Estimating Basin-Wide Salmon Escapements for Chinook Salmon Returning to the West Coast of Vancouver Island and the South Thompson River 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 (GSI) 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 from 2003 to 2006 for the South Thompson and West Coast of Vancouver Island (WCVI) ocean-type Chinook aggregates. 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. This approach can also be used to estimate terminal run size for an aggregate stock using the number of CWTs in terminal fisheries instead of the CWTs in the escapement.

South Thompson and WCVI ocean-type aggregates are genetically distinctive from other aggregates in the Northern BC troll fishery. There were few CWT recoveries in the troll fishery for age 3 and 5 fish in most years leading to greater uncertainty in escapement estimates for these ages. The sample size for GSI assignments was generally large except for age 3 fish in most years. CWT recoveries in the terminal run were relatively large for WCVI for all ages and years, but low in the escapement Shuswap indicator stock for age 3 and 5 in two of four years.

The expected total escapements (sum of escapements for ages 3-5) for the South Thompson aggregate ranged from 103,000 to 213,000 between 2004 and 2006. The CV of total escapement estimates ranged from 0.15-0.22. CV's for age 3 and 5 estimates were much larger due to low number of CWT recoveries in the fishery (for both ages) and the low number of GSI assignments for age 3 fish. The expected total terminal run for the WCVI aggregate ranged from 141,000 to 500,000 between 2003 and 2006. Uncertainty in total escapement estimates was similar to that for the South Thompson aggregate in 2005 and 2006, but CVs for the WCVI 2003 and 2004 terminal runs were

much higher owing to low CWT recoveries in the NBC troll fishery (2003) combined with a low number of GSI assignments (2004).

This analysis has shown that it is possible to reliably estimate escapement for 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. Escapement estimates were relatively precise in cases where the number of CWT recoveries in distant and terminal fisheries (or escapement) and GSI assignments was adequate. Due to low CWT recoveries in the NBC troll fishery (and occasionally in the terminal run or escapement), CV's for most age-specific estimates of terminal run size or escapement for the WCVI and South Thompson aggregates between 2003 and 2006 were generally greater than the 0.15 PSC standard. However, the CV's for the total escapement across ages were generally at or very close to the PSC standard for in all years for the South Thompson aggregated, and in 2005 and 2006 for the WCVI aggregate. Some minor adjustments to these escapement estimates may occur based on additional analyses, and such changes would be reflected in estimates entered into the Fisheries and Oceans salmon escapement database.

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. 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 estimate stock composition in specific fisheries to reduce harvest rates on weak stocks.

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. This approach can also be used to estimate terminal run size for an aggregate stock using the number of CWTs in terminal fisheries instead of the CWTs in the escapement.

In this analysis, use a Bayesian version of the ratio-method to estimate escapement for the South Thompson and terminal run for West Coast of Vancouver Island ocean-type aggregates between 2003 and 2006. A Bayesian approach offers a number of advantages compared to the existing deterministic 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.

The Fraser River Chinook Summer-Run Age 0.3 and WCVI stock aggregates are major contributors to ocean fisheries in Southeast Alaska (SEAK) and Northern British Columbia (NBC) when they are abundant and healthy. Since 2002, the Fraser River Chinook Summer-Run Age 0.3 represented upwards of 30-40% of the NBC troll fishery catches (Winther and Beacham 2006). Good quality spawning ground estimates for both stock aggregates are needed to develop accurate forecasts of the NBC and SEAK abundance indices to define allowable catch. However, the current visual survey methods in the Fraser River 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). For the WCVI aggregate, the current study design used to estimate terminal run size and spawning escapement is thought to underestimate the total abundance since only about 20 of the 101 Chinook salmon spawning rivers are surveyed annually. Since 1953, 84 of the rivers have had spawning escapement estimated in 1 or more years, and based on these historical records, the 20 rivers surveyed annually represent about 70% of the spawners outside of the main enhancement systems (i.e. Nitinat, Conuma, and Robertson).

Methods

Data

The South Thompson summer-run Chinook age 0.3 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. 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 troll fishery in Northern British Columbia (NBC).

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.

The WCVI stock group has four genetic groups (Candy et al. 2011). Northern populations in Nootka Sound and Quatsino Sound return earlier than populations in southwest Vancouver Island and Barkley Sound (Figure 3). Natural spawning escapements for 6 index rivers indicate a relatively stable abundance pattern (Figure 4). The Robertson Creek hatchery, located in Barkley Sound, is a CWT exploitation rate indicator stock that is used by the CTC to represent the WCVI stock group (PSC 2009a). Data used to estimate the terminal run of the WCVI aggregate includes information on abundance of Chinook salmon migrating past Stamp Falls to the Robertson Creek hatchery (RBT) and river spawning grounds, the recovery of RBT CWTs on the spawning grounds, RBT CWTs in terminal sport and net fisheries (inside Barkley Sound and identified as area 23A by the CDFO CWT Mark Recovery Program), RBT CWTs in the NBC troll fishery, and genetic stock identification and age data to determine the catch-by-age of the aggregate stock in NBC fisheries. We applied the model to data collected from the NBC troll fishery.

Total escapement of Chinook migrating past Stamp Falls and consequently the number of CWT'd Chinook within that escapement are estimated annually by manual counts of fish migrating through a fishway around the falls during daytime and by direct counts from video records during nighttime. CWT samples are collected from fish at Roberston Creek hatchery and by conducting carcass surveys in the river upstream of the falls.

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)

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; Beacham et al. 2006; 2008). Genetic variation at 12 microsatellite markers (*Ogo2, Ogo4, Oke4, Oki100, Ots100, Ots101, Ots104, Ots107, Ots2, Ots9, Omy325 and Ssa197*) 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) and 19 populations for the WCVI (Beacham et al. 2006; 2008).

