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Summary of a Benchmark Analysis for Lake Sockeye CUs in the Skeena Watershed

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Glossary of Terms

Bayesian refers to methods in probability and statistics based on degree-of-belief interpretation of probability. In traditional (i.e., frequentist) statistics, a hypothesis can only be true or false and the probability of being incorrect about the true/false designation is computed. Bayesian statistics has the advantage of assigning a 0-1 probability for the hypothesis directly. In stock-recruit analysis, Bayesian statistics allows the computation of probabilities for a wide-range of stock-recruit curves and associated benchmarks for any data set.

Brood Year is the year that a group or cohort of animals was born in. For example, Sockeye salmon that are 4 years old returning in 2010 were from the 2006 brood year.

Carrying Capacity is the maximum population size that can be sustained indefinitely in the absence of harvest.

Harvest Rate is the proportion of a population removed by harvest techniques like fishing.

Hierarchical Bayesian Models (HBMs) are a class of Bayesian models well suited to the analysis of data collected at different levels of aggregation. For example, in stock-recruit analysis, we may have data from individual conservation units, but may be most interested in the variation in a parameter (stock productivity) or derived parameters (optimal harvest rate) across units. Standard techniques used either assume that the data from each unit are completely independent, or aggregate the data and estimate only one parameter for all units. Hierarchical models provide an efficient way of pooling the information from different units without assuming they belong to the same population.

Maximum Sustainable Yield, or MSY is the largest yield (catch) that can be taken from a stock over an infinite period. The stock size that produces MSY (S_{MSY}) is the abundance that maximizes the population growth rate.

Overfishing occurs when fishing mortality has reached a level where the stock can no longer produce enough juveniles to replace itself. As a result, the abundance of the population will decline but will not necessarily be extirpated. Overfishing can be defined as any harvest rate (U) that is greater than the rate which maximizes yield ($U > U_{msy}$, note U_{opt} is equivalent to U_{msy}), or defined based on the more severe situation where the harvest rate limits the spawning stock to the point where so few juveniles are produced that the population will eventually be extirpated.

Photosynthetic Rate is the rate at which sugars are produced in plants and algae during photosynthesis. For algal production, it is often expressed in units of mg carbon fixed per unit area (e.g. m^2) per unit time (e.g. hr).

Recruitment is the process where juvenile organisms survive and are added to a population of interest. In salmon management, recruitment usually refers to the sum of adults caught in the fishery and that escape the fishery and can potentially spawn.

Sgen is the escapement that is sufficient for the population to recover to Smsy (the escapement that maximizes yield) in one (Sgen1) or two (Sgen2) generations.

Stock Productivity is the maximum ratio of recuits produced per spawner. This rate occurs near the origin of the stock-recruit curve where there are no density-depdendent effects on mortality. Graphically, stock productivity is the slope of the stock-recruitment curve at the origin. The harvest rate that maximizes yield is determined solely by stock productivity.

Stock-Recruitment Models are relationships that predict the expected number of individuals in one generation as a function of the number of individuals in the previous generation. There are a variety of forms of such models, with the Ricker and Beverton-Holt models being some of the most common.

Introduction

The intent of this brief report is to describe the results of a stock-recruit analysis focused on the development of possible benchmarks for Skeena lake sockeye CUs. This effort is part of broader objectives to estimate benchmarks and status for all CUs in the Skeena watershed. Some of the methods and approaches used here will apply to non-sockeye CUs in the Skeena, so a review of the analytical approach used for one species, where the data are relatively good, is a logical beginning. This work has not been vetted or endorsed by stakeholders and is an independent analysis commissioned by the Pacific Salmon Foundation. The benchmarks and status assessments presented in this report may change due to inputs from stakeholders and changes to the data that is the foundation of this analysis (e.g., changes to recruitment and harvest rate estimates based on analysis of in-river data).

Data

There are 31 lake sockeye CU's in the Skeena of which 16 have escapement data (Table 1). The stock-recruit data used here was based on escapement and recruitment estimates prepared by English et al. (2011, LGL) in consultation with S. Cox-Rogers and D. Peacock (DFO). Recruitment associated with each brood year escapement was determined based on estimates of total exploitation rate by return year and the average age compositions across years. In the case of lake sockeye in the Skeena, there is age information for 8 CUs. Age proportions for CUs with age data were mapped to CUs without age data by LGL (K. English) and DFO (Peacock). Due to missing escapement data in some years, recruitment for some brood years (especially latter ones) was incomplete. Only brood years where 95% or more of the age composition was included in the recruitment estimate was used in this analysis (see N-SR column in Table 1). Asitka had escapement data but was not included in the stock-recruit analysis because none of the recruitment estimates met the criteria (owing to missing escapement data). Escapement trends for all CUs included in the stock-recruit analysis are show in Figure 1.

Data on photosynthetic rate (PR) and other information (predators, smolt size) was used as auxiliary information in the stock-recruit analysis (see methods below). Estimates of Smax, the escapement that maximizes recruitment, determined from a PR-based model and other information, were taken from Cox-Rogers et al. (2010). Estimates of Smax from the PR model are shown in Table 1.

For the detailed analysis of Babine Lake sockeye data, we use updated enhanced and un-enhanced escapements into Babine Lake (1970-2010) to break apart the Babine brood year recruit series (Table 7 of Cox-Rogers and Spilsted 2012) into enhanced (with and without surplus) and unenhanced wild components. As age composition data were available for each year in the time series, so we used the year-specific age compositions to estimate returns for each brood year. Brood year fence count proportions of enhanced and unenhanced runs arriving at Babine Lake were first applied to the brood year returns by age to split apart Babine brood year production into enhanced and unenhanced components. We then estimated stock-recruit relationships for the following combinations:

1) All recruits vs All Babine Lake escapement (including enhanced surplus)
2) All recruits vs All Babine Lake escapement (not including enhanced surplus)
3) Early wild recruits vs Early wild escapement
4) Mid wild recruits vs Mid wild escapement
5) Late Wild Recruits vs Late wild escapement.

Methods

The following form of the Ricker model was used to predict recruitment as a function of escapement,

1) $$R_{i,t} = S_{i,t}\, e^{\alpha_i - \beta_i S_{i,t} + \omega_{i,t}}$$

where, i and t denote indices for CU and brood year, respectively, R is recruitment, S is the brood escapement for that recruitment, α is the log of the initial slope of the stock-recruitment curve (recruitment in the absence of density effects, often termed productivity), β is the rate at which recruitment declines with increasing escapement (often called the density-dependent term), and ω is a randomly distributed error term with mean 0 and standard deviation σ_i (Fig. 2).

Under this form of the Ricker relationship, $1/\beta$ is the spawning size which maximizes recruitment (i.e., Smax).

Two methods were used to estimate stock-recruitment relationships from the available data. First, the Ricker relationship was re-arranged to predict recruits-per-spawner (R/S) and log-transformed so that linear regression could be used to estimate the parameters,

$$2)\quad \log\left(\frac{R_i}{S_i}\right) = \alpha_i - \beta_i S_i + \omega$$

where, t has been omitted here and from subsequent equations for notational simplicity. We term such estimates independent linear values, since they were generated by linear regression and were independently estimated from each other.

A hierarchical Bayesian model (HBM) was the second method used to estimate stock-recruit parameters. Under this method, equation 2) is used to estimate CU-specific parameters, but the estimation further assumes that α_i estimates for each CU are exchangeable and come from a common log-normal distribution (termed a hyper-distribution),

$$3)\quad \alpha_i \sim \ln(\mu_\alpha, \sigma_\alpha)$$

where, ~ln denotes that α_i is a stochastic variable drawn from a lognormal distribution with mean μ_α and standard deviation σ_α. The parameters of this distribution (μ_α, σ_α), termed hyper parameters, are estimated along with the CU-specific values. CUs with limited stock-recruit data, or where there is considerable uncertainty in α_i estimates due to the pattern of stock-recruit data (e.g., limited variation in escapement values), will contribute less information to the hyper distribution for α compared to those CUs with where α is better defined. The hyper-distribution also affects the CU-specific estimates of α. CUs where α is poorly defined will be ‘shrunken’ towards the mean of the hyper-distribution to a greater extent than those where α is better defined. The HBM includes the use of uninformative prior distributions for the hyper parameters of α (hyper-priors) and σ_i, and informative priors for CU-specific estimates of β_i. Priors for β_i were assumed to be lognormal, with the mean determined by the PR-based estimate of Smax (Table 1), and a CV set to informative (0.3) or uninformative (3) values.

There are three advantages of the HBM compared to the linear regression method. First, the HBM incorporates prior information on carrying capacity (via PR-based Smax estimates). In most stock-recruit data sets, estimates of α and β are confounded. That is, the data can be almost equally well-described by a productive population (large α) with strong density dependence (large β) or visa-versa. This leads to considerable uncertainty in derived parameters used as benchmarks, like the escapement or harvest rate that produces MSY. By including additional information in the stock-recruit estimation via priors on β_i, this uncertainty can be reduced. The second advantage of the HBM is improved estimation of the hyper distribution of the log of stock productivity (α). In this example, the hyper-distribution is needed to estimate productivity values for the 16 of 31 lake sockeye CUs without stock-recruitment data (Table 1). One could estimate the parameters of this distribution based on independent estimates of α_i (generated by the independent linear regression method), however that distribution would be 'contaminated' by poorly defined estimates for some CUs. The HBM properly weighs the contribution of each CU to the hyper-distribution based on the amount of information in each α_i estimate. Finally, the HBM has the advantage of providing more reliable estimates of α_i for CUs where this parameter is poorly defined because the hyper-distribution acts as a prior for the CU-specific estimates.

A variety of benchmarks can be determined from the stock-recruitment parameter estimates for each CU generated from the HBM (Fig. 2). Following recommendations used for Fraser sockeye (Grant et al. 2010), Sgen1, the escapement that allows the stock to recover to the escapement that maximizes catch in one generation, was used for the lower benchmark. As an alternative lower benchmark, we computed the escapement that allows the stock to recover to the escapement that maximizes catch in two generations (Sgen2). The upper benchmark was computed as the escapement that maximizes catch (Smsy). Escapements beyond Smsy may produce additional ecosystem benefits. To account for this, we used Smax as an alternative for the upper benchmark. We also compute the harvest rate that would maximize yield for each CU for which stock-recruit data is available, generated from α_i values (Uopt). Finally, random draws of α from the posterior distributions of hyper-parameters (μ_α, σ_α) were used to estimate distributions of α values and optimal harvest rates (Uopt) for lake sockeye CUs within the Skeena without stock-recruit data.

Stock status was determined by comparing the average escapement from 2004-2008 with Sgen1 and Smsy, and exploitation status was computed by comparing the average exploitation rate over this period with Uopt. The 5 yr. period from 2004-2008 was selected because it was the last five years in the data series where both escapement and exploitation rate estimates are consistently available for the CUs used in the analysis.

We estimated stock-recruit parameters for the five strata in the detailed Babine Lake sockeye analysis independently using a Bayesian model with uninformative priors on Smax and based on linear regression.

Results

Stock-recruit plots for Skeena lake sockeye CUs show typical 'shotgun' patterns in the data (Fig. 3). Only 10 of 15 CUs had more than 15 data points. Given these characteristics, it is not surprising that there was large uncertainty in the shape of the stock-recruit curves, even when they were estimated from the HBM which included prior knowledge about Smax and exchangeability in α_i estimates (note wide credible intervals in Fig. 3). Stock-recruit curves based on independent and linear estimation (gray lines) were similar to those estimated from the hierarchical Bayesian model (HBM) for CUs where the stock-recruit based-estimates of Smax were consistent with estimates from the PR model (e.g. Asuklotz, Babine, Stephens). However, the PR-based estimate of Smax were much greater for other CUs (e.g. Morice, Tahlo/Morrison), which in turn led to lower estimates of productivity from the HBM relative to the linear independent model.

Estimates of α_i and β_i were confounded in most cases, which is not surprising given the limited information about productivity and density dependence in the stock-recruit data (Fig. 4). The use of informative priors for β_i reduced the extent of the correlation between parameters (results not shown for brevity). The posterior distributions of β_i were generally very close to the prior distributions (Fig. 5), either because the prior and stock-recruit based estimates were consistent, or because of strong confounding between α_i and β_i estimates. We examined the temporal trend in residuals from the stock-recruitment curve to evaluate whether there was evidence for temporal changes in productivity (Fig. 6). Ten of 15 CUs showed a negative trend in residuals through time indicating that productivity has been declining, however a significant negative slope was found for only two CUs (Azuklotz and Swan). Five of 15 CUs showed a positive time trend in residuals, but only one of these cases was significant (Motase). Statistical evidence for temporal changes in productivity was therefore quite limited, however the sample size for many of the CUs was low and the extent of variation in residuals was often very high, so statistical power to detect such trends was poor.

