

Accounting for Uncertainty in Estimates of Escapement Goals for Fraser River Sockeye Salmon Based on Productivity of Nursery Lakes in British Columbia, Canada

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Abstract.—For certain populations of sockeye salmon *Oncorhynchus nerka*, spawner and recruit data are either absent or too limited to estimate escapement goals (target abundance of spawners). In some cases, scientists instead use data on productivity of nursery lakes; however, many such analyses have not accounted for uncertainties. We therefore extended a previously developed lake productivity method for estimating escapement goals (the photosynthetic rate [PR] model) by using a Bayesian statistical approach that takes several sources of uncertainty into account. Utilizing data for Fraser River, British Columbia, sockeye salmon stocks, we compared this Bayesian PR method with stock–recruitment analysis. In six of seven cases, probability distributions of spawner abundance goals from the Bayesian PR method were 27% narrower on average than those from the stock–recruitment method. In four of seven cases, the Bayesian PR method produced higher median estimates of target spawner abundance than did stock–recruitment analysis; the other three pairs of estimates were within 7% of one another. We suggest that the Bayesian PR method is a potential alternative to using stock–recruitment data to estimate escapement goals for sockeye salmon populations.

Historically, management goals for escapement in populations of salmon *Oncorhynchus* spp. have been estimated using stock–recruitment (S–R) analyses, habitat-based models, or both. Stock–recruitment analyses require data series gathered over at least a decade, while a relatively short-term study might be sufficient for a habitat-based model (Koenings et al. 1993; Hume et al. 1996). Habitat-based models have been used to estimate escapement goals when S–R data are limited, nonexistent, or of poor quality (e.g., Cox-Rogers et al. 2004). For instance, even though long time series of data on spawning populations and the resulting adult recruits are available for many commercially important salmon stocks, estimates of escapement targets from S–R analyses can be inaccurate and imprecise due to measurement error in data and low contrast (range of variation) in historical spawner abundances (Hilborn and Walters 1992). Nevertheless, estimates of escapement goals from habitat-based models, which are usually based on measures of quantity and quality of freshwater habitat (e.g., Chaput et al. 1998; Bradford et al. 2000a), can

also be imprecise. Although the precision and bias of estimates based on S–R analyses are well studied and documented (e.g., Hilborn and Walters 1992; Hill and Pypers 1998), habitat-based models have yet to be similarly scrutinized. Therefore, in this paper, we develop an extension to a habitat-based model in which we explicitly account for uncertainties in the model's components and produce a probability distribution of estimates of escapement goals for each salmon stock or lake.

When applied to sockeye salmon *O. nerka*, the existing habitat-based models are founded on the observation that the maximum abundances of many (but not all) populations are limited by the quality and size of freshwater rearing lakes. The frequent occurrence of this freshwater limitation for sockeye populations has been noted by Koenings and Burkett (1987) and Shortreed et al. (2000). For oligotrophic lakes in Alaska that are rearing limited (i.e., where juvenile output is constrained by processes in the lake rather than by spawner numbers or amount of spawning area), Koenings and Burkett (1987) found good correlations between an index of lake productivity, euphotic volume (EV), and both total abundance and biomass of sockeye salmon smolts (i.e., juveniles that migrate to the sea). Euphotic volume is calculated from lake surface area and euphotic zone depth

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(Koenings and Burkett 1987). To apply this model to British Columbia (BC) lakes, Hume et al. (1996) adapted the relations of the EV model to use photosynthetic rate (PR), a more direct measure of lake productivity, and called it the PR model (Hume et al. 1996; Shortreed et al. 2000). Both EV and PR are indices of whole-lake productivity.

Both of these habitat-based models use a relation between EV (or PR) and juvenile sockeye salmon abundance to estimate the maximum capacity of a nursery lake to produce smolts, in units of biomass as well as numbers of smolts. The EV model then uses smolt numbers and an average spawner-to-smolt survival rate for sockeye salmon to back-calculate the spawner abundance required to achieve the maximum abundance of smolts (Koenings and Kyle 1997). In the PR model as developed by Hume et al. (1996) and Shortreed et al. (2000), the spawner abundance goal is the spawner number per PR unit that maximizes adult recruitment, based in part on data from Koenings and Burkett (1987). Thus, the EV and PR models are not life history models for calculating annual abundances of sockeye salmon populations but rather are models for estimating how those abundances might be constrained by the productive capacity of nursery lakes.

Although both the EV and PR models have been used to estimate escapement goals (e.g., Shortreed et al. 2000; Cox-Rogers et al. 2004; Witteveen et al. 2005), neither model has been adapted to account for uncertainty about both the data inputs and components of the models. Therefore, the objectives of this study were to (1) develop a systematic method that explicitly takes several uncertainties into account while using productivity of nursery lakes to estimate a reference point, the spawner abundance that maximizes smolt production for sockeye salmon stocks; (2) apply the method to Fraser River, BC, sockeye salmon stocks; and (3) compare these habitat-based estimates with those estimated from standard S-R analyses for the same stocks. We refer to our habitat-based method as the "Bayesian PR method" because we extended the PR method of Hume et al. (1996) and Shortreed et al. (2000) by estimating Bayesian posterior probability distributions for the parameters, variables, and output indicators.

In theory, estimates of escapement targets from two independent sources of information such as lake productivity and S-R analyses can be combined, which may be an improvement simply because more information can be used. Geiger and Koenings (1991) took this approach when estimating optimal escapement for sockeye salmon stocks in Chilko Lake in southeast Alaska by combining estimates of capacity of

the freshwater habitat with S-R data. They used a Bayesian approach to take into account uncertainty in each component. However, they inadvertently combined contradictory information in a way that led to high confidence for specific estimates of optimal escapement that were unwarranted by either information on habitat capacity or S-R data (Adkison and Peterman 1996). In light of this result, we chose not to combine the escapement targets generated by our Bayesian PR method with independent estimates from S-R analyses but rather to report each separately and to describe uncertainty in those estimates. In general, a Bayesian method for combining different sources of data should be considered very cautiously if both prior information and data entering the likelihood are relatively informative and appear contradictory.

Methods

We estimated the escapement required to maximize smolt production using the Bayesian PR method for six sockeye salmon nursery lakes (Chilko, Francois, Fraser, Pitt, Quesnel, and Shuswap lakes) and two stocks (early and late stocks that rear in the Stuart lakes complex: Stuart, Takla, and Trembleur lakes) of the interior Fraser River system, BC (Figure 1). Despite possible spawning limitation in the largest lakes, the nursery lakes of the Fraser River system are useful for this work because good estimates of both lake productivity and salmon abundance are available. Furthermore, these lakes create good contrasting situations because they range widely in physical and trophic characteristics (Table 1).

To reflect freshwater rearing capacity for sockeye salmon, we defined the escapement that maximized production in two ways, depending on the types of data available. The Bayesian PR and spawner-to-juvenile abundance (S-J) methods both estimated escapement target reference points $S_{MAX_{PR}}$ and $S_{MAX_{S-J}}$, respectively, as those that would maximize annual production of juveniles (in biomass and numbers, respectively). The S-J analyses were conducted for the three lakes (Chilko, Quesnel, and Shuswap lakes) where juvenile data (fall fry or smolt abundance) were available. For comparison, we fit an S-R model to estimate the escapement $S_{MAX_{S-R}}$ that would maximize total adult recruitment (numbers of fish). We applied the S-R method to all lakes and stocks except Quesnel Lake, as explained later. We used these definitions of the reference point, S_{MAX} , so that our results could be related to those of other researchers. Although we compare the estimates from different methods, we do not expect them to be exactly equivalent because each method integrates a slightly different combination of density-dependent processes. Note that none of these

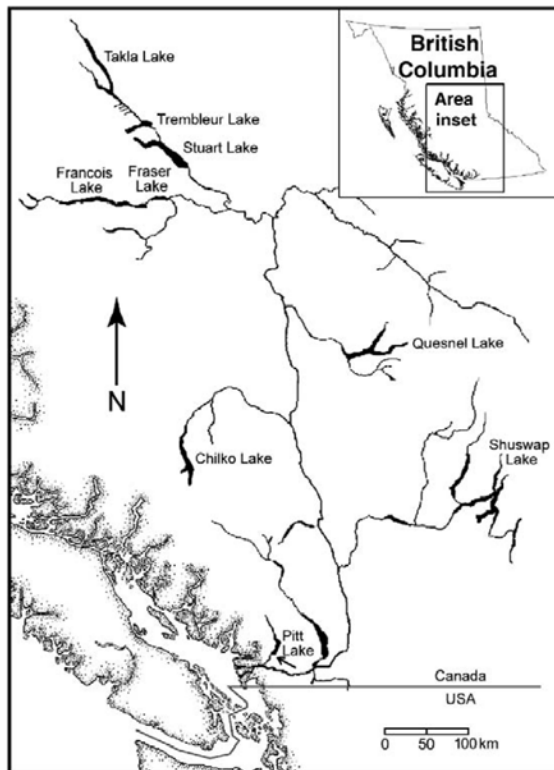


FIGURE 1.—Map showing the location of the sockeye salmon nursery lakes in the watershed of the Fraser River, British Columbia, used in an analysis of methods for estimating escapement goals.

escapement targets corresponds to the spawner abundance that produces the maximum sustainable yield (S_{MSY}), but the latter can be estimated, if desired, via iterative search from the estimated parameters of the S-R curve (Hilborn and Walters 1992).

