>79%</i>
recent	2000	43%	55%	55%	66%
		<i>42%</i>	<i>57%</i>	<i>55%</i>	<i>62%</i>

3.2. Model selection

Most of the stocks have either the Ricker model or the Larkin with three lag β coefficients as the model with the lowest DIC value (Table 3.2). Only five out of 18 stocks shows one of the other Larkin variations with the lowest DIC value. If the only two choices were Ricker or Larkin, then Chilko would be classified as an Undetermined-type stock. Ricker-type stocks tend to have the Ricker model as the only possible model, with the exception of Weaver. The blue boxes in Table 3.2 show different levels of support when the DIC evaluation is run on the Larkin model forms with normal lag β priors. None of the classifications into Ricker, Larkin, or Undetermined-type stocks are affected by the DIC results using alternate priors.

The DIC results and the individual parameters implied by the step() function are not always consistent. For instance, the Fennell Creek step() probabilities for all three lag β coefficients are over 80% (Table 3.3), suggesting that the model with the lowest DIC value would be the Larkin with three lag β coefficients, but for Fennell, the Ricker model is the lowest DIC model (Table 3.2). However, the DIC is evaluating the fit of the model to the data and the step() is evaluating the probability of a coefficient being consistently positive or negative, so differences are to be expected. The step() function identifies at least one non-zero lag β coefficient for every stock. Bowron and Harrison are the only two stocks that show a strong signal for any negative lag β coefficients with the step() function.

Table 3.2. Deviance Information Criterion (DIC) results for the eight Larkin model forms applied to each stock. The number(s) following “Larkin” indicates the lag β coefficients included in the model form evaluated and correspond to eq. 1-8. The model form with the lowest DIC values within a row are in bold with model forms within a value of 5 of the lowest in green. The DIC values for the base case (uniform lag β prior) are shown. The blue boxes indicate where different results are obtained when evaluating models with normal lag β priors, with respect to whether the model form is within 5 DIC values of model form with the lowest DIC. The stocks are grouped into Larkin-type (Early Stuart to Late Shuswap at the top), Ricker-type (Fennell to Weaver), and Undetermined-type (Upper Pitt to Birkenhead).

stock	model type							
	Ricker	Larkin	Larkin1&2	Larkin1&3	Larkin2&3	Larkin1	Larkin2	Larkin3
Early Stuart	-81.11	-86.43	-87.05	-84.75	-81.01	-85.86	-81.33	-80.12
Stellako	20.94	0.68	21.53	-0.72	0.06	20.47	22.41	-1.33
Chilko	123.99	120.67	119.08	119.57	124.13	118.00	122.52	124.29
Late Shuswap	-33.70	-39.63	-38.00	-32.28	-32.62	-33.26	-33.73	-29.83
Fennell	-220.69	-201.18	-201.10	-200.13	-201.00	-198.66	-200.89	-198.62
Bowron	-283.72	-267.74	-269.65	-269.05	-269.42	-270.95	-271.15	-270.87
Gates	-170.59	-154.68	-150.17	-149.63	-154.71	-144.70	-151.30	-149.00
Nadina	-130.03	-116.30	-116.56	-117.08	-117.96	-117.52	-118.38	-118.63
Raft	-307.32	-294.63	-295.03	-294.01	-296.23	-294.30	-296.70	-295.73
Portage	-244.14	-221.85	-223.05	-222.82	-218.97	-223.93	-220.27	-219.81
Harrison	-197.80	-181.42	-183.31	-183.22	-183.59	-185.24	-185.33	-185.54
Weaver	1.22	7.85	9.13	5.94	6.58	7.37	8.35	4.73
Upper Pitt	-194.70	-193.01	-192.79	-187.01	-193.80	-185.93	-193.46	-186.46
Scotch	-125.11	-126.85	-114.51	-120.82	-112.43	-113.91	-110.21	-112.24
Seymour	-168.31	-167.93	-166.08	-167.31	-163.04	-163.42	-163.71	-159.01
Late Stuart	-34.98	-33.34	-34.92	-33.46	-31.46	-34.92	-33.20	-31.78
Quesnel	-161.46	-165.17	-154.18	-160.01	-162.28	-142.49	-154.35	-152.10
Birkenhead	-0.76	0.80	-0.35	-0.46	3.89	-1.78	2.92	3.01

Table 3.3. WinBUGS step() function probabilities for lag β coefficients. Lag β coefficients with values >0.8 are shown in green (indicating that these coefficients are consistently positive) and <0.2 are in yellow (indicating that these coefficients are consistently negative). The stocks are grouped into Larkin-type (Early Stuart to Late Shuswap at the top), Ricker-type (Fennell to Weaver), and Undetermined-type (Upper Pitt to Birkenhead).

stock	lag β		
	β_1	β_2	β_3
Early Stuart	1.00	0.96	0.75
Stellako	0.78	0.60	1.00
Chilko	0.99	0.69	0.32
Late Shuswap	1.00	1.00	0.95
Fennell	0.83	0.88	0.83
Bowron	0.31	0.50	0.19
Gates	0.84	0.99	0.98
Nadina	0.44	0.79	0.83
Raft	0.29	0.92	0.79
Portage	0.97	0.45	0.54
Harrison	0.03	0.38	0.29
Weaver	0.64	0.21	0.96
Upper Pitt	0.72	1.00	0.89
Scotch	1.00	1.00	1.00
Seymour	1.00	0.92	0.96
Late Stuart	0.96	0.86	0.41
Quesnel	0.99	0.99	1.00
Birkenhead	0.99	0.53	0.53

3.3. Assessing bias in parameter estimation

3.3.1. Parameter estimates - representative stock

Uniform lag β priors

The representative parameter sets are generally close to the medians for the individual α and β_0 (Table 3.4). The Ricker α and β_0 parameters are all smaller than the corresponding Larkin parameters.

Table 3.4. Stock-recruit parameters used to model each type of stock. The median values estimated from historical data for each individual parameter are shown in italics below the parameter set.

	stock-recruit parameter					
	alpha	β_0	β_1	β_2	β_3	sigma
<i>Ricker model actual parameters</i>						
Ricker-type	2.39	59.33	0	0	0	0.79
	<i>2.39</i>	<i>59.49</i>				<i>0.80</i>
undetermined	2.47	1.38	0	0	0	1.38
	<i>2.47</i>	<i>1.38</i>				<i>1.36</i>
Larkin-type	2.06	0.28	0	0	0	1.04
	<i>2.06</i>	<i>0.29</i>				<i>0.99</i>
<i>Larkin model actual parameters</i>						
Ricker-type	2.69	67.52	19.29	21.16	6.87	0.83
	<i>2.69</i>	<i>68.03</i>	<i>16.80</i>	<i>20.63</i>	<i>12.96</i>	<i>0.85</i>
undetermined	2.75	1.48	2.47	1.99	0.89	1.36
	<i>2.75</i>	<i>1.52</i>	<i>2.05</i>	<i>1.36</i>	<i>0.63</i>	<i>1.35</i>
Larkin-type	2.8	0.63	0.75	0.68	0.48	0.98
	<i>2.80</i>	<i>0.65</i>	<i>0.78</i>	<i>0.77</i>	<i>0.44</i>	<i>0.90</i>

3.3.2. Estimating parameters for each stock type

The least biased and most precise estimates are made when the simulation and estimation models are the same, (top of Table 3.5 and bottom of Table 3.6). The worst case is when the data for the Undetermined stock and the Larkin stock is simulated with a Larkin model and estimated by a Ricker model (top of Table 3.6), implying that the Ricker model will tend to give negatively biased and imprecise estimates of stock-recruit parameters for cyclic or potentially cyclic stocks. The Larkin model estimating parameters from Ricker simulated stocks (bottom of Table 3.5) performs intermediate of the two extremes. The Larkin model estimating the Ricker parameters does estimate non-zero lag β coefficients, particularly for the Ricker stock. Neither the Ricker model estimating the Larkin data or the Larkin model estimating the Ricker data does particularly well estimating the α parameter – the Ricker model underestimates α by 15-40% and the Larkin model overestimates α by 10-15%. When the Larkin model estimates the lag β coefficients from the Larkin data, the estimates are least biased and most precise for the Undetermined and Larkin-type stocks.

Table 3.5. Results of simulations to test bias and precision of the Ricker and Larkin model estimates from data generated by a Ricker model in the base case scenario. The lowest MPE and MAPE when comparing the values in Table 3.5 and Table 3.6 are in bold and bright green, the values within 2.5% of lowest in light green and within 5% in gray.