Stock productivity (e^{α}, the initial slope of the stock-recruit curve) is a key management parameter as it determines the harvest rate that maximizes yield. There was considerable uncertainty in α_i estimates from the HBM with the exception of Babine and Kitsumkalum (Fig. 7). Most independent estimates of α_i were shrunk towards the mean of the hyper distribution, and the extent of shrinkage was quite large for many CUs where information to estimate stock-recruit parameters was limited (e.g., Kitwancool, Fig. 7). This shrinkage is not surprising considering the uncertainty in α_i estimates. The hyper-distribution of α from the HBM and a lognormal distribution fit to independent estimates was similar, although the latter had a slightly larger mean and showed greater variation (solid and dashed lines in Fig. 7). Thus, the effect of the hierarchical α-exchangeability assumption appears to be quite modest. The expected value for the hyper distribution of α from the HBM was 1.3 (3.7 recruits/spawner) with a CV of 0.46 and there was modest uncertainty in the hyper-distribution (Fig. 8). Based on random draws from hyper-parameters, 95% of α estimates for lake Sockeye within the Skeena watershed were between 0.48 and 3.5 with a median of 1.3 (Fig. 9, top). Optimal harvest rates translated from random draws of α produced a distribution with a mean of 0.54 and a 95% credible interval of 0.22-0.88 (Fig. 9, bottom). The wide range in optimal rates reflects the considerable variation in productivity among CUs estimated by the HBM.

Benchmarks for the 15 lake sockeye CUs with stock-recruitment data are presented in Table 2. These estimates were determined based on posterior distributions of α_i and β_i and reflect the uncertainty in these estimates. The ratio of Sgen1 to Smsy ranged averaged 0.36 and the ratio of Smsy to Smax averaged of 0.53. Optimal harvest rates ranged from 0.38 to 0.74 across CUs with an average of 0.55. Bear, Lakelse, and Johnston had the lowest productivities and optimal harvest rates of all CUs. There was very large uncertainty in optimal harvest rates within CUs due to uncertainty in α_i, with an average relative error (2 * difference in 95% credible interval / mean) across CUs of 1.22. Sgen1 was on average 3-fold greater than Sgen2 and differences between these two lower benchmarks increased with stock productivity.

Status for the 15 lake sockeye CUs with stock-recruitment data was determined by comparing the average escapement and total exploitation rate between 2004 and 2008 with estimates of Sgen1 (lower), Smsy (upper), and Uopt benchmarks (Table 3). Probabilities of being in red (below Sgen1), amber (Sgen1-Smsy), and green (>=Smsy) status zones for each CU reflect the uncertainty in Sgen1 and Smsy values generated from the posterior distributions of α_i and β_i from HBM. Similarly, the probability of over fishing between 2004 and 2008 was computed by comparing average exploitation rate over this period relative to the posterior distribution of Uopt values. Six of 14 CUs where status could be assessed (Johnston was excluded as there was no exploitation or escapement data available for the 2004-2008 period) had a probability of 0.5 or higher of being in the "red" status zone (Bear, Kitwancool, Morice, Motase, Swan, Tahlo/Morrison) with the remaining having higher probabilities in amber (Babine, Lakelse) or green (Azukoltz, Alastair, Damshilgwit, Kitsumakalum, Mcdonell, Stephens) zones. The probability that the 2004-2008 exploitation rate exceed the rate that produces MSY was very low for all CUs except Bear (p=0.31). Time trends in abundance and exploitation rate relative to the benchmarks are shown in figures 1 and 10, respectively. With the exception of Bear, the historical average exploitation rate has been at or less than the estimated optimal rate (Fig. 11). There was a significant positive relationship between the optimal exploitation rate and the historical average among the 15 CUs (r=0.55, p=0.03) indicating that management has been able to reduce harvest rates on less productive populations and increase it on more productive ones. Although all CUs have likely been under exploited over the last 5 years of available data (2004-2008) , Bear, Kitwancool, Morice, Motase, Swan, and Tahlo/Morrison have the highest probability of being in the red abundance zone given their recent escapements (Fig. 12).

The strength of the prior on Smax could have important effects on benchmark and status assessments since it effects estimation of productivity and density dependent parameters in the Ricker model. The HBM was rerun with the default informative prior with a CV of 0.3 for all CUs changed to an uninformative value of 3. Surprisingly, there was little effect of the prior on the expected estimates of α_i; eight of 15 CUs showed a small increase in expected values under an uninformative prior while seven showed a very small decrease (Fig. 13). Uncertainty in CU-specific Ricker parameters increased under the uninformative prior (note increased vertical width of credible interval relative to horizontal width). The hyper-distributions generated under both prior information scenarios were similar (Fig. 14). This occurred because effects of the Smax prior were limited for the more informative CUs that had the greatest influence on the hyper distribution for α.

The majority of CUs had only one or two years of age data (Table 1), so all the recruitment estimates used in this analysis were computed assuming that age composition does not vary among years. However, one would expect substantial variation in age composition due solely to variation in the strength of some brood years, let alone density dependent effects on age-at-return. For example, a strong brood in 2000 would result in a higher than average return of age 3 fish in 2003, age 4 fish in 2004, and age 5 fish in 2005. Using an across-year average age composition to compute recruitments, as done for all CUs in the HBM analysis, would lead to a reduction in the extent of variation in recruitment among brood years, which could affect stock-recruitment parameter estimates. To evaluate this effect, we compared benchmarks for the Babine and Nass sockeye CUs estimated using recruitments generated by year-specific and average age composition estimates. This analysis could only be done for these two CUs as they were the only ones with sufficient age information (e.g. see Table 1). Differences in benchmarks were substantial in the case of Babine sockeye where productivity decreased and Smax increased based on year-specific age compositions relative to values generated using the average age composition (Table 4). This resulted in a 55% increase in Sgen1 and a 12% decrease in Uopt under year-specific age composition. The effect was particularly strong for the lower confidence limit for Uopt (0.51 vs. 0.36). However, differences in benchmarks for the Nass comparison were small.

The detailed analysis of Babine Lake sockeye stock-recruit data showed substantial differences in productivity among some stock groups. Examination of the average escapement for the five stock groups examined (Table 5) and the stock-recruitment curves (Fig. 15) showed that the aggregate stock (with our without surplus escapement to the spawning channels) is dominated by enhanced fish, with wild stock groups comprising 2-6% of the aggregate. As expected, the productivity for the aggregate stock (with or without surplus) was higher than productivity for any of the wild stocks. This occurred because the aggregate was largely composed of enhanced fish which have higher survival in the spawning channels. Harvest rates which maximize yield averaged 0.45 over the 3 wild stock components, compared to 0.55 and 0.68 for the aggregate stock with and without surplus escapement, respectively. The early wild run appears to be the least productive stock, and has an optimal harvest rate that is almost 0.27 units lower than the optimal rate for the aggregate stock without surplus escapement. There is considerable potential to overharvest the less productive wild stock components, and especially the early run, if these stocks are fished at an exploitation rate that maximizes yield for the aggregate.

Summary

Assuming the posterior distribution of Ricker stock-recruit parameters generated for the 15 lake sockeye CUs in the Skeena are unbiased, this analysis leads to the following conclusions:

1. 6 of 14 CUs (43%) where status could be assessed based on recent average escapement (2004 and 2008) were most likely in the 'red' status zone (below lower benchmark Sgen1);

2. There was very little evidence to suggest that any of the 15 lake sockeye CUs have been overfished, and the most recent exploitation rates (2004-2008) are approximately one-half of the rates which would maximize yield. That said, any harvest of stocks in the red zone reduces the rate at which they can potentially recover;

3. There is very wide variation in productivity among CUs, indicating wide variation in exploitation rates that optimize yield. If these CUs are fished under a common exploitation rate, considerable losses in yield will be required to protect weaker stocks.

4. There was wide variation among stock groups within the Babine Lake system, with wild stocks being less productive than the aggregate, which is dominated by fish produced

from the spawning channels. Thus, wild stocks will be overfished if the exploitation rate on Babine Lake sockeye is set to maximize yield for the aggregate.

There were modest differences in benchmarks based on year-specific age composition compared to across year-averaged values for the Babine CU, but not for Nass CU. The different response of these CUs was likely driven by the extent of differences in brood strength among years, and perhaps other factors (exploitation history, contrast in stock-recruit data). Time series and observation error biases could also lead to overestimates of stock productivity and underestimation of carrying capacity, which would in turn affect the benchmarks. A logical next step in this analysis is to conduct a simulation exercise to estimate the potential extent of the biases for benchmarks within the context of Skeena River sockeye data. We suspect that time series and observation error biases could be substantive due to the short-time series of stock-recruit data combined with implementation of what generally appears to be a fixed exploitation rate strategy. However, the use of semi-informative priors on carrying capacity and the use of the HBM could reduce the extent of the bias.

The use of benchmarks developed in the analysis for future management depends on the assumption the historical data used to estimate them are representative of future conditions. Our analysis indicates that for the most part, Skeena sockeye have not been overexploited and that escapements over the last decade or so for some CUs are low because productivity has dropped, likely because marine survival is lower. There was very weak statistical evidence for declining productivity based on the temporal trend in residuals from the stock-recruit curves, but the power of these tests for most CUs was generally low due to limited sample size. The fundamental question is whether any productivity changes are permanent or temporary. If the change is permanent, then use of benchmarks developed in this analysis for future management is not appropriate because they are based on data from an era that does not represent future conditions. One could argue that, in the absence of convincing scientific data suggesting that the productivity change is permanent, there is no reason to assume that it is, and therefore that benchmarks developed in this analysis can be used for future management. However, based on the precautionary principle, one could also argue that we should assume that a permanent drop in productivity has occurred and benchmarks should be adjusted to reflect this fact. While this latter argument is also logical, we do not know of any defensible methodology to determine which data are representative of future conditions and which are not. Time series methods, like the Kahlman filter approach, provide estimates of how much productivity could be changing over the historical time series (conditional on some restrictive assumptions) but do not provide a reliable means of forecasting what productivity will be in the future. In addition, the low sample size of most sockeye CUs in the Skeena makes it difficult to apply such a model even if it was useful. In our view, concerns about the nuances of statistical methodology, or the accuracy of historical data, are relatively minor compared to the issue of whether historical information is representative of future conditions. This is a fundamental issue that needs to be addressed by stakeholders involved in Skeena River sockeye management.

The hierarchical Bayesian model provides a defensible means to estimate the distribution of productivities for the 16 of 31 lake sockeye CUs in the Skeena that do not have stock-recruitment data. The hyper-distribution of productivity can be used to define optimal harvest rates for these CUs and could also be used to drive a management strategy evaluation model (similar to Cox-Rogers et al. 2010 as proposed by Walters and Hawkshaw, UBC). If PR-based methods are used to estimate Smax, it would be possible to combine them with the α hyper-distribution to generate abundance-based benchmarks such as Sgen1 and Smsy. However, considering there is no historical data to compare to these benchmarks, and the likelihood of collecting reliable information on escapement for these CUs in the future is probably low, there does not appear to be a strong rationale to produce them. Furthermore, the lower and upper benchmarks used here and in other analyses (e.g., Grant et al. 2010) are quite arbitrary and fraught with uncertainties about the ecological benefits of higher escapements and the population risks associated with low escapements. Focusing a future management strategy evaluation on fixed exploitation rate strategies, or variable exploitation rates based on the abundance of weak stocks with escapement data, seems like the most logical way to proceed.

The analyses we have conducted assumes that the escapement and recruitment values are estimated without any bias. In fact, the expansion of counts to escapement estimates for some systems, and the changes in these expansion factors over time in cases where methodology changed, are quite uncertain. A similar argument applies to the recruitment estimates (see English et al. 2011). Incorporating these uncertainties directly in the modelling is not possible because there is no information to estimate the potential extent of bias or expansion uncertainty.

However, we could repeat the analysis under alternate assumptions used to generate the escapement and recruitment data to evaluate the sensitivity of benchmarks to these assumptions. Factors affecting the scale of the data (expansions) will effect abundance-based benchmarks (e.g. Sgen1, Smsy) but are unlikely to affect harvest rate one (e.g., Uopt). This is another reason to focus management strategy evaluations on fixed exploitation rate strategies rather than on policies which require an understanding of absolute abundance.