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. 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. No information on ageing error for the WCVI aggregate was available, so we only used prior information from other studies (McNicol and MacLellan 2010) to characterize uncertainty in age assignments in this case.

Model Structure

We developed a Bayesian model to estimate the annual spawning escapement or terminal run 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 or terminal run. The ratio method that we implement relies on the key assumption that the ratio of CWTs for the indicator stock in the escapement (or terminal run) to CWTs in a distant 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 (or terminal run size) 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 5.

The total spawning escapement or terminal run 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 sum of estimated number of CWTs in the in-river ($C_{E,a}$) and hatchery escapement ($C_{B,a}$) or terminal fishery ($C_{E,a}$) to the estimated number caught in the distant 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 the aggregate for 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 the sum across estimation strata (eqn. 1.10), determined as the number of CWTs that are caught ($m_{F,a}$) expanded by the effective sampling rate for CWTs in the catch (λ_F, eqn. 1.11). λ_F is fixed by strata 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 or terminal run 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. 1.12). The expected value for each strata $C_{E,a,s}$ 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. 1.13a). In the case where the escapement of the indicator stock is estimated, $P_{E,s}$ 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. 1.14). $P_{AFS,s}$ 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. 1.15). $\lambda_{E,s}$ 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. A modification of this structure is required in the case when information on terminal run size for the indicator stock, rather than escapement, is available, which is the case for the Roberston Creek Hatchery indicator stock for WCVI. In this case, the expanded number of CWTs in the terminal run for each strata is computed based on eqn. 1.13b, which depends only on the actual CWT recoveries and the estimated effective sampling rate of the terminal run (which does not depend on estimates in eqn's 1.14 and 1.15). The expanded number of CWTs in the escapement in the hatchery ($C_{B,a}$) is simply the sum across estimation strata (eqn. 1.16), determined as the ratio of CWT recoveries ($m_{B,a,s}$) by the effective sampling rate in the hatchery ($\lambda_{B,s}$).

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 for each strata ($C_{F,a,s}$) is assumed to be a binomially-distributed random variable (eqn. 2.6) that depends on the number of CWTs recovered from the catch ($m_{F,a,s}$) and the effective sampling rate on the catch for CWTs ($\lambda_{F,s}$). The estimated number of CWTs in the escapement (or terminal run) of the indicator stock by strata ($C_{E,a,s}$) is also assumed to be a binomially-distributed random variable that depends on the number of CWTs recovered in the escapement ($m_{E,a,s}$) and the effective sampling rate on the escapement ($P_{E,s} P_{AFS,s} \lambda_{E,s}$ in eqn. 2.7a for South Thompson, $\lambda_{E,s}$ in eqn. 2.7b for WCVI). For the South Thompson aggregate, $P_{E,s}$ 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 if there are substantive 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 uniform (eqn.'s 3.6-3.8). 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. Upper limits for the uniform distributions of expected CWT recoveries in the fishery (p_F in eqn. 3.6), escapement or terminal run (p_E in eqn. 3.7), and broodstock (p_B in eqn. 3.8) were set at 5 times the expected values determined from equations 1.11, 1.12, and 1.17, 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 deterministic version. Estimates from the latter model were determined from the expected value equations of the Bayesian model (eqn.'s 1.1-1.17). Variance in estimates from the deterministic model were computed 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).

Results and Discussion

South Thompson and WCVI ocean-type aggregates are genetically distinctive from other aggregates in the NBC troll fishery (Fig.'s 6 and 7). As a result, the probability of fish sampled in the 2003-2006 NBC troll fisheries belonging to these aggregates was either very low or very high. In cases like these, there is very little uncertainty associated with assignment error, so the Bayesian implementation is simplified because it does not have to account for this uncertainty. That is, $x_{i,s}$ in eqn. 2.1 can be treated as fixed (a fish is always a member of the aggregate or not) rather than as a random Boolean variable.

There was very little ageing error for the South Thompson aggregate, which was consistent with results for South Thompson and WCVI stocks from an independent study for a larger number of stocks (Table 4). Thus ageing error will contribute very little uncertainty to escapement or terminal run estimates for these aggregates.

GSI assignments to the aggregate stocks and CWT recoveries in the NBC troll fishery and in the return (escapement or terminal fishery) are presented in Table 4. These data, which sum assignments and recoveries across strata, show few CWT recoveries in the troll fishery for Age 3 and 5 fish in most years. The sample size for GSI assignments was generally large except for age 3 fish in most years. CWT recoveries in the terminal run were relatively large for WCVI for all ages and years, but low in the escapement Shuswap indicator stock for age 3 and 5 in two of four years.

The expected total escapements (sum of escapements for ages 3-5) for the South Thompson aggregate ranged from 103,000 to 213,000 between 2003 and 2006 (Table 5). The CV of total escapement estimates ranged from 0.15-0.22. CV's for age 3 and 5 estimates were much larger due to low number of CWT recoveries in the fishery (for both ages) and the low number of GSI assignments for age 3 fish (Table 4). The expected total terminal run for the WCVI aggregate ranged from 141,000 to 500,000 between 2003 and 2006. Uncertainty in total escapement estimates was similar to that for the South Thompson aggregate in 2005 and 2006, but CVs for the WCVI 2003 and 2004 terminal runs were much higher owing to low CWT recoveries in the NBC troll fishery (2003) combined with a low number of GSI assignments (2004).