		<i>simulated with Ricker</i>					% bias	
stock	parameter	True	Estimate				(median)	
type			mean	p10	median	p90	MPE	MAPE
<i>estimated with Ricker</i>								
Ricker	α	2.39	2.37	2.06	2.38	2.68	-0.6	6.9
	β_0	59.33	57.59	33.60	57.27	80.46	-3.5	20.0
	<i>sigma</i>	0.79	0.79	0.66	0.78	0.94	-0.8	9.3
	$\alpha\beta_0$	na	na	na	na	na	-1.7	13.5
undetel	α	2.47	2.45	2.01	2.45	2.88	-0.8	9.5
	β_0	1.38	1.32	0.74	1.34	1.78	-2.7	15.8
	<i>sigma</i>	1.38	1.38	1.15	1.37	1.64	-0.7	9.3
	$\alpha\beta_0$	na	na	na	na	na	-1.1	17.1
Larkin	α	2.06	2.07	1.76	2.07	2.39	0.3	8.2
	β_0	0.28	0.35	0.12	0.29	0.59	1.8	36.7
	<i>sigma</i>	1.04	1.04	0.86	1.03	1.23	-1.0	9.3
	$\alpha\beta_0$	na	na	na	na	na	2.0	23.1
<i>estimated with Larkin</i>								
Ricker	α	2.39	2.74	2.34	2.73	3.14	14.1	14.4
	β_0	59.33	57.33	32.50	56.58	81.93	-4.6	21.4
	β_1	0.00	14.02	1.76	10.57	30.97	0.0	0.0
	β_2	0.00	13.47	1.72	10.22	29.52	0.0	0.0
	β_3	0.00	13.00	1.70	9.97	28.35	0.0	0.0
	<i>sigma</i>	0.79	0.81	0.66	0.80	0.97	0.7	10.2
	$\alpha\beta_0$	na	na	na	na	na	5.0	18.9
undetel	α	2.47	2.77	2.27	2.77	3.27	12.0	13.9
	β_0	1.38	1.29	0.69	1.32	1.77	-4.3	16.7
	β_1	0.00	0.29	0.03	0.19	0.66	0.0	0.0
	β_2	0.00	0.26	0.03	0.17	0.58	0.0	0.0
	β_3	0.00	0.25	0.03	0.16	0.58	0.0	0.0
	<i>sigma</i>	1.38	1.41	1.15	1.39	1.70	0.8	10.4
	$\alpha\beta_0$	na	na	na	na	na	4.0	17.6
Larkin	α	2.06	2.38	2.00	2.37	2.77	15.2	15.7
	β_0	0.28	0.38	0.12	0.29	0.62	1.8	38.8
	β_1	0.00	0.24	0.02	0.11	0.46	0.0	0.0
	β_2	0.00	0.15	0.01	0.09	0.35	0.0	0.0
	β_3	0.00	0.17	0.02	0.10	0.39	0.0	0.0
	<i>sigma</i>	1.04	1.06	0.86	1.04	1.27	0.3	10.1
	$\alpha\beta_0$	na	na	na	na	na	9.0	28.0

Table 3.6. Results of simulations to test bias and precision of the Ricker and Larkin model estimates from data generated by a Larkin model in the base case scenario. The lowest MPE and MAPE when comparing the values in Table 3.5 and Table 3.6 are in bold and bright green, the values within 2.5% of lowest in light green and within 5% in gray.

stock type	parameter	<i>simulated with Larkin</i>					% bias (median)	
		True	Estimate				MPE	MAPE
			mean	p10	median	p90		
<i>estimated with Ricker</i>								
Ricker	α	<i>see</i>	2.30	1.99	2.30	2.61	-14.5	14.5
	β_0	<i>below</i>	64.02	35.04	64.05	91.38	-5.1	21.5
	<i>0.65</i>		0.89	0.73	0.88	1.07	6.1	10.8
	$\alpha\beta_0$		na	na	na	na	-9.7	17.7
undeter	α		1.63	1.02	1.66	2.20	-39.7	39.7
	β_0		1.13	0.25	0.88	2.40	-40.3	55.0
	<i>1.26</i>		2.30	1.46	2.04	3.53	50.1	50.1
	$\alpha\beta_0$		na	na	na	na	-40.8	47.8
Larkin	α		1.85	1.46	1.86	2.23	-33.5	33.5
	β_0		0.47	0.15	0.42	0.86	-34.0	43.1
	<i>0.86</i>		1.45	0.99	1.36	2.03	38.8	38.8
	$\alpha\beta_0$		na	na	na	na	-34.1	38.3
<i>estimated with Larkin</i>								
Ricker	α	2.69	2.84	2.43	2.84	3.26	5.5	8.9
	β_0	67.52	63.46	36.51	62.91	90.11	-6.8	20.7
	β_1	19.29	26.20	5.53	23.86	49.54	23.7	59.0
	β_2	21.16	27.16	6.29	24.90	50.71	17.7	54.2
	β_3	6.87	17.46	2.69	14.48	36.27	110.8	110.8
	<i>0.62</i>	0.83	0.84	0.68	0.83	1.00	-0.3	10.0
	$\alpha\beta_0$	na	na	na	na	na	-0.4	15.6
undeter	α	2.75	2.75	2.26	2.74	3.26	-0.3	9.6
	β_0	1.48	1.32	0.47	1.26	2.20	-14.9	32.4
	β_1	2.47	2.53	1.61	2.55	3.40	3.2	16.8
	β_2	1.99	2.00	1.08	2.02	2.81	1.3	20.1
	β_3	0.89	0.99	0.27	0.92	1.76	2.9	40.6
	<i>1.00</i>	1.36	1.37	1.12	1.35	1.64	-0.5	10.1
	$\alpha\beta_0$	na	na	na	na	na	-7.0	21.8
Larkin	α	2.80	2.80	2.39	2.80	3.22	-0.1	7.6
	β_0	0.63	0.60	0.28	0.58	0.91	-7.8	26.1
	β_1	0.75	0.75	0.40	0.75	1.07	0.4	21.5
	β_2	0.68	0.67	0.33	0.67	1.01	-1.7	24.1
	β_3	0.48	0.52	0.22	0.50	0.83	3.9	30.3
	<i>0.73</i>	0.98	0.99	0.81	0.98	1.18	-0.5	10.0
	$\alpha\beta_0$	na	na	na	na	na	-3.7	17.6

3.4. Population trajectories with different models

In forward simulations, both the Ricker and the Larkin models show the Ricker-type stock increasing to a stable abundance after approximately three generations (Figure 3.1). The graphs show the historical range of abundances for comparison. The middle 50% of the historical data is shown: the base case total mortality years in the solid red lines (1980 – 2011) and that of the entire dataset in dotted red lines (1952-2011). The Ricker model projects the stock to stabilize with median run sizes close to the 75th percentile abundance in the long term dataset, while the 25th to 50th percentile of the Larkin modelled abundances are near that of the long term. Both the Ricker and Larkin modelled abundances are well above the 25th to 50th percentiles of the 1980-2011 historical data.

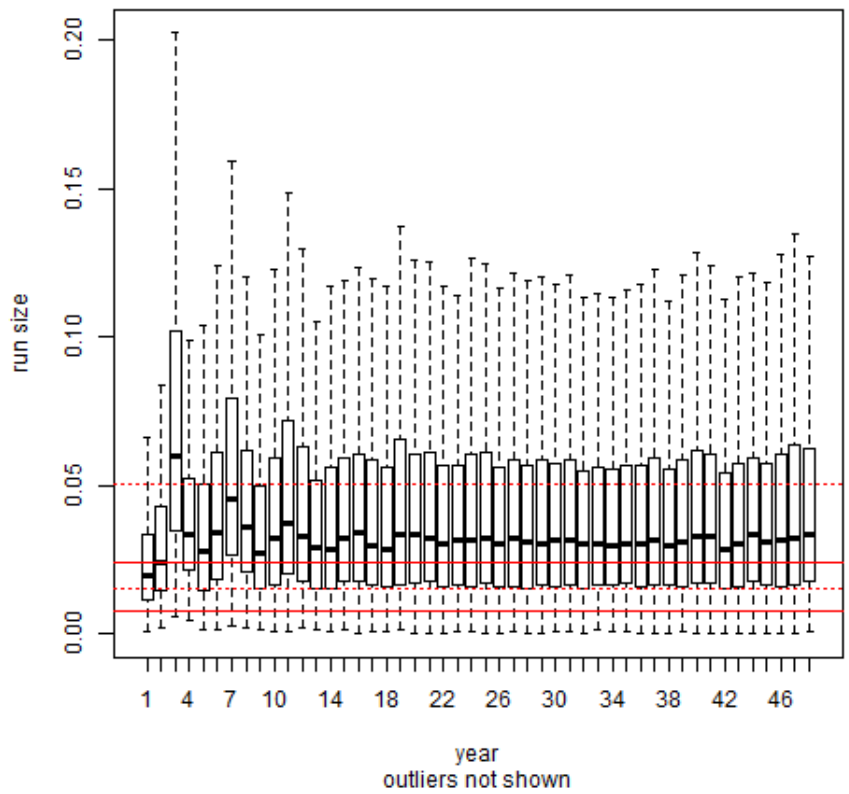
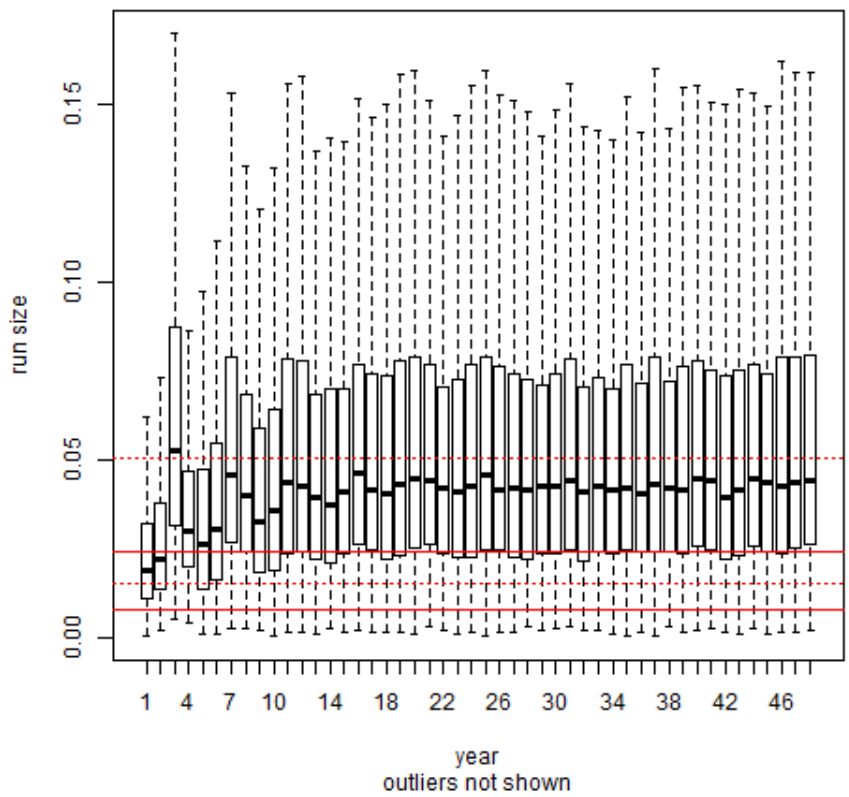


Figure 3.1. Summary of Ricker-type stock base case simulations using the Ricker model (top) and Larkin model (bottom). The results from 1000 48 year simulations are shown, excluding outliers. The historical 25th and 75th percentile ranges are shown by solid red horizontal lines (1980-2011) and dotted lines (1952-2011).