A number of revisions to the existing analysis and extension are possible. First, the stock-recruit analysis presented here could be repeated based on updated values of the CVs on Smax for individual CUs, as the confidence in the PR-based estimates among CUs is variable (see Cox-Rogers et al. 2010). That said, it is unlikely that varying the CVs in Smax among CUs will have a large effect considering the relatively small difference associated with the 10-fold change in the CV on Smax explored in this analysis. Second, the HBM analysis could be repeated based on revised estimates of escapement and recruitment based on adjustments to expansion factors, exploitation estimates, and in-river harvest data. Third, the HBM analysis could be revised so that Babine Lake sockeye stocks are broken-out into 4 components (enhanced + 3 wild stocks) rather than treated as an aggregate as done in the current analysis. Guidance from DFO and stakeholders is required here. Fourth, the simulation exercise reviewed above is needed to assess the potential for bias in benchmarks and to develop adjustments to correct for these biases if possible. Finally, a management strategy evaluation (MSE) model, similar to Cox-Roger et al. (2010) or the analysis conducted by Carl Walters as part of his work on the Independent Scientific Review Panel, is needed to evaluate the performance of alternate harvest rules. The benchmarks developed in this analysis (or revised ones from a future analysis) could be used in the MSE model to track performance, or to define harvest rate rules.

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Table 1. List of Skeena lake sockeye Conservation Units (CUs). N-SR denotes the number of stock-recruit data points for CUs with escapement and recruitment data. N-Age denotes the total number of age samples, with values in parentheses denoting the number of years where age data are available. PR-based Smax values are estimates of the spawning stock size that produces maximum recruitment based on the photosynthetic rate model and other factors (from Cox-Rogers et al. 2010). These estimates are used as priors on β_i in the stock-recruit analysis. Note that escapement estimates for Kitwancool used in this version of the report are 2-fold lower than those used in the previous version after discovering an error in the escapement expansion for this stock. The correction also resulted in a reduction in recruitment.

CU Name	N - SR	N - Age	PR-based Smax
Alastair	21	151 (2)	23,437
Aldrich			
Asitika			
Atna			
Azuklotz	13		5,933
Babine	23	17,489 (32)	1,808,245
Bear	6	46 (1)	40,532
Bulkley			
Damshilgwit	3	67 (1)	423
Dennis			
Ecstall/Lower			
Footsore			
Johanson			
Johnston	4		4,125
Kitsumkalum	19		20,531
Kitwancool	3	299 (4)	36,984
Kluatantan			
Kluayaz			
Lakelse	14	194 (1)	35,916
Maxan			
Mcdonell	6		4,072
Morice	15	98 (1)	191,362
Motase	10		1,764
Nilkitkwa			
Sicintine			
Slamgeesh			
Spawning			
Stephens	12		7,069
Sustut			
Swan	10	100 (1)	21,432
Tahlo/Morrison	18		44,587

Table 2. Preliminary benchmarks for Skeena lake sockeye Conservation Units (CU). Sgen1 or Sgen2 are two alternatives that could be used as the lower benchmark. They are the escapements that will allow the population to recover to the stock size that maximizes catch (Smsy) in one and two generations, respectively. Smsy and Smax are two alternatives for the upper benchmark, the latter being the escapement that maximizes recruitment. Prod is equivalent to e^{α}, which is the initial slope of the stock recruitment curve (maximum recruits/spawner). Uopt is the harvest rate which maximizes catch (i.e., the harvest rate at Smsy). Benchmark statistics are based on the CU-specific tock-recruit parameter values from the HBM (mean), as well as the lower and upper 95% credible intervals (LCL and UCL, respectively).

CU	Benchmark	Mean	LCL	UCL		CU	Benchmark	Mean	LCL	UCL
Alastair	Sgen2	1,144	328	2,675		Damshilgwit	Sgen2	30	5	74
	Sgen1	3,251	1,682	5,499			Sgen1	83	34	130
	Smsy	8,655	6,760	11,766			Smsy	225	153	297
	Smax	18,059	11,564	28,585			Smax	453	302	684
	Prod	3.38	2.20	5.20			Prod	3.89	1.80	7.90
	Uopt	0.49	0.34	0.63			Uopt	0.52	0.27	0.73
Azuklotz	Sgen2	214	50	570		Johnston	Sgen2	482	182	822
	Sgen1	905	391	1,690			Sgen1	953	562	1,418
	Smsy	3,586	2,500	5,270			Smsy	1,796	1,066	2,740
	Smax	5,917	3,651	9,445			Smax	5,138	3,202	7,689
	Prod	5.14	2.90	8.20			Prod	2.32	1.50	3.60
	Uopt	0.62	0.46	0.74			Uopt	0.36	0.20	0.53
Babine	Sgen2	80,879	27,850	176,678		Kitsumkalum	Sgen2	781	62	9,971
	Sgen1	307,985	159,214	550,652			Sgen1	3,183	607	36,311
	Smsy	1,072,553	792,052	1,553,761			Smsy	7,941	5,546	12,621
	Smax	1,901,936	1,213,821	3,043,237			Smax	10,840	7,168	18,610
	Prod	4.30	3.10	6.00			Prod	8.19	6.10	10.40
	Uopt	0.57	0.48	0.67			Uopt	0.74	0.67	0.79
Bear	Sgen2	3,435	906	6,990		Kitwancool	Sgen2	3,609	109	46,315
	Sgen1	7,676	3,861	13,409			Sgen1	6,834	1,563	12,269
	Smsy	17,103	6,674	33,180			Smsy	28,730	13,824	49,406
	Smax	42,509	23,341	71,998			Smax	38,734	19,990	64,854
	Prod	2.72	1.50	5.30			Prod	9.30	3.30	17.00
	Uopt	0.40	0.20	0.64			Uopt	0.74	0.49	0.85

Table 2. Con't.

CU	Benchmark	Mean	LCL	UCL		CU	Benchmark	Mean	LCL	UCL
Lakelse	Sgen2	2,024	644	4,389		Stephens	Sgen2	320	65	707
	Sgen1	4,589	2,471	8,275			Sgen1	1,526	576	2,488
	Smsy	9,820	6,518	15,673			Smsy	5,777	4,627	7,512
	Smax	24,480	14,462	44,569			Smax	8,772	6,191	12,955
	Prod	2.70	1.80	4.10			Prod	6.18	3.80	9.20
	Uopt	0.41	0.27	0.56			Uopt	0.67	0.54	0.76
Mcdonell	Sgen2	407	10	4,159		Swan	Sgen2	1,577	573	3,207
	Sgen1	925	155	13,866			Sgen1	4,572	2,487	7,647
	Smsy	2,976	2,205	4,259			Smsy	12,179	7,584	18,608
	Smax	4,032	2,667	6,147			Smax	25,270	15,271	41,180
	Prod	9.17	4.60	16.10			Prod	3.30	2.30	4.70
	Uopt	0.75	0.6	0.85			Uopt	0.49	0.37	0.61
Morice	Sgen2	10,374	3,047	22,907		Tahlo/Morrison	Sgen2	1,796	473	4,465
	Sgen1	30,953	15,335	55,946			Sgen1	6,138	2,502	11,541
	Smsy	88,943	41,143	160,944			Smsy	19,552	10,060	34,336
	Smax	177,773	92,995	305,824			Smax	36,454	17,146	63,496
	Prod	3.55	2.10	6.20			Prod	3.95	2.50	6.00
	Uopt	0.50	0.32	0.68			Uopt	0.54	0.41	0.67
Motase	Sgen2	120	49	240						
	Sgen1	300	163	520						
	Smsy	690	420	1,190						
	Smax	1,594	933	2,743						
	Prod	2.85	2.00	3.90						
	Uopt	0.44	0.32	0.55						

Table 3. Status of Skeena lake sockeye CUs based on comparing the average escapement between 2004 and 2008 relative to Sgen1 (lower) and Smsy (upper) benchmarks. The probabilities associated with each abundance status level were determined from the posterior distributions of Sgen1 and Smsy predicted from the HBM. Also shown is the average total exploitation rate (ER) between 2004 and 2008 relative to the average optimal harvest rate (Uopt) and the probability that the 2004-2008 average has exceeded the optimal exploitation rate. Status could not be computed for Johnston because no escapement or exploitation rate data is available between 2004 and 2008. Status of the Johnston CU could not be assessed because there are no escapement or exploitation rate estimates available between 2004 and 2008.

		Abundance Status					**Exploitation Rate Status**		
		Avg. Esc.	**Red**	**Amber**	**Green**		**Avg. ER**	**Avg.**	**Prob.**
CU		**('04-08)**	**(<Sgen1)**	**(<Smsy)**	**(>=Smsy)**		**('04-08)**	**Uopt**	**OverExp.**
Alastair		10,267	0	0.1	0.9		0.11	0.49	0.00
Azuklotz		3,653	0.00	0.39	0.61		0.39	0.62	0.00
Babine		907,507	0.00	0.82	0.18		0.45	0.57	0.01
Bear		1,648	1.00	0.00	0.00		0.35	0.40	0.31
Damshilgwit		271	0.00	0.09	0.91		0.32	0.52	0.06
Johnston							NaN	0.36	0.00
Kitsumkalum		12,046	0.06	0.04	0.90		0.38	0.74	0.00
Kitwancool		1,768	0.95	0.05	0.00		0.38	0.74	0.00
Lakelse		5,590	0.21	0.78	0.00		0.11	0.41	0.00
Mcdonell		4,683	0.04	0.01	0.96		0.38	0.75	0.00
Morice		20,401	0.85	0.15	0.00		0.20	0.50	0.00
Motase		282	0.50	0.50	0.00		0.32	0.44	0.02
Stephens		11,147	0.02	0.00	0.98		0.25	0.67	0.00
Swan		3,836	0.68	0.32	0.00		0.25	0.49	0.00
Tahlo/Morrison		4,356	0.75	0.25	0.00		0.23	0.54	0.00

Table 4. Benchmarks for Skeena and Nass sockeye CUs where recruitment estimates were computed using the average age composition across years compared with those computed using year-specific age composition. Parameters were estimated from a Bayesian model without prior information on β_i and where α_i estimates were assumed to be completely independent. See Table 2 for definitions of Sgen1, Smsy, Smax, Prod, and Uopt.

	Average Age Composition			**Year-Specific Age Composition**		
Babine						
	Mean	**LCL**	**UCL**	**Mean**	**LCL**	**UCL**
Sgen1	240,879	141,036	392,949	375,605	131,093	1,151,051
Smsy	898,155	708,519	1,199,148	1,001,734	604,099	2,241,124
Smax	1,539,444	1,083,354	2,270,786	2,090,271	974,564	6,003,034
Prod	4.51	3.50	5.90	3.69	2.30	5.70
Uopt	0.59	0.51	0.67	0.52	0.36	0.66
Nass						
	Mean	**LCL**	**UCL**	**Mean**	**LCL**	**UCL**
Sgen1	67,558	13,185	989,525	66,706	12,906	982,925
Smsy	229,575	162,762	355,000	221,080	156,573	352,835
Smax	316,629	198,528	552,986	306,962	194,396	559,613
Prod	8.51	5.00	13.40	8.44	4.90	13.70
Uopt	0.74	0.62	0.83	0.74	0.62	0.83

Table 5. Stock-recruitment parameter estimates and derived management parameters for the total Babine run (with and without inclusion of spawners surplus to the spawning channels) and for 3 wild run components. Average escapement is computed between 1970 and 2005, the period of record for the stock-recruit analysis.