The Bayesian PR method.—Our habitat-based Bayesian PR method for estimating S_{MAX} (Figure 2)

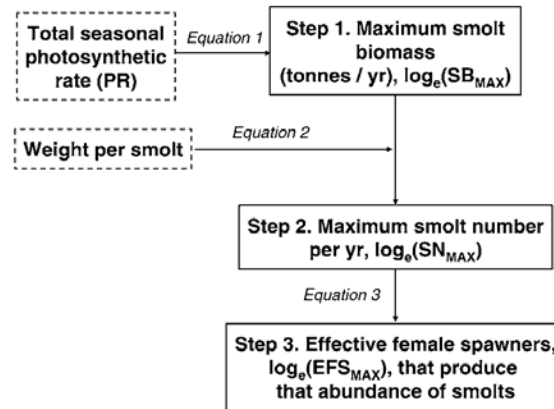


FIGURE 2.—Conceptual diagram of the three steps of the Bayesian photosynthetic rate method for estimating sockeye salmon escapement goals; the steps correspond to equations (1)–(3) in the text. Dotted-line boxes represent the input variables for which uncertainties in data were considered explicitly; tonnes = metric tons.

was adapted from the three-step procedure developed by Hume et al. (1996) and Shortreed et al. (2000). Briefly, step 1 estimates the maximum total biomass of smolts produced annually by a lake as a function of its total seasonal PR per year (1 May–31 October). Step 2 divides that maximum total smolt biomass by average weight per smolt to convert biomass into maximum total number of smolts. Step 3 estimates the number of annual spawners required, on average, to produce the maximum number of smolts annually. For the lakes examined here, the estimate in step 3 is approximately the same as the number of spawners needed to maximize smolt biomass annually; this is because smolt size varies little across the range of spawners near S_{MAX} (Hume et al. 1996). In contrast to the original PR method of Hume et al. (1996) and Shortreed et al. (2000), which used only single point

TABLE 1.—Physical characteristics and trophic status of sockeye salmon nursery lakes in the Fraser River basin, British Columbia (BC), for which data on photosynthetic rates (PR) were available.

Lake	Latitude (°N)	Longitude (°W)	Elevation (m)	Surface area (km ²)	Mean depth (m)	Trophic status
Chilko	51°16'	124°04'	1,172	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 Stobbert and Harding (1996).

^d Shortreed et al. (2000).

estimates of the two major inputs to the procedure (PR and weight per smolt), our Bayesian PR method took into account uncertainties in those quantities as well as others. This permitted a description of uncertainty in the estimated target escapement.

Details of these steps are as follows. In step 1, we estimated the maximum capacity of each nursery lake to produce sockeye salmon:

$$\log_e(\text{SB}_{\text{MAX}_i}) = \delta + \gamma \cdot \log_e(\text{PR}_{\text{TOTAL}_i}) + u_i, \quad (1)$$

where SB_{MAX_i} is the maximum annual smolt biomass (metric tons/year) that lake i can produce, δ and γ are parameters of the empirical relation between PR and maximum observed smolt biomass, $\text{PR}_{\text{TOTAL}_i}$ is the total seasonal carbon production (metric tons) in lake i , and u_i is a normally distributed random error term.

In step 2, the estimated maximum smolt production capacity for each lake was converted from units of smolt biomass to smolt numbers (abundance) by dividing by the average smolt weight:

$$\log_e(\text{SN}_{\text{MAX}_i}) = \log_e\left(\frac{\text{SB}_{\text{MAX}_i}}{W_{\text{MAX}_i} \cdot 10^{-6}}\right), \quad (2)$$

where SN_{MAX_i} is the maximum annual smolt capacity for lake i (numbers of smolts), W_{MAX_i} is the lake-specific average weight per smolt (g) at the escapement level where maximum smolt biomass is achieved as escapement increases, and 10^{-6} converts smolt weight from grams to metric tons. Density-dependent freshwater processes typically reduce weight per smolt as the density of spawners (an index of fry abundance) increases, and weight quickly reaches a lower asymptote (Hume et al. 1996; Shortreed et al. 2000; Cox-Rogers et al. 2004). Thus, within a lake, smolt weight remains relatively constant once spawner density increases above some modest level (e.g., Chilko Lake; Bradford et al. 2000b).

In step 3, we estimated the minimum number of female spawners that are required to produce the maximum number of smolts in each lake. We used effective female spawners (EFS), which is the number of female spawners adjusted for egg retention and prespawning mortality (as traditionally determined by the Pacific Salmon Commission 1998):

$$\log_e(\text{EFS}_{\text{MAX}_i}) = \kappa + \lambda \cdot \log_e(\text{SN}_{\text{MAX}_i}) + w_i, \quad (3)$$

where $\text{EFS}_{\text{MAX}_i}$ is escapement (EFS) needed to produce SN_{MAX_i} smolts, κ and λ are parameters of the empirical relation between EFS and smolt abundances at high smolt density in five BC lakes, and w_i is a normally distributed random error term.

We used \log_e transformations for equations (1) and (3) to eliminate heteroscedasticity and produce nor-

mally distributed residuals. We estimated parameter values for these equations from the data described below and then applied our three-step method to eight Fraser River sockeye salmon examples.

Data and parameter estimation.—Equation (1) was based on an empirical relation (Hume et al. 1996; Shortreed et al. 2000) between total seasonal PR (PR_{TOTAL}) and maximum observed biomass for the juvenile sockeye salmon population (SB_{MAX}) in six Alaskan and four BC rearing-limited nursery lakes. Data on PR (Table 2) were from Shortreed et al. (2000: Figure 32.2b; K. S. Shortreed, Fisheries and Oceans Canada, personal communication). Data on weight per smolt and fry biomass (Table 2) were from Hume et al. (1996), Shortreed et al. (2000), and K. S. Shortreed (personal communication). Samples of fry in the fall were used for Quesnel and Shuswap lakes because no appropriate smolt data were available in those cases. Smolt biomass data for the six Alaskan lakes (Koenings and Burkett 1987: their Table 6) were averages of 1–3 years of biomass observations. For each of the four BC lakes, we used the maximum annual juvenile biomass observed to date and assumed that these lakes were rearing limited in that peak year, as was done by Hume et al. (1996). Some of the lakes may not have been at full juvenile rearing capacity in years of historical maximum spawner abundance. We therefore conducted sensitivity analyses on assumed weight per smolt or fry, as described later.

To reflect uncertainty in the parameters of equations (1) and (3), we estimated a joint posterior probability distribution for the intercept and slope of each equation using Bayesian regression (Press 1989). We used a uniform prior probability distribution bounded by maximum likelihood estimates (MLE) \pm 3SEs for each estimated parameter. For each Bayesian regression, we used a normal likelihood function, which is consistent with the error terms assumed for equations (1) and (3). For each equation, we calculated joint posterior probability distributions across 20×20 grids of parameter values; tests with more grid points showed negligible differences in probabilities.

Figure 3 illustrates the extremes of the relations that we considered when applying equation (1) in our Bayesian analysis. The best-fit relation for equation (1) is also shown for context.

Equation (2) required input of average weight per smolt (g), W_{MAX_i} . In contrast to others who have applied the PR model (Hume et al. 1996; Shortreed et al. 2000; Cox-Rogers et al. 2004) and who have used a constant 4.5 g per smolt across all lakes, we used lake- and stock-specific weight data (Table 2). Just as with total seasonal PR, weight-per-smolt data are usually

TABLE 2.—Estimates of photosynthetic rate (PR) and weight per sockeye salmon smolt (W_{MAX}) used as input by the Bayesian photosynthetic rate method for six Fraser River, British Columbia, nursery lakes (numbers 1–6) and two Fraser River sockeye salmon stocks (numbers 7–8). The means (± 3 SE) of the input distribution are shown in untransformed units (\log_e transformation was used in analyses). Arrows at the bottom indicate that juveniles from the late stock in the Stuart lakes complex rear in Stuart and Trembleur lakes, whereas those from the early stock rear in Trembleur and Takla lakes.