The extent of agreement between escapement or terminal run estimates determined from the Bayesian and deterministic methods depended on sample size (Table 5). For example, estimates were very similar for the South Thompson aggregate in 2005 for all ages, when sample sizes were relatively high (Table 4). In contrast, the age 3 WCVI estimate in 2003 based on the Bayesian model was 25% lower (15,000 fish) than the deterministic estimate. This occurred because there was only one age 3 CWT recovery in the NBC troll fishery in that year. As a result, the estimate of the total CWT recoveries in the fishery ($C_{F,3}$) from the Bayesian model (eqn. 3.6) was higher than the deterministic estimate (eqn. 1.11) because the data were sparse and the prior had a greater effect. This reduced the ratio in eqn. 1.2, leading to a lower terminal run estimate and large uncertainty in the estimate (CV=0.79). Note that the deterministic model could not estimate age-specific escapements or terminal runs in cases where CWTs were not recovered in the fishery (e.g. South Thompson age 5, 2006) or in the escapement or terminal run (e.g., WCVI age 5 2003). Additional analyses are needed resolve differences between Bayesian and deterministic estimates. Some minor adjustments to these escapement estimates may occur based on additional analyses, and such changes would be reflected in estimates entered into the Fisheries and Oceans salmon escapement database.

This analysis has shown that it is possible to reliably estimate escapement for 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. Escapement estimates were relatively precise in cases where the number of CWT recoveries in distant and terminal fisheries (or escapement) and GSI assignments was adequate. Due to low CWT recoveries in the NBC troll fishery (and occasionally in the terminal run or escapement), CV's for most age-specific estimates of terminal run size or escapement for the WCVI and South Thompson aggregates between 2003 and 2006 were generally greater than the 0.15 PSC standard. However, the CV's for the total escapement across ages were generally at or very close to the PSC standard for in all years for the South Thompson aggregated, and in 2005 and 2006 for the WCVI aggregate.

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We thank Richard Bailey, Nicole Trouton, and Roberta Cook for mark-recapture and CWT data from the Lower Shuswap exploitation rate indicator stock. Marla Maxwell, Rob Tadey, A. Baker, and K. Buxton provided data from the Albion test fishery. We also thank Nick Komick, Erik Grundman, and Bruce Baxter for providing biological data to cross-reference scale and CWT samples collected by the Mark Recovery Program. Nora Crosby assembled the historic scale books for the Lower and Middle Shuswap stocks that were sampled by the mark recovery program. Colin Wallace modified the cBayes program to report the individual fish assignment probabilities to population-of-origin.

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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
C_B	Expanded number of CWTs for fish that entered the hatchery (broodstock)
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 from escapement for indicator stock
m_B	Decoded CWTs from indicator stock in the hatchery (broodstock)
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'

Table 1. Con't.

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
λ_B	Proportion of fish in the hatchery with an adipose fin clip 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)
p_F	Upper limit for uniform prior for expected recovery of CWTs in fishery
p_E	Upper limit for uniform prior for expected recovery of CWTs in escapement
p_B	Upper limit for uniform prior for expected recovery of CWTs in broodstock
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) $$W_{E,a} = W_{F,a} \frac{C_{E,a} + C_{B,a}}{C_{F,a}}$$

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

Table 2. Con't.

(1.10) $$C_{F,a} = \sum_s C_{F,a,s}$$

(1.11) $$C_{F,a,s} = \frac{m_{F,a,s}}{\lambda_{F,s}}$$

(1.12) $$C_{E,a} = \sum_s C_{E,a,s}$$

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

b) $$C_{E,a,s} = \frac{m_{E,a,s}}{\lambda_{E,s}}$$

(1.14) $$P_{E,s} = \frac{r_{E,s}}{R_{E,s}}$$

(1.15) $$P_{AFS,s} = \frac{N_{AFS,s}}{N_{E,s}}$$

(1.16) $$C_{B,a} = \sum_s C_{B,a,s}$$

(1.17) $$C_{B,a,s} = \frac{m_{B,a,s}}{\lambda_{B,s}}$$

Table 2. Con't.

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

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

b) $m_{E,a,s} \sim dbin(\lambda_{E,s}, C_{E,a,s})$

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

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

(2.10) $m_{B,a,s} \sim dbin(\lambda_{B,s}, C_{B,a,s})$

Table 2. Con't.

Prior Distributions

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

(3.2) $P_{F,a,s} \sim ddirch(p_{a,\ldots Nages} = .01)$

(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) $C_{F,a} \sim dunif(1, p_F)) + m_{F,a}$

(3.7) $C_{E,a,s} \sim dunif(1, p_E)) + m_{E,a,s}$

(3.8) $C_{B,a,s} \sim dunif(1, p_B)) + m_{B,a,s}$

Table 3. Data used to estimate uncertainty in age assignments for the South Thompson age 0.3 and West Coast Vancouver Island 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). No ageing error information is available for the WCVI stock, so only prior information (lower table) is used to estimate ageing error in this case.

Stock	Estimated Age ('a')	Known Age ('aa') 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 4. Summary of key data used to estimate Chinook escapement for the Southern Thompson and West Coast of Vancouver Island (WCVI) ocean-type aggregates. See Table 1 for definitions of model parameters.

Year	Data Type	South Thompson			WCVI		
		Age 3	Age 4	Age 5	Age 3	Age 4	Age 5
2003	GSI assignments for aggregate in fishery ($N_{W,a}$)	2	112	65	4	62	29
	CWT recoveries for indicator in fishery (m_F)	0	15	1	1	2	0
	CWT recoveries for indicator stock in return (m_E+m_B)	3	11	0	240	327	34
2004	GSI assignments for aggregate in fishery ($N_{W,a}$)	3	83	80	2	17	51
	CWT recoveries for indicator in fishery (m_F)	6	33	2	14	16	21
	CWT recoveries for indicator stock in return (m_E+m_B)	43	110	17	910	371	227
2005	GSI assignments for aggregate in fishery ($N_{W,a}$)	8	275	70	8	91	13
	CWT recoveries for indicator in fishery (m_F)	8	31	5	2	42	2
	CWT recoveries for indicator stock in return (m_E+m_B)	31	52	11	99	300	32
2006	GSI assignments for aggregate in fishery ($N_{W,a}$)	16	414	140	24	56	32
	CWT recoveries for indicator in fishery (m_F)	5	70	0	10	21	7
	CWT recoveries for indicator stock in return (m_E+m_B)	15	147	3	383	317	95