Recruit-Spawner Dataset	Avg. Escapement	α	β	Prod (e^{α})	Smsy	Smax	Uopt
All Babine recruits vs. all spawners+surplus	1,004,173	1.34	6.45E-07	3.8	845,356	1,550,925	0.55
All Babine recruits vs. all spawners (no surplus)	754,001	1.84	1.17E-06	6.3	584,259	856,478	0.68
Early wild recruits vs. early wild spawners	56,358	0.93	7.57E-06	2.5	53,602	132,179	0.41
Mid wild recruits vs. mid wild spawners	19,452	1.13	3.20E-05	3.1	14,848	31,236	0.48
Late wild recruits vs. late wild spawners	240,583	1.12	2.58E-06	3.1	184,135	388,193	0.47

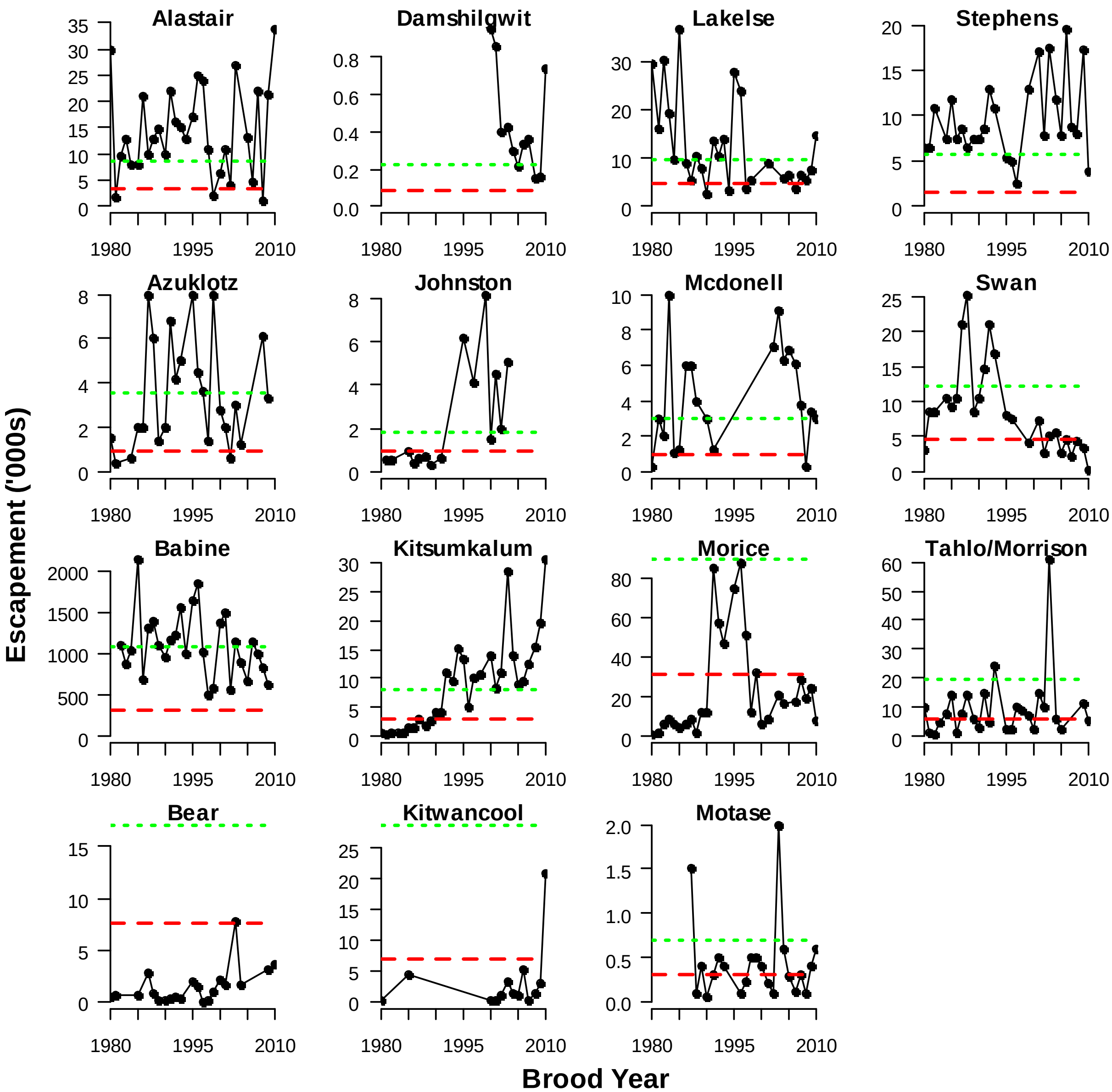

Figure 1. Tim series of escapement estimates for 15 lake Sockeye CU's in the Skeena watershed. These plots show the entire available time series, including a limited number of points which do not have complete recruitment pairs (by brood year) that would be omitted from the stock-recruit analysis. Dashed red lines and dotted green lines denote the estimated lower (Sgen1) and upper (Smsy) benchmarks generated from the hierarchical Bayesian model, respectively.

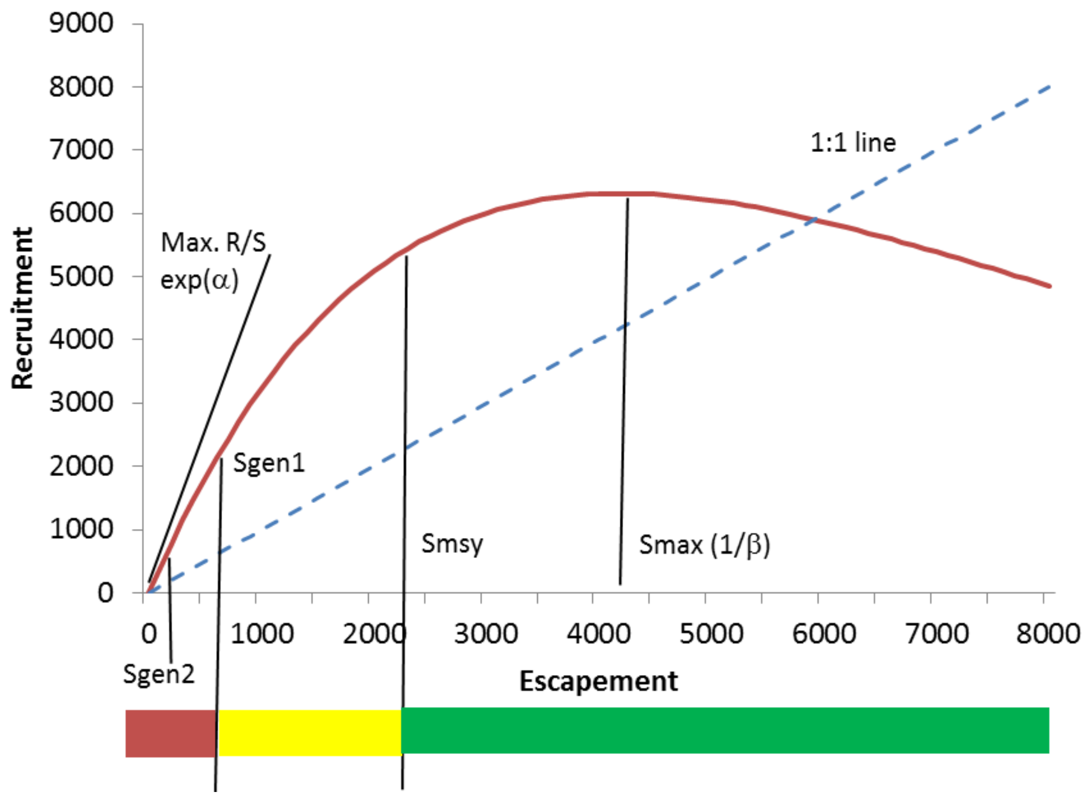

Figure 2. An example of a stock-recruitment relationship showing the abundance-based benchmarks (Sgen2, Sgen1, Smsy, Smax) used in this study as well as the estimate of maximum recruits/spawner that is used to compute the exploitation rate which optimizes yield. Stock productivity is the maximum ratio of recruits (R) to spawners (S) and is the initial slope of the stock-recruitment curve (the Max R/S tangent line). Smsy and Smax are the escapements that maximize catch and recruitment, respectively. Note that maximum catch occurs where the difference between the stock-recruit curve and the 1:1 replacement line is maximized. Sgen2 and Sgen1 are the escapements needed to recover to Smsy in two and one generations respectively. The colored status bar is defined based on escapement relative to Sgen1 and Smsy (red<Sgen1, yellow Sgen1<= and <=Smsy, green > Smsy).

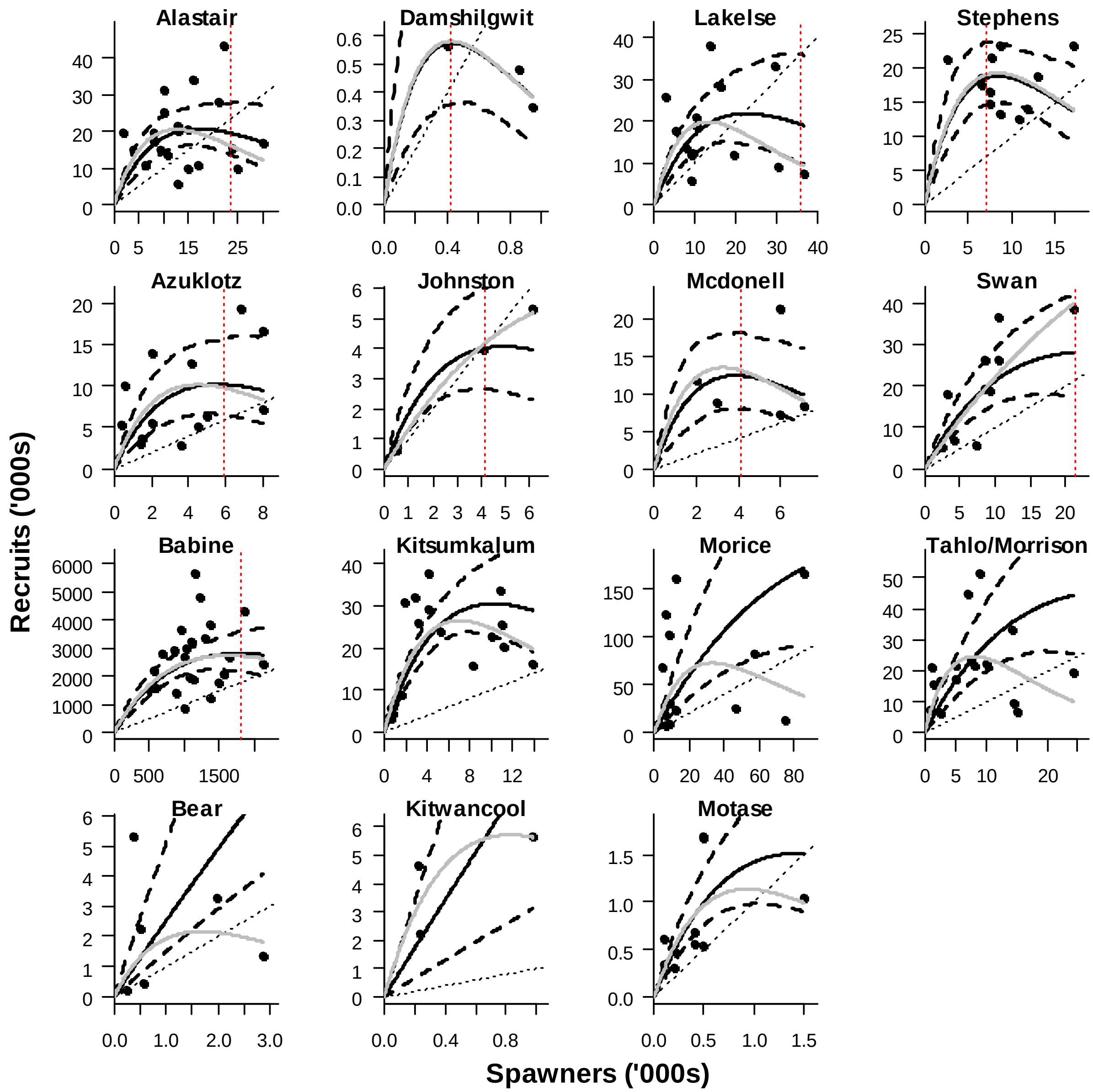

Figure 3. Stock-recruit relationships for lake sockeye CUs in the Skeena watershed. The thick black solid and dashed lines denote the expected relationship and 95% confidence limits from the hierarchical Bayesian Model. The solid gray lines show independent estimate of the relationship based on linear regression (and no effect of the prior on Smax). The thin dashed line represents a 1:1 relationship (replacement), and the vertical dashed red line denotes the mean for the prior on the escapement that maximizes recruitment from the PR model (see Table 1). This latter line is not visible for some CUs because the PR estimate is greater than the maximum escapement recorded and therefore off the x-axis scale. A CV of 0.3 for the prior on Smax was used to generate these results.