Nursery lake	Sockeye salmon population(s)	Total seasonal PR (metric tons of C/lake)		W_{MAX} at high smolt density (g)	
		Input distribution mean ± 3 SE	Number of years of data ^a	Input distribution mean ± 3 SE	Number of years of data
(1) Chilko	Chilko, Chilko south	2,541 (1,940–3,327)	5	4.2 (2.5–7.0)	28 ^d
(2) Francois	Nadina	7,225 (4,717–11,066)	2	9.7 (5.7–16.6)	1 ^e
(3) Fraser	Stellako	3,215 (2,099–4,925)	2	7.4 (4.3–12.6)	1 ^e
(4) Pitt	Pitt	606 (332–1,107)	1	5.8 (3.9–8.4)	2 ^d
(5) Quesnel	Horsefly, Mitchell	4,995 (3,814–6,541)	5	4.0 ^c (2.3–6.9)	1 ^d
(6) Shuswap	Adams, Little Shuswap, Scotch, Seymour	10,148 (7,933–12,980)	6	2.7 ^c (1.6–4.6)	1 ^d
Stuart	(7) Late Stuart	10,437 ^b (6,769–16,095)	3	6.4 (3.8–11.0)	1 ^f
Trembleur	(8) Early Stuart	2,993 ^b (2,089–4,289)	3	6.4 (3.8–11.0)	1 ^f
Takla					

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

^b Appendix 2 describes the calculation of total seasonal PR for the early and late Stuart complex juvenile rearing areas.

^c For Shuswap and Quesnel lakes, no W_{MAX} data were available, so we used the average weight of fall fry in the year of maximum observed biomass.

^d J. M. B. Hume (personal communication).

^e Shortreed et al. (1996).

^f Taylor and Bradford (1993).

available for only a few years; the average value for each lake is thus uncertain.

To characterize these uncertainties in PR and smolt weight, we used lognormal distributions, which were most consistent with the data. Means of the distributions were averages of available annual estimates for each lake (Table 2). Standard errors were based on the

amount of lake-specific data available and an estimate of relative within-lake, year-to-year variability (Appendix A), which we assumed to be the same across lakes. Lognormal input distributions for PR and weight per smolt were described by 20 discrete values for each parameter and associated probabilities. Means and SEs for the input distributions representing PR for the early and late Stuart sockeye salmon stocks were stock-specific (Appendix B) rather than lake-specific calculations because juvenile fish from these two stocks rear in Trembleur Lake and either Stuart (late) or Takla (early) Lake. Hence, stock-specific estimates of PR were calculated to describe the productivity of their respective average freshwater habitats.

Equation (3) describes an empirical relation between EFS and smolt abundances at high smolt densities (SN) that approximate maximum capacity. The data used to parameterize this relation were point estimates of EFS and smolt abundances at the peak of the spawner-to-smolt relation for the five BC sockeye salmon populations for which smolt abundance data were available (described below). We derived these point estimates by fitting a Ricker model to spawner and smolt abundance:

$$\log_e(SN_{t,p}/S_{t,p}) = a_p - b_p S_{t,p} + v_{t,p}, \quad (4)$$

where $S_{t,p}$ is EFS abundance in brood year t for population p , $SN_{t,p}$ is number of smolts produced by $S_{t,p}$ spawners, and $v_{t,p}$ is the residual error term and is assumed to be normally distributed with an SD of σ_p (Peterman 1981). We used the MLEs of b_p and the

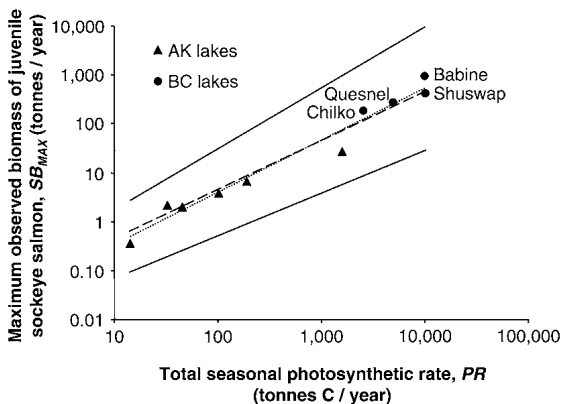


FIGURE 3.—Relation between maximum observed juvenile sockeye salmon biomass per lake per year (SB_{MAX}) and total seasonal photosynthetic rate (PR) per year in log–log space for six Alaska (AK) lakes and four British Columbia (BC) lakes; tonnes = metric tons. The dotted line represents the best-fit relationship based on the Bayesian PR method. Solid lines illustrate maximum and minimum extremes of relationships considered when we applied that method. Data were from Shortreed et al. (2000), and the dashed line represents their PR model.

arithmetic means for productivity parameters ($a'_p = a_p + (\sigma_p^2)/2$) to describe "average" spawner-to-smolt relations after correcting for back-transformation bias (Ricker 1997). By using formulas from Ricker (1997), we computed point estimates of spawner abundance ($EFS_{MAX_p} = 1/b_p$) and smolt abundance ($SN_{MAX_p} = e^{a_p-1}/b_p$) at the peak of each Ricker curve.

The five time series of EFS and smolt abundances used to estimate parameters of equation (4), and thereby EFS_{MAX_p} and SN_{MAX_p} , included cases with irregular sampling periods: 43 years of data from Chilko Lake (1949–1986 and 1993–1997), 29 years from Cultus Lake (1925, 1927, 1930, 1938–1942, 1951–1952, 1954–1961, 1965–1972, and 1974–1976), 11 years from Babine Lake prior to enhancement (1956–1966), 9 years from Port John Lake (1948–1956), and 8 years from Lakelse Lake (1944–1946 and 1950–1954). Data were from Foerster (1968), Wood et al. (1998), J. M. B. Hume (Fisheries and Oceans Canada, personal communication), and one of us (M.J.B.). Chilko Lake cohorts that would have been affected by lake fertilization experiments, including possible carryover effects (i.e., brood years 1987–1992; Bradford et al. 2000b), were excluded from all analyses to avoid biasing estimates of that lake's productivity. 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 but 1–3-year-old smolts were included in the estimates.

The resulting estimates of SN_{MAX_p} (maximum annual number of smolts per lake) and EFS_{MAX_p} (estimated EFS that produced those smolts) were used to estimate the parameters of equation (3) via Bayesian regression (Figure 4). As noted above, we also calculated uncertainty in EFS_{MAX_p} based on uncertainties in the parameters of equation (3) derived from a Bayesian analysis. The extremes of the relation that we considered (Figure 4) reflect those uncertainties.

Application of the Bayesian PR method.—We applied the three-step Bayesian PR method (Figure 2) to data for each of the six lakes and two stocks in the Fraser River watershed. We did this iteratively for the full range of uncertain conditions that we considered (i.e., the slope and intercept parameters for equations 1 and 3, as illustrated in Figures 3 and 4, respectively) and for the range of input values for PR and weight per smolt from Appendix A. Our procedure is elaborated upon in Appendix C. To describe precision of the resulting posterior probability distributions for S_{MAX} , we used an analog to a coefficient of variation ($CV = 100 \times SD/mean$), the 80% probability interval (Gelman

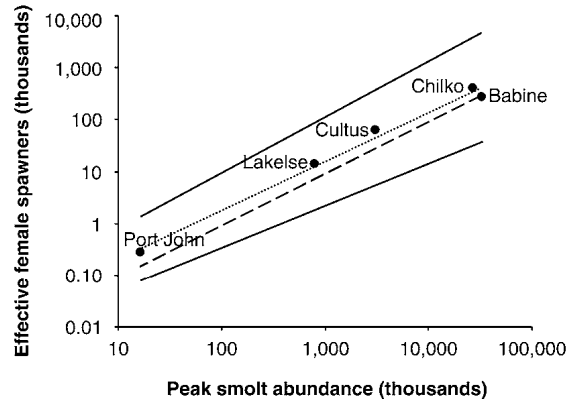


FIGURE 4.—Estimates of effective female spawners (EFS) at peak smolt abundance for sockeye salmon in five British Columbia lakes. The dotted line represents the best-fit relationship based on the Bayesian photosynthetic rate (PR) method; the solid lines illustrate the maximum and minimum extremes of relationships considered for that method; the dashed line represents the fixed smolts-per-EFS ratio used in the PR model of Shortreed et al. (2000).

et al. 1995; i.e., the 90th percentile estimate minus the 10th percentile estimate) divided by the median. Lower values of this metric reflect greater precision. For graphing, we divided results by lake surface area (ha) to standardize final results.

Bayesian stock-recruitment and spawner-to-juvenile estimates of target escapement.—For estimating S_{MAX} based on the more commonly used S-R analyses, we applied a Bayesian approach (Walters and Ludwig 1994) to account for uncertainty in parameters and to allow comparison of results among methods. We again used the Ricker S-R model (equation 4), except that the dependent variable was $\log_e(\text{adult recruits}/EFS)$.