The same general trend of run sizes settling into a stable abundance is also evident for the Undetermined-type stock (Figure 3.2). However, it takes longer for the Undetermined-type stock to reach a stable abundance than the Ricker-type stock. In particular, when modelled with the Larkin model, the cycles appear to flatten out only in the final generation. There is a stark contrast in the potential abundances implied by the Ricker versus the Larkin model simulations, with the Larkin projections ending with median abundances within the 50% range of historical run sizes and the median Ricker abundance more than double the historical range.

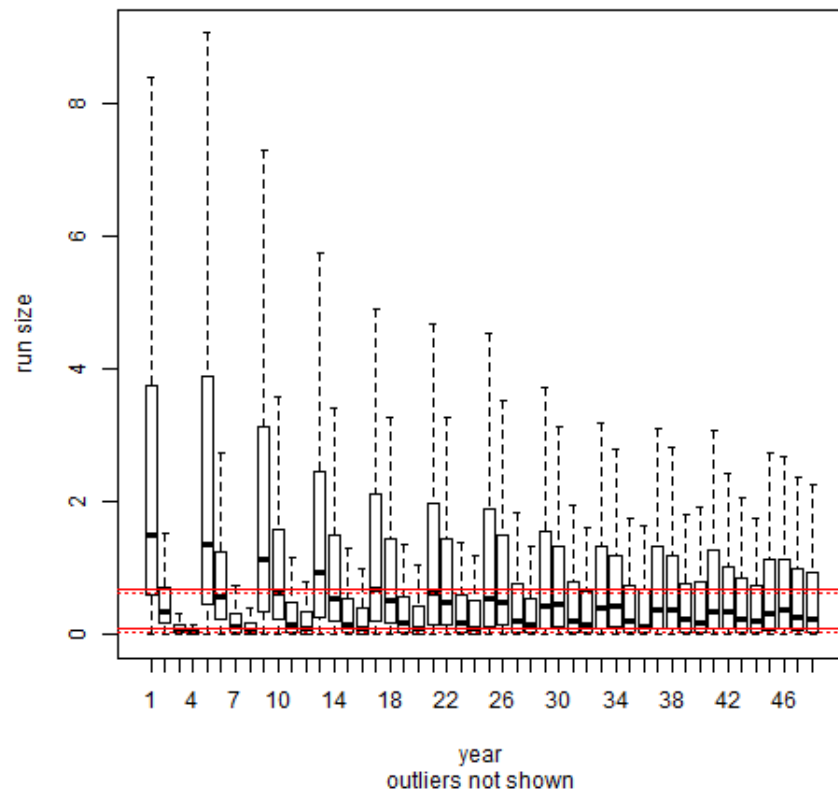
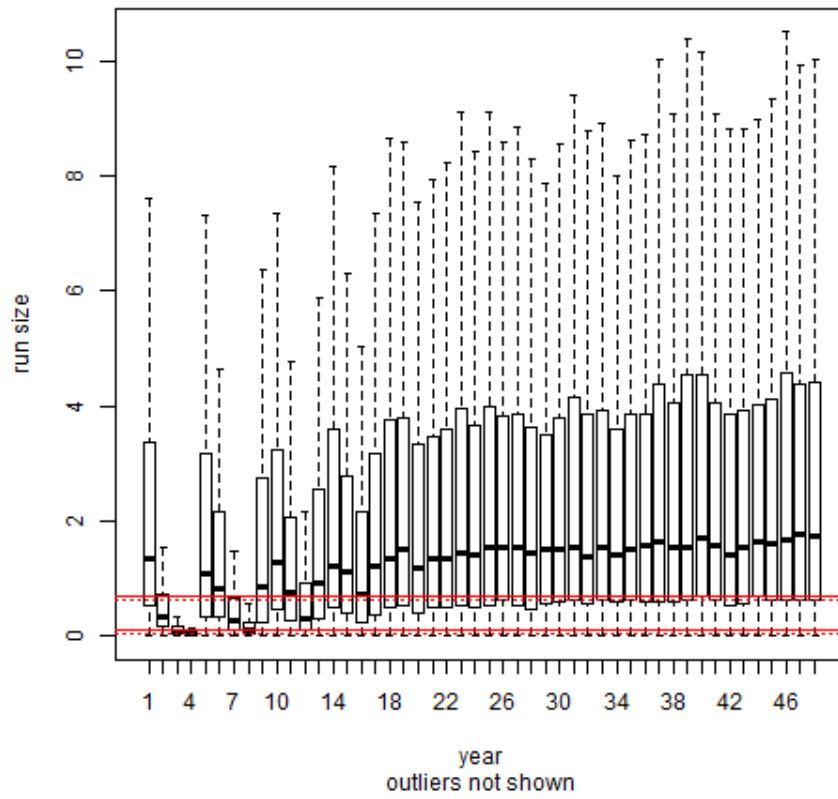


Figure 3.2. Summary of Undetermined-type stock base case simulations using the Ricker model (top) and Larkin model (bottom). The results from 1000 48 year simulations are shown, excluding outliers. The historical 25th and 75th percentile ranges are shown by solid red horizontal lines (1980-2011) and dotted lines (1952-2011).

In contrast to the Ricker-type and Undetermined-type stock, it is only in the last few generations of the 12 generation simulation that the Ricker simulation ceases to exhibit cycles for the Larkin-type stock (Figure 3.3). The Larkin-modelled trajectory never loses its cyclic pattern, but the magnitude of the differences between the dominant and off-cycle lines shows a marked decrease over time. A less extreme version of the trajectories observed in the Undetermined-type stock, where the population trajectories modelled by the Ricker model tend to increase to medians above the historical 50% range and the Larkin model trajectories decreasing to medians within the historical 50% range, is also observed for the Larkin-type stock.

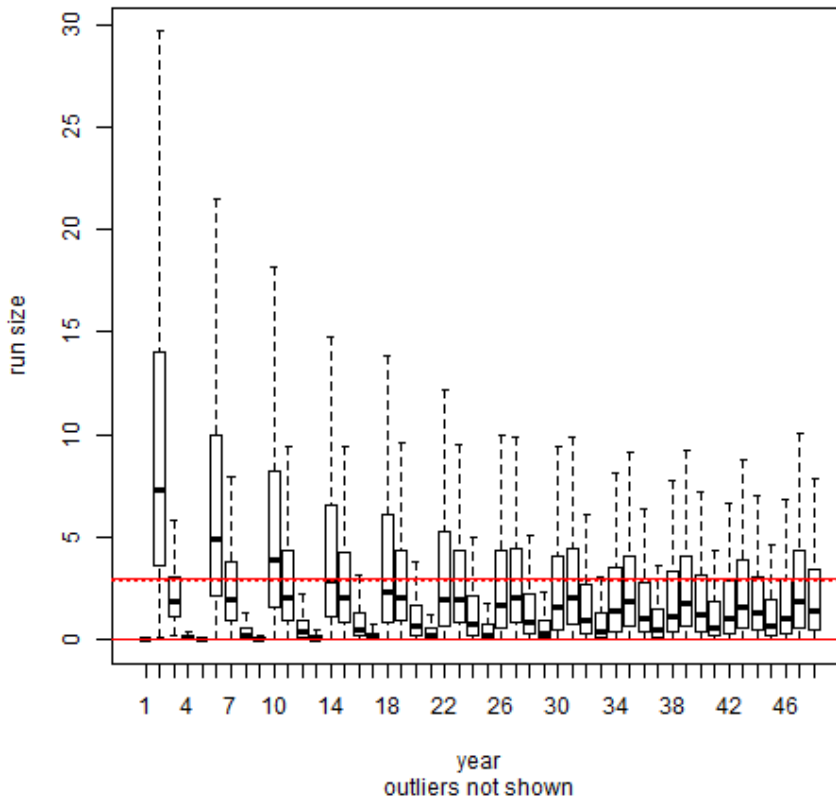
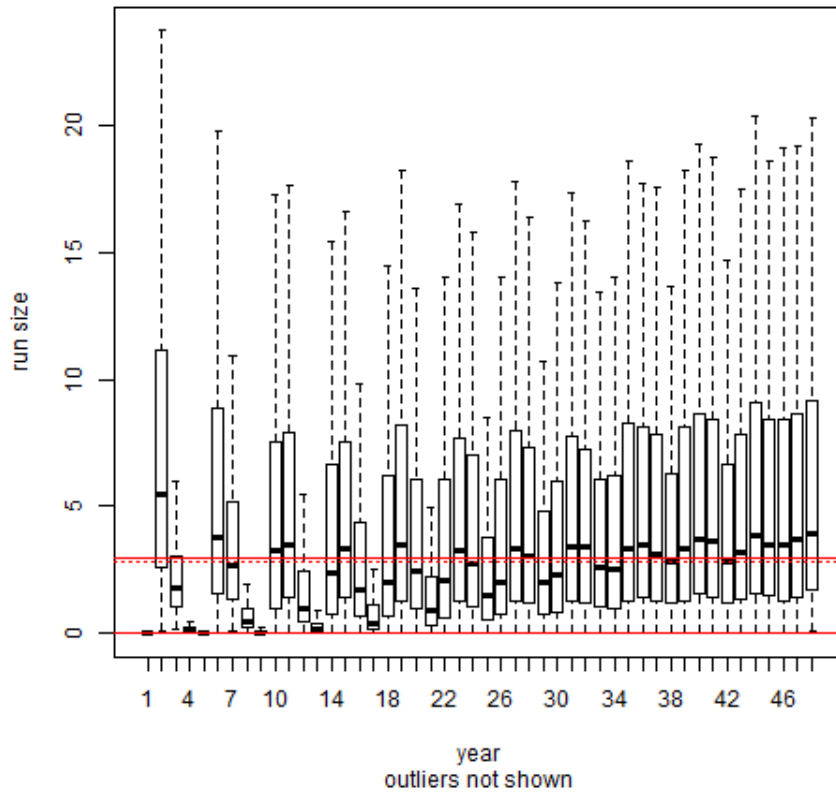


Figure 3.3. Summary of Larkin-type stock base case simulations using the Ricker model (top) and Larkin model (bottom). The results from 1000 48 year simulations are shown, excluding outliers. The historical 25th and 75th percentile ranges are shown by solid red horizontal lines (1980-2011) and dotted lines (1952-2011).