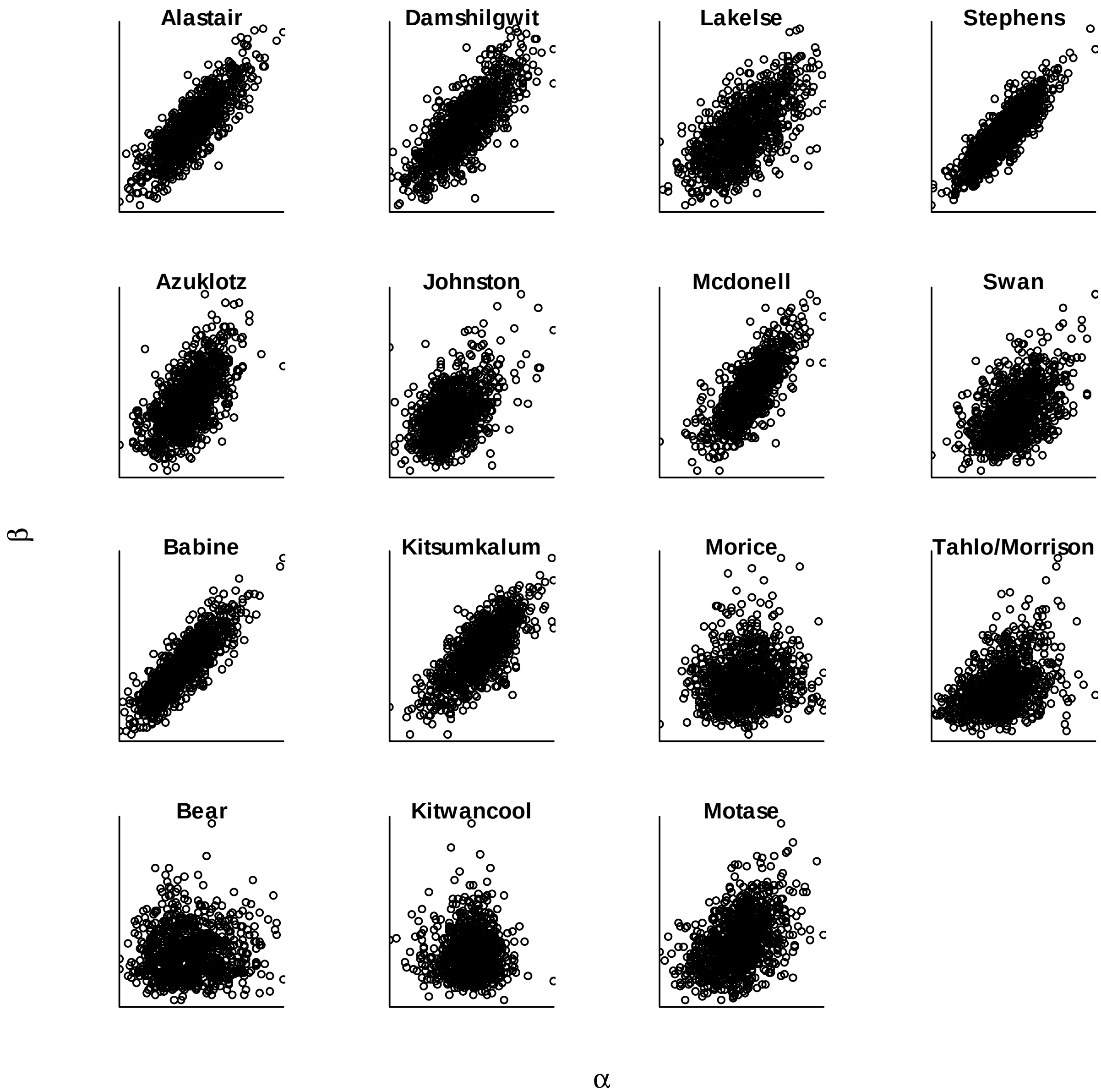

Figure 4. Scatter plots showing samples of Ricker α and β parameters for Skeena lake sockeye CUs from posterior distributions generated from the hierarchical Bayesian model. A CV of 0.3 for the prior on Smax was used to generate these results.

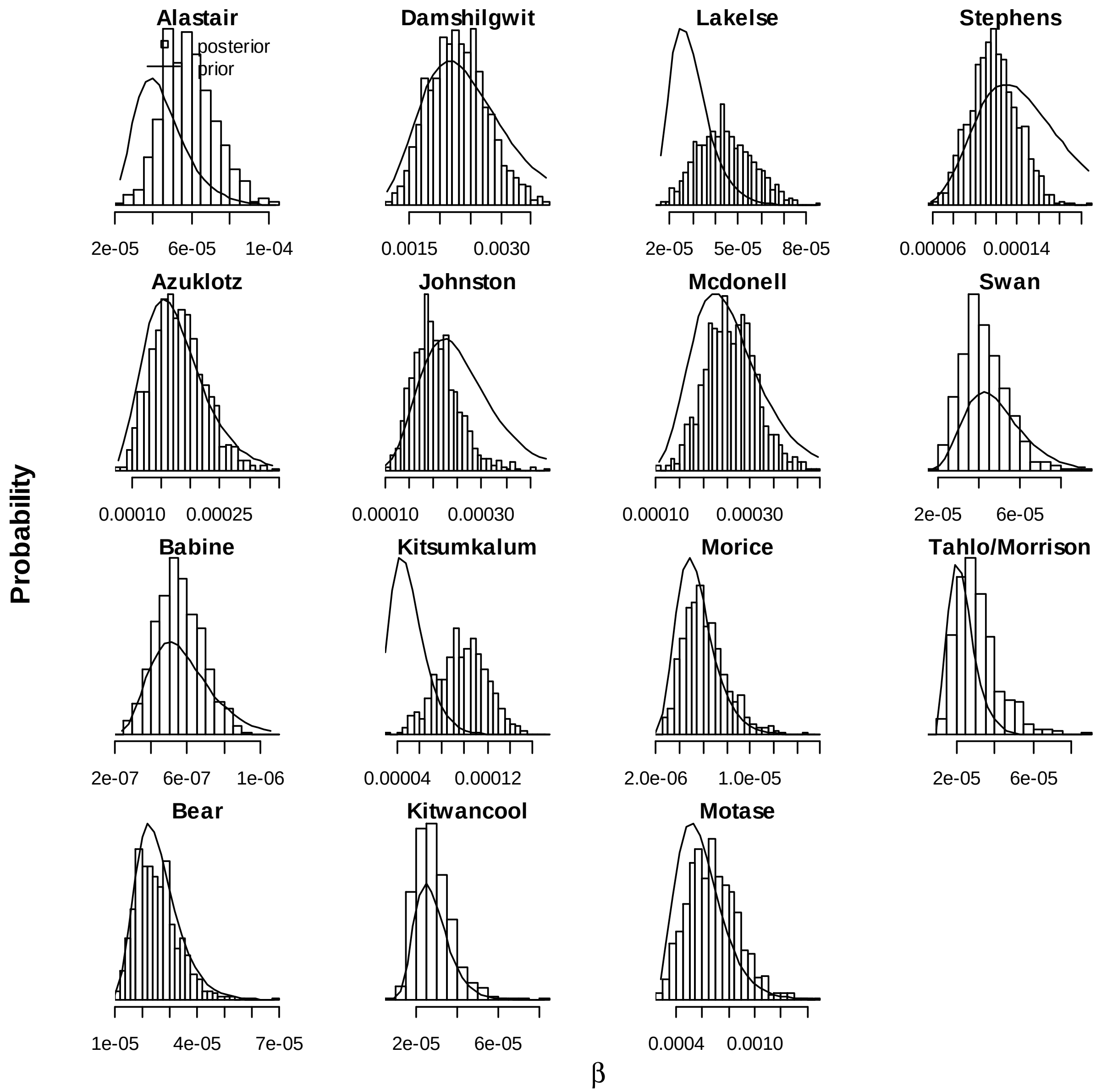

Figure 5. Comparison of the posterior distributions of the Ricker β parameter from the hierarchical Bayesian model (bars) with the prior distribution on Smax (converted to β) from the photosynthetic rate model (lines). A CV of 0.3 for the prior on Smax was used to generate these results.

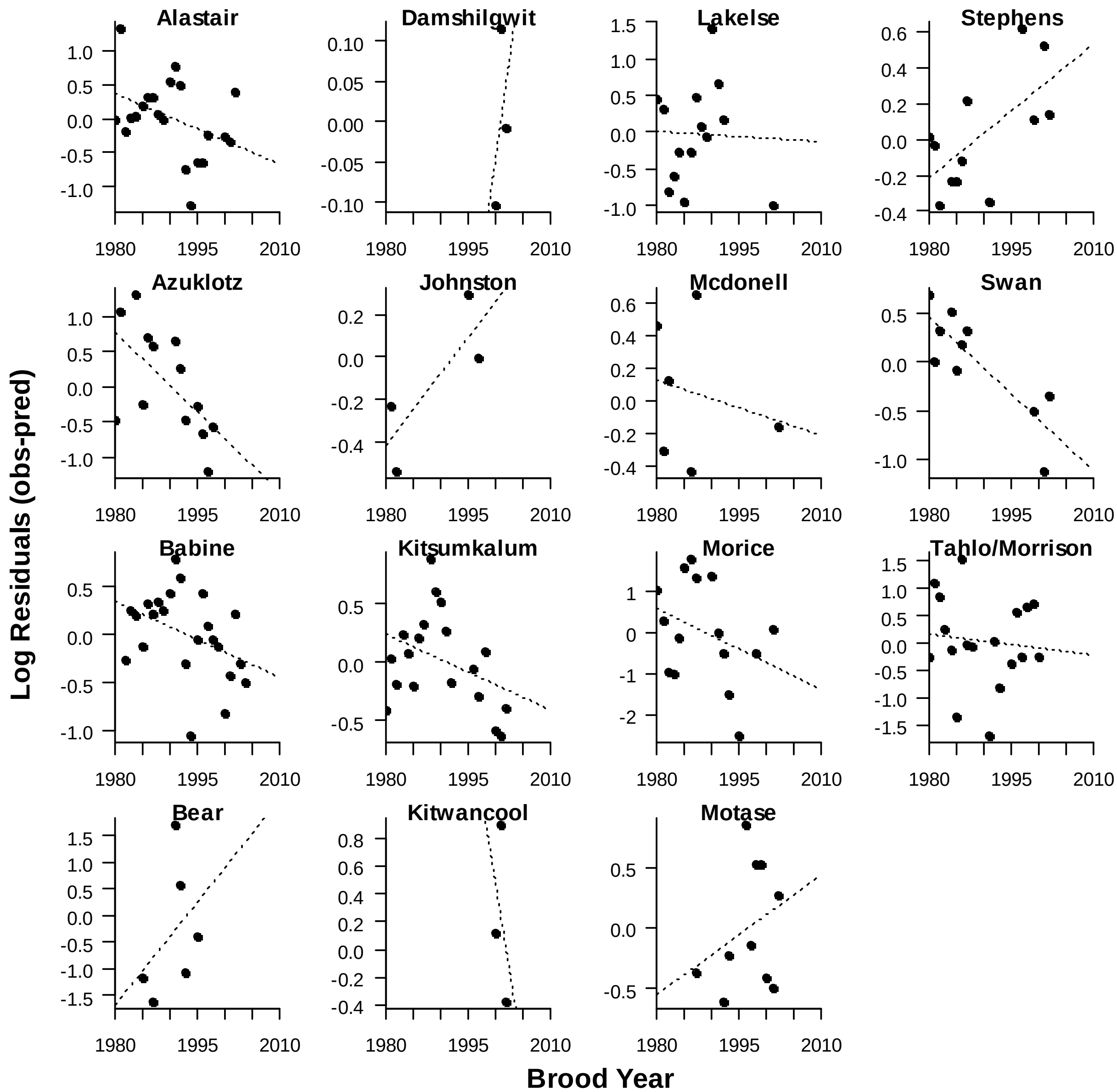

Figure 6. Residuals of recruitment from the mean stock-recruit curves from the HBM by brood year lake sockeye CUs in the Skeena watershed. The dashed line shows the trend in residuals over time. A declining slope indicates that the model is underpredicting recruitment in early years and overpredicting it in later ones, potentially indicative of a declining trend in productivity.

