Columbia River Project Water Use Plan

Lower Columbia River Fish Management Plan

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Lower Columbia River Mountain Whitefish Egg Loss Model Review

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Highlights

The updated Mountain Whitefish egg loss model (ELM) is better than earlier versions, though a few minor improvements to the calculations are identified in this review. The updated model predicts that egg loss at CPR Island is on average 55% lower than predictions from earlier versions. The updated model predicts that egg loss from dewatering over the past 23 years has generally been low, with an average of 18%

Stock recruitment analyses suggest that there is strong density-dependence in survival rates for early life history stages of MWF (larvae to age-1 recruits). As a result of this prediction, the analysis indicates that egg loss due to dewatering is mostly compensated for by higher survival rates following dewatering. Egg loss from dewatering is predicted to result in only a 10% decrease in recruitment on average.

Although there are uncertainties in the ELM and stock-recruitment analyses, MWF protection flows do not appear to be providing substantive benefits to the population. Based on these results, continuation of the MWF protective flow regime is not warranted.

Owing to current ELM predictions and significant challenges with getting reliable information on egg depth distribution for MWF in a large river, further investment in field data to improve the ELM is difficult to justify. However, continued support for the fish population indexing program is essential to track the status of the MWF population, especially in the absence of protective flows.

Summary

Operations at Hugh L. Keenleyside Dam (HLK) and the Brilliant Dam on the Kootenay River can result in dewatering of Mountain Whitefish (MWF) eggs which can potentially negatively impact spawning success and the recruitment of young individuals to the Lower Columbia River (LCR) population. The impact of flow regime on MWF egg mortality due to dewatering is predicted by an Egg Loss Model (ELM). BC Hydro implements a MWF protective flow regime to reduce the proportion of eggs that are dewatered, and uses the ELM to plan and evaluate flows. The purpose of this review is to provide additional information for decision-makers with respect to the egg loss model.

There have been substantive investments in the MWF ELM since the model was first developed. The model has improved through collection of additional field data on spawn timing, the depth distribution of eggs, and incubation duration, and improvements to the modelling framework. The most significant recent change to the ELM accounts for differences in cell area in the determination of egg loss at CPR and Kootenay spawning sites. This change has resulted in a 55% reduction in annual estimates of egg loss at the CPR island spawning site, and a 10% increase in egg loss estimates in the Kootenay River. These changes had very little effect on predictions of the relative differences in egg loss among years at both sites.

There can be very substantive differences in egg loss predictions between CPR island and Kootenay spawning sites. Thus the CPR:Kootenay weighting ratio (12.9:87.1) has a very important effect on the weighted egg loss estimate for the entire study area, which forms the basis of management decisions. Both old and new versions of the model do not account for uncertainty in the CPR:Kootenay weighting factors. The old and new versions of the egg loss model do however estimate uncertainty in egg loss predictions at each site based on interannual variation in parameter values defining the timing of spawning and incubation and the depth distribution of eggs. The current approach to estimating uncertainty does not account for potentially different amounts of information about relationships across years when data were collected, the correlation among parameters in each functional relationship, and variation in egg deposition-depth relationship among sites. In addition, the current approach uses what appear to be arbitrary cut-offs of randomly selected parameter values. Improvements to address these issues would be relatively easy to implement. It is not clear at this point whether implementing these changes will reduce or increase uncertainty in egg loss estimates, though the latter is probably more likely.

There are a number of uncertainties in the egg matt data that cannot be accounted for in the ELM. The most concerning is possible underestimation of egg deposition at greater depths due to unaccounted for depth-dependent variation in the efficiency of egg matts to index egg deposition. This issue would likely result in an underestimate of the proportion of eggs deposited at greater depths that are much less vulnerable to dessication. As a result, this potential bias could lead to overestimation of egg loss. Another issue that is not addressed in the ELM is the extrapolation of results from 3 egg matt transects at one site (CPR Island or Oxbow area of Kootenay River) to much larger areas (entire lower Columbia River or all of Kootenay River below Brilliant Dam). The model assumes that data from these two sampling sites provides a good representation the entire area that is modelled, but there are no data to confirm this assumption. This issue could lead to possible bias in egg loss estimates and underestimation of uncertainty.