There are a number of trends that appear throughout all of the forward simulations, regardless of stock-type or scenario:

1. Larger abundances are modelled with the Ricker than the Larkin model. This doesn't change over the time period of the simulation.
2. Stocks when simulated with a Ricker model show an increase in run size from the first four generations to the last four.
3. With the exception of the base case, stocks when simulated with the Larkin model also increase in run size from the first generation to the last four.
4. The abundances projected by the Ricker model and the Larkin model are more similar to each other in the first four generations than in the last four generations.

Specific to the base case scenario in Table 3.7: when simulated with the Larkin model, the Ricker-type and the Undetermined-type stocks both appear to have the same abundances in the first four generations and the last four. Figure 3.2, however, shows that while the summary statistics remain unchanged, the distribution of the abundance over the four cycle lines is quite different. Results when using the historical effective female spawners to initialize the simulations (Table 3.17) indicate that the stable abundance over time shown by the Larkin model simulations in this scenario is likely an artefact of the initial spawning stock as opposed to an intrinsic characteristic of the model or the stocks.

Table 3.7. Results of the base case scenario for all stock types. The 48 year (12 generation) run size trajectories simulated with the Larkin model is compared to historical ((simulated-historical)/historical) in the middle section. The Ricker model run size trajectories are compared to the Larkin trajectories in the table on the right ((Ricker-Larkin)/Larkin). The simulated run sizes in the min and max rows are actually the 10th and 90th percentiles out of 1000 simulations.

	Historical run size (1980-2011)	Larkin simulations compared to historical				Ricker vs Larkin	
		yrs 1-16		yrs 33-48		yrs 1-16	yrs 33-48
<i>Ricker stock</i>							
min	3,045	10,000	228%	9,000	196%	14%	59%
p25	7,875	17,730	125%	16,500	110%	11%	48%
median	16,198	32,450	100%	31,160	92%	9%	37%
mean	19,836	48,440	144%	47,950	142%	6%	27%
p75	24,286	59,220	144%	58,460	141%	7%	30%
max	58,350	101,000	73%	102,100	75%	6%	22%
<i>Undetermined stock</i>							
min	3,817	14,900	290%	9,500	149%	144%	2466%
p25	100,164	58,940	-41%	56,580	-44%	114%	974%
median	237,612	266,600	12%	268,900	13%	86%	494%
mean	701,370	1,289,000	84%	1,298,000	85%	63%	221%
p75	676,624	1,031,000	52%	1,003,000	48%	67%	309%
max	5,162,734	3,083,100	-40%	3,004,900	-42%	52%	212%
<i>Larkin stock</i>							
min	4,718	13,700	190%	78,200	1557%	61%	582%
p25	32,589	72,450	122%	323,000	891%	77%	307%
median	137,794	729,400	429%	1,093,000	693%	37%	200%
mean	2,541,710	3,033,000	19%	2,820,000	11%	20%	147%
p75	2,937,809	3,039,000	3%	2,979,000	1%	20%	166%
max	17,334,140	7,886,100	-55%	6,729,100	-61%	17%	143%

3.5. Sensitivity analyses

3.5.1. Alternate total mortality scenarios

Under the long term mortality scenario, all three stocks show a decrease in abundance compared to the base case when simulated with the Ricker model (Table 3.1). There is very little difference between this higher total mortality rate scenario and the base case for the Ricker-type and Larkin-type stocks simulated with the Larkin model. The Undetermined-type stock, however, while showing an initial decrease in abundance compared to the base case in the first four generations, shows abundances consistently higher than the base case in the last four generations. The abundances projected by the Ricker and the Larkin model are also more similar to each other than in the base case scenario, particularly in the first four generations.

Table 3.8. Results of the long term total mortality scenario for all stock types. The 48 year (12 generation) run size trajectories simulated with the Larkin model is compared to historical ((simulated-historical)/historical) in the middle section. The Ricker model run size trajectories are compared to the Larkin trajectories in the table on the right ((Ricker-Larkin)/Larkin). The simulated run sizes in the min and max rows are actually the 10th and 90th percentiles out of 1000 simulations. Note that the historical summary statistics start in 1952.

Historical run size (1952-2011)	Larkin simulations compared to historical				Ricker vs Larkin		
	yrs 1-16		yrs 33-48		yrs 1-16	yrs 33-48	
<i>Ricker stock</i>							
min	3,045	9,600	215%	8,400	176%	5%	25%
p25	15,210	17,200	13%	15,450	2%	2%	22%
median	22,816	31,750	39%	29,560	30%	1%	20%
mean	38,720	47,160	22%	46,120	19%	-2%	12%
p75	50,406	58,050	15%	56,390	12%	0%	14%
max	207,472	98,800	-52%	99,700	-52%	-2%	10%
<i>Undetermined stock</i>							
min	327	14,900	4457%	11,700	3478%	108%	1596%
p25	22,531	55,820	148%	63,490	182%	88%	693%
median	118,599	256,900	117%	297,200	151%	65%	362%
mean	534,264	1,291,000	142%	1,354,000	153%	45%	183%
p75	629,466	984,000	56%	1,069,000	70%	48%	237%
max	5,162,734	3,110,400	-40%	3,093,200	-40%	35%	182%
<i>Larkin stock</i>							
min	2,455	14,300	482%	91,900	3643%	35%	120%
p25	29,275	74,120	153%	335,400	1046%	41%	86%
median	137,794	723,200	425%	1,113,000	708%	6%	66%
mean	2,284,818	3,063,000	34%	2,846,000	25%	4%	63%
p75	2,844,683	3,044,000	7%	2,979,000	5%	0%	67%
max	17,334,140	8,074,700	-53%	6,837,100	-61%	1%	63%

The population trajectories simulated with the Ricker model under the recent mortality scenario are larger than the base case abundances for all stocks (Table 3.9). The impact of the lower total mortality rates on the Larkin simulations is more equivocal.

In the recent total mortality scenario, the Larkin model simulations of the Larkin-type and Undetermined-type stocks produce the smallest run sizes in the last four generations out of all three mortality scenarios. The Ricker-type stock exhibits very little change from the base case scenario when simulated with the Larkin model.

Table 3.9. Results of the recent total mortality scenario for all stock types. The 48 year (12 generation) run size trajectories simulated with the Larkin model is compared to historical ((simulated-historical)/historical) in the middle section. The Ricker model run size trajectories are compared to the Larkin trajectories in the table on the right ((Ricker-Larkin)/Larkin). The simulated run sizes in the min and max rows are actually the 10th and 90th percentiles out of 1000 simulations.

	Historical run size (1980-2011)	Larkin simulations compared to historical				Ricker vs Larkin	
		yrs 1-16		yrs 33-48		yrs 1-16	yrs 33-48
<i>Ricker stock</i>							
min	3,045	10,400	242%	9,400	209%	33%	91%
p25	7,875	18,220	131%	17,090	117%	28%	72%
median	16,198	33,260	105%	31,610	95%	24%	58%
mean	19,836	48,930	147%	47,360	139%	19%	44%
p75	24,286	59,960	147%	57,690	138%	20%	46%
max	58,350	101,300	74%	101,000	73%	16%	37%
<i>Undetermined stock</i>							
min	3,817	10,900	186%	9,400	146%	301%	2780%
p25	100,164	50,610	-49%	57,420	-43%	230%	1079%
median	237,612	244,900	3%	274,700	16%	160%	528%
mean	701,370	1,230,000	75%	1,267,000	81%	105%	254%
p75	676,624	996,500	47%	1,003,000	48%	116%	339%
max	5,162,734	3,122,600	-40%	3,001,800	-42%	90%	239%
<i>Larkin stock</i>							
min	4,718	12,500	165%	56,800	1104%	131%	2236%
p25	32,589	66,230	103%	275,100	744%	183%	876%
median	137,794	610,500	343%	1,005,000	629%	136%	451%
mean	2,541,710	2,955,000	16%	2,744,000	8%	56%	261%
p75	2,937,809	2,931,000	0%	2,811,000	-4%	62%	312%
max	17,334,140	7,938,000	-54%	6,630,300	-62%	47%	234%

3.5.2. Alternative prior – normal priors for lag β coefficients

Model parameters

The parameter estimates of the Ricker-type stock are the most affected by the change to a normal prior with all α and β values decreasing from the base case parameters (Table 3.10). The Larkin-type stock parameters are nearly unchanged from the base case. The changes to the Undetermined-type stock parameters are intermediate to the Ricker-type and Larkin-type, with the largest percentage change from base case occurring in the last two lag β coefficients.