For these S-R analyses, we used EFS and recruit data (brood years 1949–1996) for 11 sockeye salmon populations that rear in eight lakes (Table 2) in the Fraser River watershed (M. Lapointe, Pacific Salmon Commission, personal communication). Most Fraser River sockeye salmon juveniles migrate to the ocean as smolts after one winter in freshwater, and we included only these "1.x" age-classes in the adult recruit data. Many of the sockeye salmon populations had special aspects that we took into account. For instance, an S-R analysis for Quesnel Lake, which provides rearing habitat for the Horsefly River and Mitchell River populations, was excluded from this part of the study because an S-R analysis on the sum of those two populations provided little evidence of density dependence and did not support use of the Ricker model. For the S-R analysis of the Nadina River population that rears in Francois Lake, we summed spawner abundance from the wild with that from the Nadina River

spawning channels. Since 1963, the Pitt Lake population has been augmented by an increasing proportion of hatchery-raised fry from native broodstock (i.e., an average of 37% of total fry production in first 20 years compared with an average of 60% from 1985 to 1993; Stobbard and Harding 1996). For the two lakes (Chilko and Shuswap lakes) in which two or more populations of juveniles rear (Table 2), we summed those populations. We thus estimated S_{MAX} on a lake-by-lake basis for these population aggregates to make these estimates comparable to those from the Bayesian PR method and S-J analyses. However, stock-specific (as opposed to lake-specific) estimates of S_{MAX} were generated for the early and late Stuart stocks for comparison with estimates produced by the Bayesian PR method.

For S-J analyses, we also used equation (4) but the dependent variable was $\log_e(\text{smolts/EFS})$. Although smolt abundance data exist for Cultus, Port John, and Lakelse lakes, PR data are lacking and hence these lakes could not contribute to our comparison of methods. However, Chilko, Quesnel, and Shuswap lakes have PR and juvenile abundance data (Hume et al. 1996; J. M. B. Hume, personal communication). Smolt abundance estimates for Chilko Lake, in years described previously, were made at a counting fence at the lake's outlet. There were no smolt abundance estimates for Quesnel and Shuswap lakes, but fall fry abundances were estimated from hydroacoustic surveys for Quesnel Lake (available for brood years 1976, 1977, 1981, 1985–1987, 1989–1991, 1993, 1994, 1997, and 1998) and Shuswap Lake (brood years 1974–1979, 1982, 1983, 1986–1992, 1994, 1995, and 1998). As in Hume et al. (1996), we used these fry data under the assumption that they provided information not otherwise available.

For all Bayesian S-R and S-J analyses, we started with uniform prior probability distributions on the parameters. Upper and lower bounds for the uniform priors on a and b (equation 4) were defined by their respective MLE $\pm 3\text{SEs}$ (e.g., $\hat{a} \pm 3\text{SE}(\hat{a})$). However, we were able to use $\hat{b} - 3\text{SE}(\hat{b})$ as the lower bound on b for only three analyses (S-R analysis for Francois Lake; S-J analyses for Chilko and Shuswap lakes) without going below the biologically reasonable value of zero. For the remaining analyses, estimates of $\hat{b} - 3\text{SE}(\hat{b})$ were negative and biologically unreasonable because they implied a positive slope on the graph of $\log_e(R/S)$ versus S . For such stocks, instead of assuming that stock size could reach infinity, we arbitrarily assumed that three times the maximum observed EFS abundance ($\text{EFS}_{\text{MAXOBS}}$) was a biologically reasonable maximum bound for the parameter S_{MAX} . We thus set the lower bound on b equal to $1/$

$(3 \cdot \text{EFS}_{\text{MAXOBS}})$. Through a series of numerical trials, we found that this arbitrary choice did not substantially influence our final outcomes. 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, which is a common occurrence with salmon S-R data (Punt and Hilborn 1997; Hill and Pypers 1998).

For each S-R or S-J analysis, we calculated a 200×200 grid of posterior probabilities associated with each combination of a and b parameter values using methods outlined by Walters and Ludwig (1994). Because our reference point 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). The quantiles of each distribution of S_{MAX} and the precision estimates were calculated from the resulting marginal posterior probability distributions.

In sensitivity analyses, we evaluated the importance of errors in two key inputs to the Bayesian PR model. We determined the effect of having incorrectly estimated the PR for a lake. We also evaluated our assumption that available lake- and stock-specific smolt weight data are an accurate representation of average weight per smolt at the escapement level where maximum smolt biomass is achieved as spawner abundance increased.

Results

The posterior probability distributions of S_{MAX} that we estimated with the Bayesian PR method were generally narrower (more precise) than those calculated by estimating parameters of the standard Ricker S-R model in a Bayesian context. In six of the seven cases in which both PR and S-R analyses were feasible, the ratio of the 80% probability interval to the median S_{MAX} was 27% smaller using the Bayesian PR method than the S-R method (first two lines of each lake or stock in Table 3, last column). The precision of S_{MAX} estimates based on the Bayesian PR method was relatively consistent among lakes (range = 0.76–0.97). Although all posterior probability distributions for S_{MAX} were skewed (Figure 5) as expected, in cases where the medians were very similar the distributions resulting from S-R analyses had a longer tail at high escapements than those resulting from the Bayesian PR method (e.g., Chilko Lake and early Stuart S-R analyses; Figure 5e, h).

The Bayesian PR method produced median esti-

TABLE 3.—Range of observed sockeye salmon spawner abundances in stock–recruitment (S-R) data (units of effective female spawners [EFS]) for six nursery lakes and two stocks, and corresponding estimates of target escapement (S_{MAX}) from the photosynthetic rate (PR) model of Shortreed et al. (2000), the Bayesian PR method (with and without Babine lake), standard S-R analyses, and spawner-to-juvenile abundance (S-J) analyses. An S-R analysis was not possible for Quesnel Lake. Median S_{MAX} is the 0.5 quantile value. Precision of probability distributions is described by various quantiles and by the 80% probability interval (90th percentile estimate minus the 10th percentile estimate) divided by the median (analogous to a CV).

Nursery lake or stock and analysis method	EFS abundance range (thousands)	S_{MAX} (Shortreed et al.) ^a	S_{MAX} (EFS, thousands) percentile estimates derived from cumulative probability distributions					Precision
			0.10 ^b	0.25 ^b	0.50 ^b (median)	0.75 ^b	0.90 ^b	
Chilko Lake	7–505 ^c	265						
Bayesian PR, base case			264	312	379	465	558	0.77
S-R analysis			286	333	408	521	690	0.99
S-J analysis			339	366	402	447	496	0.39
Bayesian PR, no Babine			308	363	438	528	627	0.73
Early Stuart stock	0.8–386	280 ^d						
Bayesian PR, base case			204	244	298	366	440	0.79
S-R analysis			200	241	312	434	625	1.36
Bayesian PR, no Babine			232	274	335	410	489	0.77
Francois Lake	0.004–33	826						
Bayesian PR, base case			320	391	492	618	756	0.89
S-R analysis			11	13	15	19	24	0.81
Bayesian PR, no Babine			361	437	547	683	838	0.87
Fraser Lake	11–201	312						
Bayesian PR, base case			189	227	280	346	421	0.83
S-R analysis			115	134	163	210	279	1.01
Bayesian PR, no Babine			214	255	313	387	464	0.80
Late Stuart stock	0.02–745	976 ^d						
Bayesian PR, base case			661	820	1,042	1,332	1,664	0.96
S-R analysis			244	309	432	671	1,066	1.90
Bayesian PR, no Babine			767	945	1,195	1,516	1,874	0.93
Pitt Lake	2–22	57 ^d						
Bayesian PR, base case			46	55	67	81	96	0.76
S-R analysis			11	12	15	18	23	0.86
Bayesian PR, no Babine			52	61	73	88	105	0.72
Quesnel Lake	0.2–1,507	428						
Bayesian PR, base case			520	628	780	968	1,182	0.85
S-R analysis								
S-J analysis			421	488	597	761	1,014	0.99
Bayesian PR, no Babine			617	736	903	1,110	1,342	0.80
Shuswap Lake	2–1,836	1,007						
Bayesian PR, base case			1,454	1,800	2,286	2,923	3,668	0.97
S-R analysis			1,459	1,791	2,342	3,195	4,193	1.17
S-J analysis			534	601	704	841	1,022	0.69
Bayesian PR, no Babine			1,805	2,192	2,738	3,422	4,208	0.88

^a We converted estimates from the PR model in Shortreed et al. (2000), which were in total adult spawners, to EFS using estimates for the average proportion 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); and early and late Stuart, 50%.

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

^c Data used for the Chilko Lake S-J analysis included three extra brood years, 1997–1999, and an observed maximum EFS of 509,000, which exceeds that used for the S-R data (brood years 1949–1996).

