

**PRECAUTIONARY REFERENCE POINTS FOR FRASER RIVER
SOCKEYE SALMON ESCAPEMENT GOALS BASED ON
PRODUCTIVITY OF NURSERY LAKES AND
STOCK-RECRUITMENT ANALYSES**

by

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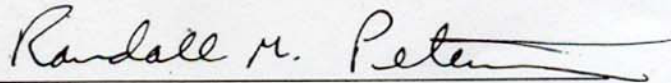
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Abstract

Accurate and precise determination of optimal spawning escapement is crucial to harvest management of sockeye salmon (*Oncorhynchus nerka*). Such escapements have been used as basis for determining biological reference points in the recent move toward implementing conservation-oriented policies related to the precautionary approach to fisheries management. Traditionally optimal escapement is estimated from spawner-recruit data, but these data are not available for all sockeye salmon populations. Recently, several researchers used data on productivity of rearing lakes to derive estimates of spawning escapement that should maximize abundance of juvenile sockeye salmon in the lake. However, only one of these studies accounted for uncertainty and that was quite limited; the rest produced point estimates. Therefore, I developed a systematic method of estimating optimal escapement for sockeye salmon based on productivity of nursery lakes that takes uncertainty into account using a Bayesian approach. Compared to estimates of optimal spawner abundance produced from Bayesian stock-recruitment analyses of Fraser River, British Columbia sockeye salmon stocks, this method based on lake productivity produced higher estimates for the optimal abundance of female spawners in all cases except one, and the precision of estimates from the two methods was similar. I also propose a scheme for determining biological reference points from estimates of optimal escapement coupled with estimates of productivity at low abundance for sockeye population aggregates. The operational performance of specific reference points developed using this approach needs to be comprehensively assessed, alongside a range of plausible harvest rules using simulation modeling.

Dedication

To my mother, Joyce Bodtker, for everything a mother provides,

To my partner in life, Dan Blondal, for his unending support and encouragement,

To my son, Ari Blondal, for helping me balance my life.

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Chapter 1: Optimal escapement based on lake productivity and stock-recruitment analyses

Introduction

Over the last few years, Pacific fisheries management agencies have developed new management policies that focus on conservation of wild salmon (*Oncorhynchus spp.*) stocks. Each agency has recognized the need to define sets of escapement goals (i.e. numbers of adult recruits allowed past the fishery to spawn) to meet different objectives, depending on the status of the stocks. 'Optimal' spawning escapement based on maximum sustainable yield (MSY), traditionally used in harvest management, is becoming a basis for calculating other escapement goals that represent more conservation-oriented policy targets (e.g., minimum and target levels of abundance might be calculated as a function of 'optimal' spawning escapement). 'Optimal' escapement goals are termed such because both lower and higher escapements have negative consequences such as reduced economic returns and/or potentially unacceptable adverse ecological consequences.

Historically, stock-recruitment analyses and habitat-based models have been used to estimate optimal escapements of salmon stocks and each method has strengths and weaknesses. Estimates based on stock-recruitment analyses can be inaccurate and imprecise due to high variability in stock-recruit data and low contrast in spawner abundances (Hilborn and Walters 1992). Habitat-based models, usually based on freshwater habitat (e.g., Bradford et al. 2000a for coho salmon), may also produce inaccurate and imprecise estimates because they rely on indirect indices of the capacity of the habitat to produce fish. However, habitat-based models can be used to generate estimates of optimal escapement where stock-recruit data are nonexistent or of poor quality. While stock-recruit data series

gathered over decades are required to support stock-recruitment analyses, a relatively short-term study or analysis might be sufficient to create a habitat-based model.

For sockeye salmon, it is possible to estimate the quality and quantity of their freshwater habitat from lake productivity because many sockeye salmon rely on lakes for their juvenile nursery. Koenings and Burkett (1987) found good correlations between euphotic volume (EV) and both total abundance and biomass of sockeye salmon smolts (i.e. juvenile salmon in the stage of migration to the sea), in oligotrophic lakes in Alaska. Euphotic volume, calculated from lake surface area (km^2) and euphotic zone depth (Koenings and Burkett 1987), is an index of lake productivity. EV is dependent on lake clarity and Hume et al. (1996) found that because British Columbia (BC) sockeye lakes had a smaller range of clarity than the Alaskan sockeye lakes, EV was inappropriate for use as an index of lake productivity in BC. Therefore, they adapted the relationships of the EV model to use photosynthetic rate (PR), a more direct measure of lake productivity. Hume et al. (1996) and Shortreed et al. (2000) developed the PR model from this adaptation of the EV model. Both models used a correlation between EV or PR and juvenile sockeye salmon abundance to estimate the maximum capacity of a nursery lake to produce smolts, in units of smolt biomass and numbers. A generally applicable average of spawner-to-smolt survival rate for sockeye salmon (Koenings and Kyle 1997) was then used in the EV model to backcalculate spawner abundances required to achieve those smolt maxima (Koenings and Kyle 1997). In the PR model, optimal spawner escapement was equated with the number of 'spawners per PR unit' that maximized adult returns (Hume et al. 1996; Shortreed et al. 2000), based on data from Koenings and Burkett (1987).

While both the EV and the PR models have been used to estimate optimal spawner abundances, neither model takes uncertainty into account. Accounting for uncertainty is important for conservation because biased expectations of productivity based on point estimates may result in overexploitation of stocks (e.g., Garcia 2000). Also, uncertainty needs to be accounted for in habitat-based models and stock-recruitment models for researchers to compare precision of estimates of optimal spawner abundance generated by these models.

The objectives of this study were to: 1) develop a systematic method of estimating optimal spawner abundance for Fraser River, BC sockeye salmon stocks based on the productivity of their nursery lakes that explicitly takes uncertainty into account, 2) apply the method to Fraser River sockeye salmon stocks, and 3) compare these habitat-based estimates with optimal escapement estimated independently from standard stock-recruitment analyses. I refer to the habitat-based method I developed as the Bayesian PR method because I used Bayesian statistical methods and represented parameters and estimates of variables with probability distributions.

In theory, estimates of optimal escapement from two independent sources of information could be combined to produce a single estimate that may be more precise simply because more information has been applied to the problem. Geiger and Koenings (1991) estimated optimal escapement for sockeye salmon stocks by combining estimates of the capacity of their freshwater habitat with stock-recruit data, using a Bayesian approach to take uncertainty into account. However, they used subjective estimates of capacity of freshwater habitat based on expert opinion instead of data and inadvertently combined contradictory information in a way that led to high confidence for specific estimates of optimal escapement that were unwarranted by both the information on habitat capacity and the stock-recruit

data (Adkison and Peterman 1996). I chose not to combine estimates of optimal escapement generated by the Bayesian PR method with independent estimates from stock-recruitment analyses but rather chose to contrast the results of the two methods.

Methods

I estimated optimal escapement based on the Bayesian PR method for six sockeye salmon nursery lakes (Chilko, Francois, Fraser, Pitt, Quesnel, and Shuswap Lakes) and two stocks (the Early Stuart and Late Stuart stocks) of the Fraser River system in British Columbia. 'Optimal' escapement here is the escapement that maximizes annual smolt biomass in the freshwater habitat. For comparison, I also estimated two other optimal escapements. The first was the escapement that maximizes annual juvenile (fall fry or smolt) sockeye salmon abundance ($S_{MAX_{S-J}}$) based on spawning stock and juvenile recruitment analysis (referred to here as S-J analysis) for three lakes where juvenile data were available (Chilko, Quesnel, and Shuswap Lakes). The second was the escapement that maximizes total adult recruitment (in numbers of fish) ($S_{MAX_{S-R}}$) based on standard stock and adult recruitment analysis (called S-R analysis) for all the lakes and stocks. Note that optimal escapement based on stock-recruitment analyses usually refers to the escapement that maximizes catch (S_{MSY}), rather than the escapement that maximizes adult recruits (S_{MAX}). I use the term optimal escapement in the latter context, defining it as the escapement that maximizes abundance or biomass (depending on the method) to make all the 'optimal' estimates comparable. These 'optimal' escapements are to be used as a basis for estimating target reference points (defining desired abundances) and limit reference points (abundances that are some small fraction of those optimal escapements and below which the spawning

stock should not drop). In each type of analysis I take uncertainty into account explicitly by using Bayesian statistical methods and representing all parameters and estimates with discretized probability distributions. Chilko Lake cohorts that would have been affected by lake fertilization experiments (i.e. brood years 1987-1992; Bradford et al. 2000b) were excluded from all analyses to avoid biasing estimates of productivity.

Fraser River sockeye salmon rearing lakes

Many lakes in the Fraser River's drainage basin provide nursery habitat for juvenile sockeye salmon (Figure 1). The nursery lakes of the Fraser River system are ideal for this work because they have relatively good estimates for abundance of major stocks and for productivity in their nursery lakes compared to other BC nursery lakes. The sockeye salmon nursery lakes in the Fraser system for which data appropriate to this study were available are Chilko, Francois, Fraser, Pitt, Quesnel, Shuswap, Stuart, Takla, and Trembleur, the latter three lakes being occupied by the two Stuart stocks. These lakes range widely in their characteristics (Table 1). The distances that sockeye salmon cover during their migrations between these lakes and the ocean range from under 100 to over 1000 km.

Habitat-based estimates of optimal escapement (the Bayesian PR method)

The Bayesian PR method consists of three steps (Figure 2): 1) first, I used lake productivity (photosynthetic rate) to estimate the maximum sockeye salmon smolt biomass (capacity) that each nursery lake can produce; 2) then I converted smolt biomass to smolt abundance, using lake-specific estimates of weight per smolt at high smolt densities; and 3) I estimated the minimal spawner abundance required to produce those smolts and called this 'optimal' spawner abundance. Empirical relationships

provide the basis for estimations in steps 1 and 3, and because both of these relationships were heteroscedastic, I used natural logarithm transformations. These three steps are detailed below.

Step 1

In step 1, I estimated the maximum capacity of each nursery lake to produce sockeye salmon:

$$(1) \quad \log_e SB_{MAX_i} = \mathbf{d} + \mathbf{g} \bullet \log_e PR_{TOTAL_i},$$

where SB_{MAX_i} is the maximum smolt biomass (tonnes year⁻¹) that lake i can produce, \mathbf{d} and \mathbf{g} are the intercept and slope parameters, respectively, of the empirical relationship between mean photosynthetic rate (PR) and maximum observed juvenile sockeye salmon biomass, and PR_{TOTAL_i} is the total seasonal (May to October) carbon production (tonnes) in lake i . Step 1 was based on a positive empirical relationship between total seasonal PR and maximum observed juvenile sockeye salmon biomass (Hume et al. 1996; Shortreed et al. 2000) in 10 rearing-limited nursery lakes (Figure 3). Rearing-limited means that juvenile sockeye salmon output from these lakes has peaked as a function of poor lacustrine conditions or fry-food interaction, instead of from limitations caused by the number of spawners or the amount of spawning area (Koenings and Burkett 1987). Data to calibrate this relationship were from Figure 32.2b in Shortreed et al. (2000) (K. S. Shortreed, Fisheries and Oceans Canada, Cultus Lake Laboratory, 4222 Columbia Valley Highway, Cultus Lake, BC, V2R 5B6, Canada, personal communication). Data were fall fry biomass for Quesnel and Shuswap lakes and smolt biomass for all other lakes. Smolt biomass data for the six Alaskan Lakes, originally from Koenings and Burkett (1987, Table 6), were averages of one to three years of biomass observations in rearing-limited lakes. For the four BC lakes, I used the maximum annual juvenile biomass observed to date and assumed these lakes were rearing-limited in that year (Hume et al. 1996).

I estimated a joint posterior probability distribution for the intercept (\mathbf{d}) and slope (\mathbf{g}) parameters (Equation 1) of the relationship between \log_e (observed juvenile sockeye salmon biomass in tonnes year⁻¹) and \log_e (total seasonal PR in tonnes of carbon year⁻¹) (Figure 3), using a Bayesian approach (Appendix A). I used uniform prior probability distributions for \mathbf{d} and \mathbf{g} , each bounded by the maximum likelihood estimate (MLE) \pm 3 standard errors (SE) and described by 20 grid points of values and associated probabilities. As a result, the joint posterior probability distribution representing \mathbf{d} and \mathbf{g} was a 20-by-20 grid of parameter values with corresponding probabilities.

The input to Equation 1 is the mean PR for a lake. PR data are usually available for only a few years, so that the true value for each lake is uncertain. To characterize the uncertainty in estimates of PR_{TOTAL_i} , I used discretized log-normal distributions. Means of those distributions were averages of available annual estimates for each lake (Table 2), while standard errors were based on the amount of lake-specific data available and an estimate of within-lake year-to-year variability in $\log_e PR_{TOTAL}$ (Appendix B), assumed to be the same across lakes. The range of possible values, defined by $\log_e (\overline{PR_{TOTAL}}) \pm 3$ SE, was divided equally into discrete bins and I used 20 grid points and associated probabilities to represent each input distribution. Means and SEs for the input distributions representing PR_{TOTAL} for the Early and Late Stuart sockeye salmon stocks were calculated (Appendix C) to be stock-specific rather than lake-specific because juvenile fish from these two stocks rear in three lakes, sharing one between them. Hence, stock-specific PR_{TOTAL} estimates were calculated to describe the productivity of their respective average freshwater habitats.

To apply Equation 1 to each lake, I took an iterative approach. For each lake i , $\log_e SB_{MAX}$ was computed according to Equation 1 using each grid point value in the discrete probability distribution for $\log_e PR_{TOTALi}$ in combination with each pair of parameter values from the grid points of the joint posterior probability distribution for \mathbf{d} and \mathbf{g} . Thus, I computed a total of 8000 possible values for $\log_e SB_{MAX}$. The probability associated with each $\log_e SB_{MAX}$ value was computed by applying the multiplication law for the probability of independent events:

$$(2) \quad P(\log_e SB_{MAXij}) = P(\mathbf{q}_k)P(\log_e PR_{TOTALim}).$$

Here, $P(\log_e SB_{MAXij})$ is the computed probability for each possible $\log_e SB_{MAXi}$ value, for $j = 1$ to 8000, $P(\mathbf{q}_k)$ is the probability associated with a set of \mathbf{d} and \mathbf{g} parameter values, for $k = 1$ to 400, and $P(\log_e PR_{TOTALim})$ is the probability associated with a $\log_e PR_{TOTALi}$ grid point, for $m = 1$ to 20.

Before proceeding to step 2, I standardized the 8000 probability values associated with $\log_e SB_{MAXi}$, so that the discrete probabilities summed to one. Then I truncated the array of $\log_e SB_{MAXi}$ values and probabilities at both ends to get the 99% interval and avoid extreme tails and standardized the truncated array so the discrete probabilities summed to one again. To make further calculations manageable, I created a discrete distribution with 20 $\log_e SB_{MAXi}$ values and associated probabilities.

Step 2

In step 2, I converted the estimated maximum capacity for each lake from smolt biomass to smolt abundance:

$$(3) \quad \log_e SN_{MAX_i} = \log_e \frac{SB_{MAX_i}}{W_{MAX_i}},$$

where SN_{MAX_i} is the maximum smolt capacity for lake i , in numbers of smolt, and W_{MAX_i} is the lake-specific weight per smolt (tonnes) at maximum smolt capacity. I described W_{MAX} by discretized log-normal distributions, which were parameterized the same way as the PR_{TOTAL} input to step 1 (Table 2, Appendix B). I used the iterative approach described in step 1 to combine the two distributions on the right side of Equation 3, resulting in 400 possible values for $\log_e SN_{MAX_i}$ each with an associated probability. Following the same procedure described at the end of step 1, I standardized, truncated, restandardized and reduced the results of step 2 into a discrete distribution with 20 $\log_e SN_{MAX_i}$ values and associated probabilities before proceeding to step 3.

Step 3

In step 3, I estimated the minimal number of female spawners (in units of "effective female spawners", EFS, or the number of female spawners reduced by prespawning mortality (Pacific Salmon Commission 1998)) required to yield the maximum smolt abundance in each lake:

$$(4) \quad \log_e EFS_{MAX_i} = \mathbf{k} + \mathbf{I} \bullet \log_e SN_{MAX_i},$$

where EFS_{MAX_i} is the minimum escapement needed to produce SN_{MAX_i} smolts and \mathbf{k} and \mathbf{I} are the intercept and slope parameters, respectively, of the empirical relationship between EFS and smolt abundances at high smolt density across lakes. The data used to calibrate this relationship were point estimates of EFS and smolt abundances at the peak of the spawner-to-smolt relationship for sockeye salmon populations in five BC lakes. These point estimates were derived using a Ricker model, shown here in the linear form:

$$(5) \quad \log_e (R_{pq} / S_{pq}) = a_q - b_q S_{pq} + v_{pq},$$

where S_{pq} is the abundance of spawners (EFS) in brood year p for population q , R_{pq} is the number of smolts produced by S_{pq} spawners, and v_{pq} is the stochastic error term, assumed to be normally distributed with standard deviation \mathbf{s}_q (Peterman 1981). First, I calculated MLEs of the Ricker a_q and b_q parameters, then I computed the arithmetic mean for each productivity parameter ($a'_q = a_q + (\mathbf{s}_q^2 / 2)$) to better describe 'average' spawner-to-smolt relationships (Ricker 1997). Next, point estimates of spawner abundance ($EF S_{MAX q} = 1/b_q$) and smolt abundance ($SN_{MAX q} = e^{a'_q - 1} / b_q$) at the peak of each Ricker curve were calculated from formulas in Ricker (1997). Finally, using these point estimates and the same Bayesian approach (Appendix A) and treatment of priors that I described in step 1, I derived a joint posterior probability distribution for parameters \mathbf{k} and \mathbf{I} (Equation 4) of the relationship between $\log_e EF S_{MAX}$ and $\log_e SN_{MAX}$ (Figure 4).