Table 5. Chinook escapement for the South Thompson Age 0.3 (a) and terminal run size for West Coast of Vancouver Island ocean-type aggregates (b), 2003-2006 (in thousands of fish). Statistics from the posterior distributions of escapement from the Bayesian model are compared to the estimate from the analytic model. CV denotes the coefficient of variation. The lower (LCL) and upper (LCL) limits of the 95% credible intervals are also shown. Blank cells under the analytic method denote cases were estimates could not be computed because no CWTs were recovered in the fishery or escapement/terminal run. Data are not available to estimate escapement for the South Thompson aggregate in 2003.

a) South Thompson Aggregate

		Bayesian				
Year	**Age**	**Mean**	**CV**	**LCL**	**UCL**	**Analytic**
2003	3					
	4					
	5					
	Total					
2004	3	23,071	0.82	2,204	71,780	19,192
	4	69,181	0.22	42,980	104,500	60,550
	5	63,436	0.41	25,950	128,000	92,168
	Total	155,688	0.22	98,420	233,000	171,910
2005	3	9,420	0.48	3,004	20,530	8,397
	4	75,525	0.19	51,520	107,500	71,555
	5	18,440	0.34	8,929	33,070	16,376
	Total	103,386	0.15	76,720	138,500	96,327
2006	3	7,927	0.46	2,830	16,990	7,411
	4	136,079	0.12	105,300	174,000	132,047
	5	68,662	0.46	26,810	149,900	
	Total	212,667	0.17	155,700	299,300	

Table 5. Con't.

b) West Coast of Vancouver Island Aggregate

		Bayesian				
Year	**Age**	**Mean**	**CV**	**LCL**	**UCL**	**Analytic**
2003	3	45,933	0.79	7,181	147,000	60,901
	4	226,434	0.58	75,440	579,600	230,165
	5	226,903	0.49	90,070	499,000	
	Total	499,273	0.35	251,600	912,700	
2004	3	175,540	0.6	30,130	429,700	147,723
	4	46,651	0.41	18,370	90,340	24,819
	5	79,472	0.34	37,160	148,800	69,023
	Total	301,666	0.36	138,400	556,300	241,564
2005	3	27,467	0.59	6,973	70,370	35,620
	4	88,576	0.21	56,970	127,700	74,024
	5	25,530	0.53	8,327	60,660	23,689
	Total	141,574	0.2	94,380	201,500	133,333
2006	3	111,410	0.32	56,260	193,700	86,502
	4	66,353	0.27	38,450	107,900	50,307
	5	12,904	0.48	4,340	27,450	8,075
	Total	190,667	0.21	125,400	274,100	144,884

