Estimating Basin-Wide Salmon Escapements using a Bayesian Model that Combines Data on Coded Wire Tag Recoveries, Genetic Stock Identification, and Scale Age Identification in Distant Fisheries

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Abstract

We developed a Bayesian model to estimate the escapement of an aggregate salmon stock based on Genetic Stock Identification data and recoveries of coded wire tags (CWTs) from a hatchery indicator stock in distant fisheries and on the spawning grounds. We applied the model to estimate escapement in 2009 for the South Thompson Age 0.3 Chinook aggregate, a significant component of the Fraser early model stock used by the Pacific Salmon Commission's (PSC) Chinook Technical Committee (CTC). The expected escapements for the South Thompson aggregate, based on data from the Fraser River gillnet test fishery (Albion) and Northern BC troll fishery were 164,000 (CV=0.06) and 152,000 (CV = 0.16), respectively. Differences in the two estimates were minor and well within variation due to sampling error. Age-specific estimates of escapement were relatively precise (0.02-0.20) in cases where the uncertainty in the expanded number of CWT recoveries in the fisheries was low. The model was not able to reliably estimate escapement for age-5 fish, as no CWTs were recovered in either fishery. Increasing the number of CWT recoveries is essential to reduce uncertainty in age-specific escapement estimates. A simulation analysis indicated that the model produced unbiased estimates of escapement under reasonable sample sizes, however large biases in escapement can result under departures from the assumption of equal harvest rates and maturity schedules for the indicator and aggregate stocks. The similarity in escapement estimates based on data from Albion and NBC troll fisheries indicates that this assumption likely holds in the case of the South Thompson aggregate, because all the Albion data are from mature fish, so there is no need to make the assumption of equal maturation schedules. Although analysis of the Albion test fishery data was not part of the proposed work for the PSC, the analysis was extremely beneficial because the estimates of spawning abundance had less uncertainty than the estimates produced from the NBC troll fishery data. The estimates based on the Albion data were more precise, met the CTC data standard for escapement indicator stocks, and required fewer assumptions than the analysis of the NBC troll fishery data.

Introduction

Accurate estimates of the spawner abundances are fundamental to manage Pacific salmon populations and the fisheries that depend on them. In the majority of cases for Chinook salmon (*Oncorhynchus tshawytscha*), catch in ocean fisheries consists of a mixture of stocks. For three fisheries managed under the Pacific Salmon Treaty, the allowable catches depend on abundance indices generated by the Pacific Salmon Commission's coastwide model which uses cohort analysis and exploitation patterns (PSC 2009a). Escapement estimates are a fundamental component of cohort analysis and are also needed to evaluate whether conservation goals and management objectives are being met. The Fraser River Chinook Summer-Run Age 0.3 aggregate stock is a major contributor to ocean fisheries in Southeast Alaska (SEAK) and Northern British Columbia (NBC). Since 2002, this stock represented upwards of 30-40% of the NBC troll fishery catches (Winther and Beacham 2006, 2009). Good quality spawning ground estimates for this stock group are needed to develop accurate forecasts of the NBC and SEAK abundance indices to define allowable catch. However, the current visual survey methods are thought to underestimate spawner numbers because of poor counting conditions experienced during helicopter surveys in the South and lower Thompson rivers (R. Bailey, DFO Kamloops, pers. Comm.). Results from the Lower and Middle Shuswap escapement survey calibration programs indicate escapements can be underestimated by 20-65% in the Fraser Summer-run Age 0.3 aggregate (Chamberlain and Parken 2007).

Obtaining unbiased and relatively precise estimates of spawning escapement for larger stock aggregates has been one of the holy grails in salmon management. Intensive methods, such as mark-recapture, can provide accurate estimates of escapements for individual stocks. These programs usually require considerable effort and resources, which limits the area and number of stocks where they can be applied. There can be considerable error introduced by setting catches based on escapements for a subset of stocks that are assumed to represent the abundance of the aggregate of stocks that are fished. This can be especially true for northern ocean fisheries which harvest stocks ranging from coastal Oregon to southeast Alaska. Less intensive methods, such as visual surveys, can be applied over a wider area and therefore potentially provide a more representative abundance index for an aggregate stock. However such indices may be quite biased and imprecise because detection probability is generally not estimated and surveys are typically only conducted for a short period relative to the duration of spawning. These characteristics limit the use of abundance indices obtained from uncalibrated visual surveys in salmon management.

In 1985, Canada and the U.S. agreed to maintain a coded wire tag (CWT) mark and recapture program designed to provide statistically reliable data for stock assessments and fishery evaluations (PSC 2009b). This program provides CWT recovery data for Chinook salmon in pre-terminal and terminal fisheries and at spawning grounds and hatcheries (PSC 2005). These data are used to estimate fishery- and age-specific exploitation rates for the indicator stocks, which are assumed to be similar to those for the larger wild stock aggregates they are meant to represent (the so-called ‘gorilla’ assumption, PSC 2005). Genetic Stock Identification (GSI) data is an emerging source of information that can be used to compliment the CWT program. For the most part, GSI has been used by fisheries management to modify fisheries reducing harvest rates on stocks of concern. Coupling the “gorilla” assumption with GSI-based estimates of stock-composition can provide a means of estimating escapements for larger aggregate stocks based on the so-called “ratio method (PSC 2005, see Appendix C). With this approach, the catch for a large aggregate stock in a fishery is first calculated from the product of the total catch and the proportion of the catch comprised of the aggregate stock as determined by GSI data. Assuming the ratio of fish in the escapement to the number in the fishery is the same for indicator and wild aggregate stocks (i.e., the gorilla assumption), the escapement for the latter is determined by multiplying the catch of the aggregate in the fishery by the ratio of CWTs in the escapement to the CWTs in the fishery.

In this analysis, we develop a Bayesian model using a variation on the ratio-method. A Bayesian approach offers a number of advantages compared to the existing analytic model. For example, estimates of uncertainty from the Bayesian model will be more realistic when sample size is small. The Bayesian model can easily incorporate uncertainty associated with age assignments from scale reading or stock assignments from GSI data. Prior information on expected CWT recoveries based on sibling models or cohort reconstruction can also be incorporated. Information can be combined across multiple fisheries to produce estimates with uncertainty based on the amount and quality of the sample data from each fishery. In this paper, we apply the Bayesian model to data for the South Thompson 0.3 Chinook aggregate to estimate escapement in 2009. A simulation exercise is used to evaluate whether estimates of the expected escapement and uncertainty are unbiased, and to evaluate the effects of sample size and departures from key model assumptions.

Methods

Data

We estimate the escapement for the entire South Thompson summer-run Chinook age 0.3 aggregate. This aggregate has represented approximately 58% of the total run size of the Fraser early CTC model stock, and visual surveys indicate that escapements have increased substantially since the mid 1990's (Fig.'s 1 and 2). The South Thompson aggregate spawns in the Lower Thompson River below Kamloops Lake, the South Thompson River mainstem, Lower and Middle Shuswap rivers, Little River, and Lower Adams River. The exploitation rate indicator stock for the South Thompson aggregate is located at the Lower Shuswap River where CWT releases for brood years (BY) contributing to the 2009 fishery were 98,000 (BY 2004), 193,000 (BY 2005) and 199,000 (BY 2006).

Data used to estimate the escapement of the South Thompson 0.3 aggregate includes information on abundance of the Lower Shuswap River indicator stock on the spawning grounds, the recovery of CWTs from this stock on the spawning grounds and in fisheries, and genetic stock identification and age data to determine the catch-by-age of the aggregate stock in fisheries. We applied the model to data collected from a gillnet test fishery, located at Albion about 50 km upstream of the Fraser River mouth, and troll fishery in Northern British Columbia (NBC). This allowed us to derive two independent estimates of spawning escapement for the South Thompson aggregate based on fishery-specific GSI, scale and CWT recovery data.

Total spawning escapement of Chinook in the Lower Shuswap River and consequently the number of CWT'd Chinook within that escapement are estimated annually from two-event sex-stratified mark-recapture experiments (Chamberlain and

Parken 2007). During the first event, a representative sample of Chinook salmon are captured by beach seining throughout the entire river and run, and subsequently tagged and released. The second event consists of a carcass recovery conducted throughout the entire system for the duration of the spawning and die-off period, where carcasses are recovered and sampled for marks and adipose fin clip (AFC) status. During the recovery portion of the project, biological information (length, sex, scales, spawning success) is collected from all fish identified with marks, as well as from a sub-sample of unmarked fish. All carcasses encountered with an AFC are sampled for the same biological information and also have their heads collected for CWT analysis.

As part of a large, coordinated program for the sampling of CWTs (Nandor et al. 2010), recoveries of CWTs are estimated by sampling fisheries and the subsequent extraction and decoding of the tags. CWT data are maintained by Canada and the U.S. and used to measure several statistics, such as fishing impacts by stock, age, and fishery, and survival and maturation rates by stock and brood year (PSC 2008). The estimated CWT recoveries for the northern BC troll fishery were extracted from the Regional Mark Processing Center (www.rmpc.org), whereas the Albion test fishery CWT recoveries were identified from biosample data maintained in DFO's Fishery Operating System and the Mark Recovery Program database. For the Albion test fishery, scale and CWT samples were collected using the methods described by Schubert et al. (1988).

Genetic samples were analyzed using methods outlined by Beacham et al. (2006). For the northern B.C. troll fishery, genetic and scale age samples were collected from commercial fishery landings (Winther and Beacham 2006, 2009; Beacham et al. 2008). In the Albion test fishery, genetic samples were collected using the methods described by Parken et al. (2008). Genetic variation at 12 microsatellite markers (*Ogo2*, *Ogo4*, *Oke4*, *Oki100*, *Ots100*, *Ots101*, *Ots104*, *Ots107*, *Ots2*, *Ots9*, *Omy325 and Ssa197*) in the test fishery samples was compared to a baseline of approximately 12,000 fish consisting of 55 Fraser River populations to assign individual fish to populations and regional reporting groups (Beacham et al. 2003a; 2003b). We used the 12-microsatellite locus baseline outlined by Beacham et al. (2006) that incorporated Chinook salmon populations ranging from the Alsek River in southeast Alaska to the Sacramento River in California to estimate stock composition of the NBC fishery samples. Individual genetic assignments were performed using the program cBayes (Neaves et al. 2005) which uses the algorithms from Pella and Masuda's (2001) program bayes. Eight chains were run for each estimate, each with a Markov Chain Monte Carlo sample size of 20,000. Estimates of individual assignments were based on the last 1000 steps of each chain combined.