The five time series of EFS and smolt abundance used here included 43 years from Chilko Lake, 29 years from Cultus Lake, 11 years from Babine Lake prior to enhancement, 9 years from Port John Lake, and 8 years from Lakelse Lake. Most juveniles (>95%) from all but one of these populations spend one winter in freshwater and migrate to sea as age-1 smolts, although some age-2 smolts were included in the abundance estimates. The exception is Port John Lake, where most smolts were age-2 and smolts of ages-1, -2, and -3 were included in the estimates. Data were from Foerster (1968), Wood et al. (1998), J.M.B. Hume (Fisheries and Oceans Canada, Cultus Lake Laboratory, 4222 Columbia Valley Highway, Cultus Lake, BC, V2R 5B6, Canada, personal communication), and M.J. Bradford (Fisheries and Oceans Canada and Cooperative Resource Management Institute,

School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada, personal communication).

Again, I used the iterative approach described in step 1 to apply Equation 4 and computed 8000 possible $\log_e EFS_{MAX}$ values and associated probabilities for each lake. Using the exponential function, I transformed these estimates to EFS abundance (from \log_e values). Results were compiled from the entire 8000-bin distribution of $\log_e SN_{MAX_i}$ values and standardized probabilities. To describe the precision of the final distributions, I used an 80% credibility interval (i.e. 90th percentile estimate less 10th percentile estimate) divided by the median. Therefore, lower values of this ratio reflect greater precision. For graphs, the arrays of 8000 $\log_e SN_{MAX_i}$ values and standardized probabilities were truncated to get the 99% interval and then described as 20-bin discrete distributions, each standardized such that the discrete probabilities summed to one.

Bayesian stock-recruitment estimates of optimal escapement

To allow the results from the Bayesian PR method to be compared with estimates of optimal escapement based on standard stock-recruitment analysis, I applied a Bayesian approach to the latter as well (Walters and Ludwig 1994). I used the same Ricker stock-recruitment model form as in Equation 5, but estimated the spawning escapement that maximizes abundance (S_{MAX}) of either total adult recruitment (S-R analyses) or juveniles at the end of their lake residence (S-J analyses). S_{MAX} is the most appropriate index from fitting the Ricker model to compare with the escapement that maximizes smolt biomass in nursery lakes (i.e. derived from the Bayesian PR method). Estimates of EFS were used in all analyses as an index of total spawners.

For the S-R analyses, I used EFS-recruit data (brood years 1949 through 1992) for 11 sockeye salmon populations that rear in 8 lakes (Table 2) in the Fraser River watershed (M.J. Bradford, personal communication). S-R analysis for the Horsefly and Mitchell populations rearing in Quesnel Lake was excluded from this study because these data show very little evidence of density dependence and do not support use of the Ricker model. Most Fraser River sockeye salmon juveniles migrate to the ocean as smolts after one winter in freshwater (Foerster 1968) and I included only these "1.x" age-classes in the adult recruit data. I summed wild spawner abundance and spawner abundance in the Nadina spawning channel for the S-R analysis of the Nadina population that rears in Francois Lake. Note also that the Pitt Lake population is augmented by a hatchery operation that uses native brood stock and releases hatchery raised fry each year. I analyzed the spawner-recruit data despite this 'enhancement.' Abundance estimates were summed for populations whose juveniles rear in the same lake (Table 2, lakes #1-4, 6) and I estimated optimal escapement on a lake-by-lake basis for these population aggregates, so they were comparable with estimates from the S-J analyses and the Bayesian PR method. However, stock-specific (as opposed to lake-specific) estimates of optimal escapement were generated for the Early Stuart and Late Stuart stocks to compare with estimates produced by the Bayesian PR method for these two stocks.

For S-J analyses, juvenile abundance data were available for Chilko, Quesnel, and Shuswap Lakes (Hume et al. 1996 and J.M.B. Hume, personal communication). Smolt abundance estimates for Chilko Lake (brood years 1949 - 1986 and 1993 – 1997) were taken from a counting fence at the outlet of the lake. Fall fry abundance was estimated from hydroacoustic surveys for Quesnel Lake

(brood years 1976, 1977, 1981, 1985-1987, 1989-1991, 1993, 1994, and 1997) and Shuswap Lake (brood years 1974-1979, 1982, 1983, 1986-1992, 1994, and 1995).

For the Bayesian stock assessments, I also used 'uninformative' priors (Punt and Hilborn 1997). Upper and lower bounds for the uniform prior probability distributions on a and b (Equation 5) were defined by their respective MLE ± 3 SE (e.g., $\hat{a} \pm 3SE(\hat{a})$). However, I was able to use $\hat{b} - 3SE(\hat{b})$ as the lower bound on b for only three analyses (i.e. S-R analysis for Francois Lake and S-J analyses for Chilko and Shuswap Lakes) without going below the biologically reasonable value of zero (Punt and Hilborn 1997; Hill and Pyper 1998). For the remainder of the analyses, estimates of $\hat{b} - 3SE(\hat{b})$ were negative and biologically unreasonable because they implied a positive slope on the $\log_e(R/S)$ vs. S graph. For such stocks, instead of assuming the stock size could reach infinity, I arbitrarily assumed that 3 times the maximum observed EFS abundance ($EFS_{MAX,OBS}$) was a biologically reasonable maximum bound for the parameter S_{MAX} , in units of EFS, and set the lower bound on b equal to $1/(3 \cdot EFS_{MAX,OBS})$. As the lower bound on b approaches zero, the precision of S_{MAX} estimates declines and the upper bound of the S_{MAX} distribution increases. Difficulty in setting a lower bound for b based on statistical analysis of the S-R data alone implies that these data are not informative about the b parameter.

A 200-by-200 grid of a and b parameter values and associated probabilities was calculated for each S-R and S-J analysis using methods outlined by Walters and Ludwig (1994). Because S_{MAX} is equivalent to $1/b$, the posterior probability distribution for S_{MAX} was converted, by inversion, from the marginal posterior probability distribution for b integrated over all probable a parameter values (Walters

and Ludwig 1994). Results describing estimates of S_{MAX} (i.e. percentile and precision estimates) were calculated from the resulting 200-value discrete marginal posterior probability distributions, but for graphs distributions were reduced to 20 grid points and standardized such that the discrete probabilities summed to one.

Results

The spawning escapement required to maximize biomass of juvenile sockeye salmon in nursery lakes (S_{MAX}), as estimated by the base case of the Bayesian PR method, was generally higher than the spawning escapement required to maximize either total adult sockeye salmon recruits or juvenile abundance in nursery lakes as estimated by the S-R and S-J analyses, respectively (Table 3, medians). The only exception was Chilko Lake, where estimates of optimal escapement from the three methods are similar, but the Bayesian PR method produced the lowest of the three estimates. Estimates of optimal escapement based on the Bayesian PR method are independent of estimates based on stock-recruitment analyses for all but three of the examples. Estimates for Chilko, Quesnel and Shuswap Lakes are not independent because estimates of maximum observed juvenile biomass from these three lakes were used to help parameterize the Bayesian PR method.

Estimates of optimal escapement from the Bayesian PR method were slightly more precise than those from S-R analyses and less precise than those from S-J analyses, with the exception of Francois Lake (Table 3, Figure 5). Precision of estimates of optimal escapement, S_{MAX} , based on S-R or S-J analyses varied greatly among lakes and was best when the observed data showed clear evidence of density dependence (e.g., S-R analyses for Francois and Pitt Lakes or any of the S-J analyses, Figure 5). These are the few cases where posterior probability distributions for S_{MAX} were largely contained

within the range of historical observations. The precision of estimates of S_{MAX} based on the Bayesian PR method was relatively consistent among lakes and improved as the median value for S_{MAX} decreased. Although all the posterior distributions for S_{MAX} were skewed, those resulting from S-R analyses were often more skewed to the right (i.e. had a longer tail at high escapements) than those resulting from the Bayesian PR method. Thus, S-R data can be poor at defining the upper limit for S_{MAX} (e.g., Early Stuart S-R analysis, Figure 5).

Sensitivity analyses

Exclusion of data from Babine Lake

I examined the sensitivity of results of the Bayesian PR method to the inclusion of Babine Lake data in the calibration of both of the predictive relationships (used in steps 1 and 3) because my assumption that Babine Lake was producing smolts at its peak capacity may not be valid. Abundance of juvenile sockeye salmon in Babine lake was limited by the capacity of its spawning grounds prior to enhancement with spawning channels in 1965 and it may still be, despite enhancement (West and Mason 1987). When I removed the Babine data point from each of the predictive relationships (Figures 3 and 4) and repeated the Bayesian PR analyses, the medians of the resulting probability distributions for S_{MAX} were 10 to 20 percent higher (Table 3).

Additional years of photosynthetic rate or smolt weight data

The base case analyses of the Bayesian PR method were mostly based on few years of photosynthetic rate (PR) and smolt weight (W_{MAX}) data for each lake, so I asked how the precision of the S_{MAX} estimates would change with additional years of input data. To do this, I simulated the effect of acquiring additional years of PR or W_{MAX} data by increasing n in Equations B1 and B2, which

narrowed the input distributions. As expected, increasing the data available improved the precision of estimates of S_{MAX} (Figure 6), but not by much. The greatest relative gains in precision were made when available data were doubled from one to two years and relative gains in precision diminished as more years of data were added.

Inaccurate photosynthetic rate or smolt weight input data

I also examined how inaccurate input data for PR or W_{MAX} might affect estimates of S_{MAX} produced by the Bayesian PR method. When few data are available, estimates of the means for PR and W_{MAX} could be inaccurate. I adjusted the base case mean of the input distribution for PR or W_{MAX} by ± 2 SE (leaving the standard errors of the input distributions at their base case values). Since the method relies on linear relationships, changes in S_{MAX} were proportional to changes in the inputs (Table 4, Figures 7-8). The effect of using potentially inaccurate inputs for PR and W_{MAX} was substantial. However, the medians of these adjusted S_{MAX} estimates from the sensitivity analyses were still within the 80% credibility interval of S_{MAX} values estimated by the base case Bayesian PR method, with the exception of the results from the PR ± 2 SE analyses for Pitt Lake (Figure 7), which were within the 99% credibility interval of base case S_{MAX} . The relative adjustment to the mean PR for Pitt Lake was the largest (amongst the lakes) because the SE estimated for Pitt Lake PR was large, as only one year of PR data was available. The precision of the estimates of S_{MAX} changed very little as a result of changes to the mean input values for PR or W_{MAX} .

Number of discrete parameter values explored

Results of Bayesian analyses can potentially be affected by the number of discrete parameter values used in calculations (as opposed to assuming a continuous range of values) (Walters and Ludwig 1994). Therefore, to examine the sensitivity of my results for the Bayesian PR method to this potential bias, I compared results using 20 (base case), 40, and 100 discrete parameter values for the two input distributions (PR and W_{MAX}) and for the intermediate results calculated by steps 1 and 2. I also compared results using a 20-by-20 grid (base case) and a 40-by-40 grid to define the joint posterior probability distributions for parameters of the two predictive relationships, combined with trials of 20 and 40 discrete parameter values for the input distributions (PR and W_{MAX}) and the intermediate results. I found very small differences in the probability distributions for S_{MAX} , indicating that the discretized ranges of parameter values provided a close approximation to the true probability distributions.

Discussion

Estimates of optimal escapement from habitat-based analyses were generally higher than estimates of optimal escapement based on stock-recruitment analyses. Contradictory results are not surprising because the methods analyze different sets of processes. Also, because the results are contradictory, they cannot be combined to estimate optimal escapement with greater precision. However, because the differences were generally in the same direction for most sockeye salmon stocks, they may be indicative of general mechanisms acting to different degrees in each lake. In addition, the lake-specific differences between estimates can be examined to learn more about individual systems. While the precision of estimates from the different analyses did not differ greatly overall, $S_{MAX_{S-R}}$

distributions from the standard adult S-R analyses were often more skewed to the right than those from the Bayesian PR method, suggesting that habitat-based analyses may be more useful than S-R analyses in defining an upper limit for optimal escapement when the range of S-R data is limited.

Comparison of estimates of optimal escapement

There are several plausible explanations of my finding that estimates of optimal escapement, S_{MAX} , from the Bayesian PR method were generally higher than estimates based on S-R or S-J analysis. First, the range of historically observed escapements is often below the range of $S_{MAX_{S-R}}$ estimates (Figure 5). If there is substantial measurement error in the historical estimates of spawner abundance and the range of these estimates is small, S-R analysis will always underestimate optimum stock size (Hilborn and Walters 1992, p. 287). If this were the case, I would expect PR-based estimates of S_{MAX} to be greater than S-R based estimates and I would expect estimates from the two methods to converge when the range of spawner abundance estimates was large. However, spawner abundance estimates for Fraser Lake span only 2 orders of magnitude and the S_{MAX} estimates from the two methods overlap considerably. Additional lakes where PR-based and S-R based S_{MAX} estimates overlap (Chilko, Quesnel, and Shuswap Lakes) have estimates of spawner abundance spanning 3 to 5 orders of magnitude, but these are also the lakes included in the calibration of the Bayesian PR method, so S_{MAX} estimates from the two methods are not independent. On the other hand, spawner abundance estimates for Francois Lake cover 5 orders of magnitude, suggesting that $S_{MAX_{S-R}}$ should be relatively unbiased, but S-R based and PR-based S_{MAX} estimates still differ by an order of magnitude. Thus, while bias due to measurement error and limited contrast in spawner abundance estimates is certainly an issue, it alone cannot explain the results.

Second, S_{MAX} estimated by the Bayesian PR method is the stock size that maximizes smolt abundance, while S_{MAX} estimated by my S-R analyses is the stock size that maximizes total adult recruits. If marine abundance of a given population influences its reproductive fitness as adult sockeye salmon or their survival rate during the smolt-to-adult life stages (e.g., Peterman 1982; Peterman 1984; Bugaev et al. 2001), estimates of $S_{MAX_{S-R}}$ would be lower than those from the Bayesian PR method. However, it is hard to imagine that either of these first two explanations could account for the large discrepancies between estimates of S_{MAX} illustrated by the Francois, Pitt, and Late Stuart examples (Figure 5).

Third, when I used the Bayesian PR method, I generalized from the lakes for which rearing-limited data were available (i.e. those in Figure 3) and assumed that other lakes were similar. If these other lakes are different, results from the Bayesian PR method might reflect a capacity that cannot actually be achieved. There are several plausible mechanisms, not necessarily independent of each other, that would limit the abundance of sockeye salmon smolts produced in nursery lakes and cause S_{MAX} estimates from S-R analyses to be significantly lower than estimates based on the Bayesian PR method. For instance, Shortreed et al. (2000) noted mechanisms such as limited spawning habitat, predator and competitor populations, thermal regimes that limit juvenile sockeye salmon feeding territory, and predation-resistant plankton community structures, all of which can affect a lake's ability to produce sockeye salmon. These mechanisms, examined in more detail below, are accounted for in habitat-based analyses (i.e. EV and PR models and Bayesian PR method) only to the extent that they may be acting in some of the lakes used to parameterize the models.

Some examples of these mechanisms illustrate the potential caveats of using any method based on photosynthetic rate. Limited spawning habitat may mean that the capacity of a lake to produce sockeye salmon smolts estimated based on PR will be under-utilized. For instance, the spawning habitat around Francois Lake has been enhanced with an artificial spawning channel. Total natural and enhanced spawning ground capacity was estimated at 50 thousand spawners (Rosberg et al. 1986 as cited in Shortreed et al. 1996), or about 26 thousand EFS, which is a full order of magnitude below the S_{MAX} estimate from the Bayesian PR method (320-750 thousand EFS, Table 3). In contrast, S-R based estimates optimal escapement (median of 13 thousand EFS, Table 3) are about half of the estimated spawning ground capacity. This example illustrates that estimates of optimal escapement based on the Bayesian PR method in the absence of other stock size information or estimates of spawning ground capacity could be quite unrealistic.

In cases where competitors or predators of juvenile sockeye salmon reduce the maximum achievable abundance of sockeye salmon juveniles in a lake, the Bayesian PR method may overestimate the capacity of the lake to produce sockeye salmon smolts. However, while other planktivores are present in most of the study lakes (e.g., kokanee or smelt), they are not always competitors with juvenile sockeye salmon (Diewert and Henderson 1992). In addition, significant populations of potential predators of sockeye salmon juveniles may be present in the lakes (e.g., juvenile chinook salmon or rainbow trout), but sockeye salmon are not always a major component in their diet (Diewert and Henderson 1992). Because the food webs are complex and unique among lakes, experiments may be required to estimate optimal escapement for these systems independently.