To evaluate effects of egg loss on recruitment for the LCR MWF population, a stock-recruitment relationship have been used to estimate the extent to which density dependence in larvae - age 1 survival rates can compensate for losses due to egg dewatering. Analyses to date indicate there is strong density

dependence which limits the effect of egg loss from dewatering on abundance. Inferences from these analyses are limited by: 1) large uncertainty in estimates of age-1 abundance and stocks size (age 2+) from the indexing program; 2) no observations at very low stock size where density-dependent mortality is low and where we would expect limited compensation in survival rates from lower density due to egg loss; and 3) large uncertainty in egg loss estimates. The recruitment ratio approach, which is based on relative differences in age-1 and age-2 MWF abundance in each year, potentially mitigates issues with error in estimates of absolute abundance. However, this approach is not useful in the current management context because purposeful alternation of high and low egg loss between adjacent years cannot be achieved.

This review brings into question whether it is worth continuing with the MWF egg loss monitoring program and the current egg loss experiment which attempts to create contrast in egg loss rates among years. In spite of limitations in how the ELM accounts for uncertainty and possible biases, the model predicts low rates of egg loss which are likely biased high due to under-representation of egg deposition at greater depths. The suggested modelling revisions are unlikely to change this conclusion. A very large increase in field effort would be required to address limitations in the input data to the ELM, but low estimates of egg loss from the current model make it difficult to justify this additional investment. The current stock-recruitment analysis, although uncertain, suggests very limited benefits of the protective flow regime on recruitment over the observed range of spawning stock sizes. Owing to stock assessment challenges, the likelihood of reducing uncertainty in the stock-recruitment analysis seems low. If protective flows are discontinued, monitoring of the MWF population from the indexing program should continue to determine if higher levels of egg loss in the absence of protective flows result in lower abundance.

1.0 Introduction

Mountain Whitefish (MWF) are the most abundant sportfish in the lower Columbia River (LCR) downstream of Hugh L. Keenleyside Dam (HLK). Operations at HLK and the Brilliant Dam on the Kootenay River can result in dewatering of MWF eggs which can potentially negatively impact spawning success and the recruitment of young individuals to the LCR population. To mitigate these impacts, BC Hydro implements a MWF protective flow regime to reduce the proportion of eggs that are dewatered by limiting maximum flows during the peak spawning period (January 1-21) and the extent of stage reductions during the incubation period (January 22 – Apr 1). As a result of annual variation in hydrology, power demand, dam operating conditions, and other factors that govern the flow regime of the Columbia River, there is annual variation in the extent of egg loss due to dewatering.

The impact of flow regime on MWF egg mortality due to dewatering is predicted by an Egg Loss Model (ELM). This model couples output from a 2D hydraulic simulation that predicts water depth and velocity as a function of discharge from HLK and in the Kootenay River, with biological models predicting the timing of spawning, the depth distribution over which eggs are deposited, and the duration of incubation. The model makes predictions of egg loss each year in the Columbia River below HLK and in the Kootenay River below Brilliant Dam, and also combines these predictions into a weighted average. Annual MWF weighted average egg mortality is categorized into 0-20% (tier 1), 20-40% (tier 2), and 40-60% (tier 3) classes. In 2004 BC Hydro and Department of Fisheries and Oceans agreed to an acceptable frequency of 60%, 30%, and 10% over a 5-year period for tier 1, 2, and 3 categories, respectively. The Columbia River Water Use Plan (WUP) was completed in 2007 and included an experimental element to better evaluate the biological effects of MWF egg loss from dewatering on the population and the benefits of protection flows (BC Hydro 2007). The WUP directed BC Hydro to continue with protective flows for an additional 5 years after the WUP was implemented after which an interim analysis of the effects of the MWF flow regime would then be conducted to determine whether to continue or stop the protective flow regime for the following five years. Based on the interim analysis and later discussions (e.g., Feb 2015 workshop in Castlegar, BC on MWF flows), an experimental flow proposal was recommended to have alternating years of egg losses (Tier 3 high egg loss vs. Tier 1 low egg loss). Achieving this alternating egg loss impact has been challenging due to Treaty obligations and water conditions in the basin.