To characterize the accuracy of scale age identifications for ocean-type Chinook salmon originating from the South Thompson aggregate, we assembled paired CWT and scale age data that had been collected from 1987 to 2009 by commercial fishery sampling programs in northern B.C. and at the Albion test fishery. The CWT ages were considered the true age (McNicol and MacLellan 2010). We used the DFO CWT mark recovery program sample data base to identify the scale book and scale numbers that were associated with CWTs originating from the Middle and Lower Shuswap River hatchery stocks, and extracted scale age identifications from DFO's Pacific Age Data System. For some years, all the scales were re-read because the aging procedures and criteria used previously were not the same as those applied currently. Also, scales were read for fish that were not aged previously when the samples had been sent directly to archives before aging. Overall, 303 paired CWT and scale samples were available for fish with Middle or Lower Shuswap CWTs, and after exclusion of scales that were unreadable or had partial ages, there were 218 fish that were age 0.2, 0.3, and 0.4. There are a relatively few Chinook salmon in the south Thompson watershed with stream-type life history compared to ocean-type life history. The stream-type populations have had fewer CWT fish released from hatcheries, relative to the ocean-type fish, which produced too few paired scale and CWT samples to characterize the accuracy for fish with stream-type life history in the South Thompson genetic regional reporting group.

Model Structure

We developed a Bayesian model to estimate the annual spawning escapement of an aggregate salmon stock based on catch in a distant fishery and the recovery of CWTs from its associated exploitation rate indicator stock in the fishery and in the spawning escapement. The ratio method that we implement relies on the key assumption that the ratio of CWTs for the indicator stock in the escapement to CWTs in the fishery is the same for wild aggregate and indicator stocks. Under this "gorilla" assumption, which holds if maturation schedules and harvest regimes among stocks are similar, the catch of the aggregate in a fishery, determined by GSI data, can be converted into an escapement estimate by multiplying it by the ratio of CWTs in the escapement to CWTs in the fishery. A detailed description of the model is provided below and a graphical representation of the model is provided in Figure 3.

The total spawning escapement for the aggregate stock (W_E, see Table 1 for parameter definitions) is the sum of age-specific estimates ($W_{E,a}$, eqn. 1.1 from Table 2). The expected value for the age-specific escapement estimates of the aggregate stock are determined by the product of the expanded catch of fish from the aggregate in the fishery ($W_{F,a}$) and the CWT expansion ratio (eqn. 1.2). The CWT expansion ratio is simply the estimated number of CWTs in the escapement ($C_{E,a}$) to the estimated number caught in the fishery ($C_{F,a}$). The total expanded number of fish from the aggregated stock in the fishery by age ($W_{F,a}$) is the sum across strata (eqn. 1.3). The expanded number of fish from the aggregate stock caught in the fishery by age and time-area strata ($W_{F,a,s}$) is the product of the strata-specific total catch ($N_{F,s}$), the estimated proportion of the aggregate in the catch determined by the GSI data ($P_{F,s}$), and the estimated proportion of fish in each age (sum of product of $P_{F,a,s}$ and $P_{S,a,aa}$, eqn. 1.4). This latter term is based on age determinations in the GSI sample (which determine $P_{F,a,s}$) and error in age assignments (as determined by $P_{S,a,aa}$). The expected proportion of fish from the aggregate stock in the GSI sample by strata ($P_{F,s}$) is the number assigned to the aggregate ($N_{W,s}$, eqn. 1.6) divided by the total size of the GSI sample ($N_{GSI,s}$ eqn. 1.5). The expected proportion of fish by age ($P_{F,a,s}$) is simply the ratio of the number of fish at each age that are assigned to the aggregate stock ($N_{W,a,s}$, eqn. 1.8) to the total number assigned that have been aged (eqn. 1.7). The expected proportion of fish assigned to age ‘a’ that are actually age ‘aa’ ($P_{S,a,aa}$) is simply the ratio of the former number to the total number of fish assigned to age ‘a’ in the ageing error matrix (eqn. 1.9).

The expected value for the expanded catch of CWTs from the indicator stock in the fishery by age ($C_{F,a}$) is simply the number of CWTs that are caught ($m_{F,a}$) expanded by the effective sampling rate for CWTs in the catch (λ_F, eqn. 1.10). λ_F is fixed and is the product of the sampling rate on the catch, the proportion of heads removed from fish with adipose fin clips, the proportion of those heads that make it to the decoding lab, and the proportion of heads with CWTs that are successfully decoded. The expected value for the expanded number of CWTs in the escapement of the indicator stock by age ($C_{E,a}$) is simply the sum across escapement estimation strata (male and female, $C_{E,a,s}$, eqn. 1.11). The expected value for $C_{E,a,s}$ is the number of CWTs recovered in the escapement ($m_{E,a,s}$) divided by the product of the proportion of the indicator stock escapement that is handled ($P_{E,s}$) during the recovery effort (dead-pitch), the proportion of those fish where the presence of an adipose fin can be unambiguously determined ($P_{AFS,s}$), and the decoding rate of CWTs for fish with adipose fin clips ($\lambda_{E,s}$, eqn. 1.12). $P_{E,s}$ is determined based on the ratio of Petersen tags recaptured to Petersen tags released during the mark-recapture experiments to estimate the escapement for the indicator stock (eqn. 1.13). $P_{AFS,s}$ is determined by the ratio of the number of fish where the status of adipose fin clip can be determined (N_{AFS}) to the total recovered ($N_{E,s}$, eqn. 1.14). $\lambda_{E,s}$ is fixed and is the product of the proportion of heads removed from fish with adipose fin clips, the proportion of those heads that make it to the decoding lab, and the proportion of heads with CWTs that are successfully decoded.

The aggregated stock escapement estimation approach is implemented in a Bayesian framework and therefore requires specification of probability distributions to represent uncertainty in parameter estimates. The number of fish from the GSI sample that are assigned to the aggregate stock within a stratum depends on the individual probabilities of assignment for each fish. Individual fish are assigned to the aggregate stock ($x_{i,s}$ = 0 (no) or 1 (yes)) in proportion to their estimated assignment probabilities ($p_{W,i,s}$) by drawing from a Bernoulli distribution (eqn. 2.1). The proportion of the aggregate stock ($P_{F,s}$) in the total catch by strata is assumed to be a binomially-distributed random variable (eqn. 2.2) which depends on the number of fish assigned to the aggregate stock ($N_{W,s}$) and the total sample size of the GSI sample ($N_{GSI,s}$). Note that there is very little uncertainty in $N_{W,s}$ in cases when the GSI sample size is large and the assignment probabilities to the stock of interest are highly informative (i.e., either very low or high values). In this situation, $N_{W,s}$ can be treated as data (i.e., fixed) rather than a random variable. The proportion-at-age for fish from the GSI sample that are assigned to the aggregate stock by strata ($P_{F,a,s}$) is assumed to be a multinomially-distributed random variable (eqn. 2.3) that depends on the number of assigned fish of each age ($N_{W,a,s}$) and the total number of fish that were assigned and aged. Age assignments based on scales can be incorrect, so the effects of ageing error are incorporated in the model. The proportion of fish of estimated age ‘a’ that are actually age ‘aa’ in the ageing error matrix ($P_{S,a,aa}$) is assumed to be a multinomially-distributed random variable (eqn. 2.4) that depends on the number of assigned fish in strata ‘a’, ‘aa’ ($n_{a,aa}$) and the total number of fish assigned to age ‘a’. Finally, the expanded catch of fish from the aggregate stock by age and strata ($W_{F,a,s}$) is assumed to be a Poisson-distributed random variable (eqn. 2.5) that depends on total catch ($T_{F,s}$), the proportion of the GSI sample assigned to the aggregate stock ($P_{F,s}$), and the age structure for those assigned fish that accounts for ageing error ($\sum P_{F,a,s} P_{Sa,aa}$). We used a Poisson rather than binomial distribution for this component because the former distribution is computationally more efficient than the latter and yields equivalent results because the total catches within strata are large numbers.

The estimated catch of CWTs from the indicator stock in the fishery ($C_{F,a}$) is assumed to be a binomially-distributed random variable (eqn. 2.6) that depends on the number of CWTs recovered from the catch ($m_{F,a}$) and the effective sampling rate on the catch for CWTs (λ_F). The estimated number of CWTs in the escapement of the indicator stock by strata ($C_{E,a,s}$) is also assumed to be a binomially-distributed random variable (eqn. 2.7) that depends on the number of CWTs recovered in the escapement ($m_{E,a,s}$) and the effective sampling rate on the escapement ($P_{E,s} P_{AFS,s} \lambda_{E,s}$). $P_{E,s}$ is assumed to be a binomially-distributed random variable (eqn. 2.8) that depends on the number of tags recaptured and the total number released. $P_{AFS,s}$ is also assumed to be a binomially-distributed random variable (eqn. 2.9) that depends on the number of fish recovered where the presence of an adipose fin clip is known ($N_{AFS,s}$) and the total number recovered ($N_{E,s}$).

The model estimates escapement for each age independently, but can also be run in an age-aggregated mode, where the data is pooled across ages prior to estimation. Precision based on this latter approach will be better because of the reduced number of parameters and increased sample size due to pooling. However, age-aggregated estimates based on pre-terminal data will be biased when one does not account for any differences in maturity schedules and differential exploitation between CWT fish and the rest of the stock aggregate (see discussion). The Bayesian model can also be simplified to avoid computations that address uncertainty in individual stock assignments (eqn. 2.1). In cases where the GSI total sample size is large, and where individual assignment probabilities to the aggregate ($P_{W,i}$) are either very small or very large, because the stock aggregate is genetically distinctive relative to others, the total number of individuals from the GSI sample assigned to the aggregate stock (N_W in eqn. 1.5) will be very well defined. In this situation, run-times for the Bayesian model can be substantially reduced by aggregating the GSI information prior to running the model. To do this, fish are assigned to the South Thompson aggregate if the probability of belonging to that stock group is greater than the probabilities for other stock groups included in the GSI analysis. The number of South Thompson assignments are then summed to compute N_W and $N_{W,a}$.

Bayesian implementation requires specification of prior probability distribution for all parameters that are estimated. For estimates of proportions, beta or dirichlet distributions were used (eqn.'s 3.1-3.5). Prior parameters were set so the prior distributions were uninformative, except in the case of the prior for ageing error, where information was available for DFO scale readers from another study for 13 ocean-type hatchery stocks: Big Qualicum, Chilliwack, Harrison, Lower Shuswap, Nitinat, Priest Rapids, Queets, Quinsam, Robertson, Salmon, Samish, Sooes, and Stillaguamish (McNicol and MacLellan 2010). The estimates of expanded catch or escapement of fish with CWTs from the indicator stock in the fishery or escapement were based on uninformative lognormal priors (eqn.'s 3.6 and 3.7). Note that the expanded CWTs returned from this prior distribution represent the number of CWTs not recovered, so these values are added to the actual recoveries to determine the prior for the total expanded number of CWTs.