Another mechanism that would limit abundance of sockeye salmon juveniles in a nursery lake is thermal stratification resulting in an epilimnion warm enough to restrict foraging fry in their use of this productive area of the lake. Evidence suggests this may be the case in Shuswap Lake (Hume et al. 1996) and such an effect would be consistent with the density dependence evident in the Shuswap fall fry data (Figure 5). This could be related to my results showing that the PR-based median estimate of S_{MAX} is approximately three times larger than the S-J based median estimate of S_{MAX} (Table 3) for that lake. In addition, the S-R data for the Shuswap aggregate show total adult returns decreasing above one million EFS (Figure 5), which corresponds more closely to the S-J based estimate of S_{MAX} , even though the Ricker S-R analysis estimates a much higher S_{MAX} (Table 3).

While the Bayesian PR method uses empirical data to relate primary lake productivity to maximum numbers of sockeye salmon juveniles, there is no evidence to suggest that nursery lakes can produce sockeye salmon sustainably at maximum capacities estimated by the Bayesian PR method. Maximum observed juvenile biomass data used to develop the Bayesian PR method were based on three years of observations, at most, for any one lake and were single occurrences for the five BC lakes. Plankton community structure and productivity are complex and may not be able to sustain high grazing pressure from sockeye salmon fry year after year. In addition, some evidence suggests that high grazing pressure from sockeye salmon fry may result in predation-resistant plankton communities (i.e. predominantly smaller zooplankton species) and subsequent reductions in juvenile sockeye salmon abundance (Koenings and Kyle 1997). On the other hand, repeated high escapements that maintain high levels of nutrient loading from carcasses may be necessary to bolster salmon productivity in the long term (Schmidt et al. 1998). More research is needed to explore the effects of repeated high

escapements and heavy grazing pressure of large juvenile sockeye salmon populations (i.e. maximum capacities estimated by the PR method).

The only results that are contrary to what we might expect from the above discussions are those from Chilko Lake because S_{MAX} estimated by the Bayesian PR method was slightly smaller than S_{MAX} estimated by either the S-R and the S-J analyses (Table 3). However, the distributions for S_{MAX} from all three analyses overlap considerably (Figure 5). The mode of the distribution of the S_{MAX} estimate based on the Bayesian PR method for Chilko Lake corresponds well to the observed spawner abundance that produced the greatest number of smolts (Figure 5) partly because Chilko data were used to calibrate the Bayesian PR method.

Comparing habitat-based estimates of optimal escapement (i.e. from the EV or PR models or the Bayesian PR method) with those based on S-J or S-R analyses suggests that mechanisms limiting the abundance of juvenile sockeye salmon within nursery lakes are at play to different degrees in different lakes. Comparing S_{MAX} estimates cannot differentiate between hypotheses but can support the need for additional investigation of specific mechanisms in specific lakes.

Utility of the Bayesian PR method

From a management perspective, there is great utility for the Bayesian PR method, despite its current limitations. If estimates of optimal escapement based on the Bayesian PR method are to be used in setting escapement goals, each of the mechanisms which can limit the abundance of sockeye salmon in nursery lakes needs to be considered. This is especially true if the Bayesian PR method is used as a stand-alone method of assessment. There are several sockeye salmon lakes on the west coast of North America without stock and recruit data to support adult S-R analyses (or where stock and recruit data

are of dubious quality). After PR data are collected over one or two growing seasons in those nursery lakes, smolt abundance at maximum capacity, optimal escapement, and the uncertainty around them can be estimated. The Bayesian PR method could also be applied to lakes and reservoirs that kokanee (land-locked sockeye salmon) inhabit, to estimate the maximum annual production of kokanee biomass.

The Bayesian PR method can also be used in combination with stock-recruitment analyses to identify systems that might benefit from enhancement and quantify the potential benefits. For example, this study suggests that if spawning ground capacity around Francois Lake existed for 300-750 thousand EFS, the lake could rear 31-48 million smolts (inter-quartile range) and, assuming 5% ocean survival, result in 1.5-2.5 million adults, or 5-8 times observed abundances. Such estimates of projected potential can help inform benefit-cost analyses and management decisions about whether to proceed with enhancement or costly research (e.g., to study the abundance and diet of sockeye salmon competitors and predators or plankton community structure).

When S-R data show little or no evidence of density dependence, sockeye salmon populations are suspected of being recruitment-limited (e.g., Early Stuart, Late Stuart, and Fraser Lake examples, Figure 5). In these cases, estimates of S_{MAX} from the Bayesian PR method, such as most of those reported here, can support calls for larger escapements for two reasons. First, they give managers confidence that nursery lakes can support the additional sockeye salmon fry produced by higher spawning escapements, especially when S-R analyses provide no such evidence. Second, additional data from subsequent larger escapements can be used to recalibrate relationships and refine the Bayesian PR method. Specifically, data from BC nursery lakes where empirical evidence strongly

suggests that sockeye salmon juveniles are rearing-limited may reduce the uncertainty implicit in the Bayesian PR method.

The utility of the Bayesian PR method discussed thus far has been implicitly related to harvest management, in terms of setting escapement goals for healthy stocks that can support harvest, assessing enhancement potential to increase harvest, and providing estimates of the maximum capacity of nursery lakes independent from S-R data, again to maximize harvest. Chapter two discusses the utility of this method in the context of conservation-oriented policies and develops a scheme to quantify biological reference points based on estimates of optimal escapement from either the Bayesian PR method or Bayesian stock-recruitment analyses.

Comparison of the Bayesian PR method with the PR and EV models

The most significant difference between the Bayesian PR method developed here and the PR model of Shortreed et al. (2000) is that the first accounts for uncertainty. However, because these methods used different data to calibrate the two predictive relationships and different estimates for smolt weight as input, estimates of maximum smolt abundance and optimal escapement differ for a given lake. The Bayesian PR method produced median estimates of S_{MAX} that were higher than, or nearly the same as, the point estimates produced by the PR model (Shortreed et al. 2000), with the exception of Francois Lake (Table 3). While lake-specific mean PR values were identical for each method, they estimated different quantities for the maximum capacity of smolt biomass in a given nursery lake because the Bayesian PR method included four BC lakes in the calibration of the PR versus maximum smolt biomass relationship and its parameters were estimated in \log_e space. As a result, for large lakes with

high total seasonal PR, the Bayesian PR method estimated higher maximum capacities of juvenile sockeye salmon biomass (Figure 3, dotted line) than did the PR model (Figure 3, dashed line).

Differences between the Shortreed et al. (2000) PR model and my Bayesian PR method in estimates for smolt weight used as input and smolts/EFS had a greater effect on the results than differences in the calibration of the first predictive relationship. The PR model used a point estimate of 4.5 g per smolt for all lakes, while the Bayesian PR method used lake-specific estimates whose means range from 2.7 to 9.7 g (Table 2). Also, the Bayesian PR method consistently estimated that more EFS were required to produce the same number of smolts than did the PR model. The average smolts/EFS ratio used by the base case Bayesian PR method varied from 51 to 78 smolts/EFS over the range of observed smolt abundances (Figure 4, dotted line), based on analysis of data from 5 BC lakes. When the Babine Lake datum was removed from the model fitting for sensitivity analysis, the slope became almost constant at 57 to 59 smolts produced per EFS. The PR model (Shortreed et al. 2000) used a constant estimate of 108 smolts/EFS (Figure 4, dashed line), while the EV model used a smolts/EFS ratio of 54 (Koenings and Kyle 1997). Average egg-to-smolt survival rate (2%) for sockeye salmon reported by Bradford (1995) translates to 70 smolts/EFS at an average fecundity of 3500 eggs per effective female. Bradford (1995) found significant differences in egg-to-smolt survival rate among populations of sockeye salmon and large interannual variation, which emphasizes the importance of taking uncertainty into account. Note that my estimate of average smolts/EFS may be similar to Bradford's (1995) estimates because I used data from 4 of the 7 sockeye salmon populations upon which Bradford's (1995) estimates were based.

Improving the Bayesian PR method and its application

Because the Bayesian PR method represents the first attempt to quantify and account for uncertainty in a habitat-based model for sockeye salmon, improvements can certainly be made to it, or at least to data used as its input. While it is reassuring that optimal escapement estimates for Fraser River sockeye salmon using this method are higher and no more uncertain than optimal escapement estimates produced by S-R analyses, it is disappointing that they are not more precise. Both of the predictive relationships used in the Bayesian PR method lack sufficient data to precisely estimate their parameters and the uncertainty in them. It was necessary to extrapolate beyond the ranges of observed data for both relationships in order to apply the Bayesian PR method to the larger lakes in this study and the true variability in these relationships may actually be underestimated. PR data and information quantifying maximum juvenile abundance in both small and large BC sockeye salmon lakes that are clearly rearing-limited would be extremely valuable, as would estimates of the smolt/spawner ratio at high smolt abundance. Since I completed this analysis, data have become available to suggest that Meziadin Lake, a small sockeye salmon nursery lake (36 km²) in the Nass River watershed on the North coast of BC, may be rearing-limited (R.C. Bocking, LGL Limited, 9768 Second St., Sydney, BC, V8L3Y8, unpublished data). If the data from this lake were included in the model fit to define parameters for the predictive relationship between PR and maximum sockeye salmon biomass, it would reduce estimates of maximum smolt biomass based on the Bayesian PR method by 7 to 15%.

The Bayesian PR method could be modified to consider some of the mechanisms that constrain the abundance of sockeye salmon smolts produced in a lake such that maximum rearing potential estimated by PR is underutilized. For example, PR could be used to calculate the abundance or biomass

of 'pelagic fish' across several species and that abundance could be prorated according to the relative abundance of sockeye salmon juveniles. One could also develop models, with additional data, that quantify the effects of independent variables such as temperature or abundance of predators or competitors on maximum juvenile sockeye salmon abundance. Implementing these ideas might improve the precision of results overall, but each adds to the data required by the method.

My application of the Bayesian PR method failed to explicitly consider uncertainty in the proportional distribution of sockeye salmon fry from the Early and Late Stuart runs among the three lakes of the Stuart complex (Appendix C). Even if my assumption that juveniles rear directly downstream of their natal habitat holds true, the area of the rearing habitat available to each stock varies annually with the relative abundances of the two stocks, and I failed to take this variability into account. No matter how it is partitioned, the total capacity of the nursery habitat of the three Stuart lakes to produce juvenile sockeye salmon, in terms of the EFS required, should be approximately equal to the sum of the PR-based estimates of S_{MAX} for the Early and Late Stuart runs.

Finally, accurate estimates of weight per smolt at high densities are crucial to obtain the best possible estimates of S_{MAX} using the Bayesian PR method. As the sensitivity analysis showed, use of inaccurate mean values for weight per smolt can have a large effect on the estimated optimal escapement. The lake-specific estimates I used for smolt weight were based on very little data (except for Chilko, Table 2). If the estimates I used were biased at all they would be biased high because they would represent smolt weight resulting from density-independent growth and, as a result, S_{MAX} estimated by the Bayesian PR method may be biased low for some lakes. However, the implications of my findings do not change because estimates of S_{MAX} based on the Bayesian PR method were already

generally higher than estimates of S_{MAX} based on S-R or S-J analyses. Again, additional lake-specific weight per smolt data over a range of smolt densities would be extremely valuable and they are relatively easy to obtain.

Chapter 2: Developing biological reference points based on estimates of optimal escapement

Introduction

Many stocks of wild salmon, steelhead, and trout have declined along the west coast of North America recently and these declines have precipitated wide-ranging policy reviews within government organizations across the Pacific Northwest. Development of conservation oriented policies is part of a growing trend worldwide that recognizes factors of non-sustainability in fisheries and seeks to implement a precautionary approach to fisheries management (FAO 1995a; Garcia 2000). The precautionary approach suggests that agencies should be more biologically conservative in setting management regulations due to large uncertainties and the failure of past regulations to prevent severe declines in fish abundance. Specifically, in order to be fully implemented, the precautionary approach to fisheries has three required components: 1) key indicators must be identified to monitor the state of the fishery in terms of spawning stock size, fishing pressure, and critical habitats, 2) biological reference points, related to these indicators, must be determined by methods that take uncertainty into account, and 3) pre-agreed management decisions corresponding to critical states of the system must be documented (Garcia 2000). Biological reference points are biologically derived indices of stock status, which are used to trigger management actions to achieve management goals (Gabriel and Mace 1999). A limit reference point (LRP) is often defined as a threshold not to be crossed or a highly undesirable state, whereas a target reference point (TRP) describes the desired state of the stock or the fishery from a management perspective (Caddy and McGarvey 1996).

Among the fisheries management agencies across the Pacific Northwest that have developed new policies expressing conservation concern and/or mandating new precautionary regulations are the Oregon Department of Fish and Wildlife (ODFW), the Washington Department of Fish and Wildlife (WDFW), the Alaska Department of Fish and Game (ADF&G), and Fisheries and Oceans Canada (DFO). Recent policies developed by these agencies all refer to the issue of sustainability and the concept of conservation, but they differ in the extent to which they embrace the precautionary approach to fisheries management and in the depth to which new operational regulations are developed.

Oregon, the first in the Pacific Northwest to develop a policy aimed at the restoration of wild salmonids, adopted a "Wild Fish Management Policy" in 1990 (ODFW 1992), which was intended to "restore wild stocks while maintaining fishing important to Oregon's economy." While restoration implies conservation, there is no specific mention of a precautionary approach and the concept of sustainability is introduced only in relation to harvest. Expanded in 1992, Oregon's policy specifically directs Oregon department biologists to identify wild populations, assess wild fish health and related habitat conditions, document hatchery fish influence on wild stocks, and manage natural and hatchery production to minimize impacts of fisheries (ODFW 1992). The absolute priority of management there is maintaining fisheries rather than wild salmon.

In Alaska, the state Constitution mandates ADF&G to manage fishery resources "on the sustained yield principle" (ADF&G 2001). In general, Alaska's wild stocks of anadromous Pacific salmon are healthier than those of its neighbors to the south. In the early 1990's, ADF&G developed an "Escapement Goal Policy" establishing a constant escapement strategy that explicitly declares maximum sustainable yield (MSY) to be optimal (Eggers 2001). However, it also defines a set of escapement

goals (i.e. analogous to reference points) that delineate levels of concern about stock status in conceptual terms (not quantitative terms) including conservation concern, management concern, and yield concern. These escapement goals or reference points are to be defined as ranges and uncertainty must be taken into account in their estimation, but there is no mention of specific estimation procedures. ADF&G staff perform stock assessments and set escapement goals, but the Alaska Board of Fisheries (BOF) is responsible for allocation and periodic reviews of the management plans for all Alaskan salmon stocks. In March 2000, ADF&G and BOF jointly adopted a "Sustainable Fisheries Policy" (Alaska Department of Fish and Game and the Alaska Board of Fisheries 2000). The goal of this policy is to ensure conservation of salmon and their habitats, protection of customary, traditional and other uses, and the sustained economic health of Alaska's fishing communities. Calling for conservative management in the face of uncertainty, the policy refers to "a precautionary approach," but provides no guidance for implementing it.

In December 1997, four years after the Washington State Legislature had directed its Department of Fish and Wildlife to develop a policy to protect the state's wild salmonids, the Washington Fish and Wildlife Commission adopted the "Joint Wild Salmonid Policy." It was developed in consultation with the public and the Western Washington Treaty Tribes. Its stated goal is to "protect, restore, and enhance the productivity, production, and diversity of wild salmonids and their ecosystems to sustain ceremonial, subsistence, commercial, and recreational fisheries, non-consumptive fish benefits, and other related cultural and ecological values" (WDFW 1997). The document is a list of policy statements addressing critical issues of fishery management, hatchery operations, spawning numbers, and habitat protection and restoration. The spawning escapement policy, applicable only to "primary"

populations and/or management units identified by "pertinent management agencies," states that escapement rates, levels, or ranges shall be designed to achieve MSY and "will account for all relevant factors, including current abundance and survival rates, habitat capacity and quality, environmental variation, management imprecision, and uncertainty, and ecosystem interactions." The policy declares that MSY shall be calculated by using long time series of accurate spawner and recruit statistics for each population, and when these are not available, historical production, habitat availability, or best available methods for calculation may be used. No additional details are provided about estimating procedures for MSY. If escapement levels that produce MSY are not achieved for three consecutive years, the policy also dictates that within six months a management assessment be completed to identify the problem and devise a plan for recovery. Currently, in Washington State, nearly every watershed is affected by salmonid stocks listed as endangered or threatened under the federal Endangered Species Act (ESA), but the Joint Wild Salmon Policy gives little direction for a course of action.

In 1998, Fisheries and Oceans Canada (DFO) released a new policy document called "A new direction for Canada's Pacific Salmon Fisheries" (Fisheries and Oceans Canada 1998). According to this document, conservation of Pacific salmon is the primary objective of management and use of the precautionary approach should ensure that resource conservation takes precedence over other shorter-term objectives. The 'New Directions' policy anticipated further policy documents intended to specify operational policies and guidelines. With this purpose, The Wild Salmon Policy (WSP) was developed and released in 2000 for public and federal review. This document embraces the global conservation ethic and draws upon the United Nations (UN) Convention on Biological Diversity, the Code of Conduct for Responsible Fisheries adopted by the Food and Agriculture Organization (FAO) of the

UN (FAO 1995b), and the UN Agreement on Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks (United Nations 1995) which commits Canada to apply the precautionary approach to fisheries management. The explicit goal of the WSP is to ensure the long-term viability of Pacific salmon populations in natural surroundings and the maintenance of fish habitat for all life stages for the sustainable benefit of Canada (Fisheries and Oceans Canada 2000). While the policy outlines principles to guide the conservation and management of wild Pacific salmon, it defines management units for salmon populations, called "conservation units," as aggregates of closely related populations with similar productivity and vulnerability to fisheries. The policy also introduces two types of reference points, target reference points (TRP) and limit reference points (LRP), which define three zones of abundance or status. Abundance above the TRP is in the "target" zone, between the LRP and the TRP is the "rebuilding" zone, and abundance below the LRP implies "collapse." According to the policy, target and limit reference points will be determined for each salmon conservation unit based on estimates of productive capacity. In addition, DFO's WSP states that annual management plans, specified through pre-season consultation, should contain harvest rules based on a range of abundance forecasts to ensure that in-season management actions can be taken without delay. Because this policy document is based upon the precautionary approach to fisheries, it addresses each of the three required components, but only conceptually. The draft WSP fails to outline a plan for implementation, including assigning the responsibility to develop methods to estimate reference points and operationalize them.