Table 3.10. Stock-recruit parameters used to model each type of stock with forecast lag β priors (normal prior). The median values for each individual parameter is shown in italics below the parameter set.

stock-recruit parameter						
	alpha	β_0	β_1	β_2	β_3	sigma
<i>lognormal β_0, normal lag β priors (forecast lag β priors)</i>						
Ricker type	2.29	59.67	-17.07	-0.54	-9.40	0.80
	<i>2.28</i>	<i>59.63</i>	<i>-6.82</i>	<i>0.71</i>	<i>-13.31</i>	<i>0.83</i>
undetermined	2.63	1.60	2.47	0.94	-0.66	1.33
	<i>2.63</i>	<i>1.48</i>	<i>1.89</i>	<i>1.12</i>	<i>-0.25</i>	<i>1.35</i>
Larkin type	2.79	0.64	0.91	0.62	0.51	0.86
	<i>2.79</i>	<i>0.64</i>	<i>0.77</i>	<i>0.77</i>	<i>0.43</i>	<i>0.91</i>

Bias in estimated parameters

There is a general improvement in the bias and precision associated with estimating parameters with the Larkin model with normal priors from data generated by the Ricker model for all stock types (bottom Table 3.11) compared to the base case (Table 3.5 and Table 3.6). There is also a general improvement in the bias and precision when the Ricker model estimates the parameters from Larkin generated data, as well (top Table 3.12). However, this combination of estimating parameters with the Ricker model from Larkin generated data continues to be the most biased and imprecise for the Larkin and Undetermined-type stocks. There is some improvement from base case when the Ricker model estimates the α parameter from the Larkin data, but estimates are still 3-33% less than the true value. There are improvements to the α parameter

estimated by the Larkin model from Ricker generated data from base case, with less than 4% bias for all stock types. The Ricker model parameters and priors used in this section are identical to the base case.

The Larkin model parameter estimates of the Larkin generated data (bottom Table 3.12) are generally worse in terms of bias and precision compared to base case. The precision for the Larkin-type stock is comparable to base case for all parameters estimated, but there is an increase in bias. The Undetermined-type stock improvement is most noticeable in the decreased bias of the β_0 and combined $\alpha\beta_0$ estimates, but there are substantial increases to bias and decrease in precision of the β_2 and β_3 estimates. The Ricker-type stock shows mild improvement in the precision of the β_0 estimate, but does substantially worse for nearly every other performance measure. In particular, the median estimates are underestimated for the lag β coefficients by 100-200%, and the MAPE is at least double that of the base case.

The lag β coefficients estimated by the Larkin model with normal priors on data generated by the Ricker model are approximately 80% closer to the true parameter value of zero than the lag β coefficients estimated by the Larkin model with bounded-uniform priors for the Ricker-type stock. The median lag β coefficients estimated by the Larkin model with normal priors for the Undetermined and Larkin-type stocks are near zero. These results show that the Larkin model with normal priors is even less prone to estimating lag β coefficients that don't exist than the base case Larkin model.

Table 3.11. Results of simulations to test bias and precision of the Ricker and Larkin model estimates from Ricker generated data (normal priors for lag β coefficients). The lowest MPE and MAPE when comparing the values in Table 3.11 and Table 3.12 are in bold and bright green, the values within 2.5% of lowest in light green and within 5% in gray.

		<i>simulated with Ricker</i>					% bias	
stock		True	Estimate				(median)	
type	parameter		mean	p10	median	p90	MPE	MAPE
<i>estimated with Ricker</i>								
Ricker	α	2.39	2.37	2.06	2.38	2.68	-0.6	6.9
	β_0	59.33	57.59	33.60	57.27	80.46	-3.5	20.0
	<i>sigma</i>	0.79	0.79	0.66	0.78	0.94	-0.8	9.3
	$\alpha\beta_0$	na	na	na	na	na	-1.7	13.5
undet.	α	2.47	2.45	2.01	2.45	2.88	-0.8	9.5
	β_0	1.38	1.32	0.74	1.34	1.78	-2.7	15.8
	<i>sigma</i>	1.38	1.38	1.15	1.37	1.64	-0.7	9.3
	$\alpha\beta_0$	na	na	na	na	na	-1.1	17.1
Larkin	α	2.06	2.07	1.76	2.07	2.39	0.3	8.2
	β_0	0.28	0.35	0.12	0.29	0.59	1.8	36.7
	<i>sigma</i>	1.04	1.04	0.86	1.03	1.23	-1.0	9.3
	$\alpha\beta_0$	na	na	na	na	na	2.0	23.1
<i>estimated with Larkin</i>								
Ricker	α	2.39	2.44	1.99	2.44	2.91	2.2	10.2
	β_0	59.33	57.52	32.67	57.02	81.64	-3.9	20.9
	β_1	0.00	2.48	-19.30	2.55	24.20	0.0	0.0
	β_2	0.00	2.96	-18.37	2.91	24.62	0.0	0.0
	β_3	0.00	1.59	-17.95	1.43	21.43	0.0	0.0
	<i>sigma</i>	0.79	0.79	0.65	0.78	0.95	-0.9	10.0
	$\alpha\beta_0$	na	na	na	na	na	-0.5	16.4
	undet.	α	2.47	2.51	1.94	2.51	3.07	1.5
β_0		1.38	1.31	0.71	1.33	1.78	-3.4	16.3
β_1		0.00	0.09	-0.41	0.06	0.61	0.0	0.0
β_2		0.00	0.04	-0.45	0.04	0.54	0.0	0.0
β_3		0.00	0.01	-0.45	0.00	0.49	0.0	0.0
<i>sigma</i>		1.38	1.39	1.13	1.37	1.67	-0.6	10.2
$\alpha\beta_0$		na	na	na	na	na	-0.5	15.8
Larkin		α	2.06	2.14	1.69	2.13	2.58	3.5
	β_0	0.28	0.37	0.12	0.29	0.60	2.0	37.8
	β_1	0.00	0.08	-0.21	0.04	0.37	0.0	0.0
	β_2	0.00	-0.01	-0.29	0.00	0.29	0.0	0.0
	β_3	0.00	0.02	-0.24	0.02	0.30	0.0	0.0
	<i>sigma</i>	1.04	1.05	0.85	1.03	1.26	-0.8	10.1
	$\alpha\beta_0$	na	na	na	na	na	3.8	25.8

Table 3.12. Results of simulations to test bias and precision of the Ricker and Larkin model estimates from Larkin generated data (normal priors for lag β coefficients). The lowest MPE and MAPE when comparing the values in Table 3.11 and Table 3.12 are in bold and bright green, the values within 2.5% of lowest in light green and within 5% in gray.

stock type	parameter	True	<i>simulated with Larkin</i>				% bias (median)	
			Estimate				MPE	MAPE
			mean	p10	median	p90		
<i>estimated with Ricker</i>								
Ricker	α	<i>see</i>	2.63	2.21	2.61	3.04	-3.0	8.4
	β_0	<i>below</i>	57.61	37.88	57.82	75.57	-14.4	17.6
	<i>sigma</i>		0.94	0.68	0.83	1.07	0.5	11.6
	$\alpha\beta_0$		na	na	na	na	-7.8	13.5
undet.	α		1.81	1.20	1.87	2.39	-32.2	32.2
	β_0		1.32	0.35	1.20	2.43	-18.7	42.2
	<i>sigma</i>		2.28	1.41	1.96	3.51	44.3	44.3
	$\alpha\beta_0$		na	na	na	na	-26.8	38.2
Larkin	α		1.87	1.53	1.88	2.21	-32.8	32.8
	β_0		0.47	0.16	0.42	0.85	-33.0	42.0
	<i>sigma</i>		1.25	0.89	1.19	1.70	21.4	22.9
	$\alpha\beta_0$		na	na	na	na	-33.1	37.2
<i>estimated with Larkin</i>								
Ricker	α	2.29	2.41	1.96	2.40	2.86	-10.8	12.3
	β_0	59.67	58.88	39.47	59.07	76.74	-12.5	16.2
	β_1	-17.07	-11.85	-28.16	-13.20	6.31	-168.4	168.5
	β_2	-0.54	1.60	-15.14	1.35	18.67	-93.6	94.3
	β_3	-9.40	-6.50	-21.35	-7.34	9.66	-206.9	215.2
	<i>sigma</i>	0.80	0.80	0.65	0.79	0.96	-4.8	10.7
	$\alpha\beta_0$	na	na	na	na	na	-11.7	14.9
undet.	α	2.63	2.64	2.09	2.64	3.19	-4.1	10.9
	β_0	1.60	1.49	0.61	1.49	2.28	0.3	26.9
	β_1	2.47	2.52	1.66	2.53	3.32	2.3	14.5
	β_2	0.94	0.94	0.14	0.97	1.69	-51.1	51.6
	β_3	-0.66	-0.59	-1.41	-0.62	0.30	-169.5	169.8
	<i>sigma</i>	1.33	1.33	1.08	1.32	1.60	-3.1	10.5
	$\alpha\beta_0$	na	na	na	na	na	-1.3	19.8
Larkin	α	2.79	2.77	2.37	2.77	3.18	-0.9	7.4
	β_0	0.64	0.62	0.30	0.60	0.94	-4.3	26.6
	β_1	0.91	0.87	0.50	0.90	1.22	19.4	28.8
	β_2	0.62	0.61	0.24	0.61	0.96	-10.5	26.6
	β_3	0.51	0.52	0.19	0.52	0.86	9.0	33.6
	<i>sigma</i>	0.86	0.87	0.71	0.86	1.04	-12.5	13.8
	$\alpha\beta_0$	na	na	na	na	na	-2.4	17.6

Modelled run sizes compared to historical range

When simulating with the Larkin model with normal priors, three differences when compared to the bounded-uniform normal base case stand out (Table 3.13): (1) the abundances for the Ricker-type and Undetermined-type stocks are larger, (2) the run sizes in the last four generations are larger than the first four generations for all stock types, and (3) while the median abundances in the final four generations of the Larkin-type stock is larger than the base case, the mean abundances are smaller.