When the combination of CWT releases, survival, exploitation rate, and sampling rate are insufficient to result in CWT recoveries for an age class in a fishery, a more informative prior distribution of the recoveries can be used to improve the precision of the spawning escapement estimate. In the case of the northern BC troll fishery in 2009, there were no age-5 CWTs recovered from the lower Shuswap River indicator stock. Accordingly, we developed an alternate prior distribution for the expanded number of age-5 CWTs in the fishery using the results from the CTC cohort analysis for the lower

Shuswap River indicator stock. Given the number of CWTs released 5 years earlier (~98,000), an assumed survival rate to age 5 among fisheries and natural mortality sources (0.014%), an expected exploitation rate in the fishery in 2009 (0.13, the average from 2003-2008), and a sampling rate in the fishery for CWTs (0.32), the expected number of CWTs in the fishery in 2009 should be approximately 2. Uncertainty in this expectation was calculated assuming binomial error, which was approximated using a gamma distribution with shape and rate parameters of 0.43 and 0.50, respectively.

The Bayesian escapement model is implemented in WinBUGS version 1.4 called from the 'R' statistical package via the R2WinBUGS library. Posterior probability distributions for model parameters were estimated using the Markov chain Monte Carlo (MCMC) sampling method as implemented in WinBUGS. A total of 2,500 iterations were conducted with the first 500 discarded to remove potential effects of the random parameter values used to initiate the simulation. Posterior distributions were based on saving every second sample from the remaining 2000 iterations. This sampling approach was sufficient to achieve model convergence in all cases. The mean and standard deviation from the posterior distribution was used to compute the coefficient of variation (CV) of parameter estimates. Uncertainty in parameter estimates was also quantified by determining the 95% credible interval from the posterior distribution based on the 2.5% and 97.5% quantiles.

We compared results from the Bayesian escapement model with those from the analytic version. Expected values for this latter model were determined from the expected value equations of the Bayesian model (eqn.'s 1.1-1.14). Variance in estimates from the analytic model were based on methods described in Bernard and Clark (1996) and PSC (2007) for analysis of CWT data, and in later work focusing specifically on GSI and CWT data (PSC 2005, Appendix C) using variance approximations described by Goodman (1960).

Simulation to Evaluate Model Bias

We used a simulation-estimation framework to evaluate the extent of potential bias in parameter estimates and their confidence limits from the Bayesian model, resulting from violations in the model assumptions. Model input data were simulated using the same distributions in the estimation framework (Table 2). The simulated data depend on the specified aggregate and indicator stock escapements, harvest rates in the fishery, and the combined harvest/and mortality between the fishery and return. These values are used to compute the abundance of both stocks before the fishery and hence the catch in the fishery. Additional parameters define conditions which determine the precision of the escapement estimate for the number of fish with CWTs on the spawning ground which includes: the fraction of the indicator stock that is given a CWT, the fraction of the observed escapement from the indicator where the status of the adipose fin can be determined, capture probability for the escapement of the indicator stock by strata, the proportion of escapement in each strata, the decoding rate for fish with adipose fin clips, and the total marks applied to estimate escapement. GSI data are simulated by specifying the sample size by fishery strata, the proportion of the aggregate stock in the fishery, and the age structure of the aggregate in the fishery. This latter component is simulated by specifying the age structure on the spawning grounds and a maturation schedule. Age proportions and maturity schedules for aggregate and indicator stocks are assumed to be equivalent unless stated otherwise. The recovery of CWTs from the indicator stock in the fishery depends on the predicted total harvest of CWTs and the effective sampling rate. For simplicity, we assumed there is no error in age assignments in the simulated GSI data.

The Bayesian estimation model was applied to the simulated data. We simulated 500 datasets with similar characteristics to the 2009 South Thompson aggregate data. The expected value (mean) from the posterior distribution was compared to the known values used in the simulation to evaluate bias for each trial. We also computed the fraction of trials where the estimates of the 95% credible interval included the true simulated values. This coverage probability should be 0.95 if the estimated mean and variance from the posterior distributions are unbiased.

Results

Application to South Thompson Chinook Aggregate Data

There was considerable variation in the quality of information for the South Thompson Chinook aggregate in 2009 needed to define the key components of the model (terms in eqn. 1.1). Sample size and capture probabilities used to estimate escapement of the Lower Shuswap exploitation rate indicator stock were high (Table 3). Over 10,000 spawners were handled in the dead-pitch, leading to the recovery of over 400 CWTs. Many CWTs were recovered in both escapement strata (male and female) for two ages (3 and 4), but there were very few recoveries of CWTs from age-5 spawners. Recoveries of CWTs in both the Albion gillnet test and NBC troll fisheries were low in all cases except for age-4 fish in the latter fishery. No CWTs from age-5 fish were recovered in either fishery. The total catch in the NBC troll was very high but was low in the Albion test fishery, however the CWT sampling rate was 100% in the latter case. GSI sample sizes for Albion and NBC troll fisheries were approximately 2,000 each, with 43% and 24% of the catch assigned to the South Thompson aggregate, respectively.

There was little uncertainty in assignments of individual Chinook in the Albion gillnet and NBC troll fisheries to the South Thompson aggregate based on GSI data. The majority of samples had either very low or high probabilities of originating from the aggregate for both fishery samples (Fig. 4). By examining only Chinook whose highest probability of assignment was to the South Thompson, we found there to be more uncertainty in the assignments of Chinook collected from the NBC troll fishery than for Chinook collected from the Albion gillnet fishery (Mann-Whitney U = 113,115; $P < 0.001$). However, overall this bimodal distribution of assignment probabilities, coupled with the large GSI sample sizes, resulted in very low uncertainty in the estimated proportion of the catch comprised of the aggregate stock (see results below). There was also very little uncertainty in age assignments in both the analysis of fish belonging to the South Thompson aggregate and from a wider distribution of stocks (Table 4).

The expected escapement of the South Thompson Chinook aggregate in 2009 estimated by the Bayesian model was 164,000 and 152,000 spawners based on the age-aggregated model using data from the Albion and NBC troll fisheries, respectively (Table 5). There was good agreement in age-3 escapement estimates based on the two data sources. The Albion-based estimate for age-4 abundance was over 30% higher than the NBC troll-based estimate, however there was substantial overlap in 95% credible intervals (Table 5) and posterior distributions (Fig. 5). The age-5 estimates based on the age-stratified model for both data sources were highly uncertain (CVs of 0.4 and 0.93, respectively) because no CWTs were recovered in either fishery. Age-5 escapement was therefore also computed using the subtraction method, where the sum of age-3 and 4 escapements estimates was subtracted from the age-aggregated values. These estimates across data sources were closer to each other than age-stratified estimates. There was substantial overlap in the posterior distributions of escapement among the data sources for ages 3 and 5, and age-aggregated estimates, but the posterior for the age-4 distribution based on the Albion test fishery data was substantively higher than the one based on data from the NBC troll fishery (Fig. 5). The CV of spawning escapement estimates was very close to or below the CTC criterion for escapement indicator stocks of 0.15 in the case of all Albion-based estimates except age-5, and NBC troll-based estimates for age-4 fish and for the age-aggregated value. In general, there was very close agreement between estimates of expected escapement and uncertainty based on Bayesian and analytic methods within fishery data sources (Table 5).

The components of variation leading to uncertainty in escapement estimates for the aggregate stock differed based on data from the two fisheries and to some extent among ages. Uncertainty in escapement based on data from the Albion test fishery was dominated by uncertainty in the expanded catch of the aggregate stock (W_F) and number of CWTs in the escapement (C_E, Fig. 6). There was no uncertainty in the number of CWT recoveries in the Albion test fishery because the sampling rate was 100%. In contrast, uncertainty in the aggregate escapement based on data from the NBC troll was largely influenced by uncertainty in the estimated number of CWTs recovered in the fishery. CWT recoveries in both fisheries were low, however uncertainty was much higher in the NBC troll data because the sampling rate was only 32%, compared to 100% in the Albion test fishery.

We attempted to reduce uncertainty in age 5 escapement estimates based on the NBC troll fishery data by using a more informative prior calculated from the expected number of CWTs recovered in the NBC fishery determined by cohort reconstruction. This prior indicated a high probability of no to few CWTs in the total catch and was not very informative because the expected expanded number of recoveries was very low (~2). As a result, the reconstruction-based prior was similar to the default lognormal prior (eqn. 3.6, Fig. 7 top). Not surprisingly then, the resulting posterior distributions of age 5 expanded recoveries in the fishery (C_{F5}) and escapement (W_{E5}) were very similar (Fig. 7, middle and bottom).

Evaluation of Model by Simulation

Simulation parameters generally produced data sets with approximately: 1) 500 CWTs recovered on the spawning grounds over ages 3-5 and a total of 10,000 unmarked fish; 2) recovery of approximately 70 CWTs in the fishery, with few marks (~ 10) for age-5 fish; and 3) assignment of 600 fish to the aggregate from a total GSI sample size of 2000. Under these conditions, the bias in the total escapement estimate, determined as the sum of the three age-specific estimates, was 6% (Fig. 8). Most model variables exhibited little bias (median ratio ~1) and coverage probabilities (fraction of simulations where true simulated value was within the 95% credible interval) were also unbiased (~0.95). There was a positive bias in W_{E5}, which was caused by the low number of CWTs recovered in the fishery (~ 10). In this case there was considerable uncertainty in the expanded number of CWTs given a simulated sampling rate of 50%. The binomial probability distribution that determines the uncertainty in the expanded number of CWTs in the fishery ($C_{F,5}$, eqn. 2.6) will tend to favor smaller values when sample size is low. This occurs because for a given number of CWT recoveries, probabilities returned from the binomial model will be higher if C_F is lower. This small sample size bias resulted in a larger value for the W_{F5} expansion ratio (ratio in eqn. 1.2) leading to an overestimate of W_{E5}. The prior distribution for C_{F5} will also have more influence on the posterior when sample size is low, which will also contribute to the bias. To demonstrate the effect of the number of CWT recoveries on bias in escapement estimates, we estimated age-aggregated escapements under an increasing number of CWTs recovered in the fishery and escapement (Fig. 9). When the total recoveries in the fishery is low (~5) escapement can be overestimated by as much as 50%, but the bias declines to less than 10% when the number of recoveries exceeds 15.