All of these policies aim to conserve wild Pacific salmon and sustain our 'uses' of them. Undoubtedly, the respective agencies have produced internal documents to elaborate their policies for conservation. However, the following interpretations are based solely on documents available to me.

Three of the four polices recognize the need to take uncertainty into account, two mandate the use of reference points, only one introduces the idea of pre-agreed management decision rules, and none develop the requirements of the precautionary approach with enough detail to operationalize it. In Canada, managers and scientists still need to define conservation units for all salmon species, develop procedures to estimate biological reference points, and develop robust operational harvest rules that may serve as pre-agreed management actions. In this chapter, I briefly examine a few suggestions for methods to estimate biological reference points for Pacific salmon and develop one way that Bayesian S-R analyses and the Bayesian PR method can be used to develop biological reference points, specifically the LRP and TRP defined in Canada's WSP.

The use of thresholds as harvest management tools has been explored by many (e.g., Quinn et al. 1990; Myers et al. 1994). Recently, methods for developing biological reference points for Pacific salmon have been suggested (e.g., Bradford et al. 2000a for coho salmon, *Oncorhynchus kisutch*; Johnston et al. 2000 for steelhead, *Oncorhynchus mykiss*; Quinn and Eggers 2001 for all salmon species). The challenges differ among salmon species due to habitat and life history differences and the data available, but something can be learned from each approach. Schemes developed by Bradford et al. (2000a) and Johnston et al. (2000) separate freshwater and ocean life-stages. In the case of coho, limit reference points in terms of maximum allowable harvest rates can be derived from estimates of freshwater production and forecasts of marine survival rates (Bradford et al. 2000a). This permits harvest rates to track changes in ocean productivity. Johnston et al. (2000) quantify a LRP as an abundance threshold from which a population can recover, to a specified level, in one generation in the absence of harvesting. By definition, this LRP is tied to a management action (cease harvesting).

Johnston et al. (2000) and Quinn and Eggers (2001) base their reference points on estimates of S_{MSY} and focus on making the LRP robust over the most likely range of stock productivity. My approach draws upon these ideas and provides one example of how reference points might be developed for sockeye salmon and make use of estimates of optimal escapement derived using the Bayesian PR method.

Methods

In the draft Wild Salmon Policy (WSP) of DFO, the limit reference point (LRP) is defined as a minimum spawning escapement or similar measure of abundance required to ensure the long-term viability of the conservation unit. Total abundance below the LRP implies a stock collapse and indicates that the long-term viability of the conservation unit is at unacceptable risk. A target reference point (TRP), the desired state of the stock or conservation unit, might be defined as the spawning escapement that optimizes yield to the fishery (S_{MSY}) under equilibrium or average conditions, "or a higher spawning escapement that achieves a broader ecosystem objective," according to Canada's draft WSP (Fisheries and Oceans Canada 2000).

I developed a scheme to determine biological reference points that can make use of S_{MAX} estimates from S-R, S-J, or Bayesian PR analyses. It is known that for the Ricker S-R model, the ratio of S_{MSY} to unfished equilibrium, S_{equil} , (i.e. the abundance of spawners such that total adult recruits equals spawners) is dependent on the Ricker a parameter (Hilborn 1985). That ratio ranges from 0.43 to 0.29 as a function of the a parameter over the range of e^a values common to sockeye salmon, i.e. 3 to 20 recruits per spawner (Figure 9). Productivity at low abundance must be below 4 recruits per

spawner for this ratio to be above 0.40. For this reason, Quinn and Eggers (2001) suggested that setting a TRP at $0.4 \bullet S_{equil}$ is approximately equivalent to S_{MSY} and would be conservative (i.e. overestimates S_{MSY}) for most salmon populations. This fits well with the definition for TRP proposed in the draft WSP of DFO, restated above.

To estimate this TRP, I defined S_{equil} in terms of S_{MAX} . Unfished equilibrium, S_{equil} , is equal to a/b , when a and b are estimated using total spawners and total adult recruits. Because I used EFS instead of total spawners in my estimation of the Ricker parameters, S_{equil} in this case was computed by (Ricker 1997):

$$(6) \quad S_{equil} = (a - \log_e k) / b$$

where a and b are the Ricker parameters from Equation 5 and k is equal to 1 divided by the proportion of spawners that are EFS (e.g., for Chilko Lake $k = 1/0.54$). Substituting $1/b$ for S_{MAX} gives:

$$(7) \quad S_{equil} = (a - \log_e k) \bullet S_{MAX}$$

and the related TRP, $0.4 \bullet S_{equil}$, would be:

$$(8) \quad S_{TRP} = 0.4 \bullet (a - \log_e k) \bullet S_{MAX}$$

An arbitrary but related LRP might be $0.2 \bullet S_{equil}$ or in terms of S_{MAX} :

$$(9) \quad S_{LRP} = 0.2 \bullet (a - \log_e k) \bullet S_{MAX}$$

I formulated both the TRP and the LRP as functions of a and S_{MAX} , which can be estimated taking uncertainty into account as reflected by the analyses described in previous sections. The a parameter can be estimated by Bayesian S-R or S-J analysis (care must be taken to ensure correct units) or, in the absence of S-R or S-J data, a range of plausible a parameters can be taken into

account. S_{MAX} can be estimated by Bayesian S-R or S-J analyses or based on nursery lake productivity via the Bayesian PR method. Therefore, this approach for estimating reference points can use combinations of a and S_{MAX} estimates from different sources. For example, even when S-R analysis is not useful for bounding estimates of S_{MAX} because S-R data are available for a limited range of spawner abundances, it might still be useable for estimating stock productivity at low abundances and the Bayesian PR method could be used to estimate S_{MAX} . To use S_{MAX} from the Bayesian PR method or $S_{MAX_{S-J}}$ in place of $S_{MAX_{S-R}}$ would assume that ocean survival is not density-dependent.

To provide examples of this approach for estimating reference points, I applied it to the Fraser River sockeye salmon aggregates considered in this study. For each of the population aggregates except Quesnel, I calculated S_{LRP} in two ways. I used the marginal posterior distribution for the Ricker a parameter from the Bayesian S-R analysis coupled with (1) S_{MAX} from the S-R analysis or (2) S_{MAX} from the Bayesian PR method. For Quesnel, I calculated S_{LRP} in three ways. The estimate of the Ricker a parameter from S-R data was used in combination with (1) S_{MAX} estimated from the S-J analysis or (2) S_{MAX} from the Bayesian PR method. For the third estimate of S_{LRP} for Quesnel and to illustrate the case where S-R data are unavailable, I used a uniform distribution of plausible a values for sockeye salmon (i.e. a in Equation 9 ranging from 1 to 3, equivalent to 2.7 to 20 recruits per spawner at low abundance (Korman et al. 1995)) coupled with S_{MAX} based on the Bayesian PR method.

Results

Probability distributions for limit reference points derived using estimates of the Ricker a parameter from the Bayesian S-R analysis coupled with (1) S_{MAX} from the S-R analysis or (2) S_{MAX}

from the Bayesian PR method were almost identical for Shuswap and Chilko Lakes and overlapped considerably for the Early Stuart and Fraser Lake examples (Figure 10). Distributions for LRPs based on two different sources for S_{MAX} were quite disparate for the examples where estimates of S_{MAX} were contradictory (Francois and Pitt Lakes, Figure 10). As was the case with S_{MAX} distributions, estimates of LRPs calculated from PR-based S_{MAX} estimates were generally higher than those calculated from S-R-based S_{MAX} estimates. The results for the Quesnel Lake example show that the LRP calculated using a range of plausible Ricker a values (to illustrate the case where S-R data were not available to estimate this parameter) is lower than either of the estimates calculated using S-R-based Ricker a estimates (Figure 11), but the distribution overlaps considerably with the others.

Discussion

Estimates for LRPs calculated using S_{MAX} from the Bayesian PR method were higher than or roughly equivalent to estimates for LRPs calculated using S-R-based estimates of S_{MAX} and are therefore at least as precautionary in the context of spawner abundance. The Quesnel Lake LRP example calculated from a range of plausible Ricker a values and S_{MAX} as estimated by the Bayesian PR method was the lowest estimate of the three for Quesnel, because all hypothesized Ricker a values (productivity at low abundance ranging from 2.7 to 20 recruits per spawner) were given equal weight. In actual cases where no data were available for a sockeye population, it might be prudent to use a more restricted range of Ricker a values based on estimates from other sockeye salmon populations in the region. For example, Ricker a estimates for 7 of the Fraser River sockeye salmon aggregates in this

study range from about 5 to 15 recruits per spawner (Figure 9) and these data may provide a useful 'prior' for the Ricker a parameter for other Fraser River sockeye salmon populations with no S-R data.

This method for developing reference points for sockeye salmon described above uses an arbitrary threshold for a LRP (i.e. $0.2 \bullet S_{equil}$). This threshold and others need to be evaluated via Monte Carlo simulation in the context of various harvest control rules (de al Mare 1998). Although the $0.2 \bullet S_{equil}$ LRP is commonly recommended and widely applied, Johnston et al. (2000) found that it performed poorly compared to other LRPs. They used the Beverton-Holt S-R model, which is not commonly applied to sockeye salmon, but their simulation modeling framework could be adapted for use with the Ricker S-R and sockeye salmon data. It is possible and desirable to model the management regime in which these reference points and harvest control rules would be used, and include management implementation error (observed differences between the intended management action and the realized result).

Using probability distributions as estimates

Accounting for uncertainty produces estimates of S_{MAX} and reference points in the form of probability distributions that quantify the precision with which these estimates can be calculated. For reference points to be useful in practice they may have to be point estimates specified from these probability distributions. Different percentiles can be specified for such estimates according to the risks associated with over- and underestimation, which depend on the management objective. When the objective is harvest management and the sockeye salmon stock is considered healthy, escapements lower than the optimum TRP mean underutilized freshwater habitats, fewer adult returns, smaller catches, lower economic returns, and fewer salmon carcasses to add nutrients to the ecosystem.

Escapements higher than the optimum mean forgone harvestable salmon in that brood year with no increases and possibly a decrease in harvestable salmon in subsequent years (i.e. reduced economic returns). In addition, while large escapements and excessive fry abundance deplete food for salmon (Koenings and Kyle 1997) and have been linked to substantial long-term declines in total stock size (Kyle et al. 1988, Koenings and Kyle 1997), they also undoubtedly provide more salmon carcasses and nutrients for the ecosystem. Therefore, in this context, the dangers of over- and underestimation tend to offset one another to some extent and setting escapement targets that match the median S_{TRP} estimate should help to balance the risks. In contrast, when a stock is depleted and the management objective is conservation, the consequences of underestimating optimal escapement may be as serious as extinction. In this context, the only negative consequence of overestimating the minimal escapement required (such as an LRP) may be economic and, therefore, it may be prudent to use the 75th percentile estimate from the probability density function for the LRP, as an arbitrary example, for the reference point such that there is low probability of underestimation.

Implementation of biological reference points for sockeye salmon escapement goals

The issue of how to specify a point values for a reference point from a distribution of possible values is only one of several issues that needs careful consideration before any scheme for developing biological reference points for sockeye salmon is implemented. Other non-trivial issues that complicate implementation of a framework for devising reference points include the cyclic abundance of sockeye salmon populations and their harvest in mixed-stock fisheries. For some of the Fraser River sockeye salmon populations whose abundance varies greatly, often in 4 year cycles, total abundances in many of the past fifty years are less than any limit reference point determined using the scheme I devised, and yet

these populations have persisted. At the same time their past persistence does not ensure their future persistence from such low abundances, because the environment and productivity are variable. It is not clear how to specify reference points for these cyclic sockeye salmon populations and future research is required.

Finally, most of the sockeye salmon populations I considered are harvested in mixed-stock fisheries. In these cases the management unit is the scale at which harvest rates can be altered and escapements can be 'controlled,' and that differs from the scale at which data are collected that may be used for estimation of reference points. In some cases, optimal escapement estimated for a lake using the Bayesian PR method may need to be translated into target and limit reference points for two or more distinct populations from different management units that share the lake habitat. In addition, a management unit will most likely be made up of more than one conservation unit, such that more than one set of reference points and forecasts will need to be considered when drawing up annual management plans and pre-agreed harvest rules could become very complex. Again, implementation of a reference point framework will need to account for these issues.

Conclusions

Determination of optimal escapement is crucial to the management of sockeye salmon and the Bayesian PR method, developed here, provides an alternative to the standard method, stock-recruitment analysis. Comparing results from the two methods shows that estimates based on the Bayesian PR method are generally higher than estimates based on S-R analyses. Many mechanisms that limit sockeye salmon abundance in nursery lakes can explain these differences and should be considered before escapement goals are set. The Bayesian PR method is based upon empirical analyses of relatively few systems and, as such, the assumption that additional systems are not significantly different is made each time the method is applied. In addition, true variability in the relationships may be underestimated due to lack of data. Finally, there is little evidence to suggest that sustaining escapements year after year at approximately the same 'optimal' level will result in sustained high smolt abundances and high adult returns.

Utility of the Bayesian PR method is not limited to estimating optimal escapement for harvest management. The Bayesian PR method can also be used in combination with stock-recruitment analyses to identify sockeye salmon systems that might benefit from enhancement and quantify the potential benefits. My analyses suggest that the Bayesian PR method may be better at determining an upper bound for optimal escapement than is S-R analysis, especially when S-R data show no evidence of density dependence. In addition, I have proposed a scheme for determining LRPs and TRPs from estimates of optimal escapement coupled with estimates of productivity at low abundance for sockeye population aggregates. My approach, which suggests that optimal escapement estimates from S-J and habitat-based analyses are appropriate alternatives to S-R based estimates, is based on the premise that

ocean survival rates of sockeye salmon are not density dependent. The operational performance of specific LRPs and TRPs developed using this approach needs to be comprehensively assessed, alongside a range of plausible harvest rules, using simulation modeling.

My explicit consideration and reporting of uncertainty in both assessment methods acknowledges and documents the lack of precision in estimates of optimal escapement. This is important, especially in the context of conservation of fish stocks, as agencies develop ways to implement the precautionary approach to fisheries management.

Table 1. Physical characteristics and trophic status of sockeye salmon nursery lakes in the Fraser River drainage basin in British Columbia where data on photosynthetic rates (PR) are available.

Lake name	Latitude (°N)	Longitude (°W)	Elevation (m)	Surface area (km²)	Mean depth (m)	Trophic status
Chilko	51°16'	124°04'	1172	185	134	ultra-oligotrophic ^a
Francois	54°04'	125°45'	725	247	87	oligotrophic, upper range ^b
Fraser	54°05'	124°45'	670	54	13	meso-eutrophic ^b
Pitt	49°26'	122°32'	0 (tidal)	51	46	oligotrophic ^c
Quesnel	52°31'	121°00'	715	271	158	oligotrophic, lower range ^d
Shuswap	50°56'	119°17'	346	330	60	oligotrophic, upper range ^a
Stuart	54°38'	124°49'	680	360	20	oligotrophic, upper range ^d
Takla	55°15'	125°44'	689	260	107	oligotrophic, mid range ^d
Trembleur	54°50'	125°05'	686	117	40	oligotrophic, upper range ^d

^a Hume et al. 1996

^b Shortreed et al. 1996

^c Stobbart and Harding 1996

^d Shortreed et al. 2001

Table 2. Estimates of photosynthetic rate and weight per smolt used in the application of the Bayesian PR method for each of six Fraser River, BC nursery lakes (#1-6) and two Fraser River sockeye stocks (#7-8). The mean of each input distribution is an average of available annual lake-specific estimates, while bounds of the input distributions are based on interannual variance estimated across lakes (Appendix B). I show untransformed units here but \log_e values were used in the analyses.

Nursery lake	Sockeye population(s)	Total seasonal PR (tonnes C per lake)		Weight per smolt at high densities (grams)	
		mean (bounds of input distribution, +/- 3 SE)	No. of years of data ^a	mean (bounds of input distribution, +/- 3 SE)	No. of years of data
1. Chilko	Chilko, Chilko south	2541 (1940 - 3327)	5	4.2 (2.5 - 7.0)	28 ^d
2. Francois	Nadina	7225 (4717 - 11,066)	2	9.7 (5.7 - 16.6)	1 ^e
3. Fraser	Stellako	3215 (2099 - 4925)	2	7.4 (4.3 - 12.6)	1 ^e
4. Pitt	Pitt	606 (332 - 1107)	1	5.8 (3.9 - 8.4)	2 ^d
5. Quesnel	Horsefly, Mitchell	4995 (3814 - 6541)	5	4.0 ^c (2.3 - 6.9)	1 ^d
6. Shuswap	Adams, Little Shuswap, Scotch, Seymour	10,148 (7933 - 12,980)	6	2.7 ^c (1.6 - 4.6)	1 ^d
Stuart	7. Late Stuart	10,437 ^b (6769 - 16,095)	3	6.4 (3.8 - 11.0)	1 ^f
Trembleur					
Takla	8. Early Stuart	2993 ^b (2089 - 4289)	3	6.4 (3.8 - 11.0)	1 ^f

^a Source of all PR data: K.S. Shortreed, personal communication.