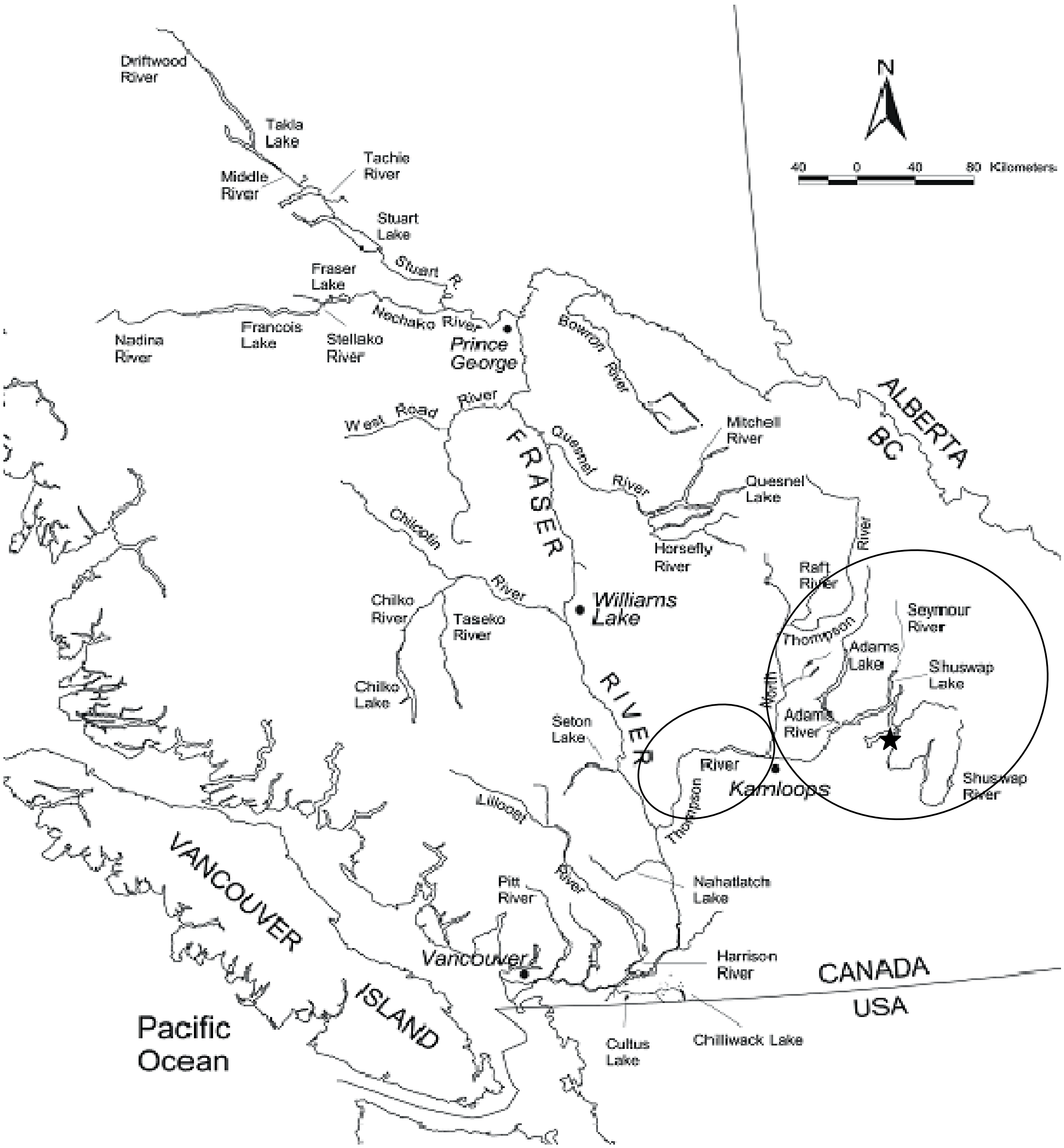

Figure 1. Map of Southern British Columbia showing the location of the major streams used by the South Thompson 0.3 Chinook aggregate stock (circled) and the location of the Lower Shuswap indicator stock (star). The Albion test fishery is located near Vancouver and the Northern BC troll fishery is located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

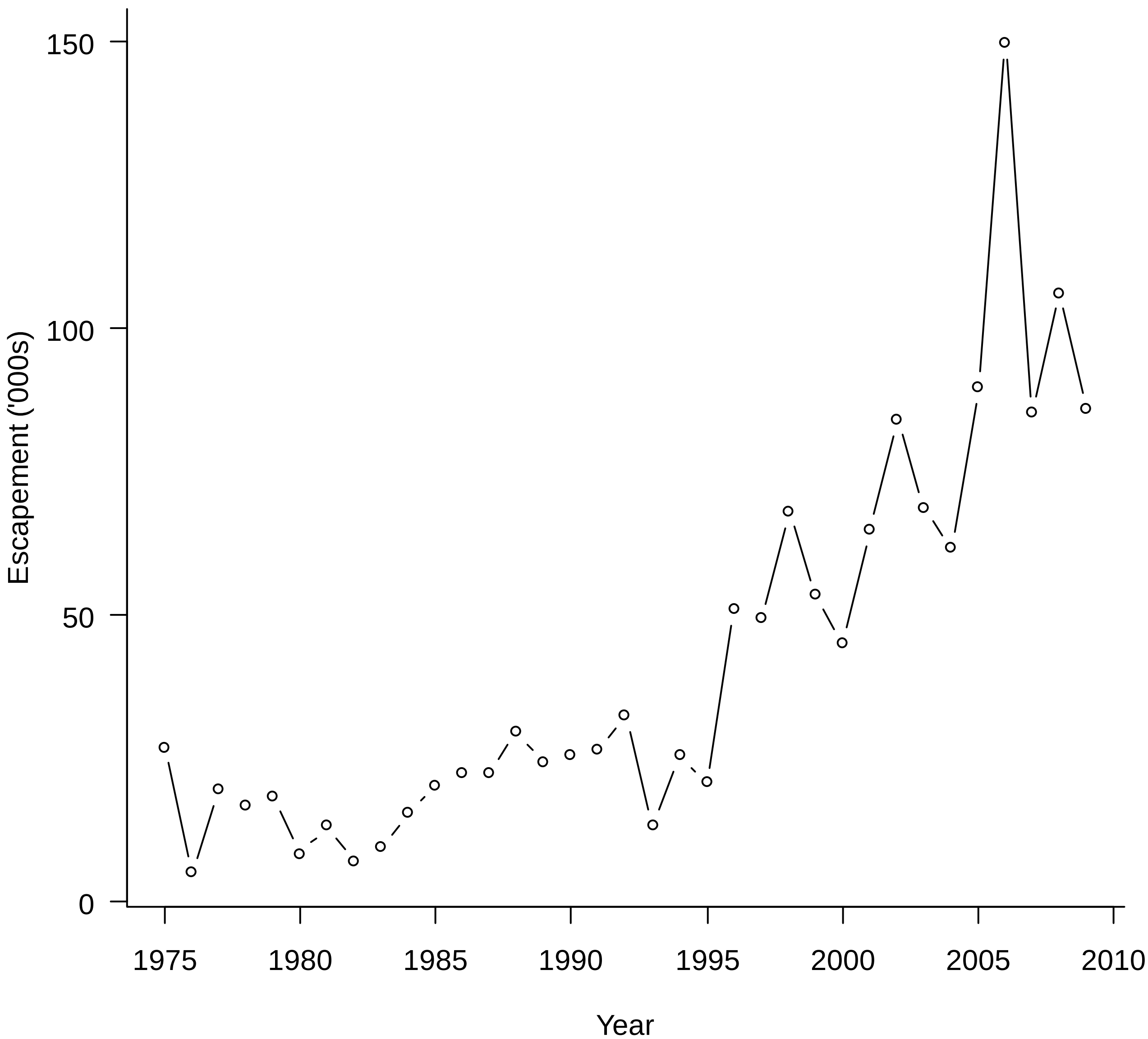

Figure 2. Historical trend in the estimated spawning escapement of the South Thompson 0.3 aggregate based on visual surveys (R. Bailey, Fisheries and Oceans Canada, unpublished data).