Bias in escapement estimates from both Bayesian and analytic models was very sensitive to simulation parameters that led to departures from the “gorilla” assumption that could arise from differences in maturity schedules or exploitation rates between indicator and aggregate stocks. We simulated the former case by using different maturation schedules for the aggregate (proportion maturing at ages 3, 4, and 5 = 0.25, 0.65, 1, respectively) and indicator stocks (proportion maturing at ages 3, 4, and 5 = 0.4, 0.8, 1, respectively). This scenario led to a 50% positive bias in the total escapement estimate (results not shown for brevity), largely due to positive biases in escapement estimates for age-3 and 4 fish. The positive bias occurred because the differences in maturation schedules led to higher proportion of recoveries on the spawning grounds for the indicator stock, leading to an underestimate in the ratio in the denominator of eqn 1.1 (relative to the unknown ratio for the aggregate) and ultimately an overestimate in escapement for the aggregate.

Discussion

This analysis has shown that it is possible to reliably estimate escapement for a large aggregate salmon stock using a combination of data for genetic stock identifications, scale age identifications, and the stock and age identifications from the recovery of CWTs in distant fisheries and on the spawning grounds. The expected escapements for the South Thompson 0.3 Chinook aggregate in 2009 based on the Bayesian model were 164,000 (CV=0.06) and 152,000 (CV = 0.16) using data from the Albion test and NBC troll fisheries, respectively. Differences in the two estimates were minor and well within the variability due to sampling error. Age-specific estimates of escapement were relatively precise in cases where the uncertainty in the expanded number of CWT recoveries in the fishery was low, which was the case for age-4 fish in the NBC troll fishery (22 recoveries with a sampling rate of 0.32) and for age-3 and 4 fish based on data from the Albion tests fishery (only 2 recoveries each, but with sampling rates of 1.0). We were not able to reliably estimate escapement for age-5 fish as CWTs were not recovered in either fishery. In these cases, age-5 estimates were derived by subtracting the sum of age-3 and 4 values from the age-aggregated totals. We consider these subtraction-based estimates of age-5 escapement to be less biased than the age-stratified estimates (due to low sample size effects), however the precision of the latter estimates was still low.

Age-aggregated estimates of escapement based on pre-terminal fishery data will be biased when the proportion of the aggregate with CWTs varies among ages. This can result from a violation of the gorilla assumption when maturity schedules vary between the CWT indicator stock and the stock aggregate. Also, the proportion of the aggregate with CWTs will likely vary, at least partially, by age due to variation in several factors including the numbers of CWTs released, the survival of CWT fish relative to the aggregate, and natural production of the aggregate. So even in the case of the age-aggregated estimates based on the Albion test fishery, where all fish are mature, we expect that the age-aggregated estimate has some unknown bias. Fisheries subsequent to the one sampled for GSI, scales, and CWTs will not contribute to bias in the age-aggregated estimate, unless they are mark-selective and change the proportion of the aggregate with CWTs. For practical purposes associated with these conditions, it is essential to design the CWT exploitation rate program with enough CWT releases to enable sufficient CWTs recoveries at each age to generate reliable age-stratified estimates.

Our analysis of the components of variance leading to uncertainty in spawning escapement estimates in 2009 can be used to focus future sampling efforts and provide guidance on future CWT releases. Increasing the number of CWT recoveries in the fisheries is essential to reduce uncertainty in the estimated escapement for age-5 fish. We attempted to reduce this uncertainty by constructing a prior distribution for CWTs in the NBC troll fishery based on cohort reconstruction. However, this prior was consistent with the data from 2009 and relatively uninformative, indicating a relatively high probability that few to no CWTs were present in the NBC troll fishery given low natural survival and modest harvest rates. Escapement estimates will be imprecise when few or no CWTs are recovered in the fishery or spawning grounds unless an informative prior distribution, which predicts a higher number of recoveries, can be justified. The most reliable and cost effective way to increase the number of CWTs that are recovered, is to increase the number that are released, since marine survival and maturation rates are uncontrollable and fishery exploitation rates are controlled by other objectives such as constraints for stocks of concern and the Pacific Salmon Treaty. Recoveries for the South Thompson indicator stock are expected to increase in the future because the release of CWTs was increased to 500,000 in 2010, from an average of 202,000 from 2004-2009. Improved precision of escapement estimates may be obtained by combining CWT, genetic and scale age identification data from multiple fisheries.

The Bayesian model we developed produced very similar results to those from the existing analytical model, but offers a number of advantages. While both models failed to directly estimate age-5 escapement, uncertainty in estimates based on the subtraction method are more readily developed using the Bayesian model. The Bayesian model can include the uncertainty in individual stock and age assignments. Both these error components were relatively minor in the case of the South Thompson age 0.3 Chinook aggregate, but could be significant for other stocks. McNicol and MacLellan (2010) reported that Chinook salmon are one of the most difficult salmon species to age due to their complexity and variable life history. Among 24 hatchery chinook salmon stocks, accuracy ranged from 100% among five readers for the Nitinat River stock on Vancouver Island down to 76% for the Nicola River stock in the Fraser River (McNicol and MacLellan 2010). Finally, extensions to the Bayesian model can be implemented to combine data sources and incorporate additional information. For example, a hierarchical version of the model could combine data from multiple fisheries (where exploitation rates are expected to differ) to derive a single escapement estimate that would essentially be an information-weighted average of the two independent estimates.

The critical assumption in the approach we used to estimate spawning escapement is that the exploitation rates and maturity schedules for the aggregate stock are similar to those from its exploitation rate indicator stock. The simulation exercise demonstrated that departures from this assumption can lead to substantial bias. Escapement estimates derived from data from the Albion test fishery are likely more reliable than those based on data from the NBC troll fishery because the "gorilla" assumption is likely more valid in the former case for four reasons: 1) the Albion test fishery harvests only mature fish based on extensive sampling and it's location 50 km upstream of the Fraser River mouth; 2) the Albion test fishery is located much closer to spawning grounds with relatively little exploitation upstream of the fishery; 3) mark-selective fisheries (MSFs), located in Juan de Fuca and Puget Sound, could reduce the percentage of the stock aggregate with CWTs between the time of the NBC troll fishery sampling and spawning ground sampling, but the estimates based on the Albion data are unaffected by these pre-terminal MSFs; and 4) the multi-panel gillnets in the test fishery are effective at sampling the full range of ages of returning fish. The first and second characteristics eliminate the effects of differences in maturity schedules among stocks, while the third and fourth characteristics limits effects of differences in exploitation rates among ages or between the exploitation rate indicator stock and its stock aggregate. The similarity in the independent escapement estimates derived from data from the two fisheries indicates that the “gorilla” assumption for the NBC troll fishery is reasonable in this case of the South Thompson 0.3 Chinook aggregate.

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References

Beacham, T.D. and nine authors. 2003a. The geographic basis for population structure in Fraser River Chinook salmon (*Oncorhynchus tshawytscha*). Fishery Bulletin 101:229-242.

Beacham, T.D. and nine authors. 2003b. Evaluation and application of microsatellites for population identification of Fraser River Chinook salmon (*Oncorhynchus tshawytscha*). Fishery Bulletin 101:243-259.

Beacham, T. D., J. R. Candy, K. L. Jonsen, J. Supernault, M. Wetklo, L. Deng, K. M. Miller, R. E. Withler, and N. V Varnavskaya. 2006. Estimation of stock composition and individual identification of Chinook salmon across thePacific Rim using microsatellite variation. Transactions of the American Fisheries Society 135:861–888.

Beacham, T.D., I. Winther, K.L. Jonsen, M. Wetklo, L. Deng, and J.R. Candy. 2008. The application rapid microsatellite-based stock identification to management of a Chinook salmon troll fishery of the Queen Charlotte Islands, British Columbia. North American Journal of Fisheries Management 28:849-855.

Bernard, D.R., and J.E. Clark. 1996. Estimating salmon harvest with coded-wire tags. Can. J. Fish. Aquat. Sci. 53: 2323-2332.

Chamberlain, M., and C.K. Parken. 2007. Enumeration and calibration of Chinook salmon escapements to two clear B.C. Interior streams. Report prepared for the Pacific Salmon Commission, Southern Boundary Restoration and Enhancement Fund, Vancouver, B.C.

McNicol, R.E., and S.E. MacLellan. 2010. Accuracy of using scales to age mixed-stock Chinook salmon of hatchery origin. Transactions of the American Fisheries Society 139:727-734.

Nandor, G.F., J.R. Longwill, and D.J. Webb. 2010. Overview of the coded wire tag program in the greater Pacific region of North America, *in* Wolf, K.S., and O’Neal, J.S., eds., PNAMP Special Publication: Tagging, Telemetry and Marking Measures for Monitoring Fish Populations—A compendium of new and recent science for use in informing technique and decision modalities: Pacific Northwest Aquatic Monitoring Partnership Special Publication 2010-002, chap. 2, p. 5-46.

Neaves, P. I., C. G. Wallace, J. R. Candy, and T. D. Beacham. 2005. CBayes: Computer program for mixed stock analysis of allelic data. Version v5.01. Free program distributed by the authors over the internet from http://www.pac.dfo-mpo.gc.ca/sci/mgl/Cbayes_e.htm

Pacific Salmon Commission. 2008. Recommendations for application of genetic stock identification (GSI) methods to management of ocean salmon Fisheries. Pacific Salmon Commission Technical Report No. 23. http://www.psc.org/pubs/psctr23.pdf

Pacific Salmon Commission. 2008. An action plan in response to coded wire tag (CWT) expert panel recommendations: a report of the Pacific Salmon Commission CWT work group. Salmon Commission Technical Report No. 25.

Pacific Salmon Commission. 2009a. 2009 annual report of the exploitation rate analysis and model calibration. Pacific Salmon Commission Report TCCHINNO (09)-3, Vancouver, B.C.

Pacific Salmon Commission. 2009b. Pacific Salmon Treaty including: Yukon River Agreement, Revisions to January 1, 2009, Memorandum of Understanding (1985), Exchanges of Notes – 1985, 1999, 2002, 2005 & 2008. Prepared by the Pacific Salmon Commission, Vancouver, B.C.

Parken, C.K., J.R. Candy, J.R. Irvine, and T.D. Beacham. 2008. Genetic and coded wire tag results combine to allow more precise management of a complex Chinook salmon aggregate. North American Journal of Fisheries Management 28:328-340.

Pella, J., and M. Masuda. 2001. Bayesian methods for analysis of stock mixtures from genetic characters. Fishery Bulletin 99:151-167.

Hankin, D.G., J.H. Clark, R.B. Deriso, J.C. Garza, G.S. Morishima, B.E. Riddell, C. Schwarz, and J.B. Scott. 2005. Report of the Expert Panel on the Future of the Coded Wire Tag Program for Pacific Salmon. PSC Tech. Rep. No. 18, November 2005. 300 p (includes agency responses as appendices).. http://www.psc.org/pubs/psctr18.pdf

Schubert, N.D., P.G. Patterson, and C.M. McNair. 1988. The Fraser River Chinook salmon test fishery: data summary, 1980-1987. Canadian Data Report of Fisheries and Aquatic Sciences 709.