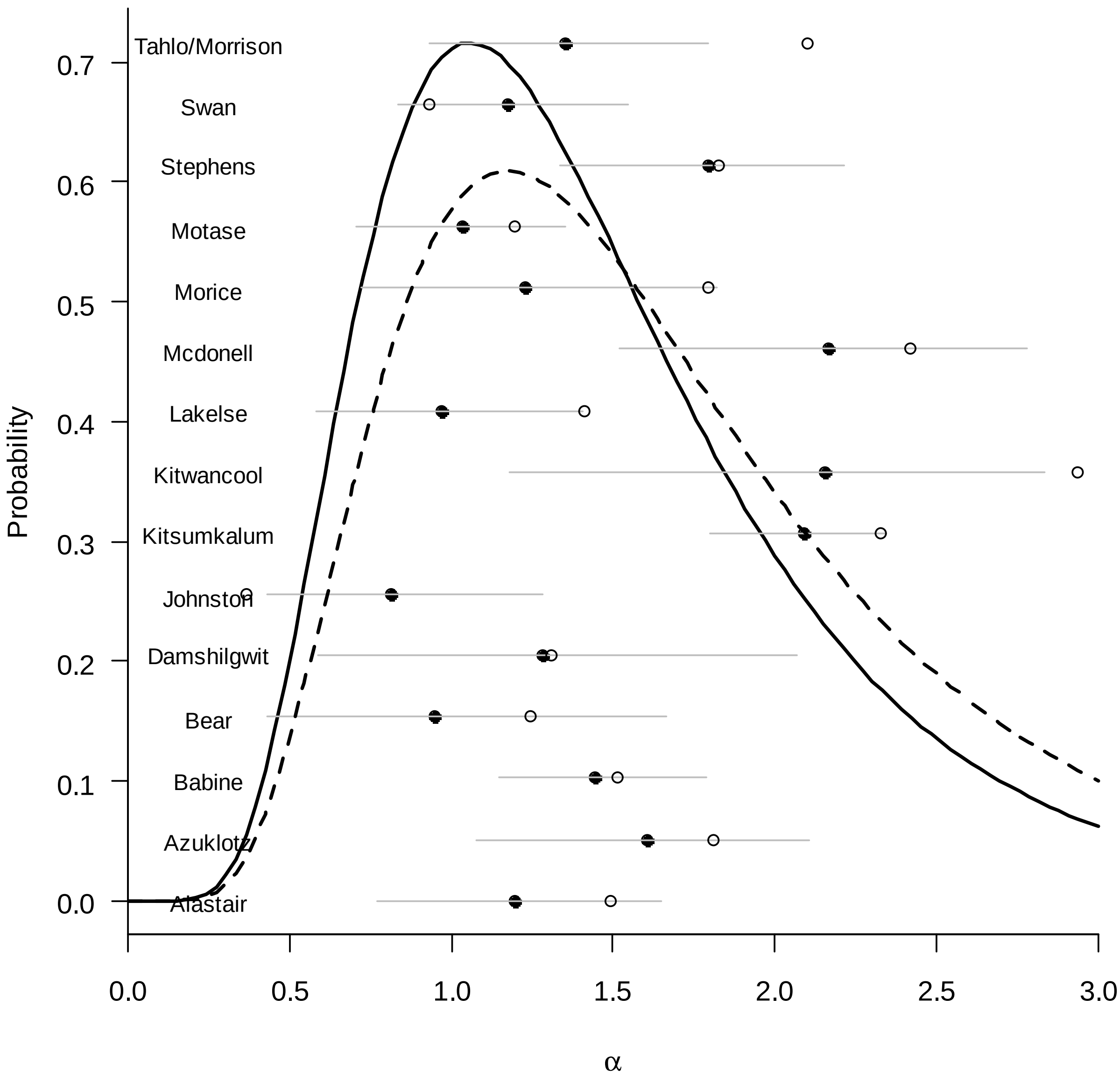

Figure 7. CU-specific mean estimates of the Ricker α parameter from the hierarchical Bayesian model (filled circles) and 95% credible intervals (horizontal lines) compared to independent estimates generated by linear regression (open circles). Note estimates of α_i from the linear regression method do not include the effects of the prior on Smax. Also shown are the mean hyper distribution of α from the HBM (thick lognormal-shaped solid line) and a lognormal distribution estimated from linear independent estimates (thick dashed line).

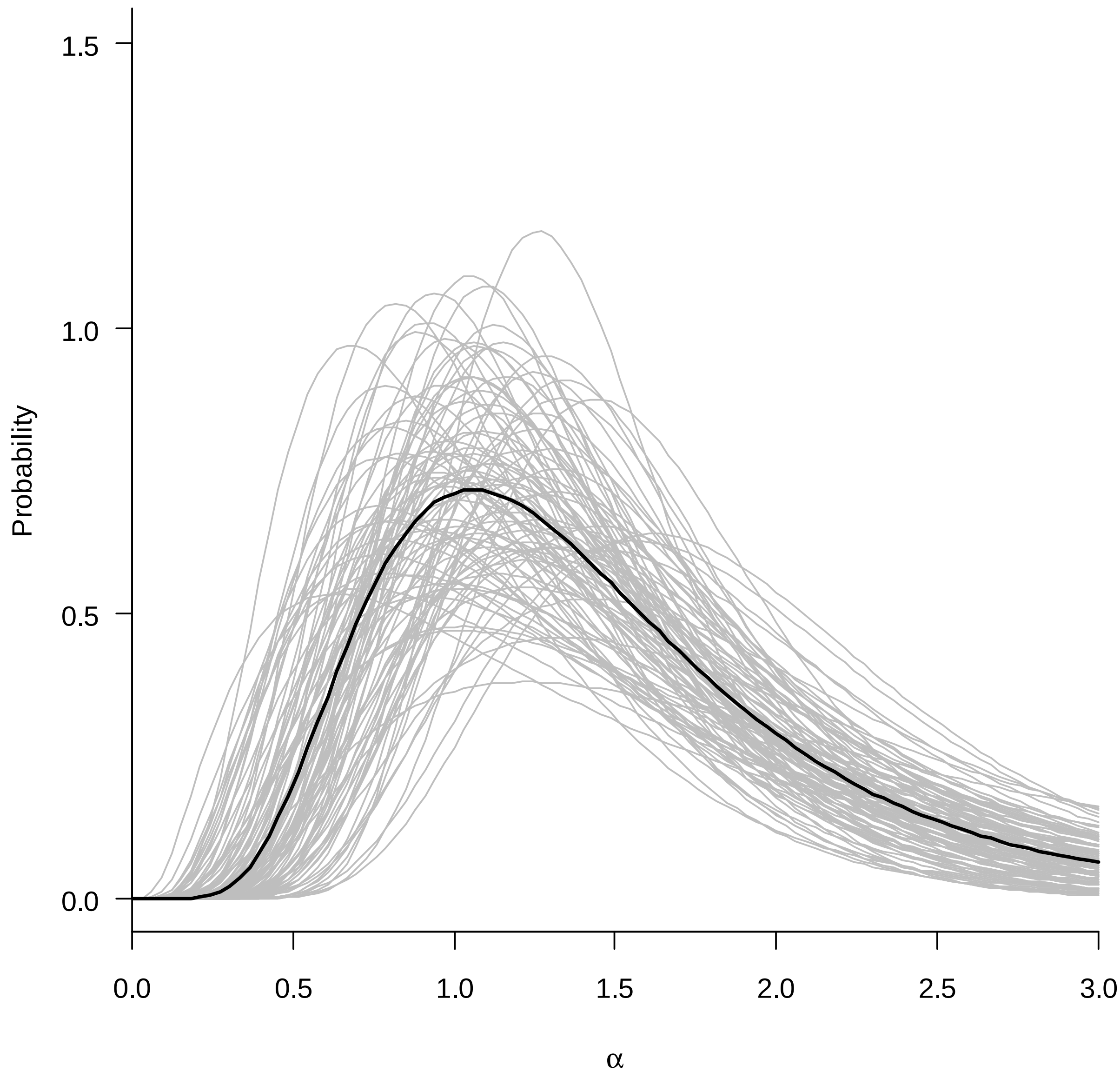

Figure 8. The mean hyper distribution of α from the HBM (solid thick line) compared to 100 random draws the μ_α and σ_α hyper parameters (gray lines). This shows the uncertainty in the α hyper distribution (bottom).

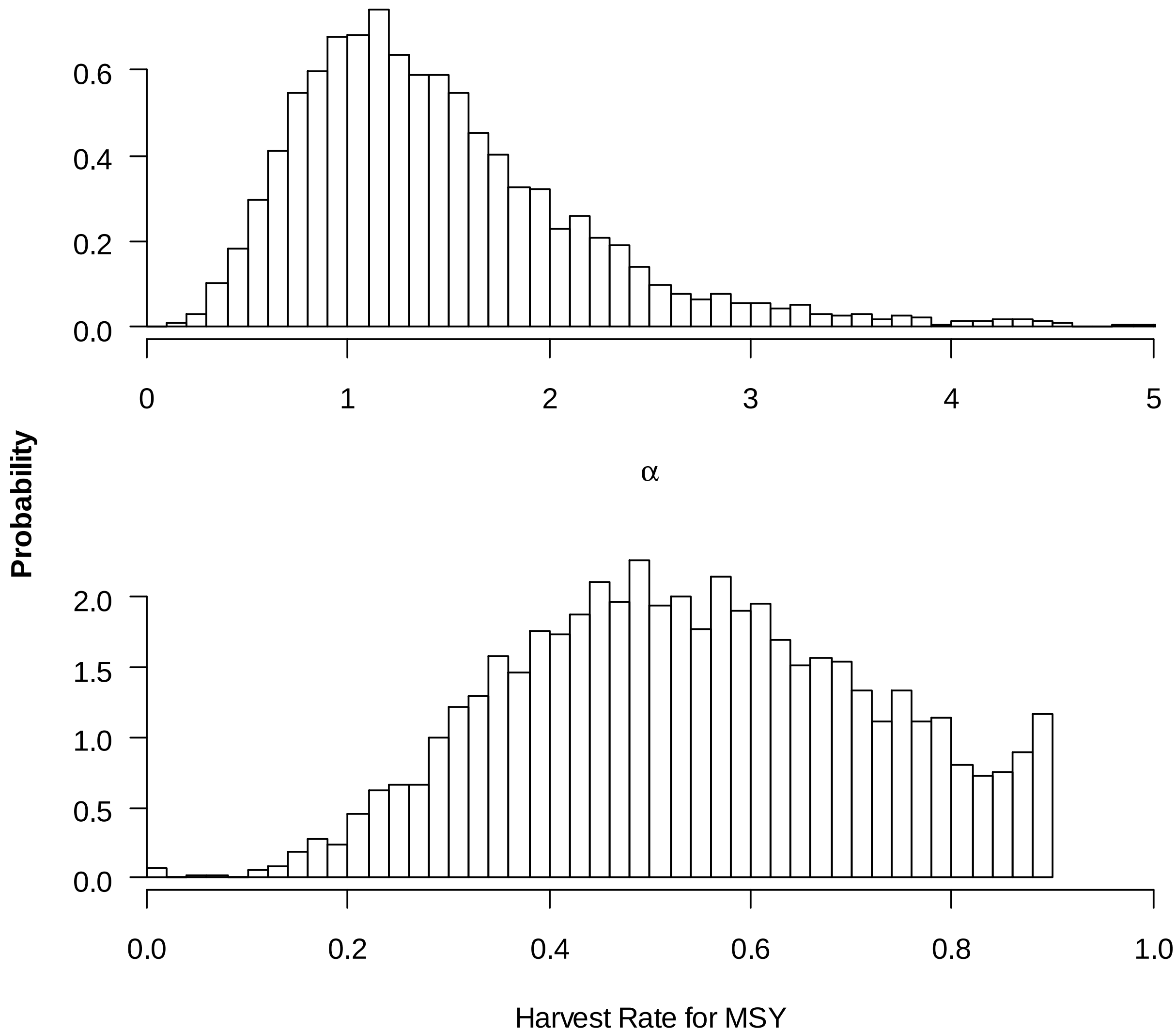

Figure 9. The distribution of Ricker α values (top) and associated optimal harvest rates (bottom) based on samples of α drawn from α hyper distributions determined from the posterior distributions of μ_α and σ_α.