Density-dependence in MWF juvenile survival rates can potentially compensate and perhaps completely mitigate losses from egg dewatering. In the absence of any density-dependent survival response there would be a linear relationship between the proportion of eggs lost due to dewatering and the reduction in the abundance of adult fish. Recruitment variability is one of the least understood processes in fisheries science (Houde 1987). It is generally accepted that recruitment strength is established early in life history by a combination of density-dependent (Vandenbos et al. 2006) and density–independent (Savoy and Crecco 1988) factors. The effects of flow-dependent mortality are potentially mitigated through compensatory (density-dependent) growth and survival responses (Fletcher and Deriso 1988, Rose et al. 2001, Korman et al. 2011). That is, a certain fraction of eggs that die due to dewatering may not have contributed to recruitment and the abundance of the adult population in the absence of dewatering because they would have died anyways due to higher natural mortality because of higher densities.

The purpose of this review is to provide additional information for decision-makers with respect to the egg loss model that is an important element used to set and evaluate the MWF protective flow regime. The first part of this report reviews the existing egg loss model and highlights recent changes to the model and their effects on predictions of egg loss (section 2). The second part of this report reviews existing information to evaluate the effects of predicted egg loss on the abundance of the population via stock-recruitment analyses (section 3).

2.0 Review of Egg Loss Model

The Mountain Whitefish egg loss model estimates the proportion of MWF eggs exposed to air (dewatered) each year due to variation in discharge (Golder 2014a). The model is based on a number of sub-routines that predict: 1) water surface elevation, depth, and velocity over a fine grid of model cells (as defined by node locations) at an hourly timestep as a function of discharge from HLK and discharge in the Kootenay River (River2D); 2) spawn timing (timing of egg deposition); 3) the vertical distribution of egg deposition with respect to water depth; and 4) incubation duration. Based on elements 1)-3), the model predicts the proportion of eggs deposited at each model cell by day. The duration that eggs are present at each cell and vulnerable to dewatering is predicted by element 4). The model then takes the hourly discharge and uses the River2D element to determine if the node is exposed to air between egg deposition and hatch. If exposure exceeds a user-defined limit (e.g., 8 hours, which is uncertain) the proportion of eggs at that node are added to a tally of the total proportion of eggs that are exposed across all cells and over the entire incubation period. A bootstrapping procedure which accounts for uncertainty in the functional relationships in 2)-4) is used to estimate uncertainty in annual egg loss estimates.

The MWF egg loss model makes predictions for CPR island in the Columbia River, and for a study site in the Kootenay River downstream of Brilliant Dam (Oxbow area). Estimates of egg loss from these two areas are combined to determine a ‘weighted egg loss estimate’ (WELE), which represents the egg loss over the entire area of interest. A key assumption in this calculation is that information from these two study sites represent the proportion of eggs lost over the entire lower Columbia River and all of the Kootenay River below Brilliant Dam. Note that Kootenay River water elevations are effected by discharge from HLK due to backwatering effects, and discharge at Brilliant Dam affects water elevations in the mainstem Columbia River both upstream and downstream of the confluence. The calculation of weighted egg loss is not available in documents describing the model (Golder 2014a and 2014b) but is included in an extension of appendix B1 in Golder 2014a (Golder, unpublished data). WELE is computed by weighting CPR and Kootenay estimates by Weighted Useable Area (WUA) for each of these areas. WUA is computed as the product of the Habitat Suitability Index (HSI) for spawning habitat for each area and the availability of spawning habitat. HSI is determined by predicting the proportion of eggs by depth based on sampling from 2009-2012 using a 5 parameter logistic regression model. This relationship does not vary across modelling years. Spawning habitat availability is determined by computing the amount of area in each depth bin from 2009-2012 from the River2D model. The average useable area across years for each depth bin is multiplied by the predicted HSI to determine WUA for each spawning area. These WUA values are summed and the proportion of each site’s WUA to the total is used as the weighting factor. The CPR:Kootenay weighting factors are 12.9 and 87.1, respectively. Thus a prediction of egg loss in the Kootenay River has over a 6-fold greater effect on the weighted estimate of egg loss compared to predictions of egg loss at CPR island.