Winther, I., and T. D. Beacham. 2006. The application of Chinook salmon stock composition data to management of the Queen Charlotte Islands troll fishery, 2002 to 2005. Canadian Technical Report of Fisheries and Aquatic Sciences 2665.

Winther, I., and T. D. Beacham. 2009. The application of Chinook salmon stock composition data to management of the Queen Charlotte Islands troll fishery, 2006. Pages 977-1004 *in* C. C. Krueger, and C. E. Zimmerman, editors. Pacific Salmon: ecology and management of western Alaska's populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

Table 1. Definition of variables used in the Bayesian model to estimate escapement for an aggregate stock.

Variable	Description
Parameter Estimates	
W_E	Escapement of wild stock
W_F	Expanded catch of wild stock in fishery
C_F	Expanded number of CWTs from indicator stock in fishery
C_E	Expanded number of CWTs in the escapement of indicator stock
P_F	Proportion of the wild stock in fishery
$P_{F,a}$	Proportion-at-age for wild stock in fishery based on scale ages
$P_{S,a,aa}$	Proportion of fish aged as 'a' that are actually age 'aa' from age-error matrix
N_W	Number of fish in GSI fishery sample assigned to the wild stock
$N_{W,a}$	Number fish in GSI fishery sample assigned to the wild stock of age 'a'
x_i	Binary value specifying whether a fish from GSI sample from fishery is assigned to wild stock or not (0=no, 1=yes)
P_E	Proportion of total escapement of indicator stock available to be sampled
P_{AFS}	Proportion of escapement where status of adipose fin (clipped or not) is known
Data	
m_E	Decoded CWTs in escapement for indicator stock
r_E	Tags recaptured in escapement of indicator stock in dead-pitch recovery
R_E	Tags applied to escapement of indicator stock
N_E	Total dead-pitch recoveries in escapement of indicator stock
N_{AFS}	Recoveries in escapement of indicator stock where status of adipose fin is known (clipped or not)
N_F	Total catch in fishery (all stocks)
m_F	Decoded CWTs from indicator stock in the fishery
$P_{W,i}$	Probability of assignment of individual fish in GSI fishery sample to wild stock
N_{GSI}	Number of GSI samples from fishery
$n_{a,aa}$	Number of fish of estimated age 'a' that are actually age 'aa'
Constants	
λ_F	Proportion of the total catch from fishery that is sampled and successfully decoded
λ_E	Proportion of sampled fish with an adipose fin clip from the escapement of the indicator stock that are successfully decoded
p_a	Prior for proportion at age in fishery (prior sample size for age 'a')
$p_{a,aa}$	Prior for proportion of fish of age 'a' that are actually age 'aa' (prior sample size)
Indices	
a, aa	Index for total age (a or aa = 3 to 5)
s	Index for fishery (time-area) strata or escapement (male, female, small) strata
i	Index for individual fish in GSI sample from fishery (i=1 to N_{gsi})

Table 2. Equations used to determine expected values and uncertainty (sampling and prior distributions) in parameters and derived variables of the Bayesian escapement estimation model. See Table 1 for definitions of model parameters, constants, and indices.

Expected Values

(1.1) $$W_E = \sum_a W_{E,a}$$

(1.2) $$W_{E,a} = W_{F,a} \frac{C_{E,a}}{C_{F,a}}$$

(1.3) $$W_{F,a} = \sum_s W_{F,a,s}$$

(1.4) $$W_{F,a,s} = N_{F,s} P_{F,s} \sum_a P_{F,a,s} P_{S,a,aa}$$

(1.5) $$P_{F,s} = \frac{N_{W,s}}{N_{GSI,s}}$$

(1.6) $$N_{W,s} = \sum_{i=1}^{n_{GSI,s}} x_{i,s}$$

(1.7) $$P_{F,a,s} = \frac{N_{W,a,s}}{\sum_a N_{W,a,s}}$$

(1.8) $$N_{W,a,s} = \sum_{i=1}^{N_{GSI,s}} x_{i,a,s}$$

(1.9) $$P_{S,a,aa} = \frac{n_{a,aa}}{\sum_{aa} n_{a,aa}}$$

(1.10) $$C_{F,a} = \frac{m_{F,a}}{\lambda_F}$$

Table 2. Con’t.

(1.11) $C_{E,a} = \sum_{s} C_{E,a,s}$

(1.12) $C_{E,a,s} = \dfrac{m_{E,a,s}}{P_{E,s} P_{AFS,s} \lambda_{E,s}}$

(1.13) $P_{E,s} = \dfrac{r_{E,s}}{R_{E,s}}$

(1.14) $P_{AFS,s} = \dfrac{N_{AFS,s}}{N_{E,s}}$

Sampling Distributions

(2.1) $x_{i,s} \sim dbern(p_{W,i,s})$

(2.2) $N_{W,s} \sim dbin(P_{F,s}, N_{GSI,s})$

(2.3) $N_{W,a,s} \sim dmulti(P_{F,a,s}, \sum_{a} N_{W,a,s})$

(2.4) $n_{a,aa} \sim dmulti(P_{S,a,aa}, \sum_{aa} n_{a,aa})$

(2.5) $W_{F,a,s} \sim dpois(N_{F,s} P_{F,s} \sum_{a} P_{F,a,s} P_{S,a,aa})$

(2.6) $m_{F,a} \sim dbin(\lambda_{F}, C_{F,a})$

(2.7) $m_{E,a,s} \sim dbin(P_{E,s} P_{AFS,s} \lambda_{E,s}, C_{E,a,s})$

(2.8) $r_{E,s} \sim dbin(P_{E,s}, R_{E,s})$

(2.9) $N_{AFS,s} \sim dbin(P_{AFS,s}, N_{E,s})$

Table 2. Con't.

Prior Distributions

(3.1) $P_{F,s} \sim dbeta(1,1)$

(3.2) $P_{F,a,s} \sim ddirch(p_{a,\ldots Nages} = 1)$

(3.3) $P_{S,a,aa} \sim ddirch(p_{a,aa} = prior\_data)$

(3.4) $P_{E,s} \sim dbeta(1,1)$

(3.5) $P_{AFS,s} \sim dbeta(1,1)$

(3.6) $C_{F,a} \sim \exp(dnorm(0,1E-6)) + m_{F,a}$

(3.7) $C_{E,a,s} \sim \exp(dnorm(0,1E-6)) + m_{E,a,s}$

Table 3. Data used to estimate escapement for the South Thompson 0.3 aggregate in 2009. See Table 1 for definitions of model parameters.

Comment [FaOC1]: Josh, there is a minor spelling mistake in the table that I can't correct. Near the bottom…Fisery

Escapement Data for Indicator Stock

	Peterson Marks		Deadpitch Recoveries			
	Applied	Recaptured	AFC Present	AFC Not Present	AFC Status Unknown	Decoding Rate
	R_E	r_E	N_{AFS}		N_E-N_{AFS}	λ_E
Male	1,710	821	208	6,023	0	0.99
Female	941	502	282	4,872	0	0.99
Total	2,651	1,323	490	10,895	0	0.99

CWT Recoveries

		Age			
		3	4	5	Total
in escapement of indicator stock (m_E)					
	Male	107	69	2	178
	Female	97	134	1	232
in fishery (m_F)					
	Albion	2	2	0	
	NBC	8	22	0	

Fishery Catch and GSI Data

	Fishery	
	Albion	NBC
CWT Sampling Rate (λ_F)	1	0.32

	Albion	NBC Strata									Total
		1	2	3	4	5	6	7	8	9	NBC
Total Catch (T_F)	1,990	16,450	12,739	9,835	8,373	11,976	7,351	2,998	3,048	100	72,870
# of GSI Samples (N_{GSI})	1,982	369	294	378	292	294	221	71	92	95	2,106
# Assigned to SoTh (N_W)	863	101	83	97	57	70	57	16	8	1	490

# of Fish by Age in GSI Sample assign

		Age			
Fisery	Strata	3	4	5	Other
Albion		78	496	154	27
NBC	1	4	58	21	5
	2	1	45	14	1
	3	2	65	11	2
	4	3	34	7	3
	5	3	47	10	1
	6	2	35	7	0
	7	1	8	1	0
	8	2	4	1	0
	9	0	0	0	0

Table 4. Data used to estimate uncertainty in age assignments for the South Thompson age 0.3 Chinook aggregate in the Bayesian escapement model. The ageing error matrices represent the number of fish assigned age ‘a’ (based on scale reading) whose actual age was ‘aa’ (as determined from CWTs). The top matrix is based on fish from the South Thompson aggregate ($n_{a,aa}$ from Table 1), while the lower matrix is based on data from a ocean-type stocks as summarized in McNicol and MacLellan (2010). Prior information on age assignment error used in the model is based on the lower matrix (prior sample size in eqn. 3.3 of Table 2).

	Estimated	**Known Age ('aa')**		
Stock	**Age ('a')**	**3**	**4**	**5**
South Thompson (data)				
	3	29	1	0
	4	0	175	1
	5	0	1	11
Ocean-type S tocks from McNicol and MacLellan (prior)				
	3	93	2	0
	4	1	126	2
	5	0	2	25

Table 5. Comparison of statistics on escapement estimates for the South Thompson Age 0.3 aggregate in 2009 determined by the Bayesian and analytic models (in thousands of fish). Mean and MLE denote the expected values for the Bayesian and analytic models, respectively, and CV denotes the coefficient of variation. The limits of the 95% credible interval are also shown. The total escapement estimate (Age=All) was determined by the age-aggregated model, where age-specific data were pooled prior to estimation, and based on the sum of age-specific estimates. Age 5 escapement statistics from the Bayesian model were computed using both the subtraction method (5=Age aggregated total–(3-4)) and the sum of all age-specific estimates. For the analytic model, the age 5 estimate could only be determined using the subtraction method, with variance estimated by the parametric bootstrap method.