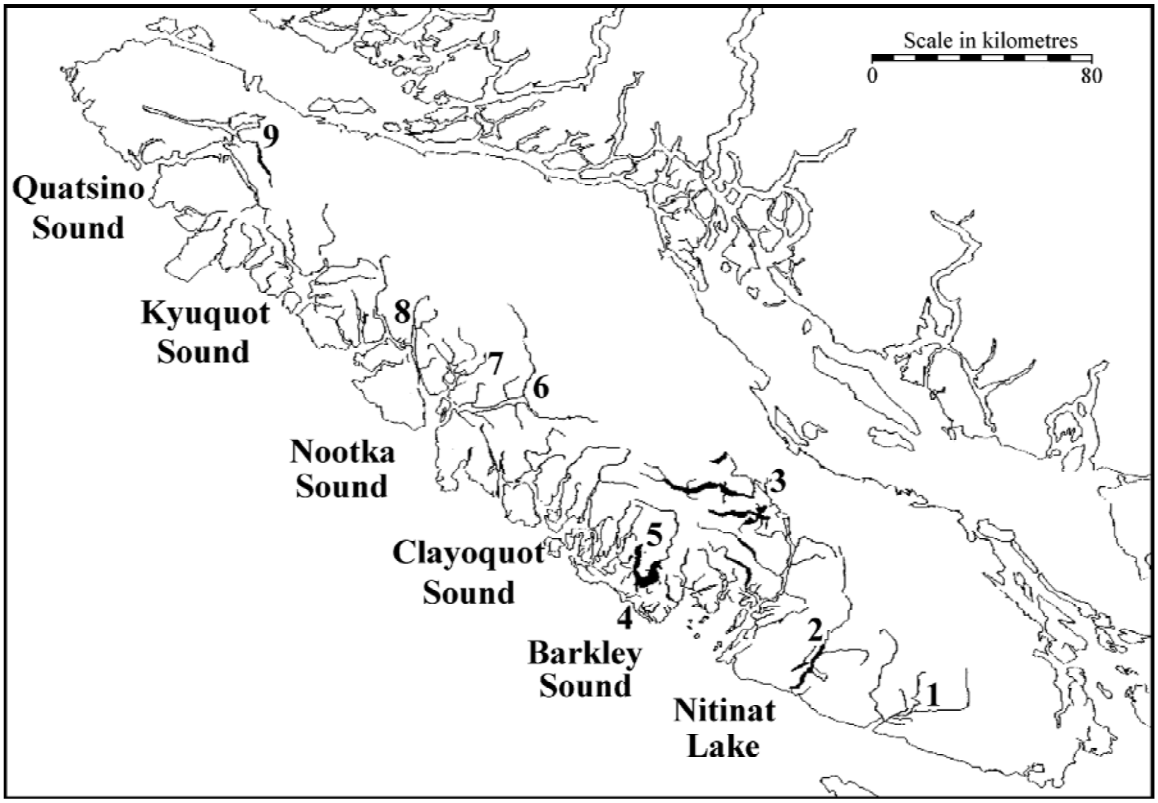

Figure 3. Map of West Coast of Vancouver Island (WCVI) showing distribution of the WCVI ocean-type aggregate and the location of 9 enhancement facilities: 1. San Juan River (Area 20-1), 2. Nitinat Lake/River (Area 22), 3. Robertson Creek Hatchery / Stamp River (Area 23), 4. Thornton Creek Hatchery (Barkley Sound Area 23), 5. Kennedy River (Clayoquot Sound Area 24), 6. Gold River and Burman River (Nootka Sound Area 25), 7. Conuma/Canton/Sucwoa/Tlupana Rivers (Nootka Sound Area 25), 8. Tahsis River (Nootka Sound Area 25), and 9. Marble River (Quatsino Sound Area 27).

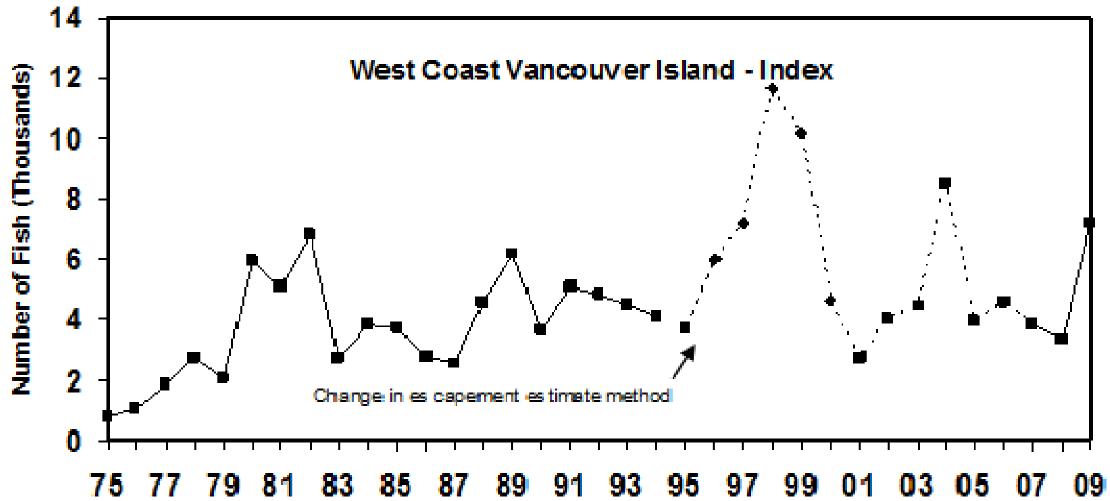

Figure 4. Historical trend in estimated spawning escapement of the West Coast of Vancouver Island for six rivers (Marble, Tahsis, Burman, Artlish, Kaouk, and Tahsish), which were chosen to provide an 'index' of escapement for wild WCVI stocks in general. These stocks were chosen based on historical consistency of data quality (reproduced from PSC 2011).