Table 3.13. Comparison of 48 year (12 generation) run size trajectories for all stock types simulated with the Larkin model with uniform lag β coefficients (middle), and Larkin with normal priors on lag β coefficients (right) are compared to historical ((simulated-historical)/historical). The simulated run sizes in the min and max rows are actually the 10th and 90th percentiles out of 1000 simulations.

	Historical run size (1980-2011)	Larkin simulations - uniform priors				Larkin simulations - normal priors			
		yrs 1-16		yrs 33-48		yrs 1-16		yrs 33-48	
<i>Ricker stock</i>									
min	3,045	10,000	228%	9,000	196%	11,700	284%	19,700	547%
p25	7,875	17,730	125%	16,500	110%	20,790	164%	34,870	343%
median	16,198	32,450	100%	31,160	92%	38,640	139%	63,870	294%
mean	19,836	48,440	144%	47,950	142%	58,640	196%	137,000	591%
p75	24,286	59,220	144%	58,460	141%	71,140	193%	117,900	385%
max	58,350	101,000	73%	102,100	75%	125,200	115%	210,200	260%
<i>Undetermined stock</i>									
min	3,817	14,900	290%	9,500	149%	26,200	586%	22,700	495%
p25	100,164	58,940	-41%	56,580	-44%	86,380	-14%	122,500	22%
median	237,612	266,600	12%	268,900	13%	328,100	38%	489,900	106%
mean	701,370	1,289,000	84%	1,298,000	85%	1,436,000	105%	1,872,000	167%
p75	676,624	1,031,000	52%	1,003,000	48%	1,145,000	69%	1,602,000	137%
max	5,162,734	3,083,100	-40%	3,004,900	-42%	3,309,200	-36%	4,392,800	-15%
<i>Larkin stock</i>									
min	4,718	13,700	190%	78,200	1557%	14,100	199%	114,400	2325%
p25	32,589	72,450	122%	323,000	891%	66,600	104%	395,900	1115%
median	137,794	729,400	429%	1,093,000	693%	674,600	390%	1,155,000	738%
mean	2,541,710	3,033,000	19%	2,820,000	11%	2,684,000	6%	2,531,000	0%
p75	2,937,809	3,039,000	3%	2,979,000	1%	2,829,000	-4%	2,858,000	-3%
max	17,334,140	7,886,100	-55%	6,729,100	-61%	7,245,700	-58%	6,082,700	-65%

3.5.3. Stock specific models

Undetermined – Larkin with 2 lag β coefficients

The individual median parameters of the stock-specific Larkin model form for the Undetermined-type stock are in between the median parameters for the base case and the normal priors scenario (Table 3.14 compared to Table 3.4 and Table 3.10). Using the

stock-specific model form to simulate forward, the last four generation abundances are larger than the first four generation (Table 3.15). This result is unlike the base case simulation, but similar to the other scenarios. Two things stand out when using the stock-specific Larkin form for the Undetermined-type stock: (1) the mean and median abundances are more similar to each other than for the base case or the normal prior scenario, and (2) there were substantially fewer simulations discarded due to the cleaning algorithm (Table 3.18).

Table 3.14. Stock-recruit parameters used to model the Undetermined-type stock using a stock-specific model (eq.2). The median values for each individual parameter is shown in italics below the parameter set.

stock-recruit parameter						
	alpha	β_0	β_1	β_2	β_3	sigma
<i>stock specific model form with lognormal β_0, uniform lag β priors</i>						
undetermined	2.68	1.47	1.39	1.43	0	1.13
	<i>2.68</i>	<i>1.5</i>	<i>1.98</i>	<i>1.34</i>	<i>0</i>	<i>1.33</i>

Table 3.15. Comparison of 48 year (12 generation) run size trajectories for the Undetermined-type stock simulated with the Larkin model base case (middle), and Larkin with the first two uniform prior lag β coefficients (right) compared to historical ((simulated-historical)/historical). The simulated run sizes in the min and max rows are actually the 10th and 90th percentiles out of 1000 simulations.

Historical run size (1980-2011)	Larkin model - three lag β terms				Larkin model - two lag β terms				
	yrs 1-16		yrs 33-48		yrs 1-16		yrs 33-48		
<i>Undetermined stock</i>									
min	3,817	14,900	290%	9,500	149%	29,900	683%	52,700	1281%
p25	100,164	58,940	-41%	56,580	-44%	94,950	-5%	187,300	87%
median	237,612	266,600	12%	268,900	13%	366,700	54%	583,800	146%
mean	701,370	1,289,000	84%	1,298,000	85%	1,319,000	88%	1,607,000	129%
p75	676,624	1,031,000	52%	1,003,000	48%	1,216,000	80%	1,614,000	139%
max	5,162,734	3,083,100	-40%	3,004,900	-42%	3,149,100	-39%	3,847,400	-25%

3.5.4. Initial effective female spawner numbers

The abundances in the last four generations when the initial effective female spawners is taken from the recent historical data (Table 3.17) is nearly an exact match with the base case summary statistics when comparing the abundances in the last four generations (Table 3.7). The historical effective female spawners are not directly proportional to the cycle line medians and means used for the base case (Table 3.16).

Table 3.16. Effective female spawner numbers used to initialize the simulations. The “base case” uses the median effective female spawners in each cycle line for S_{t-1} to S_{t-4} and the average for each cycle line for S_{t-5} to S_{t-7} rounded to the nearest 100 fish. “Historical” are effective female spawners from 2006-2012.

	Initial effective female spawners						
	S_{t-7}	S_{t-6}	S_{t-5}	S_{t-4}	S_{t-3}	S_{t-2}	S_{t-1}
<i>Ricker-type stock</i>							
base case	3,100	8,200	3,800	2,000	2,300	7,800	2,700
historical	640	1,080	280	840	4,100	2,040	30
<i>historical as % base</i>	21%	13%	7%	42%	178%	26%	1%
<i>undetermined-type stock</i>							
base case	23,300	9,600	25,600	140,900	11,100	3,700	1,700
historical	14,280	4,140	57,880	43,270	43,480	780	31,770
<i>historical as % base</i>	61%	43%	226%	31%	392%	21%	1869%
<i>Larkin-type stock</i>							
base case	1,208,200	172,400	2,900	1,800	1,041,200	119,300	2,300
historical	1,170,690	32,300	80	20,210	3,073,260	46,030	10
<i>historical as % base</i>	97%	19%	3%	1123%	295%	39%	0%

Table 3.17. Comparison of 48 year (12 generation) run size trajectories for all stock types simulated with the Larkin model base case initial spawner values (middle), and the historical initial spawners from 2006-2012 on the right ((simulated-historical)/historical). The simulated run sizes in the min and max rows are actually the 10th and 90th percentiles out of 1000 simulations.

Historical run size (1980-2011)	Larkin simulations - base case				Larkin simulations - historical EFS				
	yrs 1-16		yrs 33-48		yrs 1-16		yrs 33-48		
<i>Ricker stock</i>									
min	3,045	10,000	228%	9,000	196%	4,500	48%	9,100	199%
p25	7,875	17,730	125%	16,500	110%	10,730	36%	16,490	109%
median	16,198	32,450	100%	31,160	92%	24,430	51%	31,150	92%
mean	19,836	48,440	144%	47,950	142%	40,480	104%	47,980	142%
p75	24,286	59,220	144%	58,460	141%	50,030	106%	58,650	141%
max	58,350	101,000	73%	102,100	75%	91,400	57%	102,300	75%
<i>Undetermined stock</i>									
min	3,817	14,900	290%	9,500	149%	34,800	812%	9,500	149%
p25	100,164	58,940	-41%	56,580	-44%	118,200	18%	56,640	-43%
median	237,612	266,600	12%	268,900	13%	395,200	66%	272,200	15%
mean	701,370	1,289,000	84%	1,298,000	85%	1,314,000	87%	1,282,000	83%
p75	676,624	1,031,000	52%	1,003,000	48%	1,181,000	75%	1,001,000	48%
max	5,162,734	3,083,100	-40%	3,004,900	-42%	3,096,300	-40%	2,964,600	-43%
<i>Larkin stock</i>									
min	4,718	13,700	190%	78,200	1557%	14,900	216%	85,100	1704%
p25	32,589	72,450	122%	323,000	891%	91,530	181%	337,000	934%
median	137,794	729,400	429%	1,093,000	693%	593,400	331%	1,105,000	702%
mean	2,541,710	3,033,000	19%	2,820,000	11%	2,803,000	10%	2,832,000	11%
p75	2,937,809	3,039,000	3%	2,979,000	1%	2,620,000	-11%	3,007,000	2%
max	17,334,140	7,886,100	-55%	6,729,100	-61%	7,395,900	-57%	6,782,500	-61%

3.5.5. Number of simulations discarded due to cleaning algorithm

The Ricker-type stock, regardless of whether it was simulated by a Ricker or Larkin model had the least number of simulations discarded, with the exception of when it was modelled with the Larkin model with normal priors on the lag β coefficients (Table 3.18). The exception is an unsurprising result when the representative parameter set has

three negative lag β coefficients. The Larkin-type stock modelled with either model had the next fewest discards, with less than 5% of the simulations being discarded by the algorithm. The Undetermined-stock modelled by the Ricker model also had less than 5% of the simulations discarded. However, when modelled by the Larkin model, approximately 15% of the simulations of the Undetermined-type stock were discarded in most scenarios. The exceptions to this are the short mortality scenario, when over 20% of the scenarios were discarded and the stock-specific model form, when fewer than 5% of the scenarios were discarded.