^d S_{MAX} values for Pitt Lake and for the early and late Stuart stocks from the Shortreed et al. (2000) PR model were not published. We calculated these based on mean PR_{TOTAL} and the PR model equations.

mates of EFS abundance that were either higher than or nearly the same as those from the S-R method. Specifically, in four of the seven cases (Francois, Fraser, and Pitt lakes and the late Stuart stock), the median S_{MAX} from the Bayesian PR model was larger than S_{MAX} from the S-R analysis; the other three pairs of median estimates were within 7% of one another (Table 3). The largest discrepancy between results was for Francois Lake, where median target escapement from the Bayesian PR method was about 33-fold

greater than that from the S-R analysis (Table 3). Median target spawning escapements estimated using the Bayesian PR method also tended to be larger for nursery lakes with higher estimates of PR (Figure 6), as was predetermined by the model's equations.

It is difficult to generalize about the three lakes for which S-J analyses were possible (Chilko, Quesnel, and Shuswap lakes). In the latter two lakes (particularly Shuswap Lake), the S_{MAX} estimated by the Bayesian PR method was higher than that estimated by the S-J

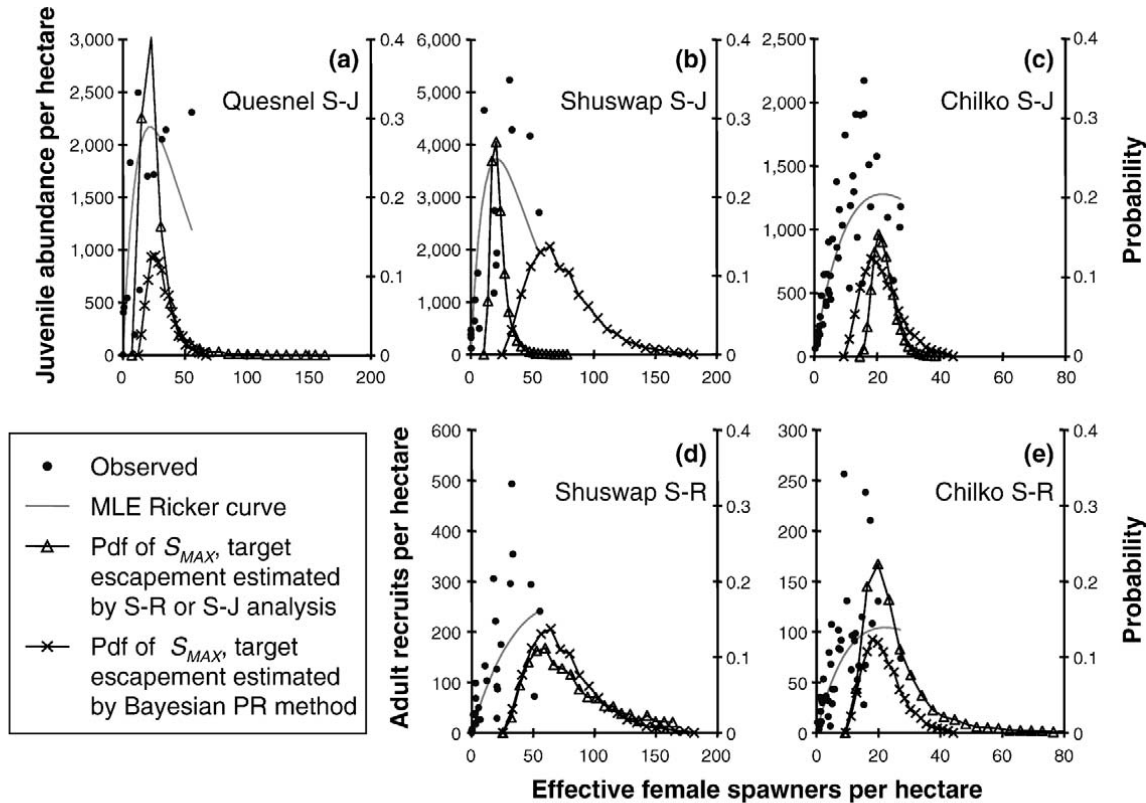


FIGURE 5.—Observed data (solid dots) for sockeye salmon spawning stock (effective female spawners [EFS]/ha of lake surface area) and the resulting juvenile abundance (fish/ha; primary y-axis of panels a–c) or number of adult recruits (fish/ha; primary y-axis of panels d–j) in British Columbia lakes. Maximum likelihood estimates (MLEs) for the Ricker curves fit to these data are indicated by curves without symbols. Curves with symbols are posterior probability distribution functions (PDFs) for estimates of the reference point, S_{MAX} (the EFS density that maximizes either juvenile abundance [a–c] or adult recruits [d–j]); posterior probabilities for these distributions are on the secondary y-axis. Posterior PDFs are from the Bayesian photosynthetic rate (PR) method (× symbols) and either stock–recruitment (S-R) or spawner-to-juvenile abundance (S-J) analyses (Δ symbols) of eight Fraser River sockeye salmon aggregates. For Francois Lake (panel f), the PDF of S_{MAX} from the Bayesian PR method occurs off-scale at a median of 20 EFS/ha.

method (Table 3). The S-J method produced a more precise distribution of estimates than the Bayesian PR method for Shuswap Lake (precision metric = 0.69 versus 0.97), but the relative precision of the methods was reversed for Quesnel Lake (Table 3). In Chilko Lake, the estimates of median S_{MAX} from the Bayesian PR and S-J methods differed by only 6%.

In six of eight cases, S_{MAX} estimated by the Bayesian PR method was greater than the estimate from the PR model of Shortreed et al. (2000; Table 3). Across all cases, the ratio of those quantities (Bayesian PR S_{MAX} /PR S_{MAX}) ranged from 0.6 to 2.3.

Sensitivity Analyses

We examined the sensitivity of results of the Bayesian PR method to the exclusion of Babine Lake data in the parameterization of both of the empirical

relationships (equations 1 and 3) because our assumption that Babine Lake was producing smolts at its peak capacity may not have been valid (Wood et al. 1998; Cox-Rogers et al. 2004). Abundance of juvenile sockeye salmon in Babine Lake was limited by the capacity of spawning grounds prior to construction of spawning channels in 1965, and this may still be the case, despite enhancement (West and Mason 1987). When we removed the Babine Lake data point from each of the empirical relationships (Figures 3, 4) and repeated the Bayesian PR analyses, the medians of the resulting probability distributions for S_{MAX} were 10–20% higher than in the initial baseline analysis in all seven cases and the precision metric was between 2% and 9% lower in all cases (rows labeled “Bayesian PR, no Babine” in Table 3).

Another sensitivity analysis was done because the

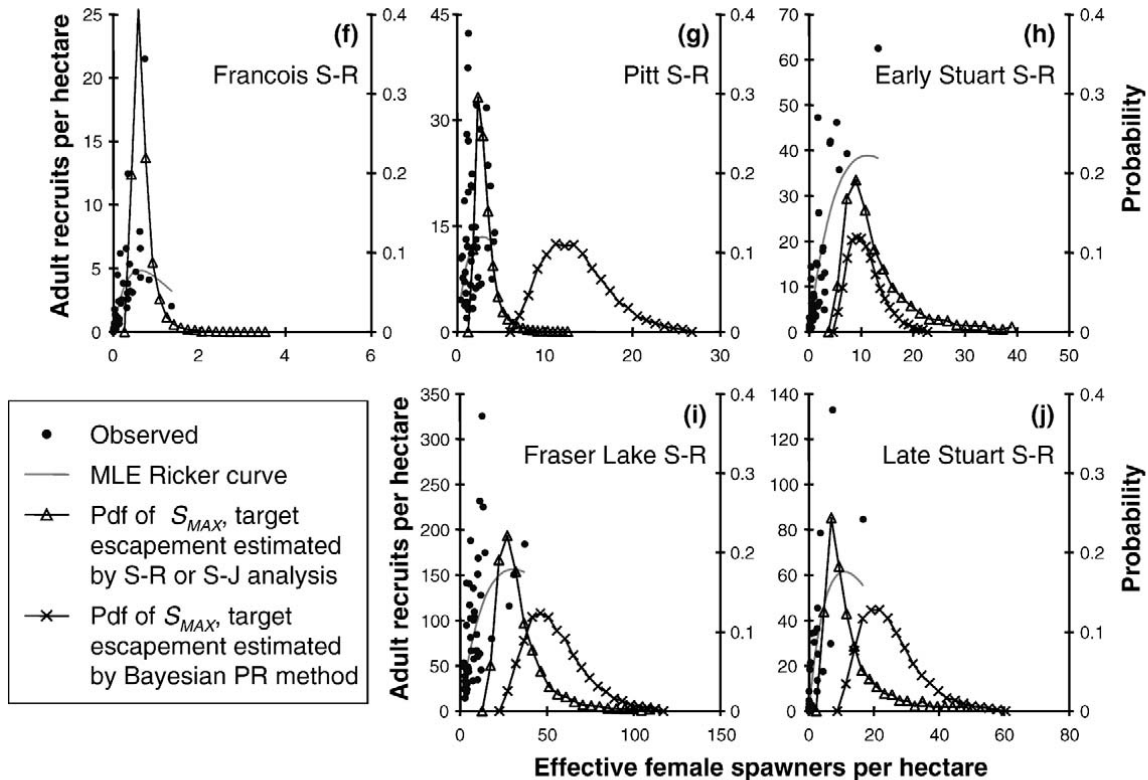


FIGURE 5.—Continued.