2.1 Modelling issues

There have been substantive investments in the MWF egg loss model since the model was first developed. The model has improved over time through collection of additional field data on spawn timing and the depth distribution of eggs, and incubation duration. The modelling framework has also been improved. The most current version of the model is well documented and changes are well described in Golder (2014a). In this review, I begin by discussing changes that have been made since the last available

WUP report on the model (Golder 2014a) was published (Cell Area), and then address more general issues that apply to both old and new versions of the model.

New Model Accounts for Differences in Cell Area

The most significant recent change to the ELM accounts for differences in cell area in the determination of egg loss at CPR and Kootenay spawning sites. The River2D model breaks the study area up into a large number of triangular-shaped cells that are defined by specifying the location and bed elevations of the nodes of each triangle. Prior to this change (~ April 2015), the egg loss in each cell was simply summed to determine the total for the entire study areas in the lower Columbia and Kootenay rivers. This summation assumed all cells with the same egg deposition and inundation history contributed equally to egg loss. A new version of the model released in April 2015 revised this approach by accounting for differences in the area each of each cell when summing egg loss estimates. This change had a large effect on predictions at CPR island where there are many cells with small areas representing an extensive shallow area. As a result, losses at CPR island were over-represented in earlier versions of the model. After accounting for cell area, annual estimates of egg loss at the CPR island spawning site were on average 55% lower compared to estimates from earlier versions of the model (Table 2). In contrast, egg loss estimates for the Kootenay River based on the new model increased by an average of 10%. The cell area revision to the model had very little effect on predictions of the relative differences in egg loss among years at both sites, as it explained 88% and 90% of inter-annual variation in egg loss predicted by the old model at CPR Island and in the Kootenay River, respectively (Fig. 1). Thus the new model changed the scale of predicted egg loss, mostly at CPR Island, but did not effect the assessment of the relative impact of various water years.

There was little effect of accounting for cell area on weighted egg loss estimates for the Columbia-Kootenay system as a whole. The Columbia and Kootenay weighting factors are 12.9 and 87.1 respectively. As a result of these weights, the Columbia predictions, which changed substantially under the new model, have only a modest effect on the weighted average (Fig. 2). Average weighted egg loss between 1992 and 2012 under old and new models were 18% and 20%, respectively (note 2013 and 2014 weighted values under old model were not available to me at the time this review was conducted), and the annual predictions from the two models were highly correlated (r^2=0.98, Fig. 2). The frequency of tier 1-3 years predicted by the new model is very close to the planned percentage of years in each category (Table 2). Thus, accounting for cell area in the new version of the model makes little overall difference to assessments based on weighted egg loss estimates, but dramatically changes interpretation of HLK effects based on estimates for CPR island, which are more than 50% lower under the new model.

Neither Model Accounts for Uncertainty in CPR:Kootenay Weights

There can be very substantive differences in egg loss predictions between CPR island and Kootenay spawning sites. Thus the CPR:Kootenay weighting ratio (12.9:87.1) has a very important effect on the weighted egg loss estimate, which is the ultimate metric used to determine the egg loss tier and potential effects on recruitment (Korman 2015, Golder 2017). Both old and new versions of the egg loss model account for uncertainty in key functional relationships determining timing of spawning and incubation and the depth distribution of egg deposition. However, neither version accounts for uncertainty in the CPR:Kootenay weighting factors. This is logically inconsistent as uncertainty in the depth distribution of egg deposition is accounted for in predicting site-specific egg loss (e.g. CPR or Kootenay predictions), but not in the prediction of the HSI curves that also depend on egg distribution depth relationship. In addition, the CPR:Kootenay weighting ratio does not vary among years, while inter-annual variation in other key functional relationships are accounted for in the model. These issues are easily rectified by revising the model to account for uncertainty in the weighting factor, using the approach described below.