Table 3.18. The number of simulations discarded by cleaning algorithm in order to generate 1,000 simulations for comparing population trajectories.

scenario	simulation model	stock type		
		Ricker	undet.	Larkin
<i>base case</i>				
	Ricker	0	19	16
	Larkin	0	184	21
<i>long term mortality</i>				
	Ricker	0	18	10
	Larkin	0	137	7
<i>recent mortality</i>				
	Ricker	0	22	24
	Larkin	1	305	38
<i>forecast priors</i>				
	Larkin	54	166	10
<i>stock-specific model</i>				
	Larkin	na	27	na
<i>historical spawners</i>				
	Ricker	0	23	19
	Larkin	0	192	15

Chapter 4. Discussion

There are relatively few studies examining how the choice of Larkin model form or priors affects the representation of the long term population dynamics of Fraser Sockeye stocks compared to the Ricker model, particularly for non-cyclic stocks. The characteristics associated with longer term simulations with the Larkin model is of particular concern for the management of fisheries on Fraser Sockeye. The Larkin model is used to simulate the population dynamics of all Fraser Sockeye stocks in the escapement plan evaluation model. I began to address this gap by classifying the Fraser Sockeye stocks with stock-recruit datasets into Ricker-type, Larkin-type, and Undetermined-types and chose a representative stock from each category to evaluate the Larkin model further. I then determined that the Larkin model estimated known parameters for all three types of stocks with less bias and more precision than the Ricker model. I also found that the Larkin model priors used in escapement plan evaluations estimates non-zero lag β coefficients that were larger for the Ricker-type stock. However, the estimate of non-zero lag β coefficients is greatly reduced for all stocks by using a normal prior. Finally, I simulated all three types of stocks using the Larkin model under different scenarios and compared the 48 year run size trajectories to a range of historical run sizes. The results from the forward simulations indicate that the choice of model form has less of an effect in the first four generations than in the last four generations and that the abundance in the last four generations tends to be larger than the historical range, regardless of model choice. These results suggest that unless the stock-recruit model form is known, performance measures should focus more on the outcomes in the first four generations instead of over the entire 48 year simulation period. In addition, the simulations suggest that using stock-specific Larkin model forms for Undetermined-type stocks could reduce the frequency of zero and infinite run sizes in longer term simulations of population dynamics.

In this section, I begin by describing some of the assumptions of the models and the sources of bias in the data. Then I discuss the results of each of my methods: model selection, bias evaluation, and comparison of population trajectories using different

models. I then discuss the implications of my results on the escapement planning process and conclude with a summary of recommendations for the process.

4.1. Assumptions and Sources of Bias

Time series bias and errors in variables biases as described by Hilborn and Walters (1992) and Walters and Martell (2004) are likely problems for the Fraser Sockeye dataset. When I plotted the stock versus recruit graph as suggested by Walters and Martell (2004) to test for potential time-series bias, the relationship for Fraser Sockeye was very strong, i.e., time-series bias should be suspected. Estimates of stock composition, spawner abundance, catch, and overall run size are all affected by changes in methodology over time and will cause errors in variables problems. The assumption of stationarity that is implied by using a single fit of the model to represent a population into the future is also not true. Grant et al. (2010) showed changing patterns in productivity for all Fraser Sockeye stocks with the exception of Late Shuswap, Raft, and Weaver. However, while it is possible to incorporate and evaluate the effects of changing productivity, it is not possible to know what future patterns of productivity will be. The Ricker and Larkin models assume that there is a capacity constraint. This is supported by the data by the negative relationship when plotting $\ln(R/S)$ versus EFS, even when fit to unconstrained Ricker β_0 , with the exception of Scotch (which has a short dataset).

4.2. Models and model selection

Martell et al. (2008) and Peterman and Dorner (2011) used Akaike's information criterion (AIC) methods to select between the Ricker the Larkin model. The DIC method that I used has been described as a Bayesian version of the AIC (Ward 2008). Of the Fraser Sockeye stocks Martell et al. tested, there was more support for the Larkin model for seven stocks (Early Stuart, Late Stuart, Stellako, Quesnel, Chilko, Seymour, and Late Shuswap) and equal support for Ricker and Larkin for two (Birkenhead and Weaver). In addition to comparing the "standard" stationary Ricker and Larkin models, Peterman and Dorner also compared non-stationary Kalman filter versions of the two models. The

results were consistent between Martell et al. and Peterman and Dorner's stationary models for all of the stocks except for Weaver. There was considerably less support for the Larkin model when comparing non-stationary Kalman filter models (Peterman and Dorner). In contrast, the DIC results shown in Table 3.2 identify only four stocks that have more support for the Larkin model than the Ricker (i.e., Early Stuart, Stellako, Chilko, and Late Shuswap). Although, in the case of Chilko, the model form with the most support is the Larkin with the first lag β coefficient. If only the DIC values the Ricker and the full Larkin models were compared for Chilko, then there is equal support for both. For the three representative stocks I selected, the Larkin model was identified as having the most support for Late Shuswap by both AIC and DIC methods. Martell et al. did not evaluate Bowron, but Peterman and Dorner's result also found the Ricker model to have the most support for Bowron. However, my results for the Undetermined-type Late Stuart differ from both Martell et al. and Peterman and Dorner, who both found that the Larkin model had the most support. Interestingly, when Peterman and Dorner compared the non-stationary Kalman filter models, there was equal support for the Ricker and the Larkin.

Martell et al. (2008) evaluated two versions of the Larkin model with AIC. The "Larkin-a" model is the same as eq. (1), while the "Larkin-b" exponentiates the lag β terms. For all of the Fraser stocks that they tested, there was equal support for both Larkin models using AIC methods, except for Early Stuart, where the Larkin-a model had more support. An alternate to AIC and DIC methods for choosing between model forms is to use the reversible jump Markov Chain Monte Carlo algorithm to sample between posterior model probabilities (Ward 2008, King 2012). I decided to use the DIC methods as they are computationally more straightforward, and sufficient for the purpose of broadly categorizing the forecasted stocks. In the future, using the posterior model probabilities could be useful for fine-tuning the model forms for the Undetermined stocks.

4.3. Assessing bias in parameter estimation

I have presented both the assessment of average directional bias using MPE and the overall magnitude of uncertainty using the MAPE metrics. The results in Table 3.5, Table 3.6, Table 3.11, and Table 3.12 show that the Ricker model and the Larkin model

estimate their own parameters with less bias and uncertainty than when estimating parameters from data generated by the other model. However, the Larkin model estimates Ricker parameters with less bias and uncertainty than the Ricker model estimates Larkin parameters. Even so, the Larkin model tends to overestimate the α parameters and underestimate the β_0 parameters, which is consistent with the effects of time series bias.

The base case Larkin model with bounded-uniform priors on the lag β coefficients estimates non-zero lag β coefficients from the dataset generated with the Ricker model (Table 3.5). This occurs to a larger degree when estimating parameters for the Ricker-type stock. The median estimates of the non-existent lag β coefficients is reduced by approximately 80% for all stock types when estimated with the Larkin with normal priors (Table 3.11). However, the bias associated with estimating Ricker-type stocks when simulated and estimated with this version of the Larkin model increases. Overall, the combined $\alpha\beta_0$ MPE and MAPE were the smallest for the Larkin model with bounded-uniform priors.

My results for the Larkin-type stock are very similar to those reported by Collie and Walters (1987), who evaluated the bias associated with estimating Larkin and Ricker parameters for Late Shuswap stocks on a much shorter dataset. With respect to model fit, they found that the third lag β coefficient was not significant - the DIC evaluation shows that there is equal support for the full Larkin (eq.1) as well as the Larkin with the first two lag β coefficients (eq.2). When evaluating bias associated with estimating stock-recruit parameters, they found: (1) that there was very little difference when the Ricker model estimated parameters from data generated by the Ricker, and the Larkin from the Larkin, (2) when using the Ricker model to estimate parameters from data generated by the Larkin model, the parameters were much more biased than vice versa, (3) not only were the Ricker estimates in the previous case more biased, the Ricker α estimates were similar to the estimates of α from Ricker-generated data, and (4) when using the Larkin model to estimate Ricker generated data, α and β_0 were slightly overestimated, but there was no tendency to estimate a value for the lag β coefficients. My results are similar to these last four results from Collie and Walters

(1987), although their last finding is more consistent with the results from the Larkin model with the normal priors on the lag β coefficients.

I would conclude that Collie and Walters' (1987) findings of lower bias associated estimating parameters with the Larkin model compared to the Ricker model and that lag β coefficients are not caused by biases in using the Larkin model to estimate parameters can also be applied to Ricker-type and Undetermined-type stocks.

4.4. Population trajectories with different models

While the previous two methods seek to answer the question of how well does the model fit the data, there is a limited ability for those methods to address the question of how well does the model predict. Although I use the term “predict” very loosely, given that the end objective is to model population dynamics 48 years into the future. Annual run size forecast methods have been tested for their predictive ability using retrospective methods. These methods use part of the historical dataset to estimate the parameters and the rest of the dataset to compare the run size predicted from the parameterized model (e.g. Haeseker 2008, Grant et al. 2010). However, retrospective methods are not available for testing a 48 year “prediction” due to the length of the dataset. The only method available for comparative purposes is the somewhat circular calculation of comparing projected run sizes to historical run sizes. This comparison does not appear in the Fraser Sockeye escapement plan literature, but I believe it would be useful for the process. Showing the range of projected run size as a percentage of the past run size range would put the future projections into perspective with historical information as well as provide a performance measure that could be compared across stocks.

Walters and Staley (1987) found that when fitting a Ricker model to Fraser Sockeye stock-recruit data that the model fit tends to “bend over” at escapement values close to or at small multiples of the historical average escapement level. When they tested this on a hypothetical stock with a high carrying capacity and subjected it to a management regime with a fixed escapement target, the estimated parameters would have indicated a lower carrying capacity consistent with the escapement target. This implies that the Ricker stock-recruit model estimates of capacity are influenced more by

the number of spawners in the past, and by extension by fishing pressure, than any real information on capacity limitations. As a number of sockeye generations have passed since the original Walters and Staley (1987) observation, I performed the same check with the current dataset and found that their observation on the relationship between the average number of effective female spawners and the abundance at which the Ricker curve bends over still holds true for a large number of forecasted stocks. There is no reason to suspect that the Larkin model is free of this dependency on past spawner data for its parameter estimates. Of the three representative stocks, only Bowron, the Ricker-type stock shows this relationship between the historical escapement and the Ricker curve. Walters and Staley's (1987) results also reinforces the caveat to not take the historical run sizes as "truths" that need to be replicated but rather more as a stable measuring stick to compare different scenarios.