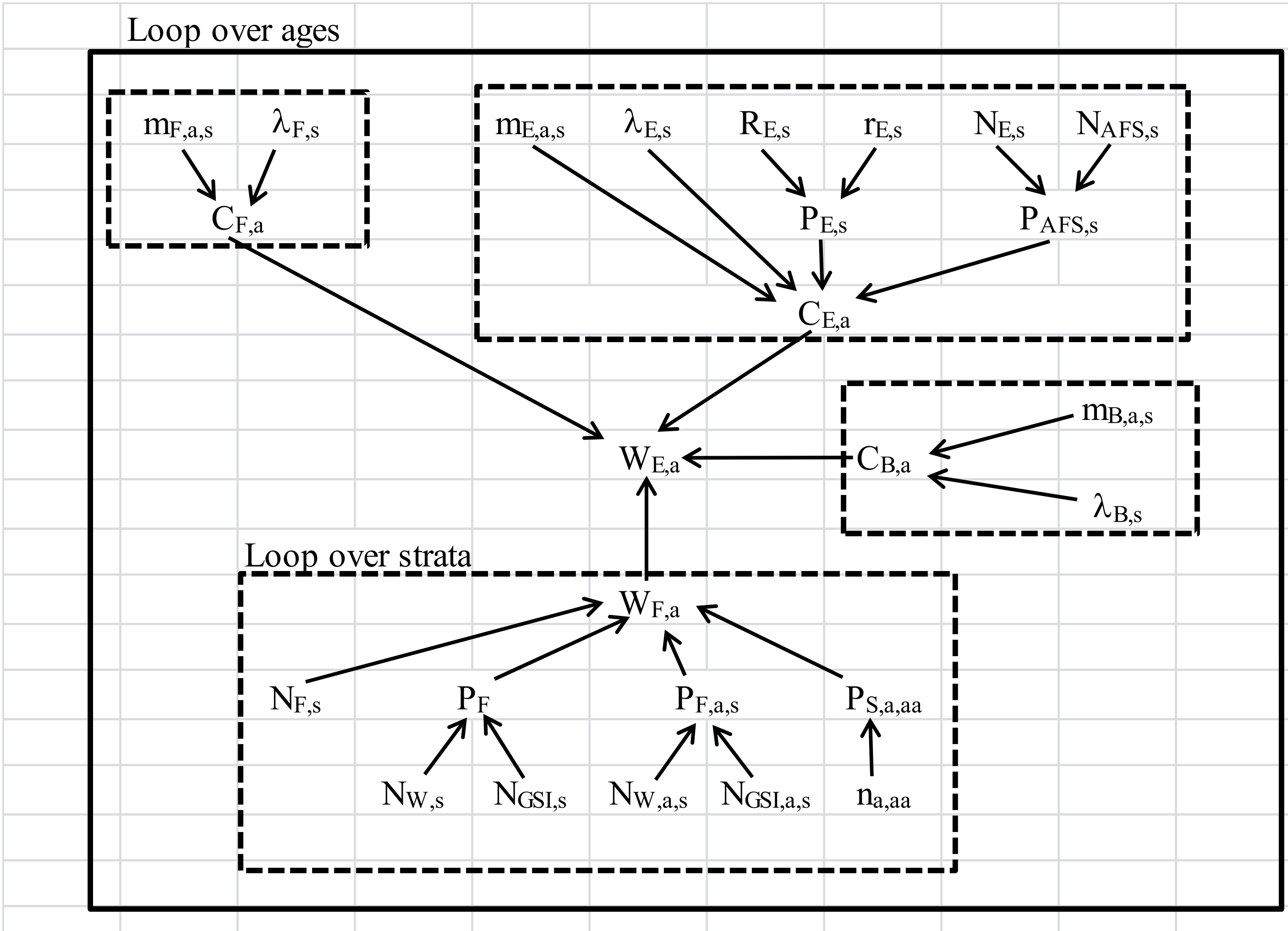

Figure 5. Visual representation of the Bayesian model used to estimate escapement of the South Thompson 0.3 Chinook aggregate. Variables are defined in Table 1. Arrows indicate conditional dependencies; the boxes represent repetition of structure over age (a) and fishery or escapement estimation (s) strata.