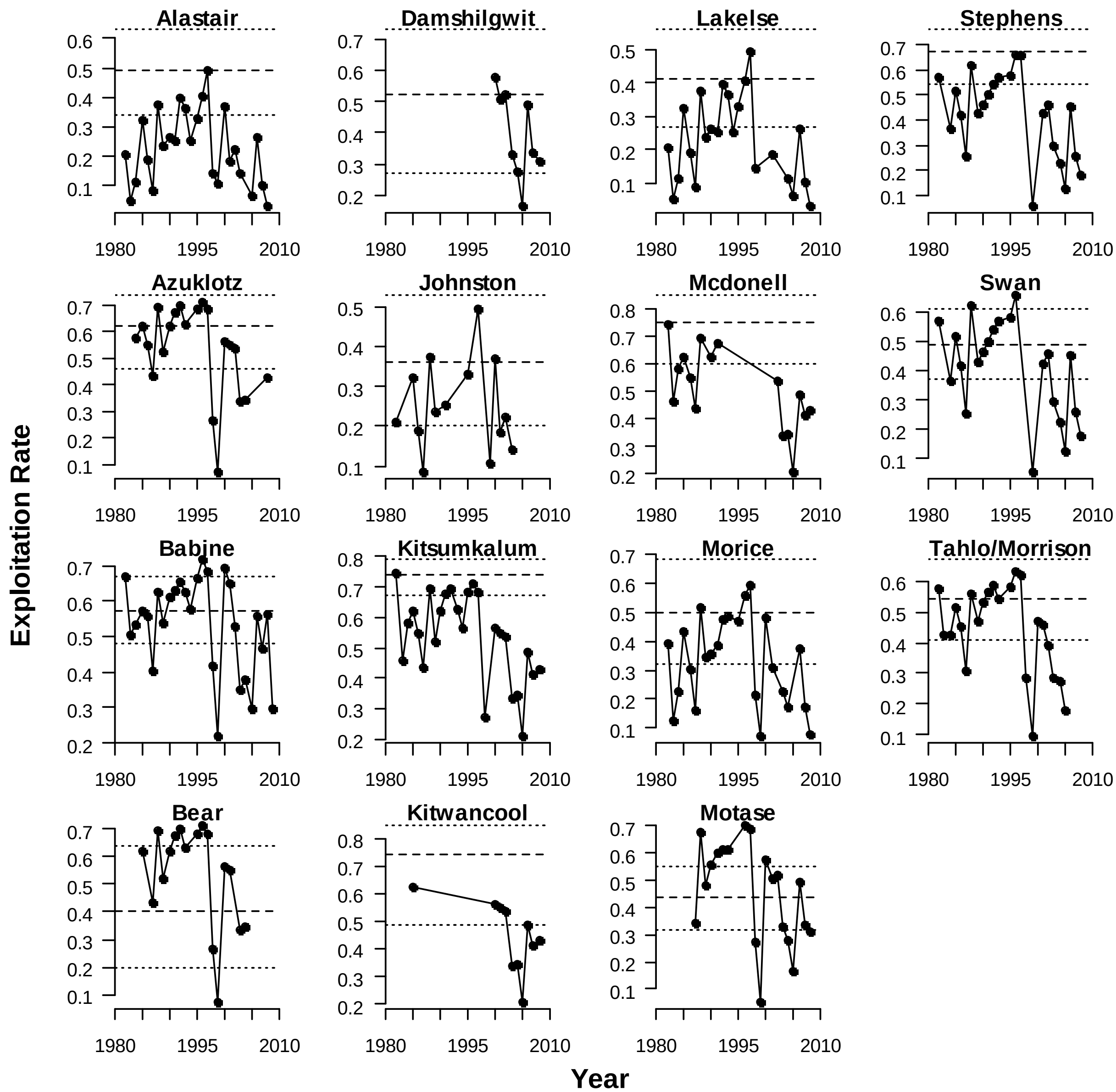

Figure 10. The historical exploitation rate for lake sockeye CUs in the Skeena relative to the mean estimate of the optimal exploitation rate (dashed horizontal line) and the 95% credible intervals of that optimal rate (finely dashed horizontal lines).

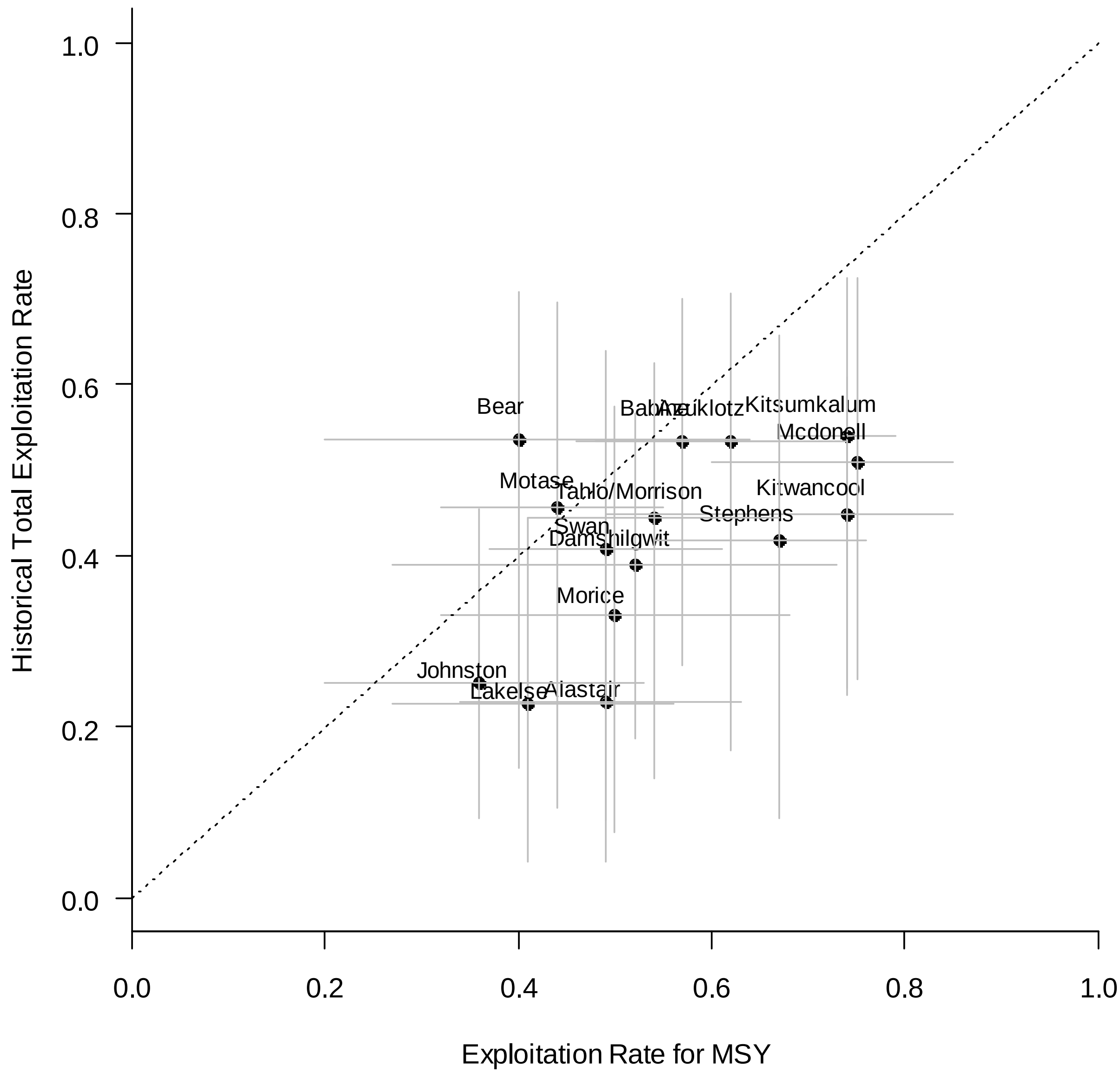

Figure 11. Comparison of the historical average (points) and the 95% quantile (vertical gray bars) of the total exploitation rate over the period of record (1980-2008 for years when estimates are available relative to the estimated optimal rate to produce the maximum sustainable yield estimate from the HBM (Uopt). Points and horizontal lines denote the mean estimate of Uopt and the 95% credible interval. Points below the 1:1 line indicate that the historical average exploitation rate is less than the optimal rate, indicating the CU has been under exploited relative to MSY.

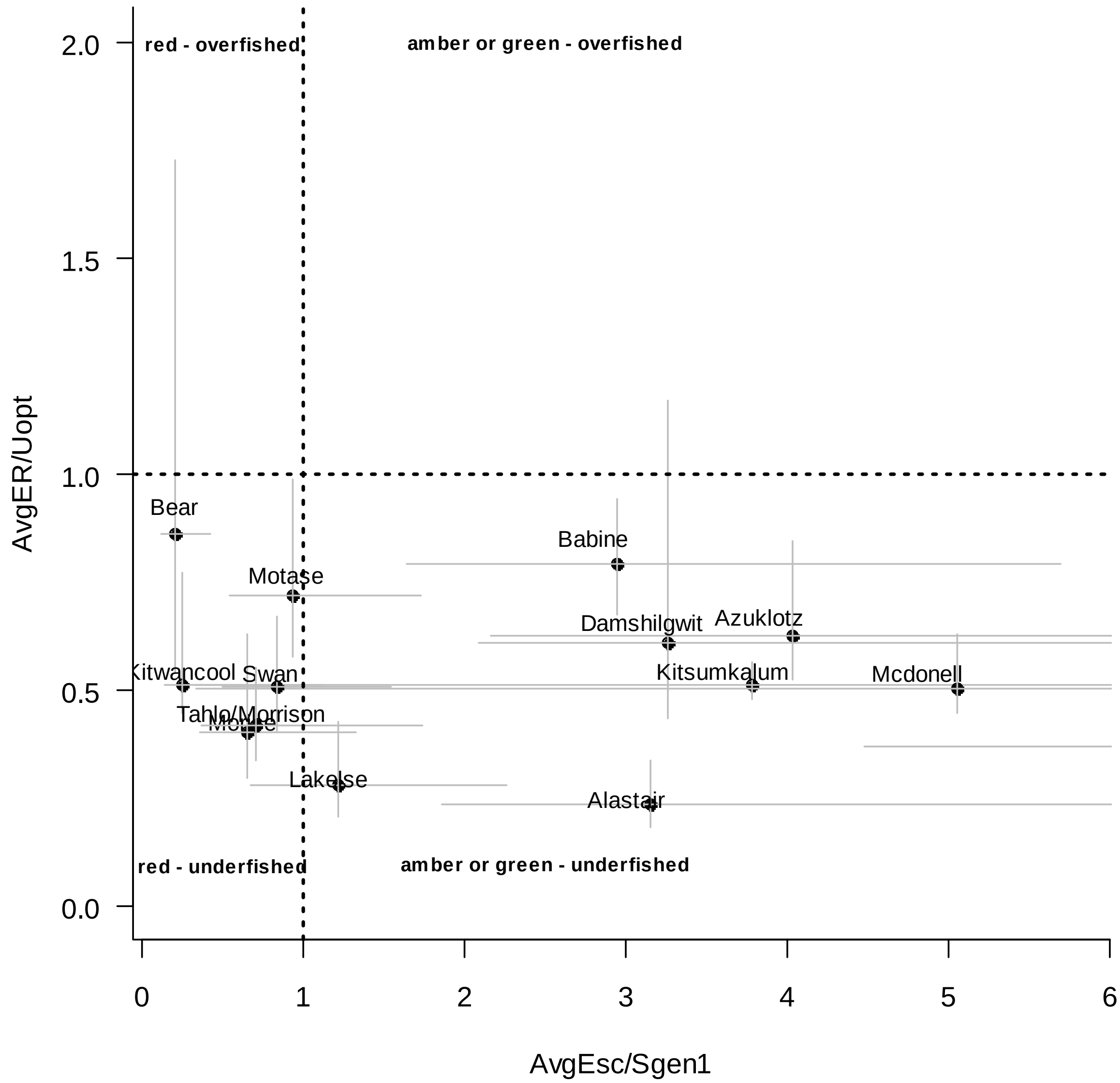

Figure 12. Status of 15 lake sockeye CUs in the Skeena based on the average escapement and exploitation rate between 2004 and 2008 data relative to abundance and exploitation benchmarks. The x-axis is the ratio of the average escapement relative to the lower benchmark (Sgen1). CUs with ratios less than one would be in the red status zone. The y-axis is the ratio of the average exploitation rate relative to the rate which maximizes yield (Uopt). CUs with ratios greater than one would be considered overfished. The solid points are the expected ratio and the gray lines represent the 95% credible intervals. The Stephens CU is not shown as the AvgEsc/Sgen ratio was greater than 8 and exceeded the x-axis scale (this CU has a AvgER/Uopt ratio of 0.37, so the stock is in the green status zone and under fished). The Johnston CU is not shown as there is no escapement or exploitation rate estimates over the 2004-2008 period.