		Bayesian Model				**Analytic Model**			
Fishery	**Age**	**Mean**	**CV**	**2.5%**	**97.5%**	**MLE**	**CV**	**2.5%**	**97.5%**
Albion Gillnet	3	17.2	0.16	12.4	22.8	18.6	0.09	15.3	21.9
	4	107.3	0.08	92.2	124.2	116.0	0.08	97.8	134.2
	5[1]	39.9	0.33	14.9	65.8	38.6	0.34	12.8	64.4
	5[2]	6.9	0.40	3.2	14.2	NC			
	All[3]	164.3	0.06	145.8	184.8	173.2	0.06	152.8	193.6
	All[4]	131.4	0.07	114.4	149.2	NC			
NBC Troll	3	20.7	0.40	9.3	43.0	14.0	0.38	3.6	24.4
	4	77.9	0.20	52.4	117.7	82.4	0.20	50.1	114.7
	5[1]	53.7	0.55	0.0	110.4	65.7	0.48	3.4	128.9
	5[2]	45.0	0.93	3.3	157.4	NC			
	All[3]	152.3	0.16	112.6	204.5	162.1	0.17	108.1	216.1
	All[4]	143.6	0.31	85.5	264.0	NC			

[1] Computed using subtraction method
[2] Computed using age-stratified model
[3] Computed using age-aggregated model
[4] Computed by summing age-specific estimates

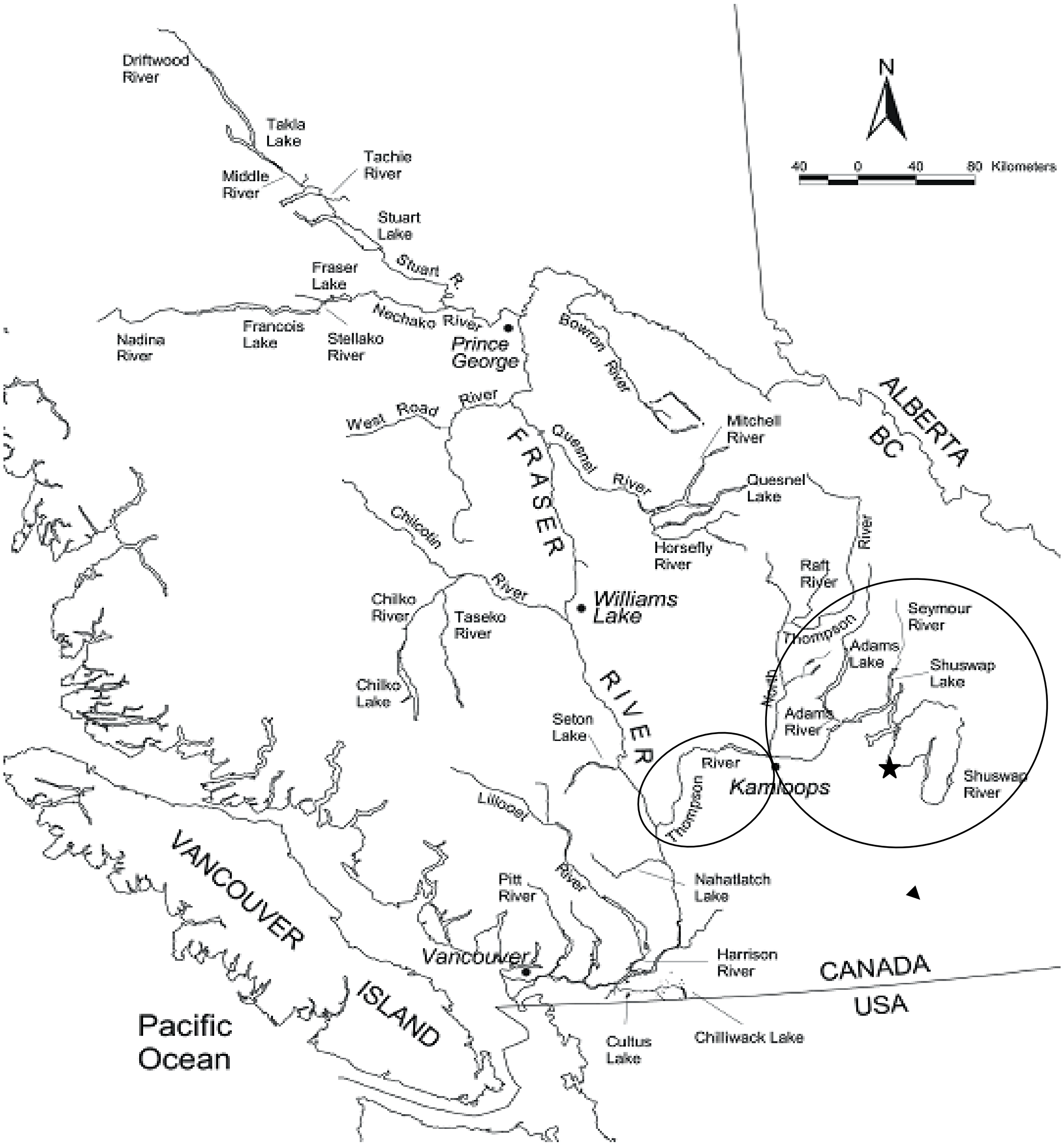

Figure 1. Map of Southern British Columbia showing the location of the major streams used by the South Thompson 0.3 Chinook aggregate stock (circled) and the location of the Lower Shuswap indicator stock (star). The Albion test fishery is located near Vancouver and the Northern BC troll fishery is located well north of Vancouver Island and is not shown on the map.

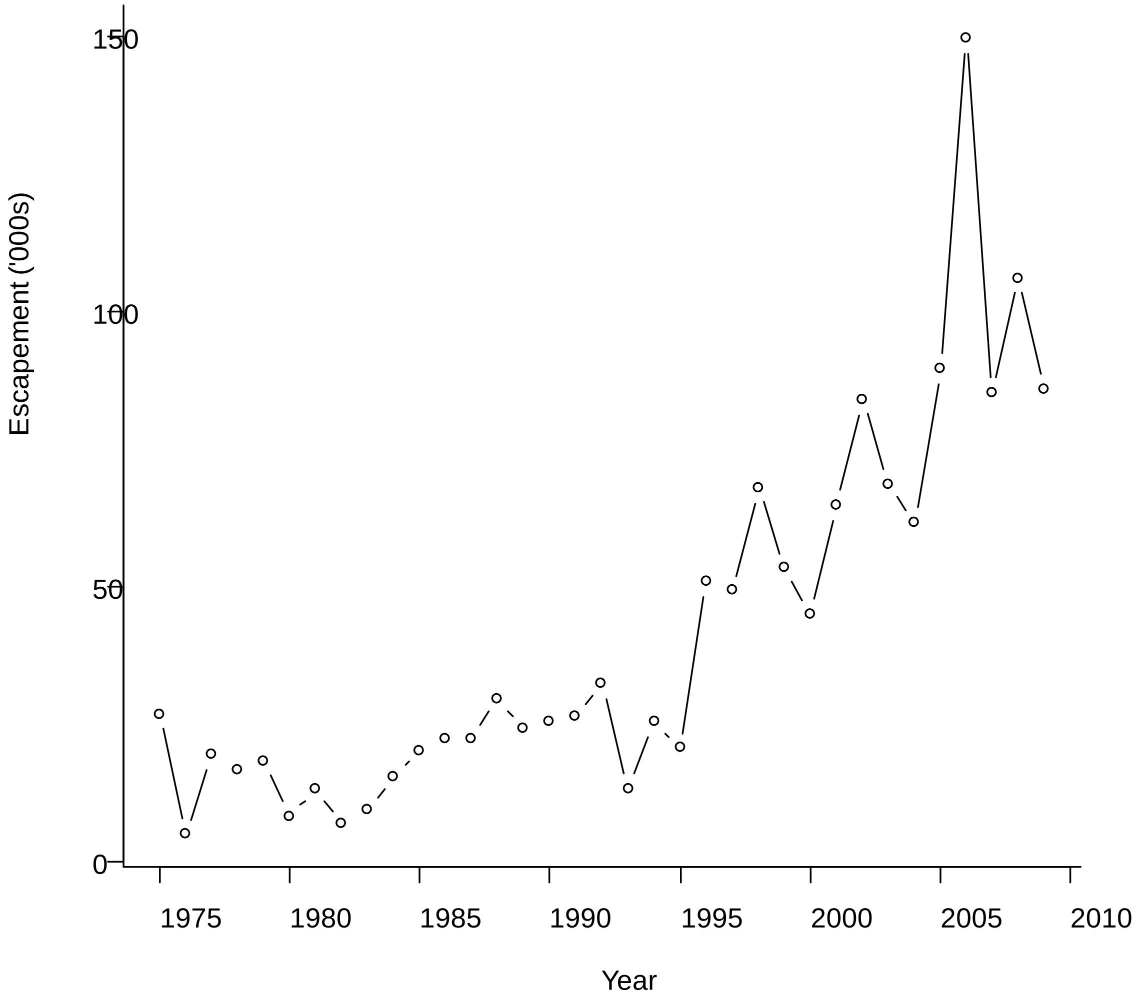

Figure 2. Historical trend in the estimated spawning escapement of the South Thompson 0.3 aggregate based on visual surveys (***R. Bailey, Fisheries and Oceans Canada, unpublished data***).

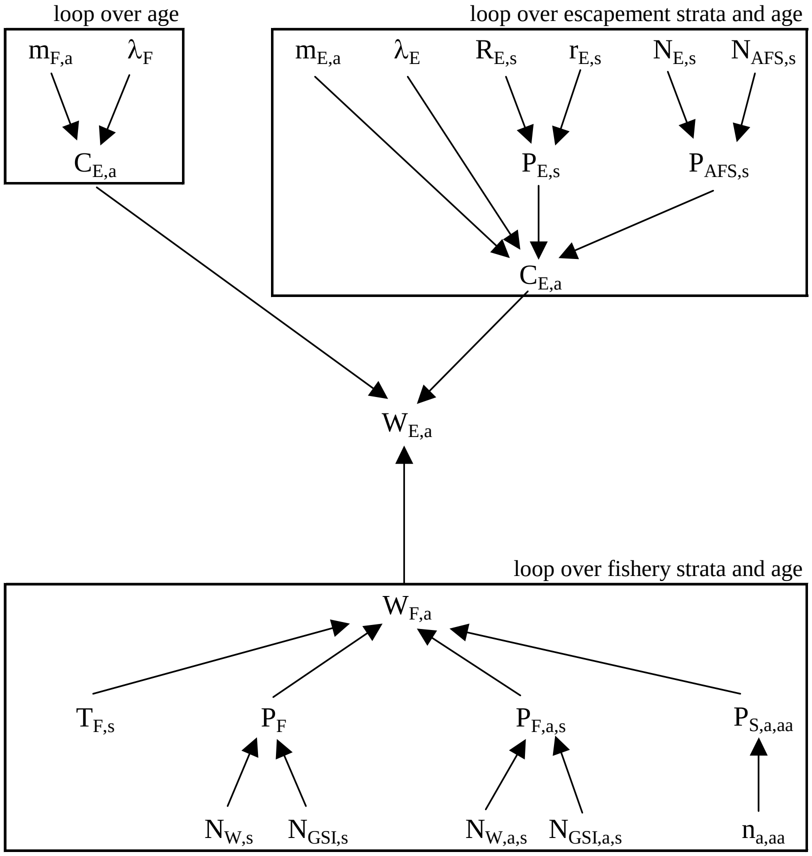

Figure 3. Visual representation of the Bayesian model used to estimate escapement of the South Thompson 0.3 Chinook aggregate. Variables are defined in Table 1. Arrows indicate conditional dependencies; the boxes represent repetition of structure over age (a) and fishery or escapement estimation (s) strata.