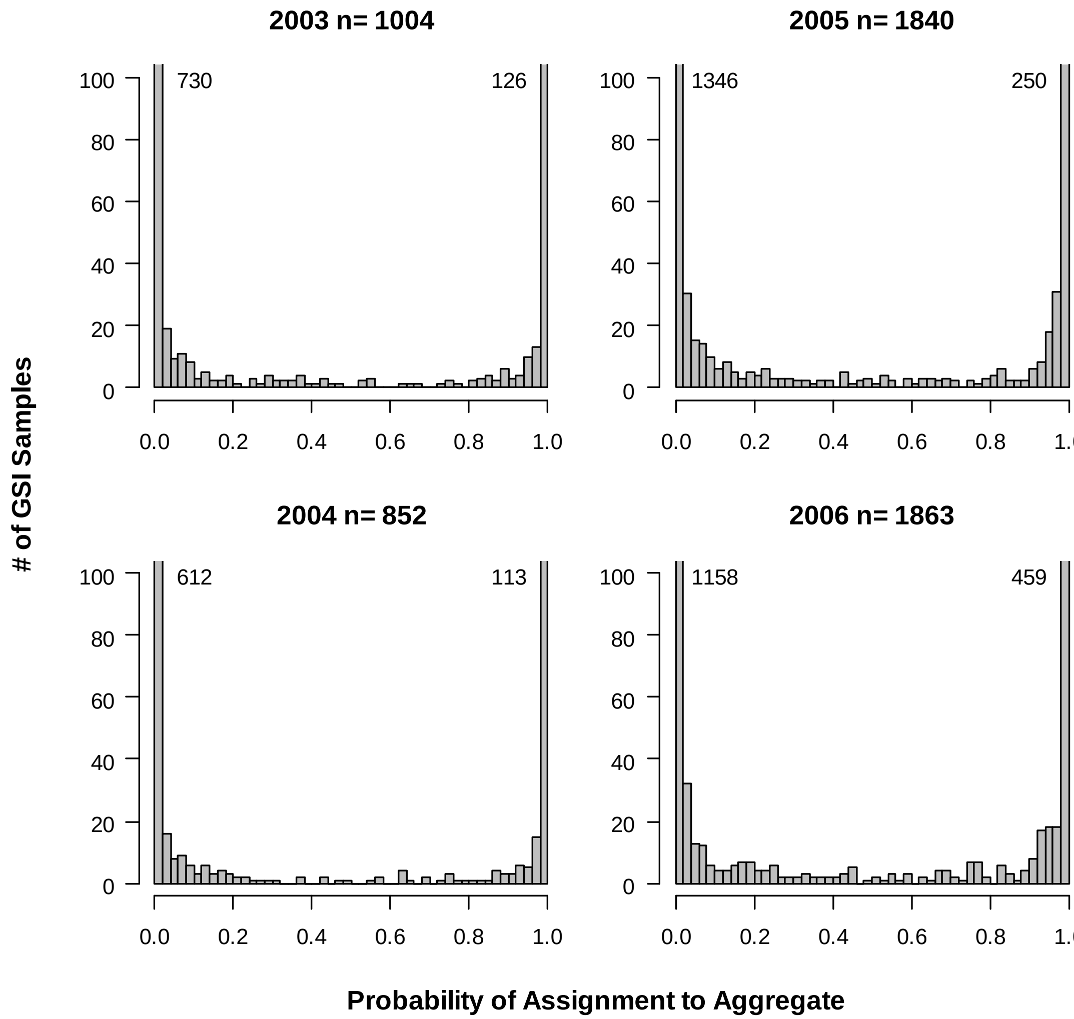

Figure 6. Frequency distributions of the number of samples with different probabilities of assignment to the South Thompson Chinook ocean-type aggregate based on genetic stock identification (GSI) data collected from the Northern BC troll fisheries, 2003-2006. 'n' specifies the total GSI sample size for each year. 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).

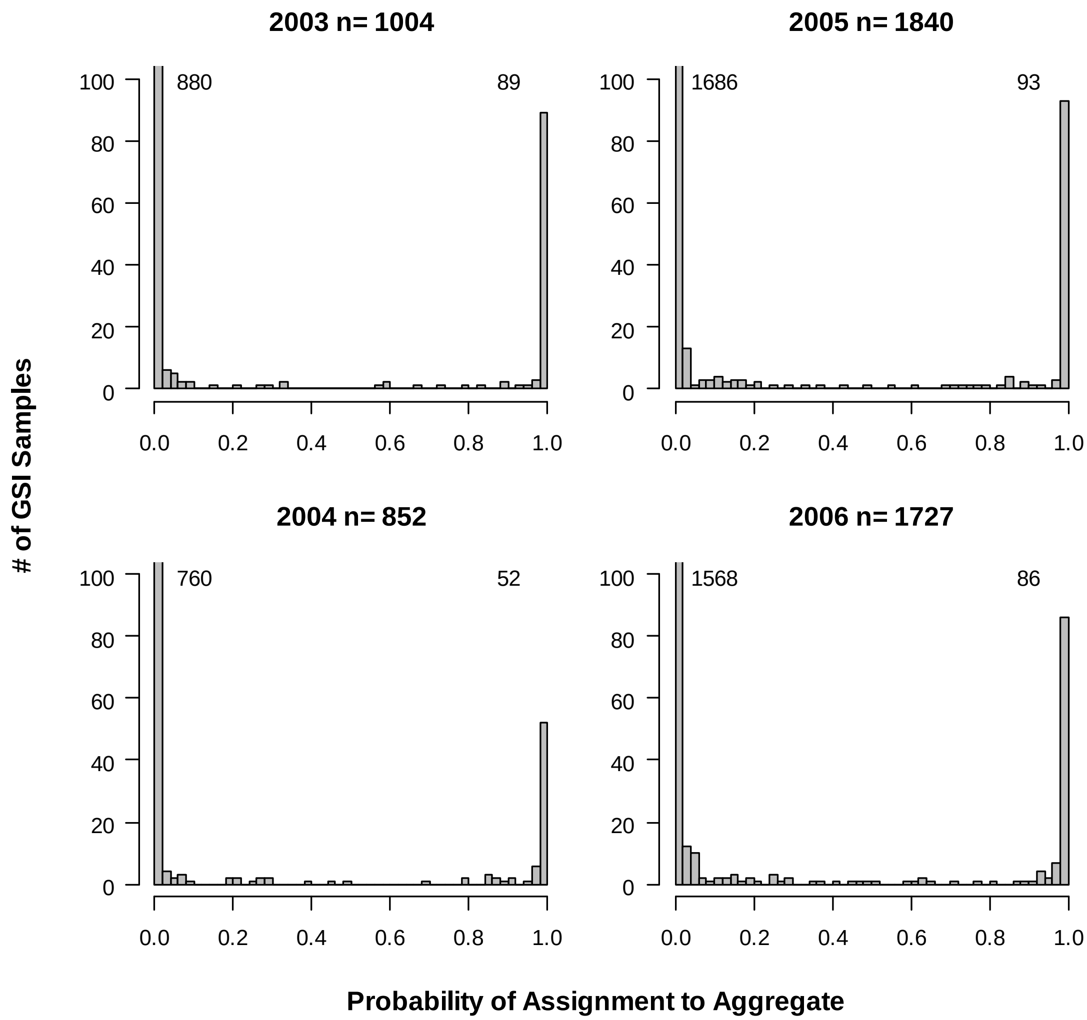

Figure 7. Frequency distributions of the number of samples with different probabilities of assignment to the West Coast of Vancouver Island ocean-type aggregate based on genetic stock identification (GSI) data collected from the Northern BC troll fisheries, 2003-2006. 'n' specifies the total GSI sample size for each year. 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).