Approach for Estimating Uncertainty in Old and New Models Could be Improved

The old and new versions of the egg loss model estimate uncertainty in egg loss predictions based on the uncertainty in parameter values defining the timing of spawning and incubation and the depth distribution of eggs. For each of these relationships, a separate curve is fit to each year when egg matt data were available, and the mean and standard deviation of parameter values across years is calculated based on year-specific parameter values. A bootstrap sample of parameter values for each relationship is drawn from normal distributions based on these statistics, and fed into the egg loss model to predict the mean and confidence intervals (uncertainty) of egg loss for each modelled year. There are three basic problems with this approach. First, the procedure doesn't account for the fact that there are potentially different amounts of uncertainty in relationships in each year. The sample size of egg depth distributions (# of eggs per depth category) undoubtedly varies by year which will lead to varying degrees of certainty in the relationship for each year. The current approach treats each year as having equal information about egg depth distribution and therefore having equal weight in calculating the across-year average values. Second, the approach does not account for the fact that parameter estimates for each functional relationship in each year are not independent but instead correlated. Finally, the model assumes that the relationship between depth and relative egg deposition can be represented by a single relationship for each year. It seems likely that this relationship would vary spatially and depend on the interaction between spawning locations and depth resulting in considerable spatial variation that is not accounted for in the model.

The first issue of the computation of an average relationship across years can be addressed by using a hierarchical Bayesian model to estimate the annual relationships along with a hyper-distribution which describes the inter-annual variation in parameter estimates. When applying the ELM, random draws from these hyper-distributions, that account for correlation among parameter estimates (see below), can be used to represent the relationship in the simulation for each simulated year. Such an approach more accurately accounts for variation in parameter estimates across years then the current approach. This approach may be challenging to implement owing to the limited number of years (2009-2012) when egg matt data are available.

With respect to the issue of parameter correlation, the approach used in the bootstrapping of the ELM is to take random normal draws of each parameter value defining that functional relationship (across years) based on the most likely estimate and standard deviation of the parameter (calculated when fitting these models), and then restrict draws to the central 60th percentile. This is repeated for each parameter. Model calculations of egg loss are then calculated by combining the random draws for each parameter to calculate new function values (e.g. predicting egg distribution with depth) and then running the ELM with these functions. The fundamental error in this computation is that it does not account for the correlation among parameters values within a relationship. Consider a simply linear regression y = b0+b1*x, where x is the predictor variable (e.g., date for spawn timing relationship), y is the dependent variable (e.g. proportion of spawning occurring on that day in logit space) and b0 and b1 are the constant and slope of the relationship. As for any linear regression, estimates of b0 and b1 are not independent. Lower estimates of b0 are more likely to be associated with higher estimates of b1 and visa-versa. This can be visualized by an isopleth diagram which shows the joint probability of b0 and b1. The peak of this plot represents the maximum likelihood estimates of b0 and b1, and the contour lines represent joint probability of different values. The shape of these isopleths is not circular which would indicate independence among parameter estimates, but is instead oblong due to parameter correlation. The current bootstrapping approach assumes these parameters are uncorrelated when they are surely not. Not accounting for this correlation will result in an overestimation of uncertainty in egg loss estimates.

Golder (2014a) states that random samples of parameter values are restricted to lie between the 20th and 80th quantiles (e.g. the central 60% of the normal distribution) to avoid unrealistic estimates of depth and spawn timing distribution. I have two concerns about this approach. First, it isn't clear how the authors determined what was unrealistic and what wasn't and the extent to which this constraint eliminated the problem. Second, it is likely that this restriction is only needed because the random parameter selection does not account for parameter correlation. This error is easily corrected by using an alternate approach where a table of hyper-parameter values for each relationship is generated from an MCMC sampling procedure of the hierarchical Bayesian model. The R script for the bootstrapping of the egg loss model can randomly sample the rows from such a table to select hyper-parameter values. Parameter values to use for each ELM trial would be based on random draws from the hyper-distributions. Draws of hyper-distribution parameters and the trial-specific estimates can account for the covariation among parameters by modelling these correlations explicitly using multivariate normal distributions. This process will better account for both inter-annual variation in parameter values and account for correlation among parameters. A modest amount of work will be required to estimate hierarchical Bayesian models (HBMs) for the three functional relationship in the ELM to implement this recommendation.