Bayesian PR method was based on only a few years of PR and smolt weight (W_{MAX}) data for each lake. We therefore indirectly evaluated the effect of acquiring additional years of similar PR or W_{MAX} data by increasing the sample size n in equations (A.1) and (A.2) for an example case, Pitt Lake. Increased sample sizes narrowed the input distributions and improved the precision of S_{MAX} estimates, but not dramatically (Table 4). The greatest relative gains in precision were made when sample sizes for both types of data were doubled from 1 to 2 years (e.g., precision for Pitt Lake S_{MAX} estimates decreased from 0.82 to 0.67). Relative gains in precision per year diminished as more years of data were added.

When few data are available, as was the case here, estimates of mean PR and W_{MAX} could also easily be inaccurate; therefore, we examined how biased PR or W_{MAX} estimates might affect the S_{MAX} estimated by the Bayesian PR method. We did this by adjusting the base-case mean of the input distributions for both PR and W_{MAX} while leaving the SEs of the input distributions at their base-case values. We found that varying PR by +2SEs and -2SEs caused median S_{MAX} to shift by an average of 29% and -22%, respectively, relative to base-case estimates (Figure 7a). Similarly,

varying W_{MAX} by +2SEs and -2SEs caused shifts of -28% and 38%, respectively, in median S_{MAX} (Figure 7b). Changes to mean input values for PR or W_{MAX} had little effect on the precision of estimated S_{MAX} (i.e., the precision metric shifted by an average of 2% and not more than 7%; Figure 7), providing evidence that the precision of S_{MAX} estimated by the PR method is dominated by the variance terms in the method rather than uncertainty in the means of the input distributions.

Discussion

Our results suggest that the habitat-based Bayesian PR method for estimating S_{MAX} for Fraser River sockeye salmon is a viable alternative to commonly used S-R analyses, even when the latter are conducted in a Bayesian context. First, in six of seven cases, the posterior probability distributions of spawner abundance at S_{MAX} derived from the Bayesian PR method were 27% narrower on average (reflected by the precision) than the distributions calculated by the standard Ricker S-R analysis. Second, the improved precision of Bayesian PR estimates of S_{MAX} was relatively insensitive to the potential inaccuracy of input estimates of lake productivity (PR) or body size of smolts. Also, when we omitted the Babine Lake data

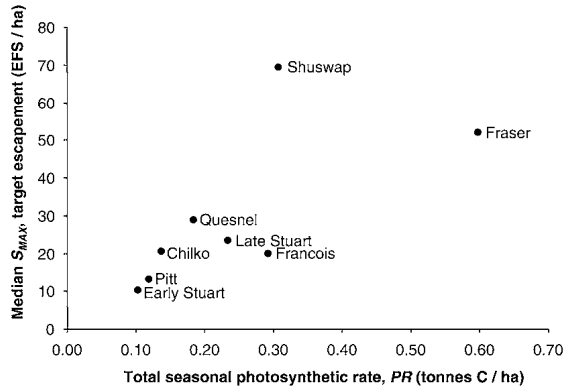


FIGURE 6.—Median S_{MAX} (effective female spawner (EFS) target escapement/ha) as estimated by the Bayesian photosynthetic rate (PR) method as a function of total seasonal PR per hectare for eight Fraser River, British Columbia, sockeye salmon aggregates; tonnes = metric tons.

point from our input data set due to concerns that it might not be a rearing-limited lake, our precision of Bayesian PR estimates of S_{MAX} improved. On the other hand, precision of our standard Ricker S-R estimates was influenced by our arbitrary choice of bounds for the prior on the b parameter, especially when the range of spawner abundances was limited. However, if we had solely let the S-R data determine the bounds ($\pm 3SEs$) in such cases, some parameter values would have been biologically unreasonable (e.g., no compensation in the S-R relation) and the posterior distributions would have been even wider than those already shown for the Ricker S-R method.

Even though the estimates from the Bayesian PR approach were relatively precise, this could be misleading because our estimation of precision was limited to the uncertainties that we could account for with data. For instance, when we applied the Bayesian PR method to the larger lakes in this study, it was necessary to extrapolate beyond the ranges of observed data for both component empirical relationships. The true variability in these relationships may be underestimated due to lack of data. In addition, quantifying more of the inherent uncertainties in the Bayesian PR method may decrease the precision of the results. For example, our application of the method did not explicitly consider uncertainty in the proportional distribution of sockeye salmon fry from the early and late Stuart stocks among the three lakes (Appendix B). Quantifying this uncertainty would probably widen the probability distributions of S_{MAX} estimates for the Stuart lakes stocks.

Perhaps more importantly, the accuracy of S_{MAX} estimates is unknown for the Bayesian PR and S-R analyses because simulations have not been conducted

TABLE 4.—Results of sensitivity analyses to determine the effects of obtaining additional years of input data for photosynthetic rate (PR), weight per smolt (W_{MAX}), or both, on estimates of target escapement (S_{MAX}) produced by the Bayesian PR method for Pitt Lake, British Columbia, sockeye salmon. Precision of probability distributions is described by the 80% probability interval (90th percentile estimate minus the 10th percentile estimate) divided by the median S_{MAX} (analogous to a CV).

Years of input data		S_{MAX}	
PR	W_{MAX}	80% probability interval (EFS, thousands)	Precision
1	2	50.4	0.76
2	2	44.7	0.67
4	2	41.6	0.62
6	2	39.9	0.60
8	2	39.3	0.59
10	2	38.9	0.58
1	1	54.7	0.82
1	4	48.1	0.72
1	6	47.1	0.71
1	8	46.8	0.70
1	10	46.6	0.70
4	4	38.2	0.57
6	6	35.8	0.53
8	8	34.5	0.52
10	10	34.3	0.51

for these particular situations. However, if two or more methods produce similar estimates of S_{MAX} , this will increase confidence in those numbers, but it of course does not guarantee their accuracy. For instance, medians and posterior probability distributions for estimates of S_{MAX} from Shuswap, Chilko, and early Stuart S-R analyses were similar to Bayesian PR results (Table 3; Figure 5d, e, and h, respectively), as were the Quesnel and Chilko S-J estimates (Figure 5a, c). For Quesnel, Chilko, and Shuswap lakes, this similarity may have been partly due to our use of data from these lakes to parameterize one of the two relations in the Bayesian PR method (Figure 3). However, that is not the sole reason for the similarity; results for the early Stuart stock from the S-R and Bayesian PR methods were similar, yet these data were independent of those used to parameterize the Bayesian PR method.

In contrast, there are several potential sources of bias in the Bayesian PR method. First, a sensitivity analysis (Figure 7) showed that estimates of S_{MAX} will be biased if the Bayesian PR method uses biased inputs of a lake's PR or weight per smolt at peak smolt biomass. It is thus very important to gather sufficient data on these two parameters to reduce bias.