^b Appendix C describes the calculation of total seasonal PR for the Early and Late Stuart juvenile rearing areas.

^c For Shuswap and Quesnel lakes no weight per smolt data were available, so the average weight of fall fry in the year of maximum observed biomass was used.

^d Data source: J.M.B. Hume, personal communication.

^e Data source: Shortreed et al. 1996

^f Data source: Taylor and Bradford 1993

Table 3. Range of observed spawner abundances in S-R data (in units of effective female spawners, EFS) and estimates of optimal escapement, S_{MAX} , from the PR model of Shortreed et al. (2000), the Bayesian PR method, S-R, and S-J analyses for six BC sockeye nursery lakes and two sockeye stocks. Precision of Bayesian posterior probability distributions is described by the 80% credibility interval (90th percentile estimate less 10th percentile estimate) divided by the median (i.e. analogous to a C.V.).

Nursery lake or sockeye stock; Analysis method	Range of observed spawner abundances (thousands of EFS)	PR model of Shortreed et al. (2000) ^a	Estimates of optimal escapement, S_{MAX} (thousands of effective female spawners, EFS)					Precision
			Percentile estimates derived from cumulative probability distributions					
			0.10 ^b	0.25 ^b	0.50 ^b (median)	0.75 ^b	0.90 ^b	
Chilko	7 - 369 ^c	265						
Bayesian PR, base case			264	312	379	465	558	0.77
S-R analysis			291	348	440	583	770	1.09
S-J analysis			330	364	412	477	552	0.54
Bayesian PR, no Babine			308	363	438	528	627	0.73
Early Stuart	0.8 - 211	280 ^d						
Bayesian PR, base case			204	244	298	366	440	0.79
S-R analysis			131	155	196	263	359	1.16
Bayesian PR, no Babine			232	274	335	410	489	0.77
Francois	0.004 - 33	826						
Bayesian PR, base case			320	391	492	618	756	0.89
S-R analysis			10	11	13	16	20	0.73
Bayesian PR, no Babine			361	437	547	683	838	0.87
Fraser	11 - 201	312						
Bayesian PR, base case			189	227	280	346	421	0.83
S-R analysis			113	135	169	224	310	1.16
Bayesian PR, no Babine			214	255	313	387	464	0.80

Late Stuart	0.02 - 327	976 ^d						
Bayesian PR, base case			661	820	1042	1332	1664	0.96
S-R analysis			147	187	259	398	600	1.75
Bayesian PR, no Babine			767	945	1195	1516	1874	0.93
Pitt	2 - 22	57 ^d						
Bayesian PR, base case			46	55	67	81	96	0.76
S-R analysis			10	12	14	18	23	0.90
Bayesian PR, no Babine			52	61	73	88	105	0.72
Quesnel	0.2 - 1507	428						
Bayesian PR, base case			520	628	780	968	1182	0.85
S-J analysis			416	487	599	776	1049	1.06
Bayesian PR, no Babine			617	736	903	1110	1342	0.80
Shuswap	2 - 1836	1007						
Bayesian PR, base case			1454	1800	2286	2923	3668	0.97
S-R analysis			1388	1704	2229	3084	4065	1.20
S-J analysis			545	613	716	853	1032	0.68
Bayesian PR, no Babine			1805	2192	2738	3422	4208	0.88

^a Published estimates of optimal escapement from the PR model in Shortreed et al. (2000) are in total adult spawners. I converted their estimates to EFS using estimates for the average proportion of spawners that are EFS for each lake or stock: Chilko 54% (Hume et al. 1996), Fraser 52% (Shortreed et al. 1996), Francois 59% (Shortreed et al. 1996), Pitt 50%, Quesnel 46% (Hume et al. 1996), Shuswap 53% (Hume et al. 1996), Early and Late Stuart 50%.

^b Probability that optimal escapement is less than the value in the body of the table.

^c Data used for the Chilko S-J analysis included brood years 1993 - 1997 and an observed maximum EFS of 509 thousand, which is greater than the maximum observed in the brood years used for the S-R data (1949 - 1992).

^d Estimates of optimal escapement for Pitt Lake and for the Early and Late Stuart sockeye stocks from the PR model were not published. I calculated these using my mean PR_{TOTAL} estimate and the PR model equations (Shortreed et al. 2000).

Table 4. Results of sensitivity analysis to determine the effects of inaccurate input data for photosynthetic rate (PR) or weight per smolt (W) on estimates of optimal escapement, S_{MAX} , produced by the Bayesian PR method. SE is standard error. Change is S_{MAX} median is equal to the difference between medians from sensitivity analysis and base case, divided by the base-case median. Precision of probability distributions is described by the 80% credibility interval (90th percentile estimate less 10th percentile estimate) divided by the median (i.e. analogous to a C.V.).

Nursery lake or sockeye stock; Sensitivity analysis	Mean of input parameter distribution (PR in total seasonal C per lake, or W in grams)	Change in S_{MAX} median (relative to base case)	Estimates of optimal escapement, S_{MAX} (thousands of effective female spawners)					
			Percentile estimates derived from cumulative probability distributions					
			0.10 ^a	0.25 ^a	0.50 ^a (median)	0.75 ^a	0.90 ^a	Precision
Chilko								
PR base case	2541		264	312	379	465	558	0.77
PR + 2SE	3041	0.20	314	373	456	559	674	0.79
PR - 2SE	2123	-0.16	222	261	318	387	462	0.76
W base case	4.2		264	312	379	465	558	0.77
W + 2SE	5.9	-0.28	192	227	274	334	400	0.76
W - 2SE	2.9	0.39	363	433	527	646	779	0.79
Early Stuart								
PR base case	2993		204	244	298	366	440	0.79
PR + 2SE	3804	0.27	256	307	379	468	569	0.83
PR - 2SE	2355	-0.21	161	192	235	287	345	0.78
W base case	6.4		204	244	298	366	440	0.79
W + 2SE	9.2	-0.29	146	174	212	261	313	0.79
W - 2SE	4.5	0.40	283	339	417	516	624	0.82
Francois								
PR base case	7225		320	391	492	618	756	0.89
PR + 2SE	9600	0.32	418	515	648	826	1032	0.95
PR - 2SE	5437	-0.25	243	296	367	462	567	0.88
W base case	9.7		320	391	492	618	756	0.89
W + 2SE	13.9	-0.29	230	279	349	438	538	0.88
W - 2SE	6.8	0.40	448	546	686	866	1073	0.91
Fraser								
PR base case	3215		189	227	280	346	421	0.83
PR + 2SE	4272	0.33	248	301	373	465	572	0.87

	PR - 2SE	2420	-0.25	144	172	211	259	313	0.80
	W base case	7.4		189	227	280	346	421	0.83
	W + 2SE	10.6	-0.28	136	163	200	247	299	0.81
	W - 2SE	5.2	0.40	264	316	392	486	596	0.85
Late Stuart									
	PR base case	10437		661	820	1042	1332	1664	0.96
	PR + 2SE	13931	0.34	872	1083	1396	1801	2281	1.01
	PR - 2SE	7820	-0.25	501	621	780	988	1232	0.94
	W base case	6.4		661	820	1042	1332	1664	0.96
	W + 2SE	9.2	-0.29	475	589	744	948	1179	0.95
	W - 2SE	4.5	0.40	922	1141	1462	1872	2357	0.98
Pitt									
	PR base case	606		46	55	67	81	96	0.76
	PR + 2SE	906	0.49	69	82	99	121	145	0.77
	PR - 2SE	405	-0.33	31	37	45	55	64	0.75
	W base case	5.8		46	55	67	81	96	0.76
	W + 2SE	7.4	-0.21	36	43	53	64	76	0.74
	W - 2SE	4.5	0.27	59	70	85	103	122	0.75
Quesnel									
	PR base case	4995		520	628	780	968	1182	0.85
	PR + 2SE	5979	0.19	619	747	931	1168	1432	0.87
	PR - 2SE	4173	-0.17	439	528	651	809	978	0.83
	W base case	4.0		520	628	780	968	1182	0.85
	W + 2SE	5.7	-0.29	374	450	553	687	839	0.84
	W - 2SE	2.8	0.39	724	874	1087	1365	1672	0.87
Shuswap									
	PR base case	10148		1454	1800	2286	2923	3668	0.97
	PR + 2SE	11957	0.18	1696	2109	2696	3467	4366	0.99
	PR - 2SE	8612	-0.15	1245	1534	1944	2465	3076	0.94
	W base case	2.7		1454	1800	2286	2923	3668	0.97
	W + 2SE	3.9	-0.29	1050	1288	1631	2076	2595	0.95
	W - 2SE	1.9	0.40	2018	2491	3211	4126	5206	0.99

^aProbability that optimal escapement is less than the value in the body of the table.

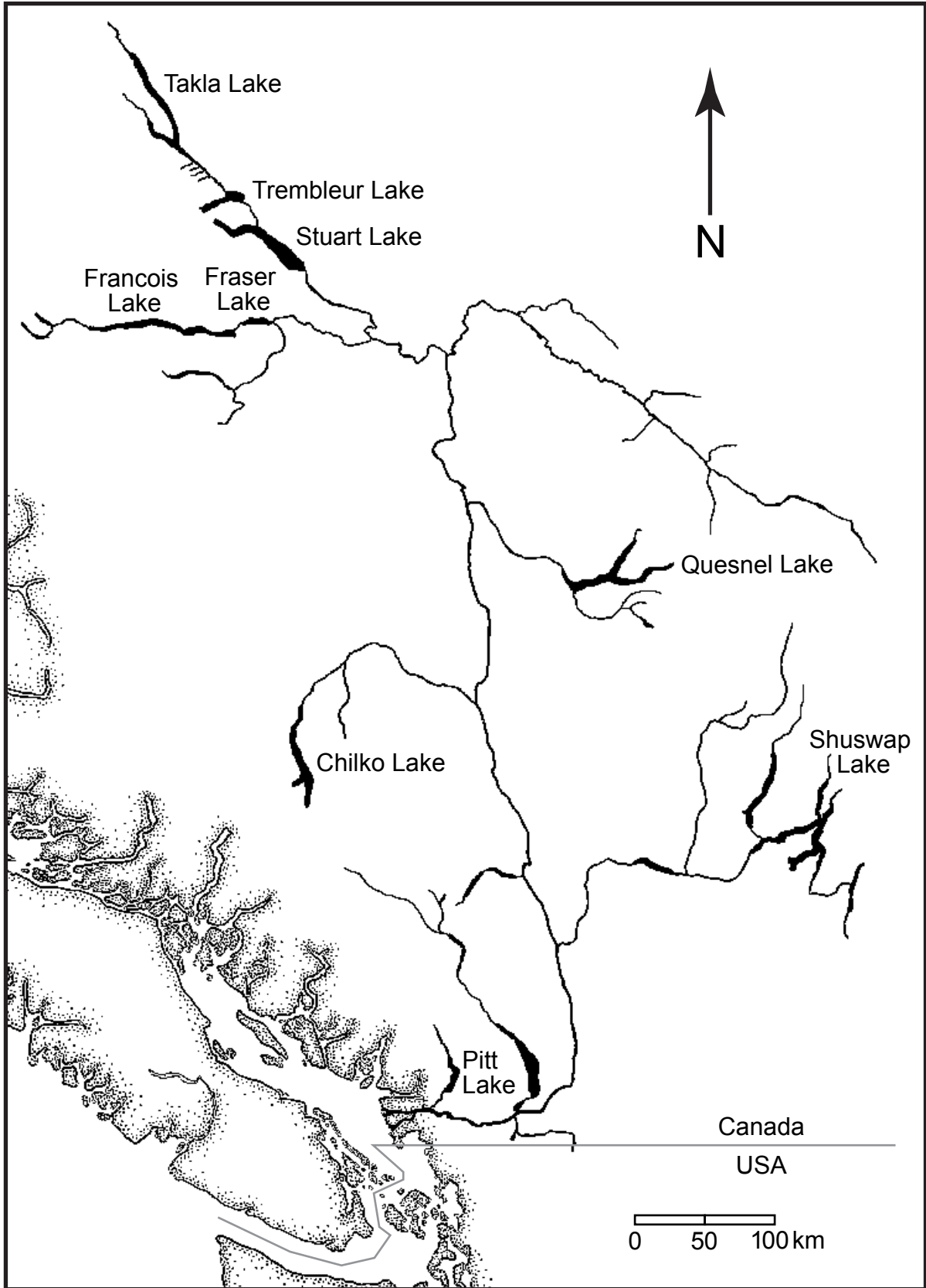


Figure 1. Fraser River watershed with major sockeye salmon nursery lakes identified.

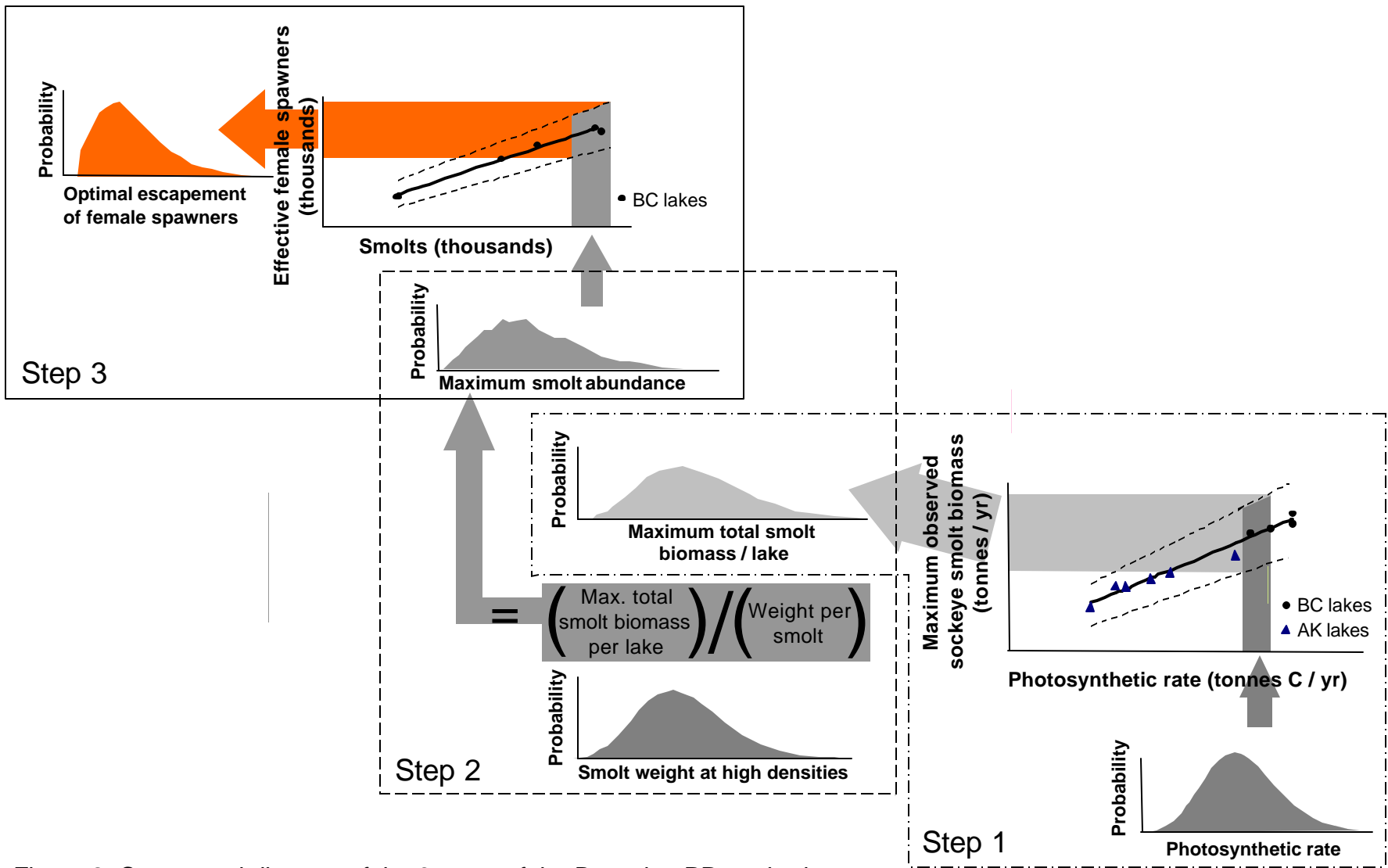


Figure 2. Conceptual diagram of the 3 steps of the Bayesian PR method.