Spatial variation in the distribution of spawners and topography would likely lead to considerable across-site variation in relative egg deposition – depth relationships within years. This variation is ignored in the ELM. It could be addressed by fitting relationships to each egg matt transect (in each year) separately within a hierarchical Bayesian framework where parameters for each site-specific relationship are drawn from hyper distributions. Separate hyper-distributions might be required for CPR and Kootenay locations. When running the ELM, random draws from these hyper-parameter distributions (that account for parameter correlation) would be used to define egg deposition-depth relationships for each node, rather than using the same relationships for all nodes (for a given ELM trial) as is currently done. This change would likely lead to additional uncertainty in egg loss estimates.

2.2 Key Uncertainties in Egg Loss Model

Uncertainty in the prediction of the spawn timing, depth distribution of eggs deposited, and incubation duration are likely the biggest source of error in egg loss estimates. Predictions of water depth which determine the inundation history for each cell are based on a well established model (River2D) that is fit to many observations of water surface elevation in this application (Golder 2014a). There is some error in water depth predictions, especially at discharges and locations not included in the River2D calibration, but I suspect these errors are modest relative to errors that summarize spawning and incubation dynamics.

Predictions of spawn timing, incubation duration, and the distribution of egg depth are based on egg matt data collection, which is challenging in large rivers like the mainstem Columbia and Kootenay rivers. Paired egg matts were deployed at only 3 depths for 3 transects in the two spawning areas (CPR Island and Kootenay River) for a total of 18 samples per area. This limited sample likely provides only a rough description of egg depth distribution at study sites because only three depth categories are sampled. As egg matts are deployed for a week prior to collection, and there can be a range of depths over each matt due to variation in discharge, there is also error in the depth assigned to each matt to compute the depth-egg distribution relationship. There are likely other important sources of error, such as variation in the location of spawning relative to where the matts are deployed, and extrapolation of relationships at each study site (e.g. CPR Island) to a much broader area (lower Columbia River). Of greatest concern are potential biases due to variation in the efficiency of mats to retain eggs which likely varies with depth.

Presumably the efficiency of mats to retain eggs will decrease with higher water velocity, which is likely higher at greater depths. Some eggs are inevitably lost as mats are pulled to the surface, and this loss rate also likely increases with depth. These processes could lead to an underestimate of the proportion of eggs deposited at greater depths which would in turn lead to an overestimate of egg loss in the ELM, since locations with greater depths are less vulnerable to dewatering.

Some of the issues above apply to the characterizations of spawn timing and incubation duration. Relationships for both of these important variables depends on the egg matt data, and the latter includes additional error associated with egg staging. ATU-hatch relationships are likely dominated by temperature effects which is modelled, but spawn timing is likely effected by factors (fish condition, water temperature) other than model day, which is the sole independent variable used in its prediction in the ELM. These potential errors and uncertainties arising from sampling error and potential bias should be kept in mind when decision-makers agonize over small differences in predicted egg loss which can lead to different predictions of the egg loss tier in any particular year. Expanding the sampling program to include more depths, more transects within study sites, and more study sites would help address some of these issues. However, as discussed below, increasing sampling effort may not be warranted given low estimates of egg loss estimated by the most recent version of the ELM.

See Table 3 for a summary of ELM issues.

3.0 Review of Effects of Egg Loss on Recruitment

An evaluation of the biological effects of MWF egg loss due to dewatering needs to consider the effects of fish density on survival rates of juveniles following the egg stage. The effects of flow-dependent mortality are potentially mitigated through compensatory (density-dependent) growth and survival responses (Fletcher and Deriso 1988, Rose et al. 2001, Korman et al. 2011). Density-dependence in MWF survival of early life stages (larvae to age-1 recruits) can potentially compensate for losses from egg dewatering. That is, a certain fraction of eggs that die due to dewatering may not have contributed to recruitment in the absence of dewatering because they would have died anyways due to higher natural mortality because of higher densities in the absence of protection flows. The objective of this element of the review is to evaluate the evidence for a relationship between egg loss and recruitment of Mountain Whitefish in the LCR to evaluate the evidence that such compensation is occurring.