Second, in the cases when Bayesian PR estimates of S_{MAX} were considerably higher than estimates from the standard S-R analyses, they ranged between 1.7 and 4.5 times higher for Fraser Lake, late Stuart complex,

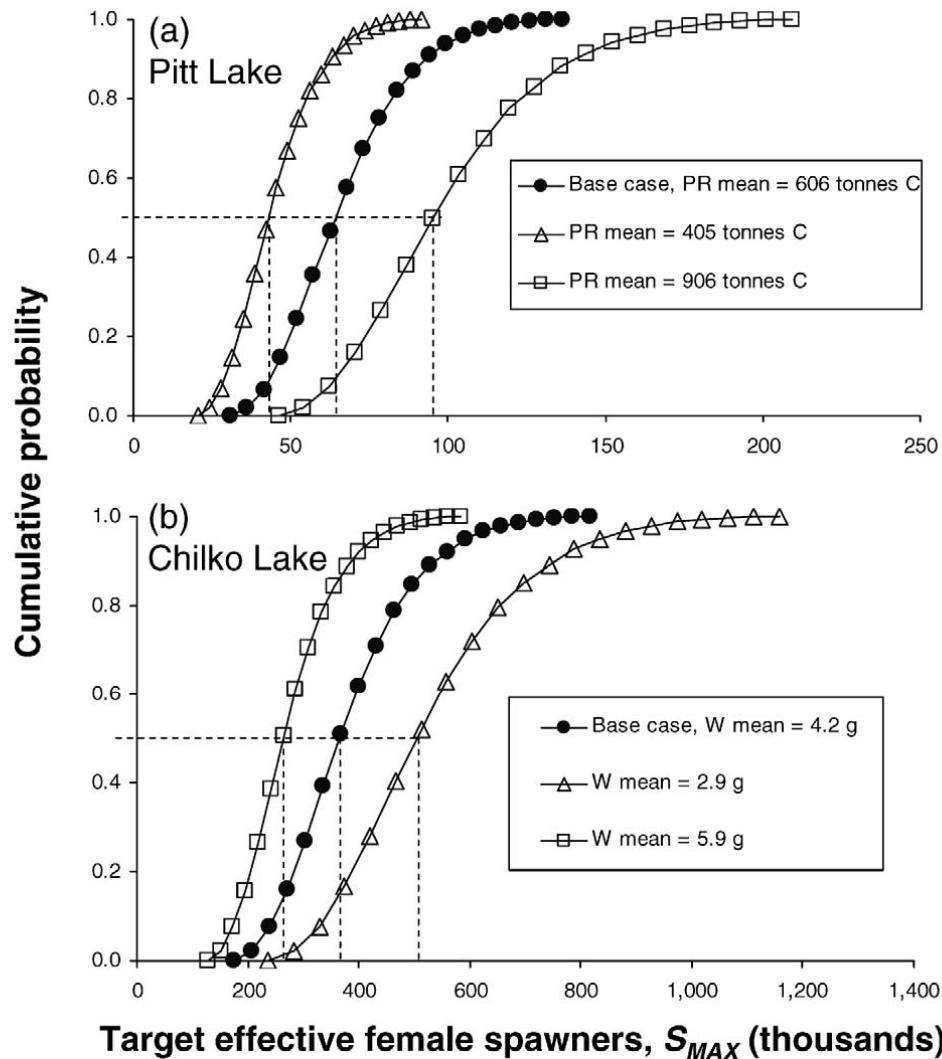


FIGURE 7.—Cumulative probability distributions of S_{MAX} , the sockeye salmon target escapement (effective female spawners [EFS]) that maximizes the number of juveniles in Pitt and Chilko lakes, British Columbia, based on the Bayesian photosynthetic rate (PR) method; tonnes = metric tons. A given point on a curve indicates the probability that S_{MAX} is less than the corresponding x -axis value. Horizontal lines represent the median probability (50th percentile), and vertical lines indicate the median S_{MAX} values corresponding to the median probability in each sensitivity analysis (e.g., in the top panel's base case, where mean PR = 606, there is a 0.50 probability that $S_{MAX} \leq 65,000$ EFS). Results for Pitt Lake (panel a) are based on three different input distributions for PR with the means indicated. Results for Chilko Lake (panel b) are from three different input distributions for smolt weight at high density (W_{MAX}).

and Pitt Lake stocks, and approximately 33 times higher for Francois Lake. Bayesian PR estimates might better approximate S_{MAX} than those from S-R analyses when substantial measurement error exists in historical estimates of spawner abundance and when the range of temporal variation in historical estimates is narrow. In such cases, S-R analysis generally tends to underestimate optimum stock size (Hilborn and Walters 1992:287). There is some evidence to support this explanation in the case of Francois Lake. The range of

escapement in Francois Lake has been very narrow; escapement has not exceeded 2 EFS/ha (Figure 5), which is substantially lower than that of all other lakes. The S-R analysis may thus have underestimated S_{MAX} .

Third, there is an opposite possible explanation for Bayesian PR estimates of S_{MAX} generally being greater than those from the S-R method. Bayesian PR values might be biased high, rather than S-R estimates being biased low. This situation could arise because the Bayesian PR method does not take into account various

mechanisms other than primary production that may limit production of juveniles from lakes. Such mechanisms are implicitly accounted for in the data used in S-R analyses but are not reflected by PR values for a lake. Shortreed et al. (2000) discussed such factors, which included limited spawning habitat, populations of predators and competitors, thermal regimes that limit feeding territories of juvenile sockeye salmon in lakes, and predation-resistant plankton community structures. In an application of the PR model to Skeena River sockeye salmon, Cox-Rogers et al. (2004) modified their estimates of S_{MAX} to account for such mechanisms, including limnetic competitors, variations in smolt size at rearing capacity, and multiple ages of smolts. These mechanisms could act independently or in unison and would cause S_{MAX} estimates from Bayesian PR analyses to be substantially higher than S-R estimates.

There is evidence that some of the above mechanisms suggested by Shortreed et al. (2000) operate in a few of our example nursery lakes, which might partially account for the large differences between estimates of S_{MAX} produced by the different methods. For example, total natural and enhanced spawning ground capacity around Francois Lake was previously estimated to be 50,000 spawners (Rosberg et al. 1986, cited by Shortreed et al. 1996), or about 26,000 EFS, which is only a small fraction of the median S_{MAX} estimate from the Bayesian PR method of 492,000 (Table 3) and about twice our median S-R based estimate of 15,000. In the Pitt Lake system, although diet sampling (Henderson et al. 1991) indicated little overlap with juvenile sockeye salmon, the presence of competitors (e.g., threespine stickleback *Gasterosteus aculeatus* and longfin smelt *Spirinchus thaleichthys*) and predators (e.g., juvenile Chinook salmon *O. tshawytscha* and rainbow trout *O. mykiss*) (Diewert and Henderson 1992) may be responsible for reducing the maximum achievable abundance of juvenile sockeye salmon in the lake and may partially explain why the S_{MAX} estimated by the Bayesian PR method (67,000 fish) is more than four times higher than the 15,000 fish estimated by S-R analysis.

When long time series of data on abundances of spawners and recruits are neither available nor reliable, it is reasonable to consider using the Bayesian PR method (but cautiously) to estimate escapement goals from data on PR in rearing lakes and average smolt body size. These data can be gathered relatively quickly and inexpensively compared with annual estimation of abundance of spawners and stock-specific catches over one or more decades (Hume et al. 1996; Shortreed et al. 2000). We also caution, though, that the Bayesian PR and original PR models

were based on data from interior BC lakes and that trophic relations may be different in other regions, such as coastal sockeye salmon rearing lakes (S. Cox-Rogers, Canada Department of Fisheries and Oceans, personal communication). Another reason for caution when using the Bayesian PR method is that, like its analog in Alaska (the EV model), no rigorous field evaluation of the model's performance has been undertaken. However, there are some indications that the EV model, for example, does not necessarily adequately reflect a lake's capacity to produce spawners (e.g., Geiger et al. 2005:70).

Comparisons of Habitat-Based Methods

Accounting for uncertainty is the main conceptual difference between the Bayesian PR method and the two methods upon which it is based, the Alaskan EV model (Koenings and Burkett 1987) and the PR model of Shortreed et al. (2000). The Bayesian PR method accounts for uncertainties in the relationships in Figures 3 and 4, as well as uncertainties in PR and smolt weight.

Three other differences in components of the analysis contributed to differences between median S_{MAX} estimates from our PR-based Bayesian method and the point estimates produced by the Shortreed et al. (2000) PR model (Table 3). First is smolt weight. Average body size of sockeye salmon smolts is not monitored for most BC sockeye salmon populations, and much uncertainty remains about the accuracy of smolt size estimates when peak biomass is achieved in a rearing lake. However, body size is a critical variable in the PR-based models. Shortreed et al. (2000) and Cox-Rogers et al. (2004) used an estimate of 4.5 g for smolt weight at peak production (originally based on Alaskan data in Koenings and Burkett 1987) for all BC sockeye salmon lakes. Although Cox-Rogers et al. (2004) used data from BC populations to support the PR model's use of 4.5-g smolts, the authors adjusted their PR model predictions for lakes that consistently produced smaller smolts even at low escapements. Because average body size of sockeye salmon smolts varies greatly among lakes in BC (Burgner 1991), we used lake- and stock-specific estimates of mean smolt weight at high spawner abundance (Table 2) when we applied the Bayesian PR method. Mean weight of smolts enters into the denominator of step 2 of our Bayesian PR method (Figure 2), so increased weights would lead to fewer estimated smolts at a given maximum smolt biomass and, hence, lower estimated S_{MAX} . The reverse would be true for decreased weights. For Pitt Lake, early and late stocks of the Stuart complex, and Fraser and Francois lakes, the mean smolt weights that we used could be biased high.