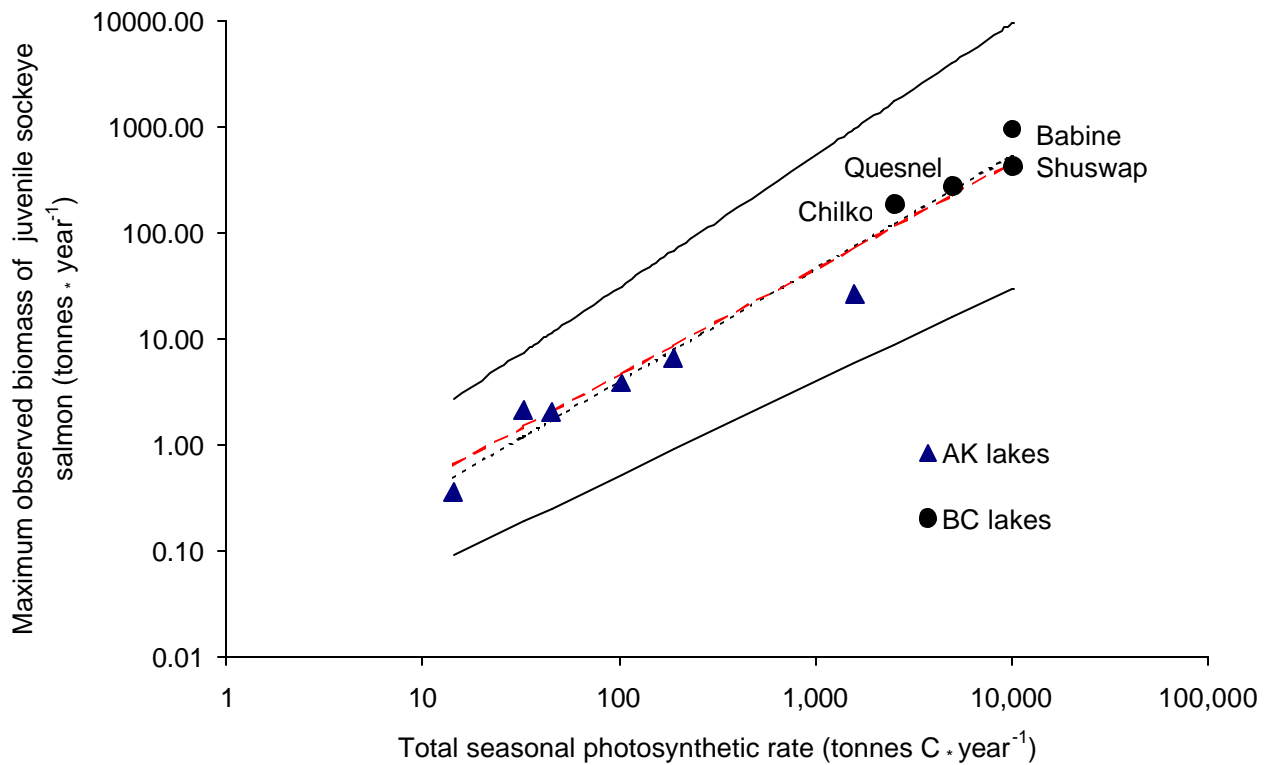


Figure 3. Relationship between maximum observed juvenile sockeye salmon biomass and total seasonal photosynthetic rate (PR) in log-log space. Data are smolt biomass except for two of the BC lakes, Shuswap and Quesnel, which are fall fry biomass. Data for Alaskan lakes (solid triangles) are from Koenings and Burkett (1987) and for BC lakes (solid circles) are from Shortreed et al. (2000). The dotted line represents the best-fit relationship of the Bayesian PR method, the solid lines illustrate the extremes of the range of relationships considered by the Bayesian approach, and the dashed line represents the PR model of Shortreed et al. (2000).

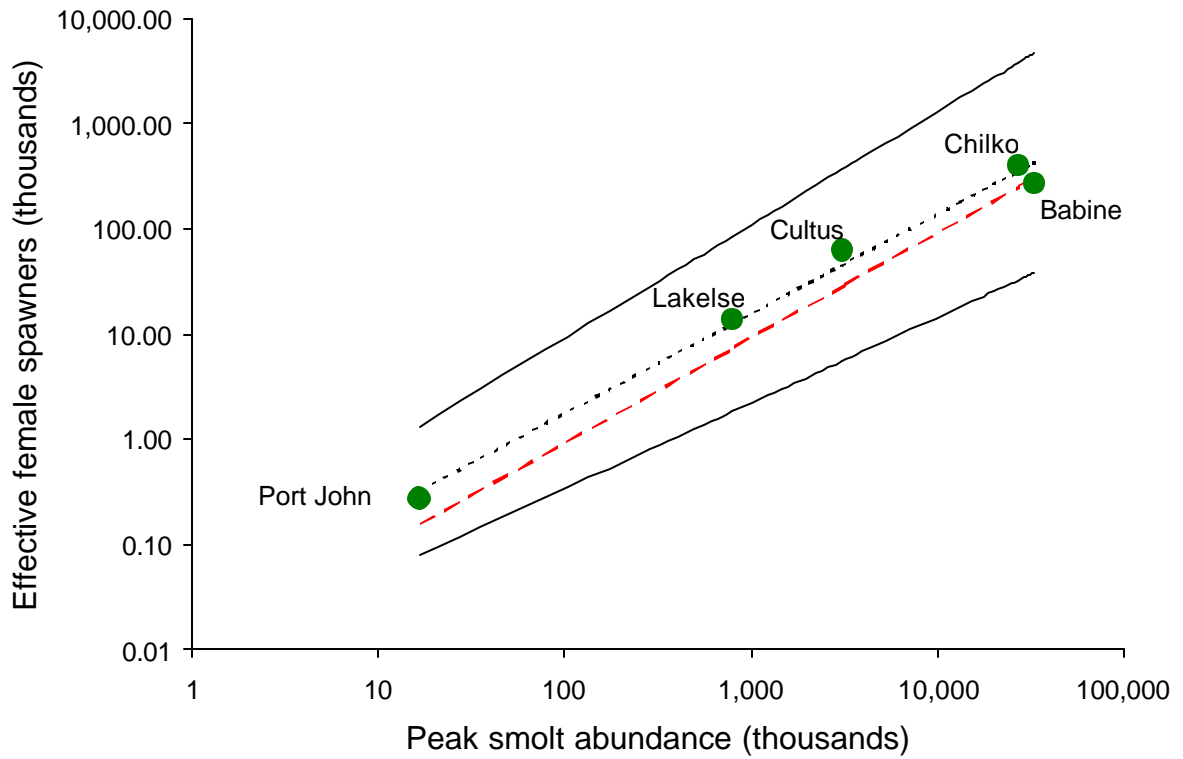
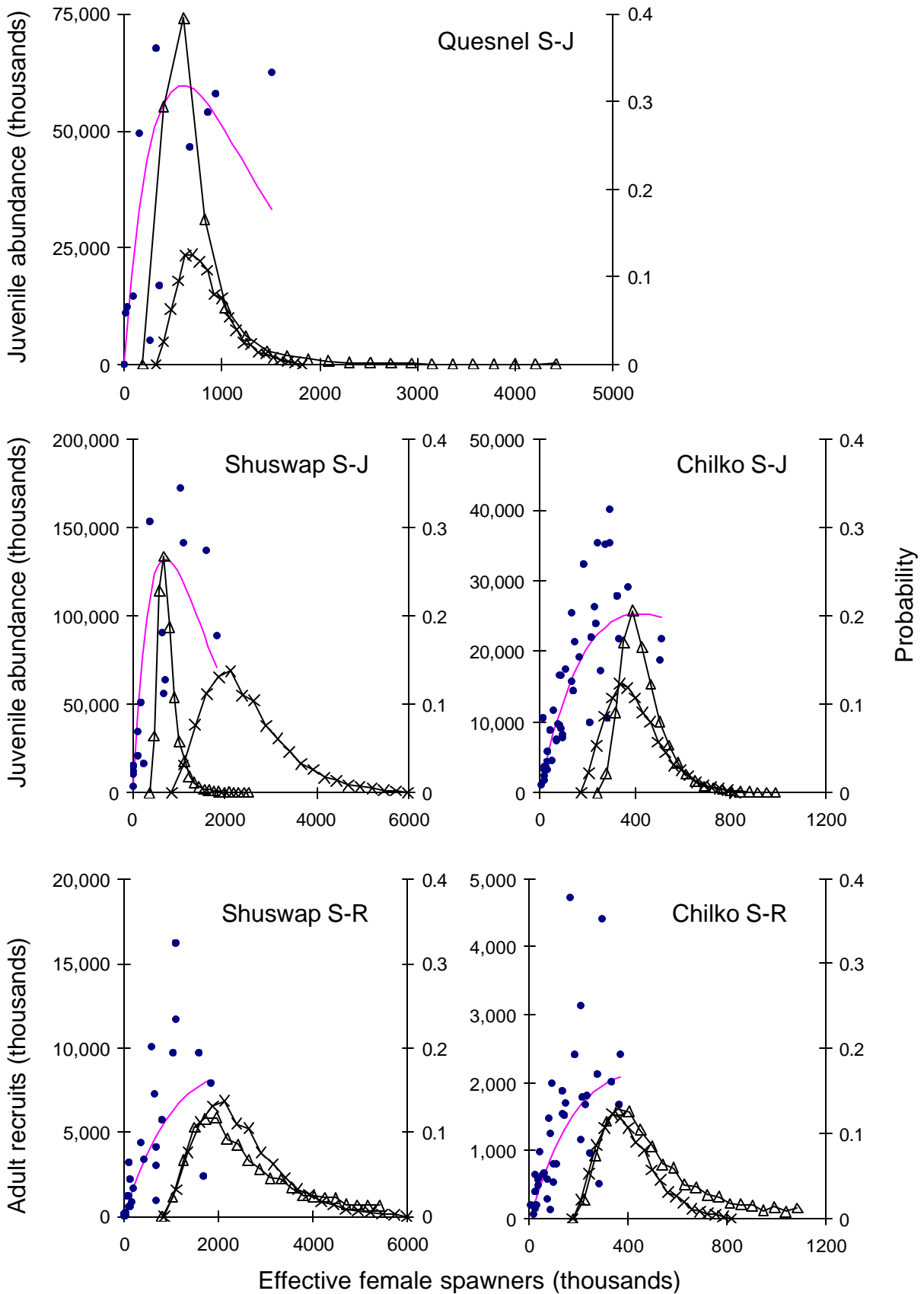


Figure 4. Estimates of effective female spawners and estimates of smolt abundance at peak smolt productivity for five BC lakes. The data are from five separate analyses of EFS and smolt data using the Ricker model to estimate EFS and smolt abundances at the peak of the curve. The dotted line represents the best-fit relationship of the Bayesian PR method, the solid lines illustrate the extremes of the range of relationships considered by the Bayesian approach, and the dashed line represents the smolts per EFS ratio used in the PR model of Shortreed et al. (2000).

Figure 5. Observed stock and recruit data, maximum likelihood estimates for the Ricker curve, posterior probability density functions (pdf) for estimates of the escapement to maximize recruits, S_{MAX} , from the Bayesian PR method and the S-R analysis or the S-J analysis of 8 Fraser River sockeye salmon aggregates. Left-hand Y axis refers to observed adult or juvenile abundance; right-hand Y axis refers to probability for the pdfs of optimal escapement estimated by S-R or S-J analysis (open triangles) and estimated by the Bayesian PR method (X's).



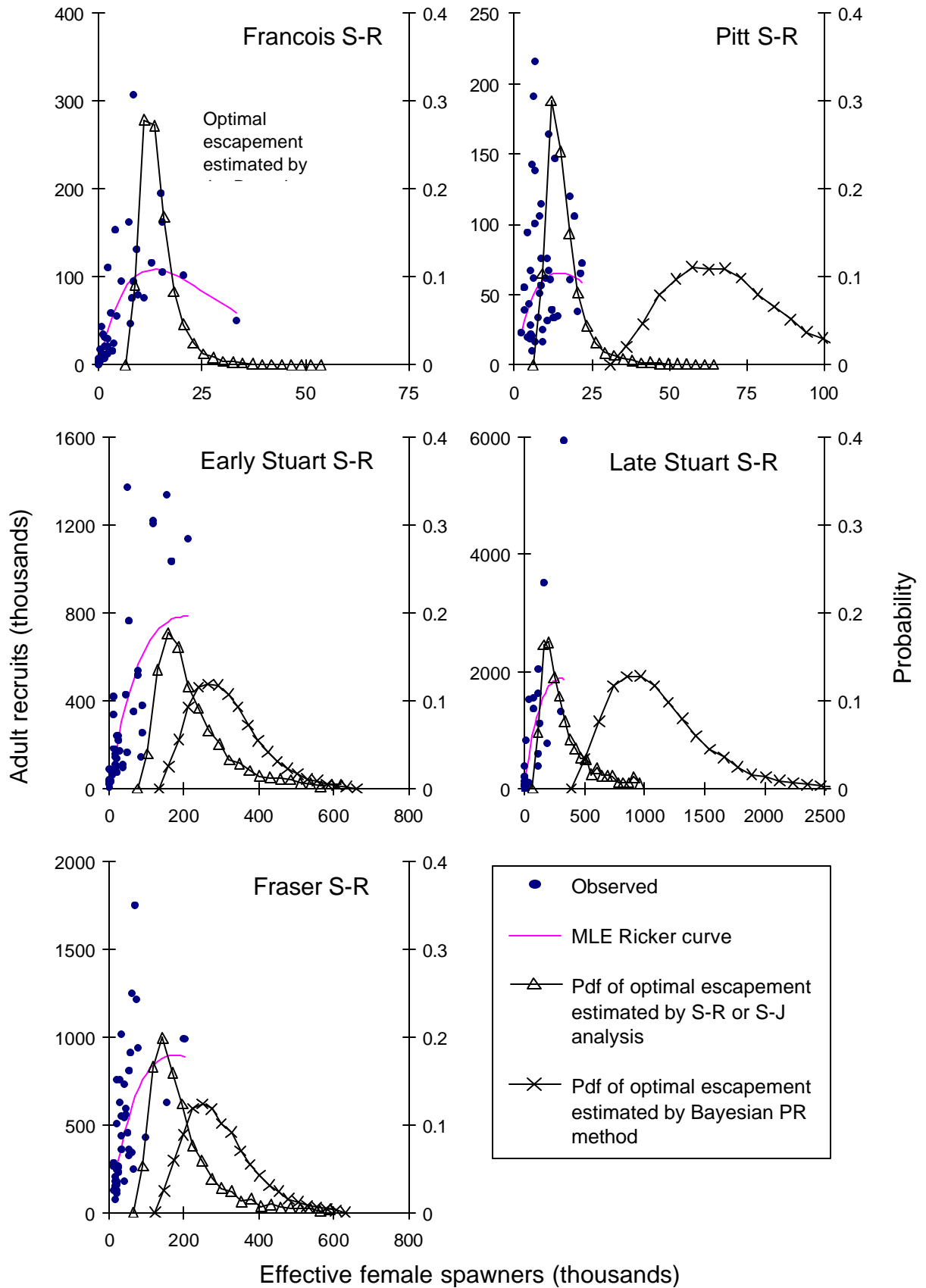
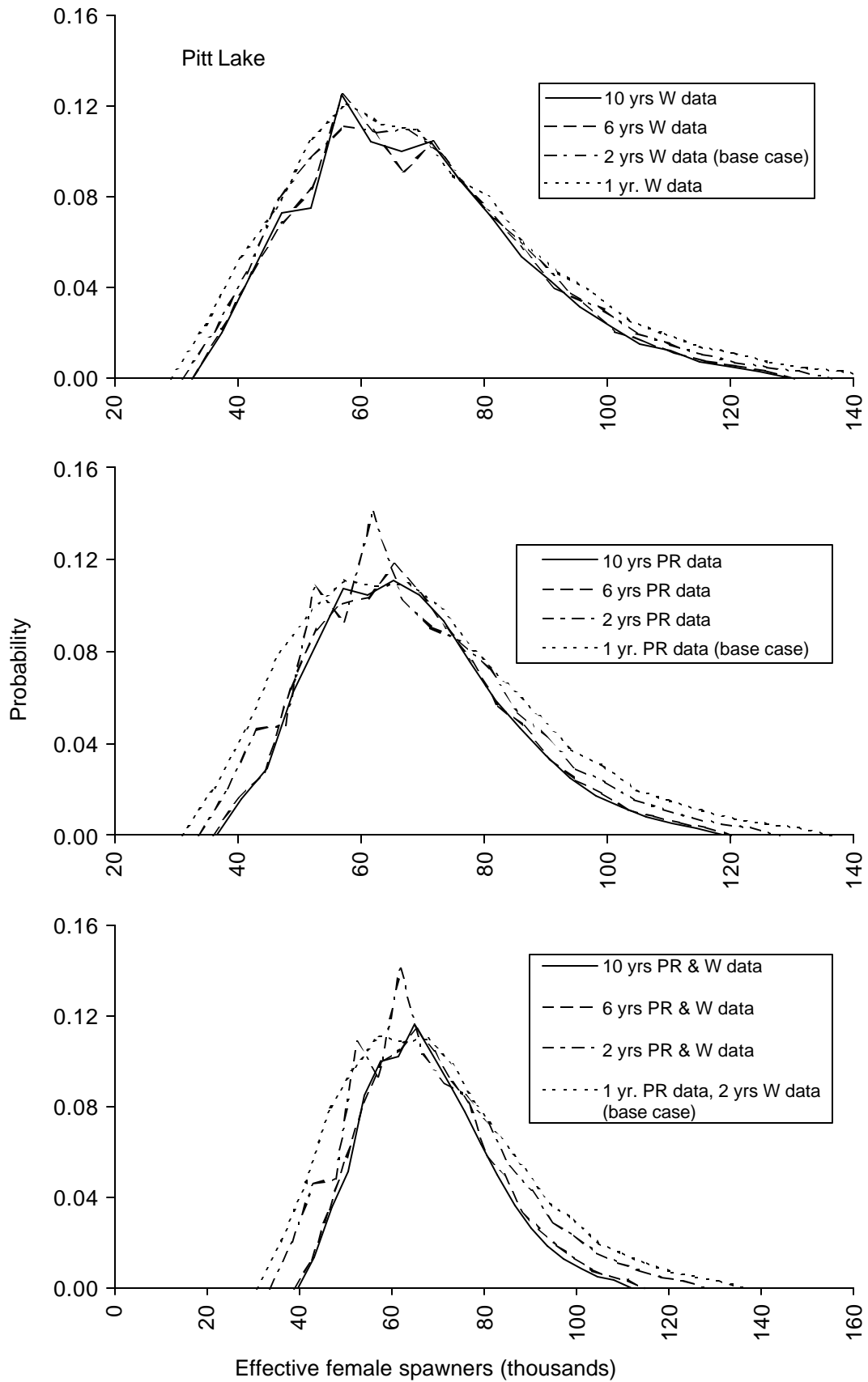


Figure 6. Changes in the precision of S_{MAX} estimates from the Bayesian PR method for Pitt Lake with additional years of photosynthetic rate (PR) and weight per smolt (W) input data.