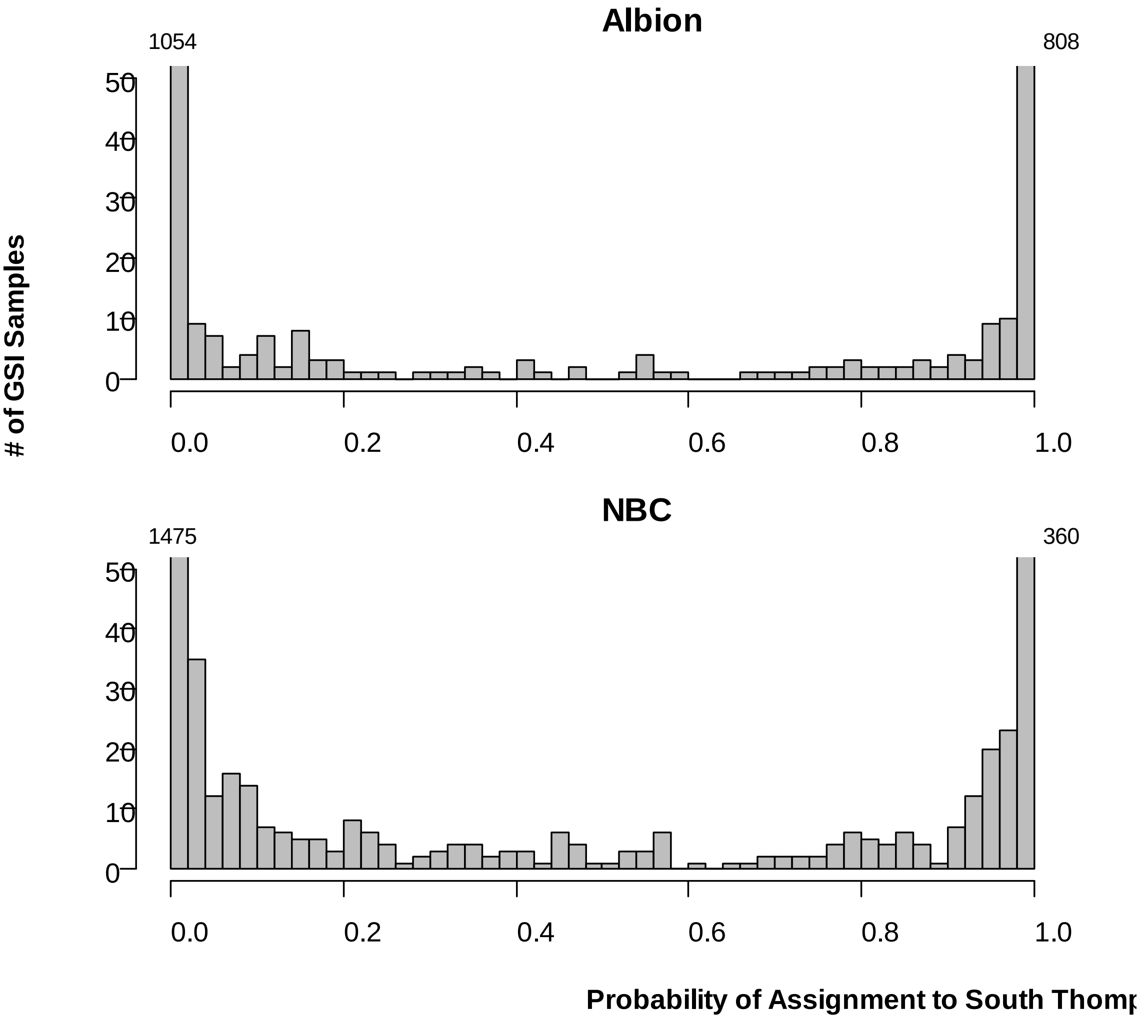

Figure 4. Frequency distributions of the number of samples with different probabilities of assignment to the South Thompson Chinook aggregate based on genetic stock identification (GSI) data collected from the Albion test and Northern BC troll fisheries in 2009. Note that the y-axes do not extend to the full range of the data and frequencies for probabilities <0.02 (first bar) and > 0.098 (last bar) are cut-off (frequencies for these cases are shown by the text at the top of the bars). The total GSI sample sizes in Albion test and NBC troll fisheries were 1977 and 2106, respectively.

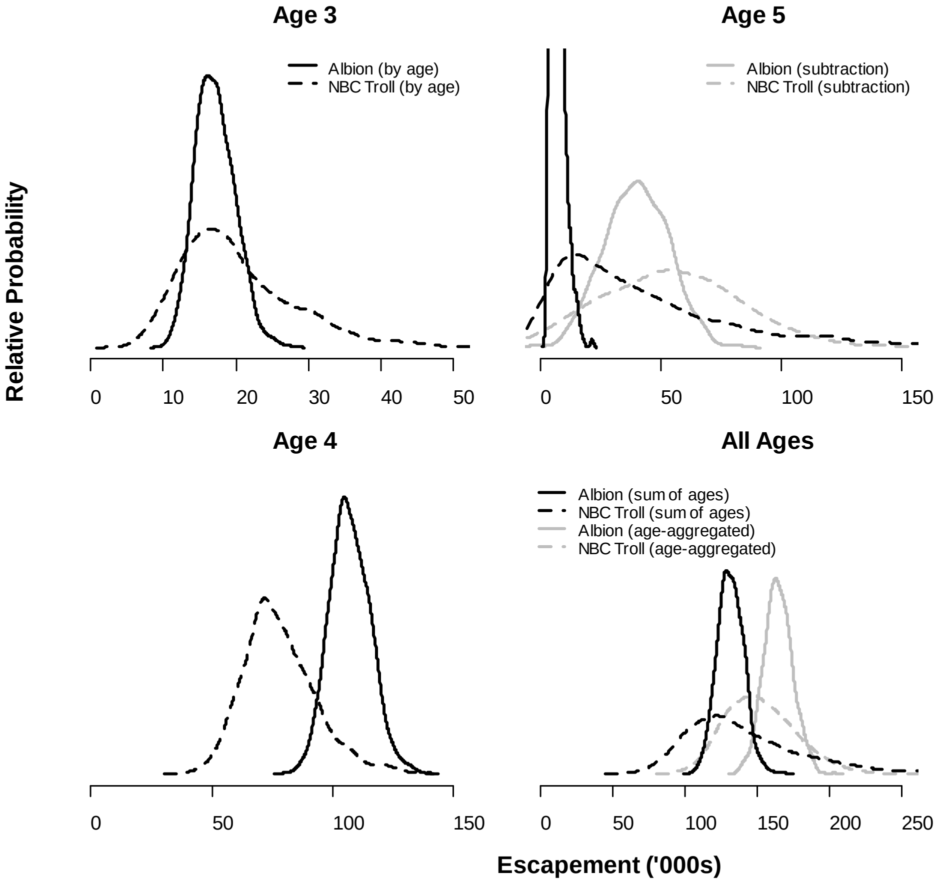

Figure 5. Comparison of posterior probability distributions of escapement for the South Thompson Chinook 0.3 aggregate in 2009 from the Bayesian model based on GSI data and CWT recoveries in the Albion test and Northern BC troll fisheries. Age-specific posteriors are based on the age-stratified model (dark lines), and the posterior for the total across all ages is based on the sum of age-specific posteriors (dark lines). An alternate posterior distribution for the total escapement across ages is based on the age-aggregated model, where the data is aggregated across ages before estimation (gray lines). In the case of age 5 fish, an alternate posterior distribution is calculated using the subtraction method where the sum of age 3 and 4 estimates is subtracted from the total based on the age-aggregated model (gray lines)

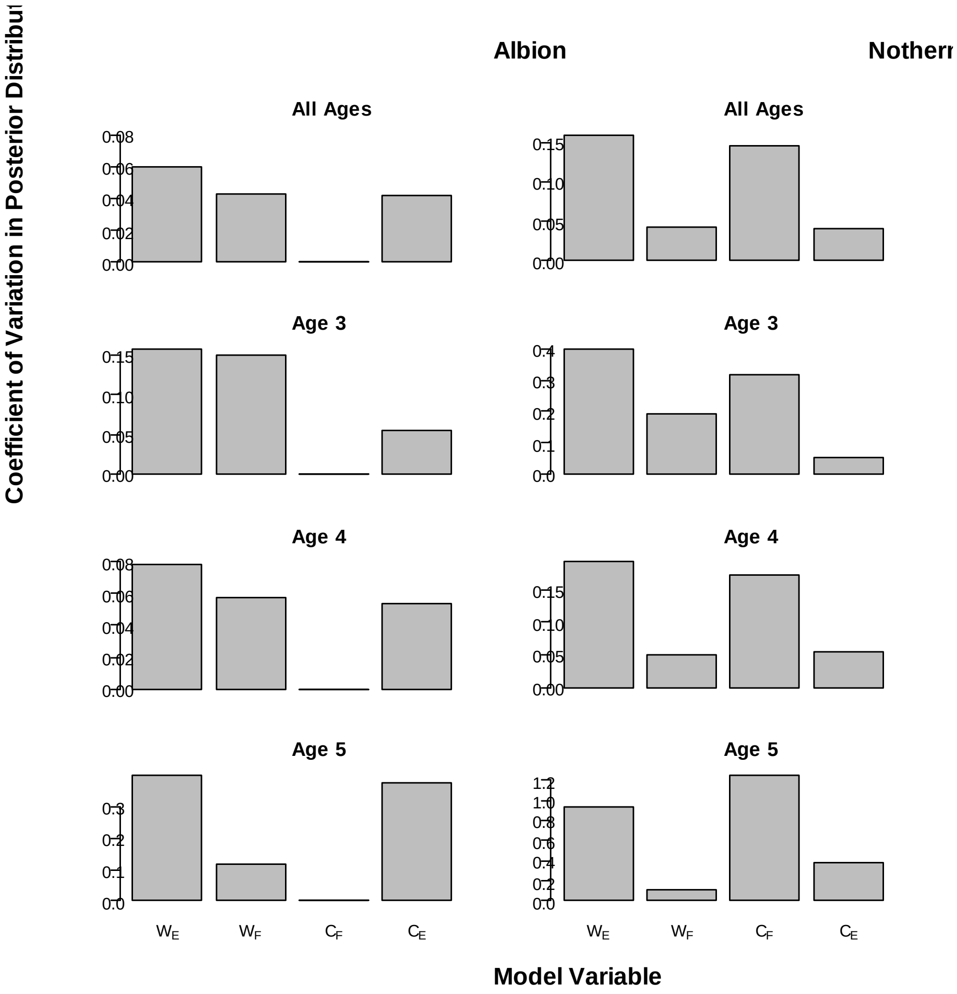

Figure 6. Comparison of the coefficient of variation of posterior distributions of key model variables used to determine escapement to the South Thompson Chinook 0.3 aggregate in 2009 based on the Bayesian model using data from the Albion test and Northern BC troll fisheries. See Table 1 for definition of model variables. Results are shown for the age-aggregated model (All Ages) as well as for the age-stratified model.