If we had used a smolt weight of 4.5 g instead (a 22–54% reduction from our data), our median estimates of S_{MAX} from the Bayesian PR method would have increased by 25–107%. In contrast, if we had used a smolt weight of 4.5 g for Shuswap, Quesnel, and Chilko lakes, (7–65% heavier than the data), our median S_{MAX} estimates would have decreased by 7–38%.

The second difference between our Bayesian PR method and that of Shortreed et al. (2000) was that our method included four BC lakes with high PRs in the calibration of the relationship between PR and maximum smolt biomass, rather than just the Alaskan lakes used by Shortreed et al. (2000). As a result, for large lakes with high seasonal PR (e.g., Shuswap and Francois lakes), the Bayesian PR method estimated slightly higher median maximum capacities of juvenile sockeye salmon biomass than did the Shortreed et al. (2000) PR model. This effect was negated when smolt size was large relative to 4.5 g and was amplified when it was small.

The final difference between the Bayesian PR method and the PR method of Shortreed et al. (2000) was that our method consistently estimated that more EFS were required to produce the same number of smolts than the Shortreed et al. (2000) PR model, based on our analysis of data from five BC sockeye salmon rearing lakes (Figure 4). Estimates of smolts per EFS in our base-case Bayesian PR analysis varied from 51 to 78 over the range of observed smolt abundances. In comparison, the PR model equations (Shortreed et al. 2000) led to a constant 108 smolts per EFS. These various factors explain why the Bayesian PR median estimates of S_{MAX} did not differ in a consistent direction from those of Shortreed et al. (2000).

Overall, the Bayesian photosynthetic rate method appears to be a useful additional stock assessment technique that, if applied carefully, will improve scientific advice to managers of salmon fisheries.

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Appendix A: Photosynthetic Rate and Weight-per-smolt Data

Shortreed et al. (2000) describe the collection of PR data in detail. As in that paper, we converted seasonal average daily PR ($\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) for each lake into total seasonal PR (metric tons of C/lake; PR_{TOTAL}) by multiplying the daily rate by lake surface area (m^2), length of the growing season (assumed to be 180 d from May 1 to October 31), and a conversion factor for milligrams to metric tons. We also averaged multiple years of annual estimates of PR, where available, to obtain mean total seasonal PR for each lake (Table 2).

Weight-per-smolt (W_{MAX}) data for Fraser River sockeye salmon (Table 2) are sparse for most lakes and stocks. Where W_{MAX} at high smolt density was not available, we used W_{MAX} data for cohorts with parental

spawning populations that were relatively abundant compared to the historical range of abundances. Lake-specific mean weight was calculated when more than one annual estimate was available.

Unlike the PR method of Hume et al. (1996) and Shortreed et al. (2000), the Bayesian PR method took into account uncertainty in inputs of PR and W_{MAX} . That uncertainty was reflected by lake-specific, normally distributed \log_e estimates of both PR and W_{MAX} . Standard errors for these distributions were based on lake-specific data and estimates of interannual variability in PR and W_{MAX} . Within-lake annual variability in \log_e estimates of both PR and W_{MAX} was approximately normally distributed. Interannual

variability in PR ($\sigma^2_{\log_e \text{PR}_{\text{TOTAL}}}$) and W_{MAX} ($\sigma^2_{\log_e W_{\text{MAX}}}$) was estimated using variance components analysis (VARCOMP procedure in the Statistical Analysis System; SAS Institute, Inc. 1988) on all multiple annual observations available. For PR, data were from eight of the nine 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). The W_{MAX} data represent only those cohorts that had relatively high abundance and that presumably had been subject to density-dependent growth. The variance components analysis assumed equal interannual variability among lakes, and the data supported that assumption (i.e., variance did not increase as a function of PR or W_{MAX}).

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

$$\log_e(\text{PR}_{\text{TOTAL}}) \sim N \left[\log_e(\overline{\text{PR}}_{\text{TOTAL}}), \sqrt{\frac{\sigma^2_{\log_e(\text{PR}_{\text{TOTAL}})}}{n}} \right], \quad (\text{A.1})$$

and

$$\log_e W_{\text{MAX}} \sim N \left[\log_e(\overline{W}_{\text{MAX}}), \sqrt{\frac{\sigma^2_{\log_e(W_{\text{MAX}})}}{n}} \right], \quad (\text{A.2})$$

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

Appendix B: Photosynthetic Rate for Early and Late Sockeye Salmon Stocks of the Stuart Lakes Complex

Quantifying normal distributions to describe PR_{TOTAL} for the rearing habitats of the early and late sockeye salmon stocks of the Stuart lakes complex required additional analysis because both stocks rear within Trembleur Lake in addition to Stuart (late) or Takla (early) Lake. There are no abundance estimates for juvenile sockeye salmon rearing in the individual lakes in the Stuart lakes system, so we apportioned the nursery habitat of Trembleur Lake between the two stocks by making various assumptions and using stock-specific estimates of escapement. We assumed that juveniles rear in the lake directly below their natal stream (J. M. B. Hume, personal communication). This means that juveniles of each stock have exclusive use of nursery habitat in either Stuart or Takla Lake and also use some portion of Trembleur Lake habitat (J. M. B. Hume, personal communication). 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, we calculated the relative proportion of spawners from each stock that used streams flowing into Trembleur Lake. On average, 26% of the spawners using these streams in years of high abundance were from the early stock and 74% were from the late stock. Assuming (1) equal egg deposition per female and equal egg-to-fry survival rates between stocks and (2) equal consumption of prey among individual fry, the estimated index of lake productivity (total seasonal PR)

for Trembleur Lake was apportioned to each stock based on the relative abundance of spawners.

The $\log_e(\overline{\text{PR}}_{\text{TOTAL}})$ representing the nursery habitat for each stock is thus a function of the $\log_e(\overline{\text{PR}}_{\text{TOTAL}})$ for the two lakes contributing to each stock's habitat:

$$\begin{aligned} \log_e[\overline{\text{PR}}_{\text{TOTAL}}(\text{early Stuart})] \\ = \log_e[\overline{\text{PR}}_{\text{TOTAL}}(\text{Takla}) \\ + 0.26 \cdot \overline{\text{PR}}_{\text{TOTAL}}(\text{Trembleur})], \end{aligned} \quad (\text{B.1})$$

and

$$\begin{aligned} \log_e[\overline{\text{PR}}_{\text{TOTAL}}(\text{late Stuart})] \\ = \log_e[\overline{\text{PR}}_{\text{TOTAL}}(\text{Stuart}) \\ + 0.74 \cdot \overline{\text{PR}}_{\text{TOTAL}}(\text{Trembleur})]. \end{aligned} \quad (\text{B.2})$$

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

$$\begin{aligned} \text{var}(\text{early Stuart}) \\ = \text{var}(\text{Takla}) + 0.26^2 \cdot \text{var}(\text{Trembleur}), \end{aligned} \quad (\text{B.3})$$

and

$$\begin{aligned} \text{var}(\text{late Stuart}) \\ = \text{var}(\text{Stuart}) + 0.74^2 \cdot \text{var}(\text{Trembleur}). \end{aligned} \quad (\text{B.4})$$

Variance for each contributing lake was computed from the SD in $\log_e(\text{PR}_{\text{TOTAL}})$ (equation A.1).

Appendix C: Details of the Bayesian Photosynthetic Rate Method

For each lake or stock, we applied each step of the Bayesian PR method (equations 1–3) iteratively across the full range of possible parameter values. For example, for each lake i we computed 8,000 $\log_e(\text{SB}_{\text{MAX}_i})$ values from equation (1), which resulted from each possible combination of the 20 discrete values of $\text{PR}_{\text{TOTAL}_i}$ with each of the 400 discrete pairs of δ and γ . Also, for each equation, the probability (P) associated with each possible outcome was the product of the probabilities of the components. For example,

$$P[\log_e(\text{SB}_{\text{MAX}_j})] = P(\theta_k)P[\log_e(\text{PR}_{\text{TOTAL}_m})], \quad (\text{C.1})$$

where $P[\log_e(\text{SB}_{\text{MAX}_j})]$ is the computed probability for each possible $\log_e(\text{SB}_{\text{MAX}_i})$ value for $j = 1\text{--}8,000$;

$P(\theta_k)$ is the probability associated with a set of δ and γ parameter values for $k = 1\text{--}400$; and $P[\log_e(\text{PR}_{\text{TOTAL}_m})]$ is the probability associated with a $\log_e(\text{PR}_{\text{TOTAL}_i})$ grid point for $m = 1\text{--}20$.

To make calculations in the subsequent step manageable, we described results from equations (1) and (2) with 20-grid-point discrete distributions and associated probabilities, standardizing solutions such that discrete probabilities summed to one. At the end of step 3, we exponentiated $\log_e(\text{EFS}_{\text{MAX}})$ values for each lake to obtain target escapement estimates in terms of EFS abundance. Percentile and precision estimates were computed from the final 8,000-grid-point distributions.