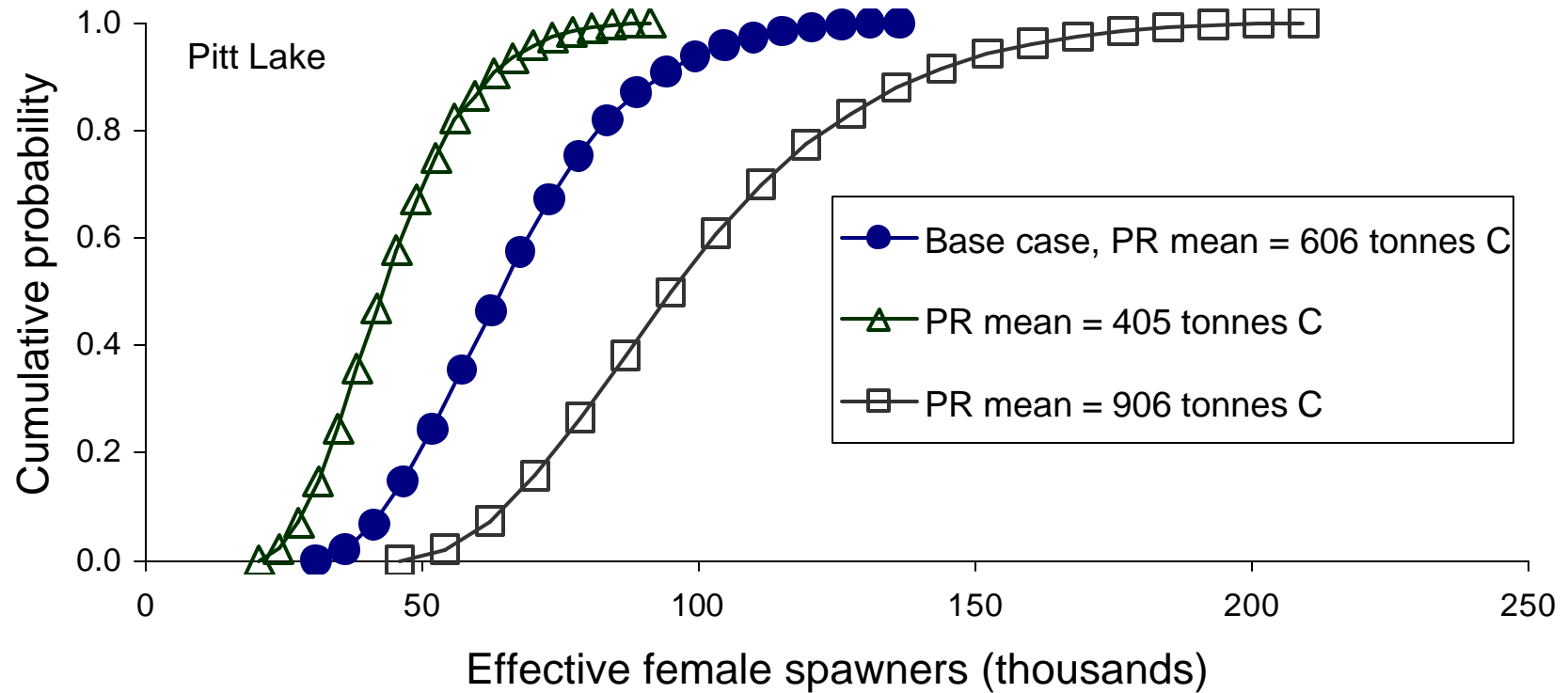


Figure 7. Cumulative probability functions comparing three estimates of the escapement to maximize recruits, S_{MAX} , for Pitt Lake sockeye salmon calculated using the Bayesian PR method and three different input distributions for photosynthetic rate (PR). The mean values of the input distributions were 606 (base case, solid circles), 906 (base case + 2SE, open squares), and 405 (base case - 2SE, open triangles) metric tons of carbon. Standard deviation of the input distribution remained at the base-case value.

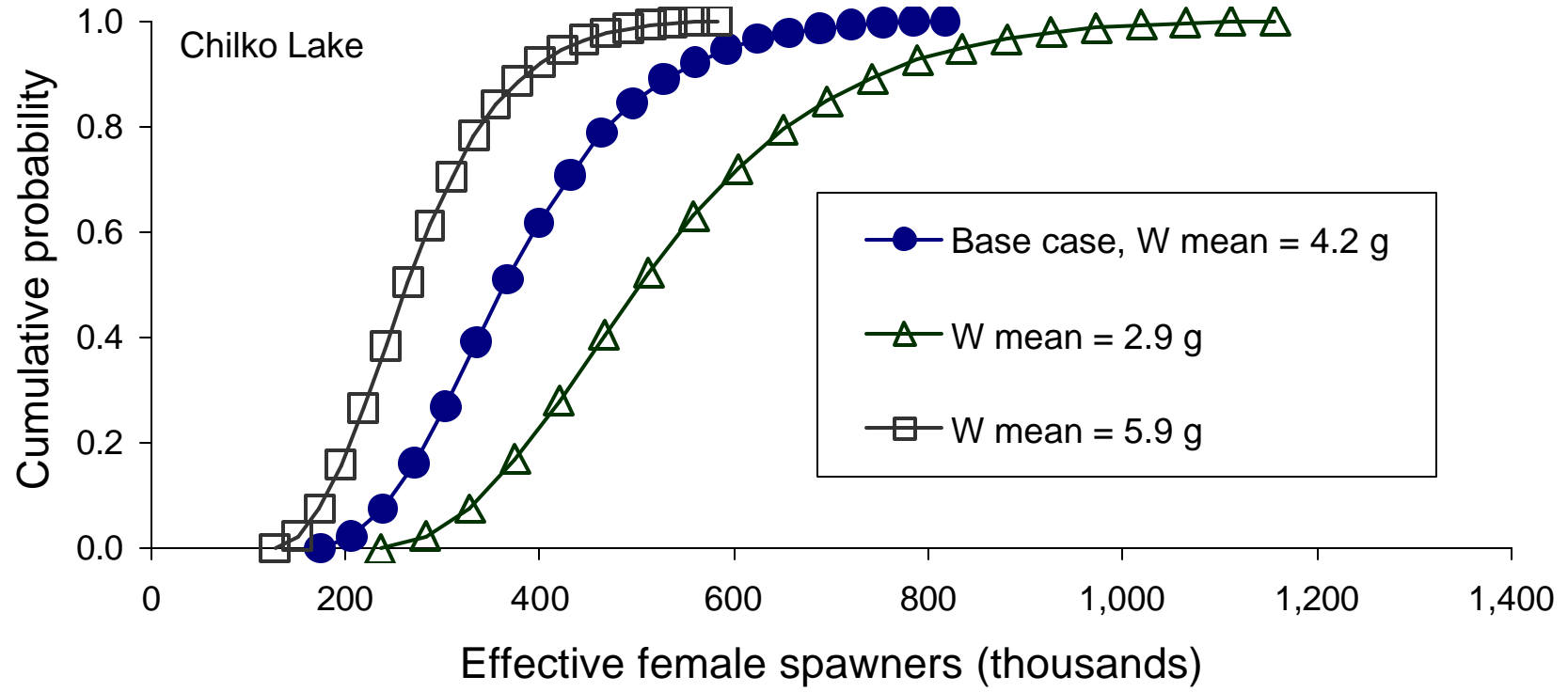


Figure 8. Cumulative probability functions comparing three estimates of the escapement to maximize recruits, S_{MAX} , for Chilko Lake sockeye salmon calculated using the Bayesian PR method and three different input distributions for smolt weight at high density (W_{MAX}). The mean values of the input distribution were 4.2 (base case, solid circles), 5.9 (base case + 2SE, open squares), and 2.9 (base case - 2SE, open triangles)

grams. Standard deviation of the input distribution remained at the base-case value.

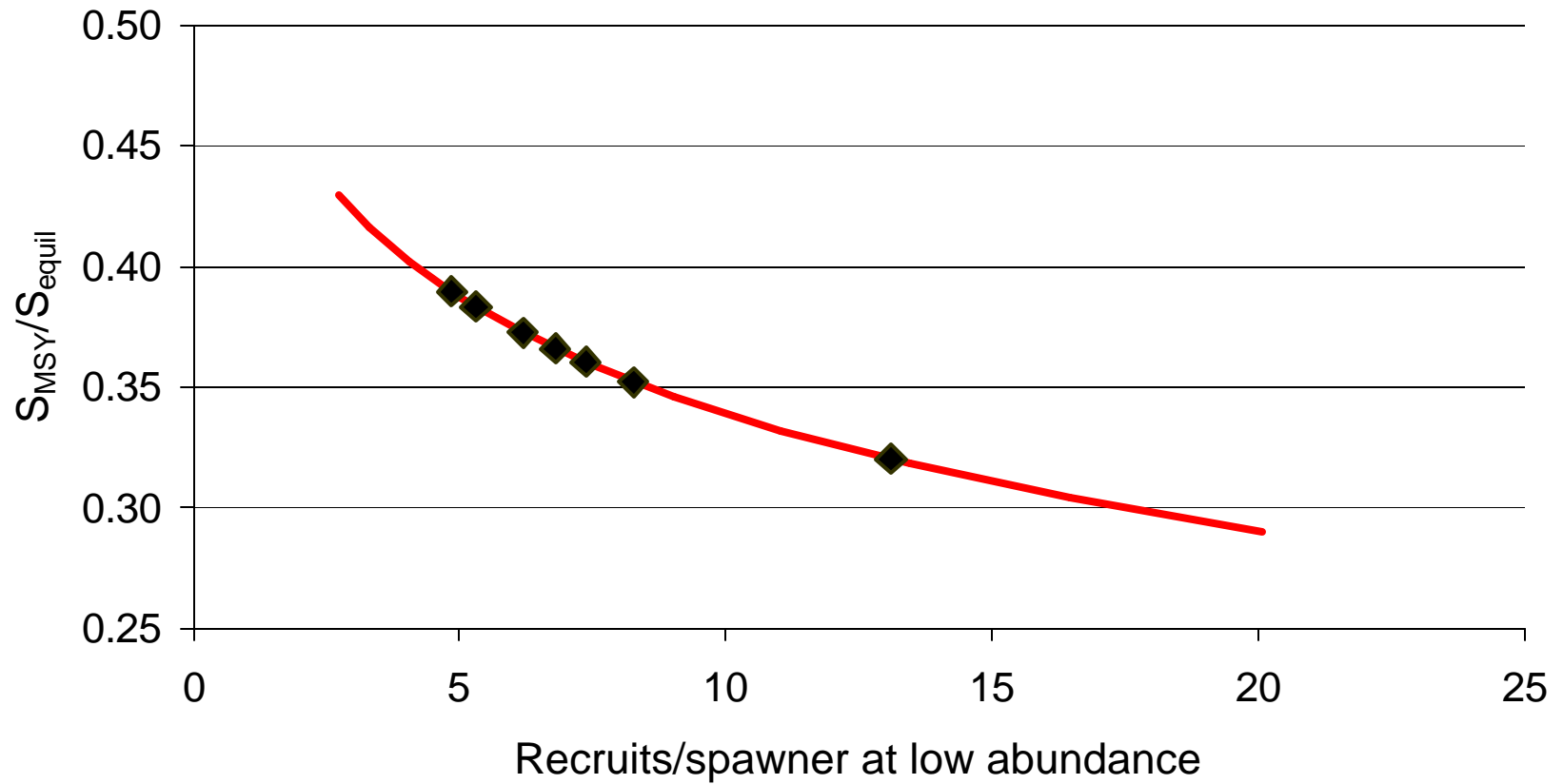
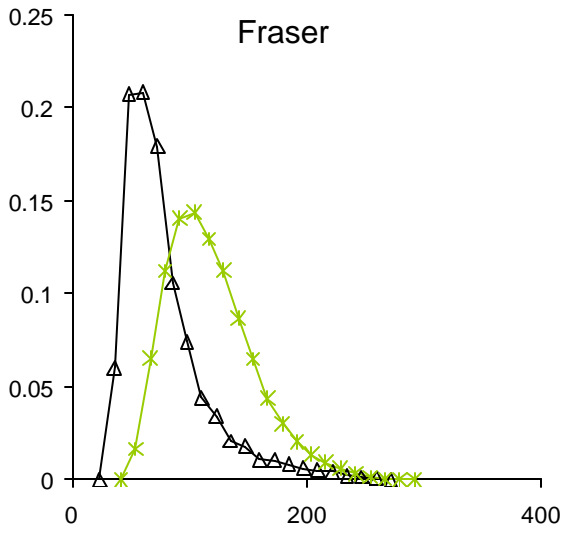
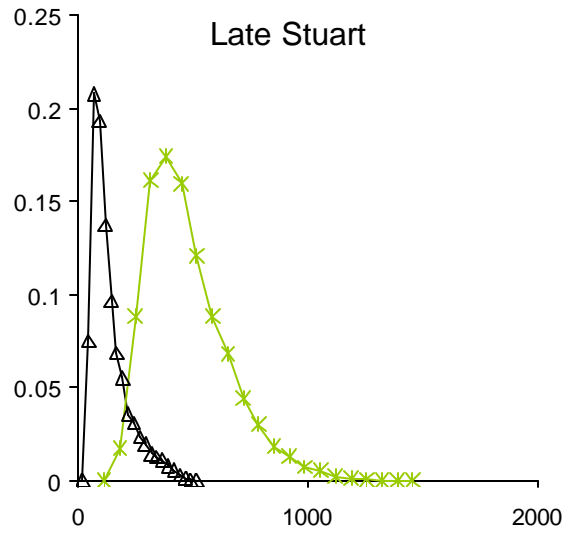
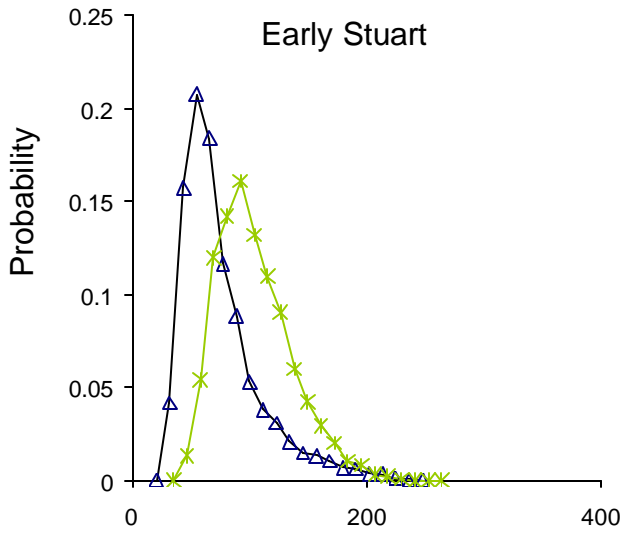
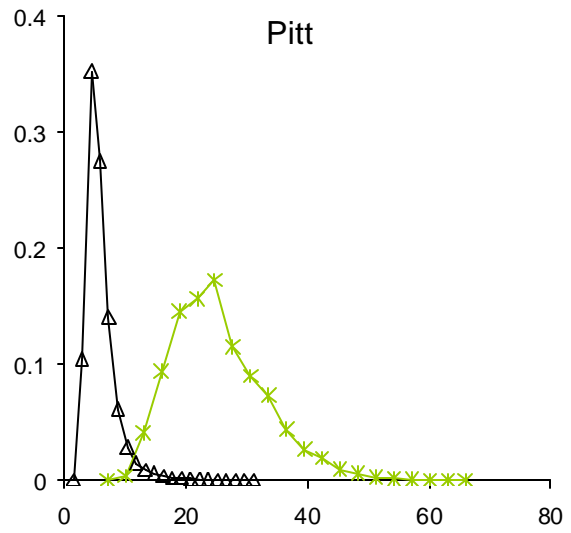
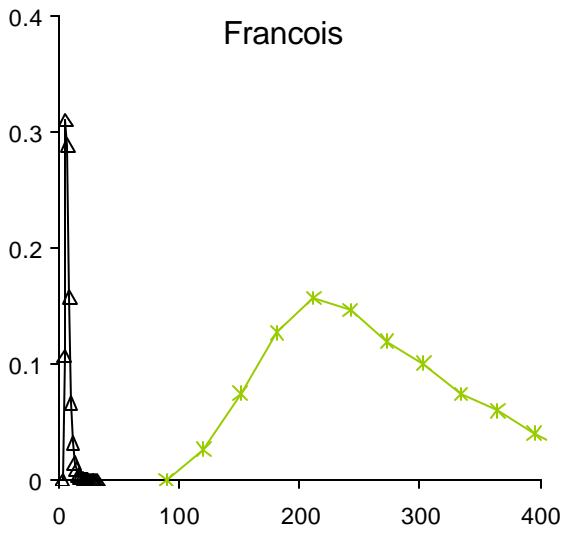