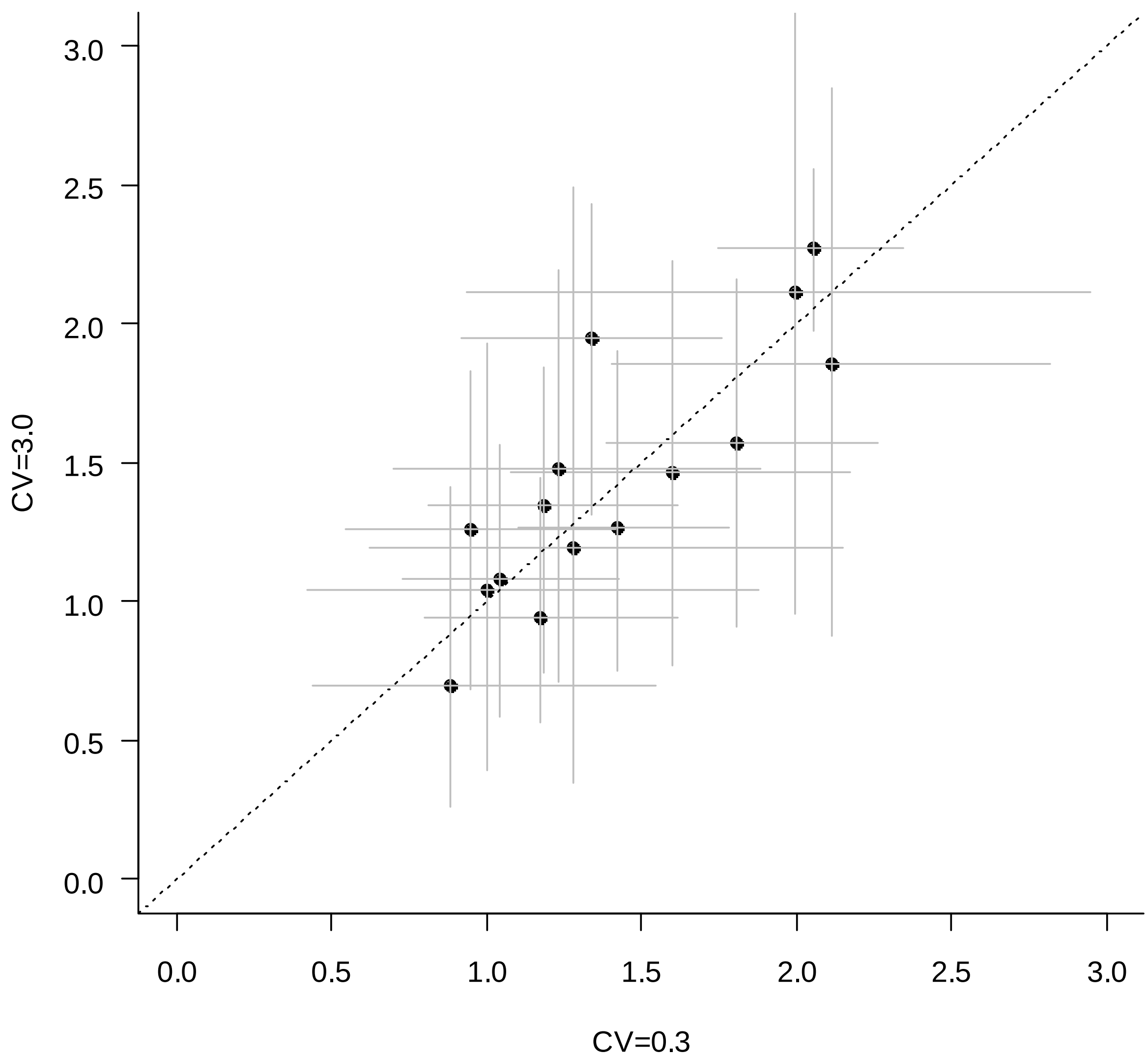

Figure 13. Comparison of HBM-based CU-specific estimates of α_i estimated with informative (CV=0.3) and uninformative (CV=3) prior distributions on Smax. Solid points and lines represent mean estimates and 95% credible intervals, respectively.

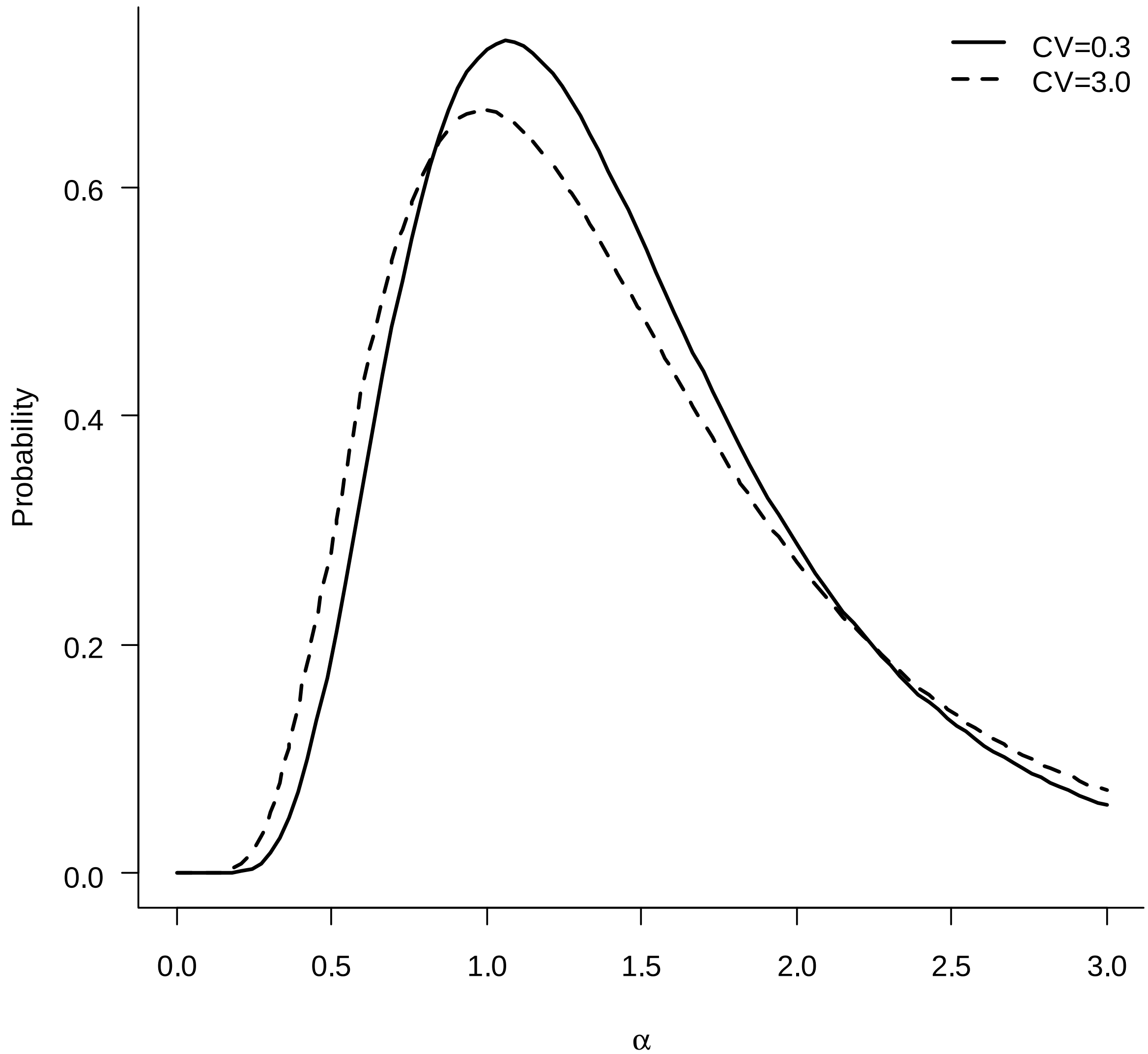

Figure 14. Comparison of mean hyper-distributions of α estimated with informative (CV=0.3) and uninformative (CV=3) prior distributions on Smax.

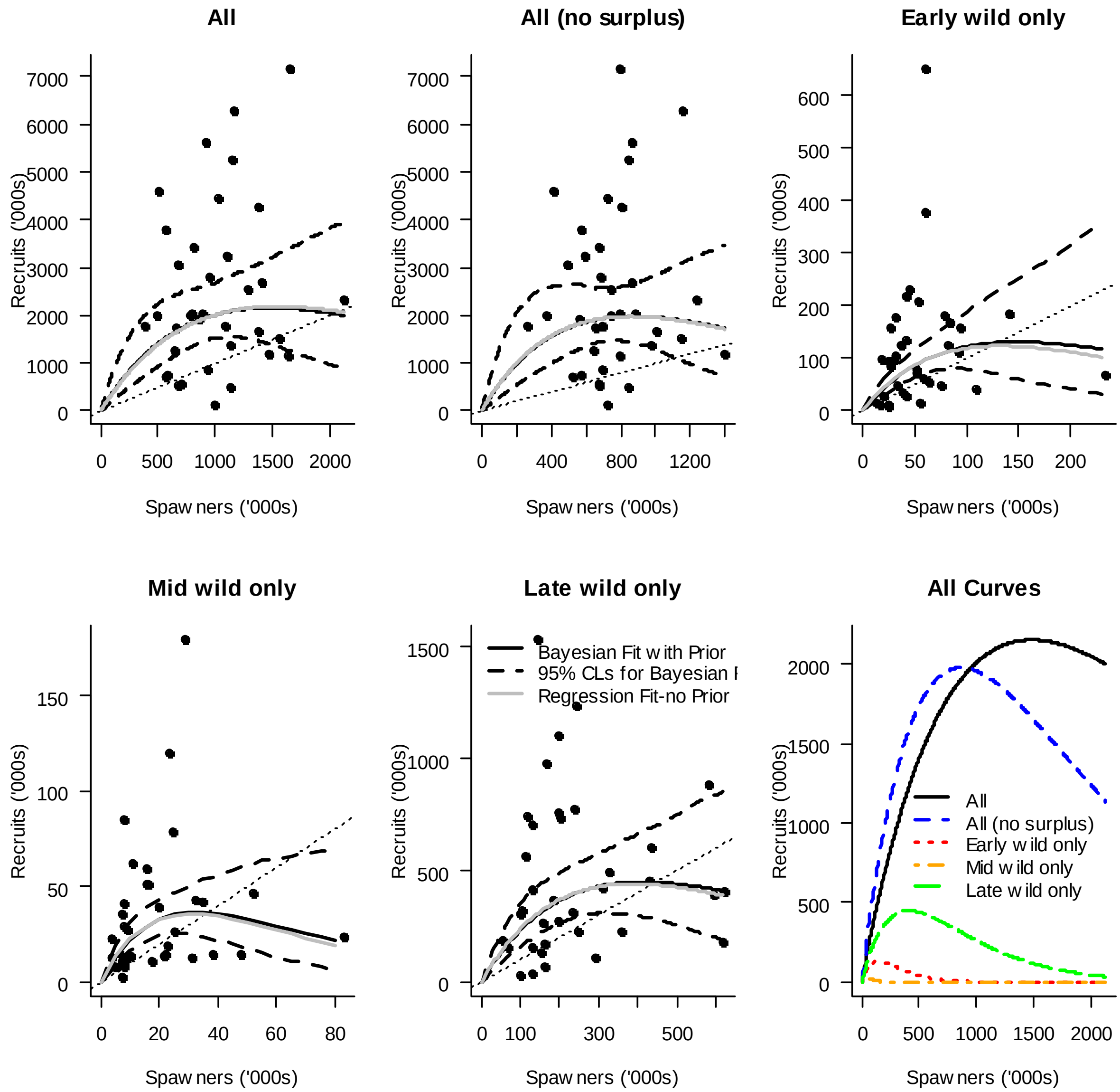

Figure 15. Comparison of stock-recruit relationships for different sockeye stocks within Babine Lake. The plots with titles beginning with "All" are based on the total recruitment estimates for the Babine aggregate and the total escapement or escapement less the surplus spawners at the spawning channel. The other relationships are based on recruitment and escapement estimates for early, mid, and late wild components. The thick black solid and dashed lines denote the expected relationship and 95% confidence limits from a Bayesian model where parameters for each stock were estimated independently. The solid gray lines show independent estimate of the relationship based on linear regression. The graph titled "All Curves" compares the relationships among all stock groups.