Effect of priors

I chose to constrain the β_0 prior for both the Ricker and Larkin to positive values. There does not appear to be a consensus in the literature on whether priors for the Ricker and Larkin model should constrain β coefficients to be positive. Rivot et al. (2001) specifically noted that they chose to allow for negative Ricker β_0 coefficients in their analysis, even though it is "highly improbable" (p. 2286). Grant et al. (2010) did not assume that any of the four Larkin β coefficients had to be positive, although they did limit the Ricker β_0 to be positive. Su and Peterman (2012) also assumed that the Ricker β_0 is positive in their choice of prior. The constraint of the Larkin lag β coefficients to positive values only is not unique to the escapement plan evaluation model for Fraser Sockeye. Although they did not state why, both Myers et al. (1998) and Martell et al. (2008) constrained Larkin lag β coefficients to be positive.

Of the three types of stocks, the Ricker-type was the most affected and the Larkin-type the least affected by choice of prior, both in terms of the abundances projected and the number of simulations discarded compared to the base case. As could be expected, allowing for positive interactions between cycle lines increased the projected abundances for all stocks. Using the normal prior decreased the number of discards for the Larkin-type and Undetermined-type stocks somewhat but increased the

number of discards for the Ricker-type stock substantially when compared to the base case.

When discarding the simulations by hand for the bias estimation methods, I noticed that the simulations with population trajectories that increased to infinity or crashed into a series of zeroes tended to do so in the later years of the simulation. This would not cause issues when forecasting run sizes, but needs to be taken into account when simulating for a number of years. For my evaluation, I chose to discard the simulations that could not be used. However, if normal priors for the lag β coefficients were used for evaluating TAM rules, alternate methods of discarding the simulations should be explored and the effects of discarding these simulations on the 48 year performance measures examined.

The Larkin model with normal priors estimates parameters from Ricker generated data with less bias and more precision than the base case model. When comparing individual parameter estimates from data generated by itself, the Larkin model performs worse than the base case. However, there is an improvement over the base case when comparing the combined $\alpha\beta_0$ performance measures. The concern I have for using the Larkin model with normal lag β priors to model Fraser Sockeye stocks is that the occurrence of discarded simulations is markedly different for this model when compared to the rest of the scenarios for the Ricker-type stock.

Effects of alternate total mortality scenarios

A 5% increase in the median total mortality from base case to the long term rate did not affect the results of the base case much. However, a 12% decrease in the median total mortality did – and not always in the direction that was anticipated. In the case of the Ricker model simulations, the decrease in total mortality led to increased abundance for all stock types. For the Larkin model simulations, the decrease in total mortality also resulted in increases to the abundance of the Ricker-type stock, and there was very little effect on the Undetermined-type stock's abundance. However, the Larkin-type stock decreased in abundance by the last four generations. This is possibly due to the between cycle interactions, with lower total mortality rates initially increasing

spawner abundances, but resulting in overall production being limited by the cycle line interactions of the Larkin model.

Stock-specific models

The abundances projected for the stock-specific model form (eq. 2) of the Undetermined-type stock are intermediary to the abundances projected with the base case Larkin and the Ricker. An incentive for using the Larkin with the first two lag β terms for this particular stock is that the number of simulations discarded due to the cleaning algorithm is much less with this model form (Table 3.18). I would recommend that stock-specific models be investigated for stocks when the DIC does not differentiate between the Ricker or the Larkin model.

Effects of changing initial spawning abundances

Most of the differences in projected run size associated with using different initial spawners occurred in the first four generations when using both the Ricker and Larkin model for all stock types. This implies that when evaluating long term performance of escapement plans, the model form used to represent a stock is more important than the abundance at the starting point. Performance measures currently used to evaluate TAM rules are probabilities calculated over the entire 48 year-12 generation simulation time frame. With the effects of initial spawning size nearly gone after four generations in my results, probable outcomes would be weighted by the longer term abundances that are determined by the choice of model. However, the total mortality regime I modelled is independent of run size, whereas TAM rules are abundance-based. I would expect that the abundance-based nature of the TAM rule, with higher exploitation rates being applied to higher run sizes, would result in the effect of initial spawner abundance lasting longer than in my results. However, the underlying long term effect of the choice of model form will still be there.

I would recommend testing in the escapement plan evaluation model how long the effects of the initial spawner abundance lasts. This would assist in putting the long term probabilities into perspective. I would recommend that the escapement planning process use probabilities calculated over the first few generations that is still affected by

the abundance of initial spawners. This would indicate near term probabilistic outcomes in addition to the current probabilities calculated over the entire 48 year period.

4.5. Potential implications for long term escapement plan

An important qualification of the results and conclusions drawn in this paper is that I examine three specific stocks as a examples of stocks that exhibit different cyclic behavior. Although the assessment is meant to inform the long term escapement planning process, I did not run any simulations within the actual escapement planning model. This was a done to separate the effect of the harvest rule from the qualities of the stock-recruit model used to simulate the population dynamics. Any results and conclusions drawn from one (or three) stock(s) should be tested on the other forecasted stocks. The results from this project raise two concerns with respect to the long term escapement plan model and process:

The first concern comes from observing the differences in abundance in the first four generations compared to the last four generations, as well as the results where the same abundance was generated at the end of 48 years regardless of starting abundances. These results imply that all stocks can increase and stabilize very quickly and to run sizes much larger than their historical range. It also affects the overall interpretation of the escapement plan performance measures. The escapement plan performance measures primarily used to select TAM rules calculate probabilities of catch and escapement over the entire 48 year simulation period. If the effect of initial spawner size is mostly gone after the first 12-16 years, performance measures will be weighted by the remaining 32-36 years and will reflect long term probabilities that will be dependent on the model form used to represent the stock as well as the TAM rule applied. Providing performance measures that are calculated on the first 12-16 years will be more indicative of what is possible at the current stock abundance. These near term performance measures would also reflect the effect of TAM rules on near term probabilities of catch and escapement, which is likely to be of interest and concern to escapement planning process participants. Abundance projections in the first four generations is also less dependent on the model form and priors used than those in the last four generations.

An additional suggestion arising from the above concern is that when there is doubt about what model form or prior to use for a particular stock, consideration should be given to incorporate multiple model forms into the escapement plan evaluation model. In this way, the uncertainty regarding stock-recruit model forms could be incorporated into the escapement plan model. The probabilities associated with each stock-recruit model form could be directly incorporated into the escapement plan evaluation model if the posterior model probabilities method for model selection is used. For example, if there was a 60% probability associated with one model form, then 60% of the 48 year simulations in the escapement plan model could be generated from that stock-recruit model form.

The second concern comes from observing the number of simulations that are discarded when modelling the Undetermined-type stock with the Larkin model (Table 3.18). Approximately 15% of the Undetermined-type base case simulations are discarded due to run sizes reaching zero compared to less than 5% for the other stock types. This implies that the model does not represent the Undetermined-type stock as well as the other stock types. It is unlikely due to high mortality rates, since the scenario that implements a smaller total mortality rate resulted in over 20% of the simulations being discarded for the Undetermined-type stock. Simulating this stock with a stock-specific model form identified using the WinBUGS step() function reduced the discarded simulations to less than 5%. Other Fraser Sockeye stocks should be checked for the frequency of zero run size occurrence and alternate models considered if the occurrence is high. Using the stock-specific model for this stock resulted in no change to the mean run size in the first four generations compared to the base case, but larger short term median run size and larger potential run sizes in the long term. The implications for other stocks will be stock dependent.

4.6. Conclusions & Recommendations

My first project questions about parameter estimation were: are the Larkin parameters that describe the interaction between cycle lines caused by biases in parameter estimation for non-cyclic stocks? Which model has the least bias and uncertainty associated with it when estimating stock-recruit parameters from all stock

types? The base case Larkin model with bounded-uniform priors does produce some non-zero parameter estimates for the lag β coefficients when estimating data generated by the Ricker model. The tendency to estimate non-zero lag β coefficients is substantially reduced by using the Larkin model with normal priors. The Larkin model estimates parameters from data generated by the Ricker and Larkin models with less bias and more precision than the Ricker model estimates them.

My second project question was: how does the choice of Larkin model form and priors that are used to model the interactions between cycle lines affect the performance measures used to evaluate TAM rules? In general, the choice of model form or the priors makes less of a difference in the run sizes projected over the first four generations than for the last four generations. Performance measures calculated over the entire 48 year simulation period may be more dependent on the choice of stock-recruit model than desired. There is evidence that using a stock-specific model form for the Undetermined-type stock decreases the occurrence of zeroes in the run size trajectories.

Based on the results of this project, I have recommendations on model forms, additional performance measures, and an overall change for the Fraser Sockeye long term escapement planning process. Regarding alternate model forms, I recommend considering alternate model forms for stocks when the DIC evaluation does not clearly differentiate between the Larkin or the Ricker model. I believe that the addition of two performance measures will help the participants of the escapement planning process better understand the implications of different TAM rules: (1) comparison of run size in the first and last 3-4 generations of the escapement plan simulations to the historical range of run sizes and (2) the probabilities of low catch and low escapement in the first 3-4 generations of escapement plan simulations while the trajectories are still influenced by the initial spawner sizes. My results show that the choice of stock-recruit model strongly affects the abundance projections in the last few generations of a 48 year simulation, whereas the choice of model has less of an influence on the projections in the first four generations. As an overall change, I would recommend that the idea of "long term" in the long term escapement plan be changed from 48 years to 12-16 years until such time that a stock-recruit model form can be empirically determined.

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