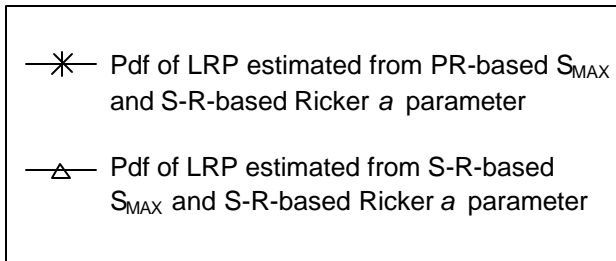
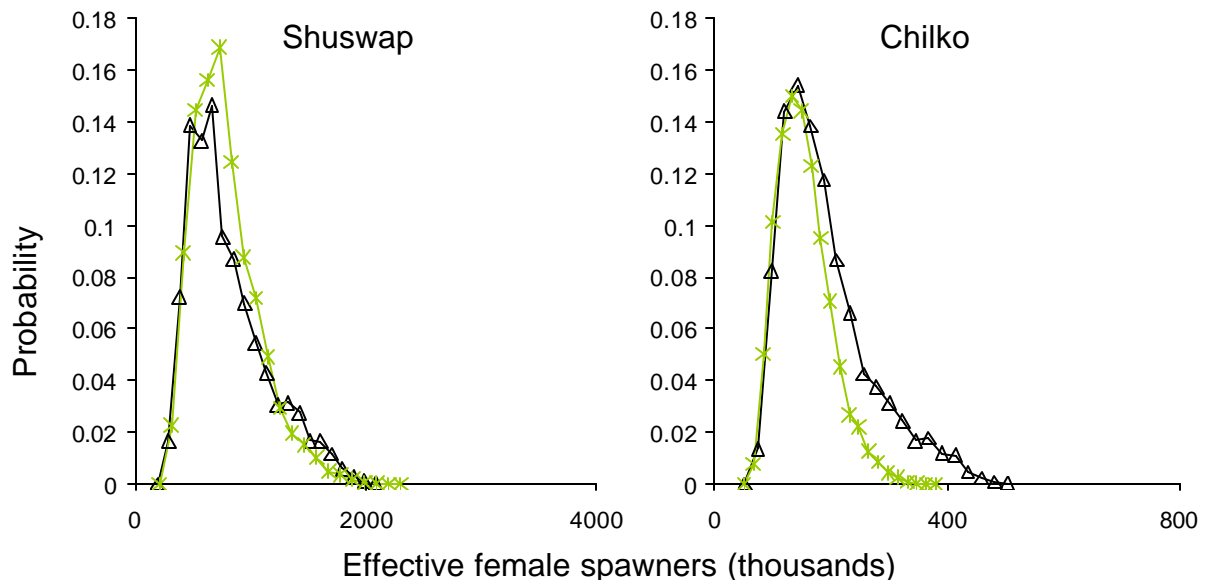
Figure 9. Ratio of S_{MSY}/S_{equil} , estimated using the Ricker stock-recruitment model, as a function of the Ricker a parameter (recruits per spawner at low abundance). The solid diamonds represent the Fraser River sockeye aggregates analyzed in this study.

Figure 10. Provisional estimates of limit reference points (LRP), as probability density functions (pdf), determined from two different combinations of estimates of optimal escapement and sockeye salmon productivity at low abundance for 7 Fraser River sockeye salmon aggregates: 1) PR-based S_{MAX} and S-R-based Ricker a parameter (stars), 2) S-R-based S_{MAX} and S-R-based Ricker a parameter (open triangles).



Effective female spawners (thousands)

60a



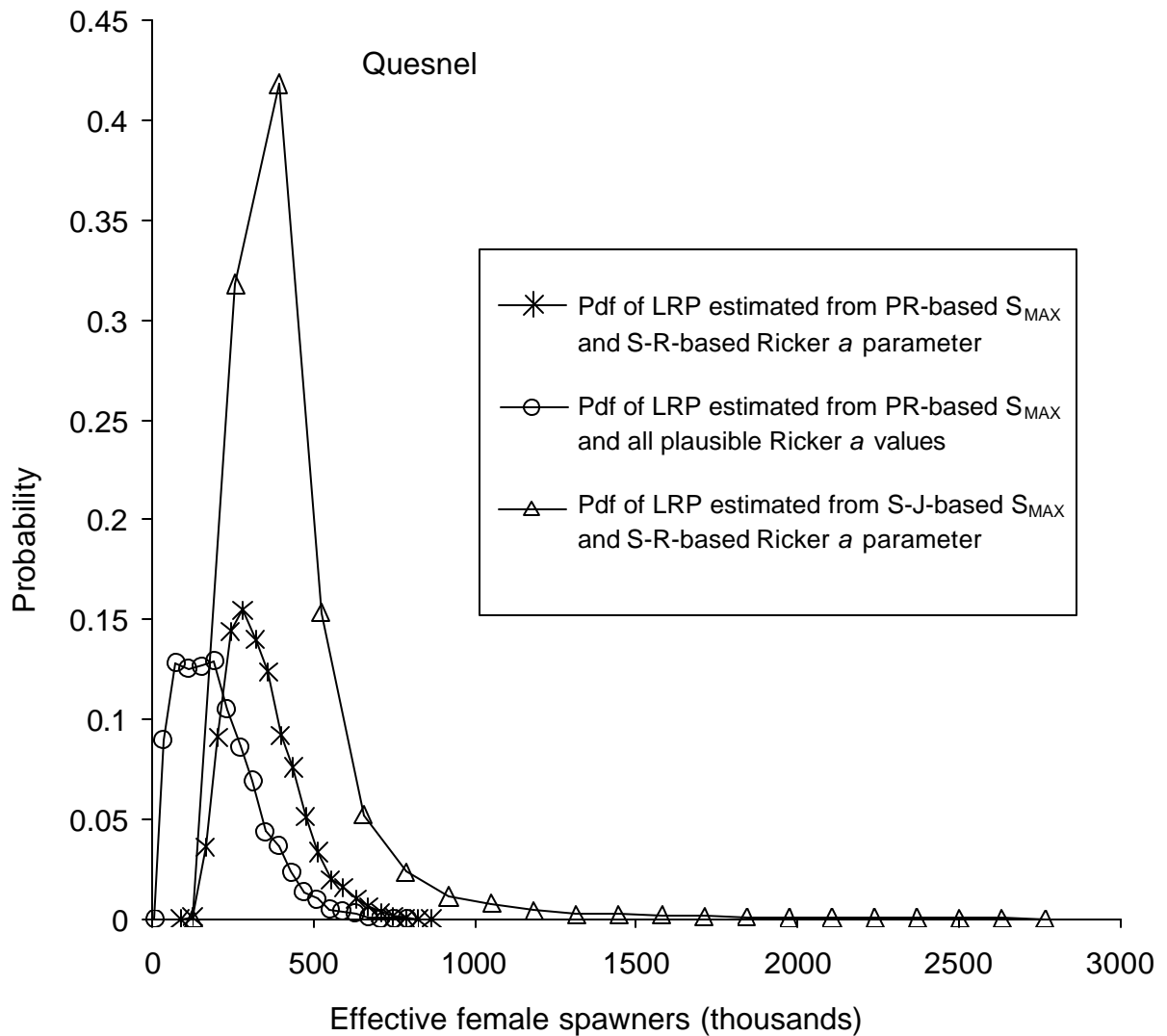


Figure 11. Provisional estimates of limit reference points (LRP), as probability density functions (pdf), determined from three different combinations of estimates of optimal escapement and sockeye salmon productivity at low abundance for the Quesnel Lake sockeye salmon aggregate: 1) PR-based S_{MAX} and S-R-based Ricker a parameter (stars); 2) PR-based S_{MAX} and all plausible Ricker a values (open circles); and 3) S-J-based S_{MAX} and S-R-based Ricker a parameter (open triangles).

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Appendix A:

A Bayesian approach to parameter estimation for linear relationships

A Bayesian approach was used to take uncertainty into account when quantifying the parameters for all of the linear relationships fit in this study (i.e. to quantify parameters for relationships used in steps 1 and 3 of the Bayesian PR method and all the S-R and S-J analyses). Bayesian methods combine prior information with likelihoods based on available data to compute posterior probability distributions for the estimates of interest. In this way degrees of belief are quantified for all probable values of the estimates, given the data. Given the linear relationship:

$$(A1) \quad Y = \mathbf{b}_0 + \mathbf{b}_1 X + \mathbf{e}$$

where Y is the dependent variable, \mathbf{b}_0 is the intercept, \mathbf{b}_1 is the slope, X is the independent variable, and \mathbf{e} is the stochastic error term assumed to be normally distributed with standard deviation \mathbf{s} , each plausible set of \mathbf{b}_0 and \mathbf{b}_1 parameters defines a different relationship between the X and Y variables. In this study, for each of the linear relationships, plausible ranges for the slope and intercept parameters were considered while \mathbf{s} was treated as known. \mathbf{q} denotes the parameter vector $(\mathbf{b}_0, \mathbf{b}_1, \hat{\mathbf{s}})$, where $\hat{\mathbf{s}}$ is the MLE for \mathbf{s} . For a given parameter combination \mathbf{q}_i , the posterior probability of \mathbf{q}_i given the observed data, D , was determined using Bayes theorem (Gelman et al. 1995):

$$(A2) \quad P(\mathbf{q}_i|D) = \frac{L(D|\mathbf{q}_i)P(\mathbf{q}_i)}{\sum_j L(D|\mathbf{q}_j)P(\mathbf{q}_j)}$$

where $L(D|\mathbf{q}_i)$ is the likelihood of the data given \mathbf{q}_i , $P(\mathbf{q}_i)$ is the prior probability assigned to \mathbf{q}_i , and $\sum_j L(D|\mathbf{q}_j)P(\mathbf{q}_j)$ is the sum of the products of the likelihoods times priors for all parameter combinations considered.

For both \mathbf{b}_0 and \mathbf{b}_1 , plausible ranges of the prior probability distribution were divided into a number of discrete bins and an equal probability (i.e. a uniform prior) was assigned to each bin. For a given \mathbf{q}_i , the likelihood of the data across all data points t was computed using the normal likelihood function:

$$(A3) \quad L(D|\mathbf{q}_i) = \prod_t \frac{1}{\mathbf{s}_i \sqrt{2\mathbf{p}}} \exp\left(-\frac{w_t^2}{2\mathbf{s}_i^2}\right)$$

where $w_t = Y_t - (\mathbf{b}_{0_i} + \mathbf{b}_{1_i} X_t)$ and \prod_t is the product of all t terms to the right. The prior probabilities and likelihoods of the various parameters combinations (\mathbf{q}_i) were then combined using Bayes' theorem (Equation A2) to generate the posterior distribution for \mathbf{q} , also called the joint posterior probability distribution for the slope and intercept parameters.

Appendix B:

Photosynthetic rate and weight per smolt data for Fraser River sockeye salmon

Photosynthetic rate (PR) data used in this study were from 9 BC sockeye salmon nursery lakes (K.S. Shortreed, personal communication). Shortreed et al. (2000) described the collection of PR data in detail. Values of seasonal average daily PR ($\text{mg C m}^{-2}\text{d}^{-1}$) for each lake were converted to total seasonal PR (tonnes C per lake) (PR_{TOTAL}) by multiplying by lake surface area and length of the growing season, assumed to be 180 days (May 1 to October 31); Shortreed et al. (2000). Where available, multiple years of annual estimates of PR were averaged to obtain mean total seasonal PR for each lake (Table 2).

Weight per smolt (W_{MAX}) data for Fraser River sockeye salmon are sparse for most stocks (Table 2). Since W_{MAX} at high smolt density was not always available, where possible I used W_{MAX} data for cohorts whose parents were *not low* in abundance relative to the range in historical records (i.e. relatively high; also, spawner abundance was used as an index of smolt density). Annual estimates of W_{MAX} were converted from grams to tonnes and lake-specific mean values were calculated in cases where more than one annual estimate was available.

Lake-specific normally distributed \log_e estimates of both PR and W_{MAX} were used in the application of the Bayesian PR method. Standard errors for these distributions were based on the amount of lake-specific data and estimates of interannual variability in PR and W_{MAX} . Exploratory data analysis revealed that within-lake annual variability in \log_e estimates of both PR and W_{MAX} was

approximately normally distributed. Interannual variability ($\mathbf{s}_{\log_e PR_{total}}^2$ and $\mathbf{s}_{\log_e SW_{MAX}}^2$) was estimated using variance components analysis (SAS VARCOMP procedure, SAS Institute Inc. 1988) on all multiple annual observations available. For PR, data were from 8 of the 9 study lakes because only one annual estimate of PR was available for Pitt Lake. Data used in the W_{MAX} variance components analysis included 34 years from Babine Lake (Wood et al. 1998), 28 pre-fertilization years from Chilko Lake (J.M.B. Hume, personal communication), and 7 years from Cultus Lake (Foerster 1954). These W_{MAX} data represent only those cohorts in relatively high abundance that had been presumably subject to density-dependent growth. The variance components analysis procedure assumed equal interannual variability among lakes and these data do not contradict that assumption (i.e. variance does not increase as a function of PR or W_{MAX}).

For application of steps 1 and 2 of the Bayesian PR method, $\log_e PR_{TOTAL}$ and $\log_e SW_{MAX}$ for each lake were described by normal distributions:

$$(B1) \quad \log_e PR_{TOTAL} \sim N \left(\log_e \overline{PR}_{TOTAL}, \sqrt{\frac{\mathbf{s}_{\log_e PR_{TOTAL}}^2}{n}} \right)$$

$$(B2) \quad \log_e SW_{MAX} \sim N \left(\log_e \overline{SW}_{MAX}, \sqrt{\frac{\mathbf{s}_{\log_e SW_{MAX}}^2}{n}} \right)$$

where n in each case is the number of annual estimates of either PR or W_{MAX} available for that lake (Table 2).

Appendix C:

Photosynthetic rate (PR) for Early and Late Stuart sockeye salmon stocks

Quantifying the normal distribution to describe PR_{TOTAL} for the rearing habitats of the Early and Late Stuart sockeye salmon stocks required additional analysis because the rearing habitats for their juveniles overlap in Trembleur Lake. There are no abundance estimates for juvenile sockeye salmon rearing in the Stuart Lakes, so I apportioned the nursery habitat of Trembleur Lake between the two stocks by making various assumptions and using stock-specific estimates of escapement. Assuming that juveniles rear in the lake directly downstream of their natal stream means that juveniles of the Early Stuart stock have exclusive use of nursery habitat in Takla Lake and use some portion of Trembleur Lake habitat, whereas juveniles of the Late Stuart stock have exclusive use of Stuart Lake and also use some portion of Trembleur Lake. Using escapement estimates apportioned to each natal stream (J.M.B. Hume, personal communication), for only the dominant cycle line where fry density was high relative to other years, I calculated the relative proportion of spawners, from each of the two stocks, that used streams flowing into Trembleur Lake. On average, 26% of the spawners using these streams in years of high abundance are from the Early Stuart stock, and 74% are from the Late Stuart stock. Assuming equal egg deposition and equal egg-to-fry survival rates between stocks, and assuming all fry consume equally, the estimated index of lake productivity (total seasonal PR) for Trembleur Lake was apportioned to each stock based on the relative abundances of the spawners. The $\log_e \overline{PR}_{TOTAL}$ representing the nursery habitat for each stock is a function of the $\log_e \overline{PR}_{TOTAL}$ for the two lakes contributing to each stock's habitat:

$$(C1) \quad \log_e \overline{PR}_{TOTAL}(EarlyStuart) =$$

$$\log_e \left(\overline{PR}_{TOTAL}(TaklaLk) + 0.26 \bullet \overline{PR}_{TOTAL}(TrembleurLk) \right)$$

$$(C2) \quad \log_e \overline{PR}_{TOTAL}(LateStuart) =$$

$$\log_e \left(\overline{PR}_{TOTAL}(StuartLk) + 0.74 \bullet \overline{PR}_{TOTAL}(TrembleurLk) \right)$$

The average variance (*var*) in $\log_e PR_{TOTAL}$ for each of the habitat areas is also a function of the variance calculated for each contributing lake:

$$(C3) \quad var(EarlyStuart) = var(TaklaLk) + 0.26^2 \bullet var(TrembleurLk)$$

$$(C4) \quad var(LateStuart) = var(StuartLk) + 0.74^2 \bullet var(TrembleurLk)$$

Variance for each contributing lake was computed from standard deviations in $\log_e PR_{TOTAL}$

(Appendix B, Equation B1).