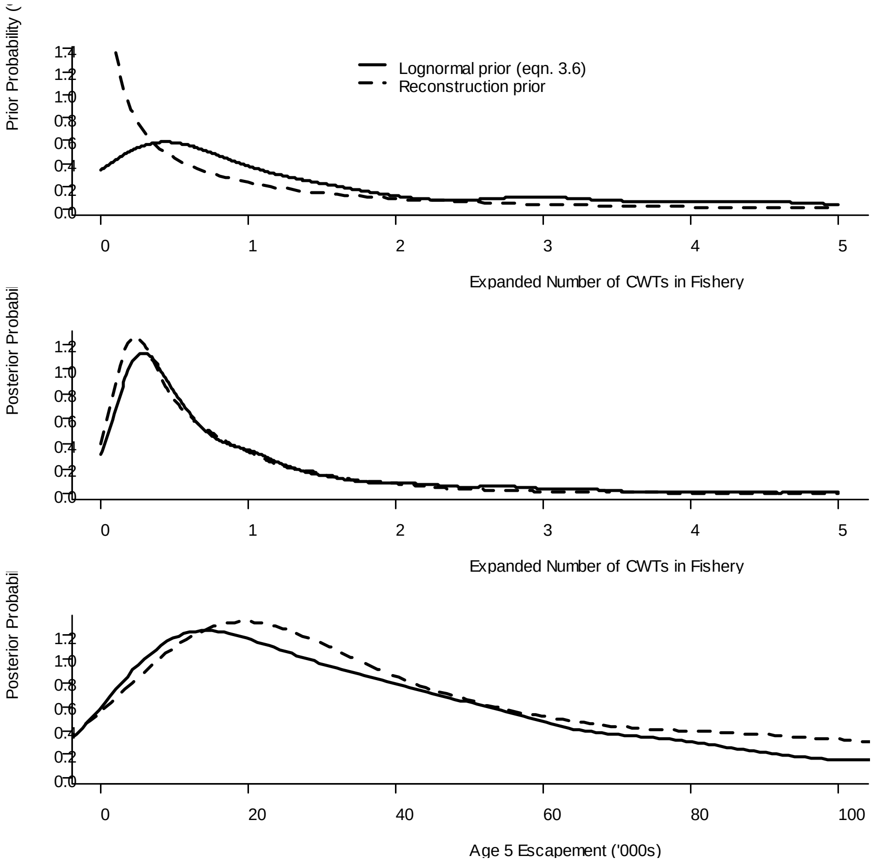

Figure 7. Effect of the prior distribution on the expanded number of CWTs in the NBC troll fishery on age 5 escapement. Two alternate priors of the expanded number of CWTs in the fishery are compared in the top figure. The posterior distributions of the number of CWTs in the fishery based on both prior distributions are compared in the middle figure. The bottom figure compares the posterior distributions of age 5 escapement under the two prior distributions.

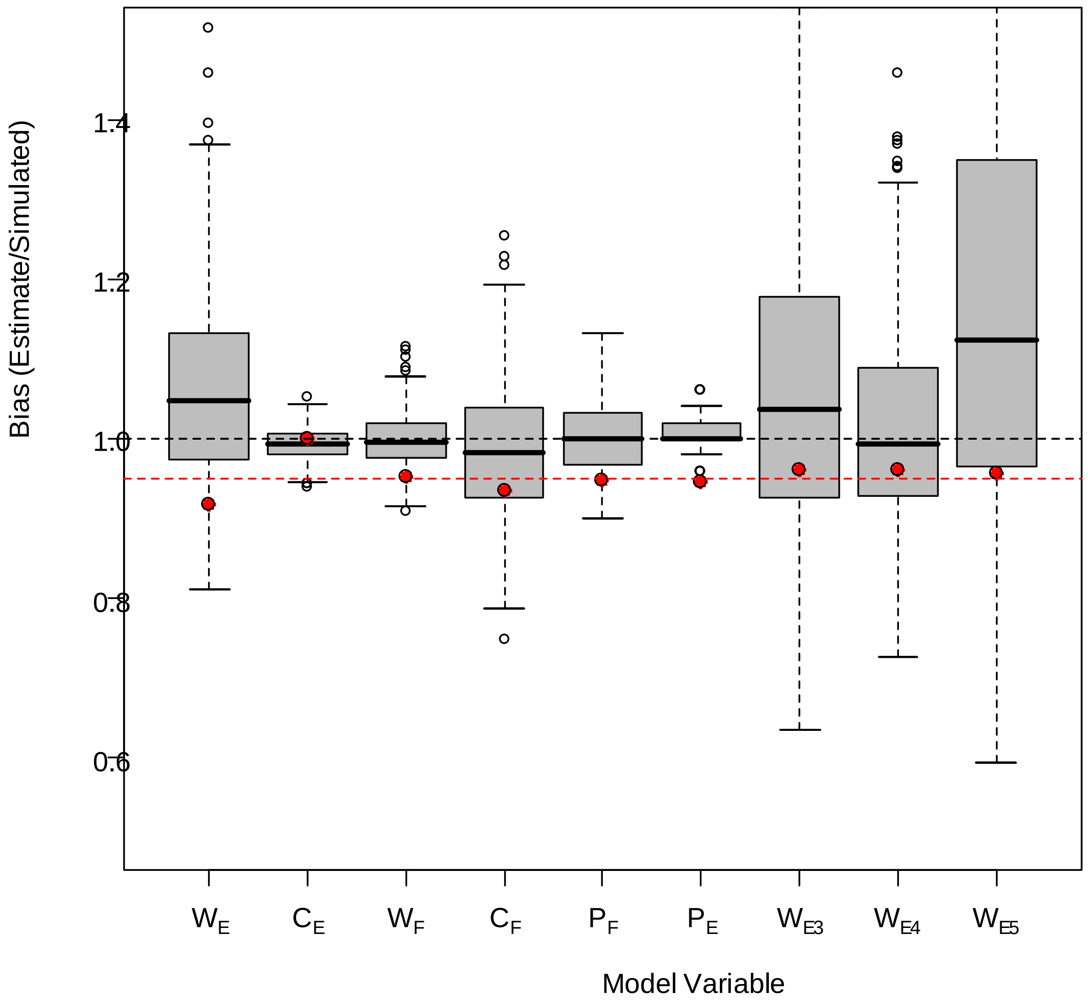

Figure 8. Extent of bias in expected values and coverage probability for key model variables. The box plots show the distribution of the ratio of the expected value to true simulated values based on 500 simulated data sets. The red points show the coverage probability, which is the fraction of simulations where the 95% credible interval included the true simulated value. The dashed black and red lines denote the ratios of no bias in the expected values and coverage probability, respectively. The thick black lines and box widths denote the median and interquartile ranges while the whiskers and open points denote more extreme values. See Table 1 for definition of variables. For brevity, the plot shows the sum of age-specific values ($W_E \ldots C_F$), the weighted averages across ages (P_F) or escapement strata (P_E), and age-specific escapement estimates (W_{Ex}).

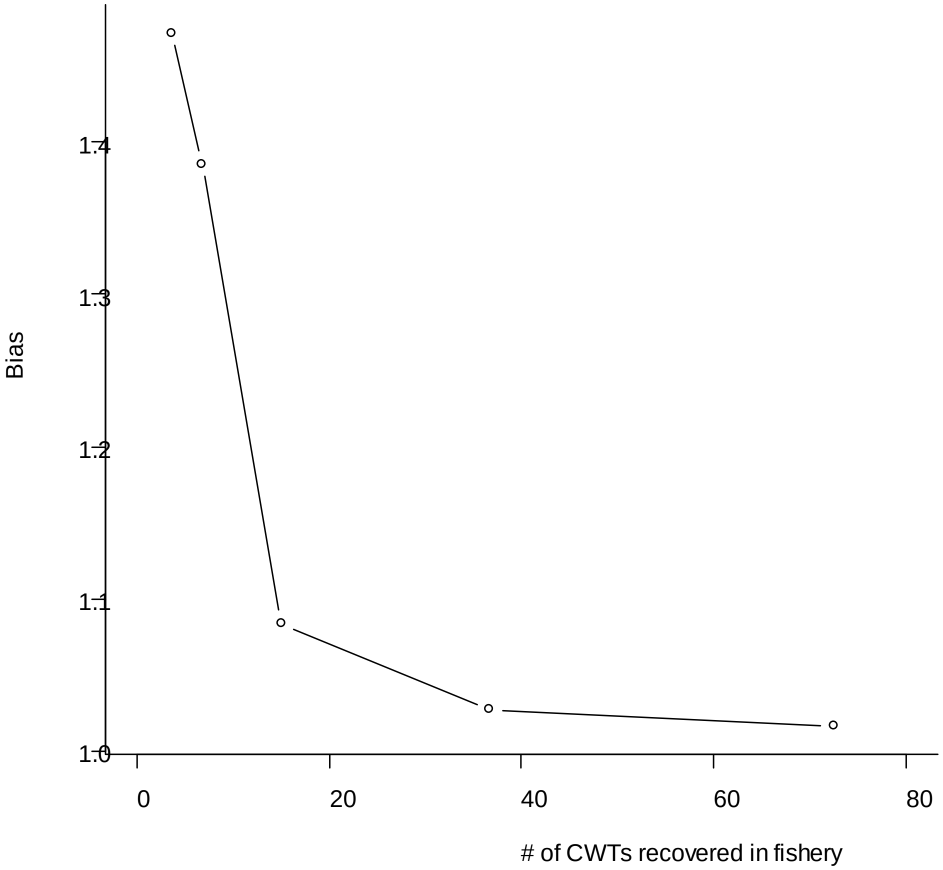

Figure 9. Effect of the simulated total number of CWTs recovered in a distant fishery on bias in age-aggregated escapement estimates for an aggregate stock. Bias is computed as the average of the ratio of the estimated to true simulated escapements over 100 trials. In this set of simulations, the number of CWTs recovered on the spawning grounds was approximately 6-fold greater than the number recovered in the fishery.