3.1 Stock-Recruitment

To evaluate effects of egg loss on recruitment, a stock-recruitment relationship is needed to estimate the extent to which density dependence can compensate for losses due to egg dewatering. A MWF stock-recruitment relationship was originally estimated by Korman (2015) based on age-1 abundance (recruits) and age-2+ abundance (stock) estimates from the index monitoring program (Ford 2013) and egg loss estimated from an earlier version of the ELM (Hildebrand 2014). Owing to the relatively flat stock-recruitment curve that arose from the data, which implies strong density-dependence in survival rates, the estimated recruitment loss due to egg dewatering was only 10% compared to an average egg loss estimated by the ELM of 19% (Fig. 3). The analysis indicated that egg loss due to dewatering has on average been relatively modest because almost half of the total egg loss from dewatering was compensated for by increased survival rates of early juvenile stages prior to age-1. More recently, Golder (2017) evaluated the effects of MWF egg loss using similar approaches (Fig. 4). They concluded that the effect of predicted egg loss from the ELM on the MWF adult-age 1 stock-recruitment relationship was not significant. This occurred because most of the stock size estimates were on the flat end of the stock-recruitment curve, thus modest reductions in stock (through egg loss from dewatering) did not substantively change recruitment. Results from both analyses are limited by: 1) uncertainty in estimates of age-1 abundance and stocks size (age 2+) from the indexing program; 2) no observations at very low stock size where density-dependent mortality is low and where we would expect limited compensation in survival rates from lower density due to egg loss; and 3) large uncertainty in egg loss estimates.

Estimates of recruitment and spawning stock size for Mountain Whitefish in the LCR are uncertain due to: 1) typical challenges of estimating fish abundance in a large river; 2) particular challenges with MWF due to their sensitivity to electroshocking and highly aggregated distribution; and 3) potential problems with the current approaches used to analyze data from the LCR indexing program. Abundance estimates of fish populations in large rivers are often uncertain because the capture probability (proportion of the population sampled per unit effort such as a week-long boat electrofishing trip) is low and variable (Korman and Yard 2017). This leads to low numbers of recaptures of marked fish, which leads to high uncertainty in abundance estimates. The problem is even worse when one considers that age- or size-specific abundance estimates are needed to separate total abundance into mature (stock) and young (recruit) components for the stock-recruitment analysis. As fish size effects boat electrofishing capture probability (Korman and Yard 2017), the analysis should be stratified by fish size, further reducing the number of recaptures and increasing uncertainty is size- or age-stratified abundance estimates. Error associated with ageing scales and assigning ages based on age-length relationships adds additional uncertainty to age-specific estimates of abundance.

Adding to these challenges, Mountain Whitefish are particularly difficult to sample because they are highly aggregated and sensitive to electrofishing. Aggregation results in low and potentially variable capture probability, while sensitivity to electrofishing makes the assumption that marked fish behave like unmarked and previously uncaptured fish more tenuous. All these issues indicate that estimates of recruitment and stock size for MWF should be treated as quite uncertain, and that uncertainty in their estimates is likely higher than presented in current assessments (see discussion below). Existing stock-recruitment analyses (Korman 2015, Golder 2017) do not account for observation uncertainty when estimating the relationships (which could easily be corrected), and doing so would add even more uncertainty into the assessment of egg loss due to dewatering on recruitment.

The analytical procedures used to estimate age-specific abundance of Mountain Whitefish and other species sampled in the LCR indexing program are unconventional and could potentially lead to biases in abundance and uncertainty estimates. Potential issues include: 1) the use of highly uncertain observed fish (but not caught) data in the assessment; 2) inconsistencies in age estimates determined by length frequency compared to length-age relationships determined from scales (that is not addressed in analytical procedures); 3) failure to jointly estimate survival, abundance, and capture probability using an integrated Jolly-Seber model. Such a model could be applied in a robust design framework to provide size-specific abundance estimates that makes much better use of all the data. This is a very standard approach and no reason in the existing documentation is provided to rationalize not adopting it. These analytical issues lead to additional uncertainty in abundance estimates beyond those related to the challenges of the sampling situation described above. See Table 4 for a summary of stock assessment issues.

Finally, estimation of stock-recruitment parameters requires a large sample size (ideally 15-20 years) and a wide spread of stock size observations. As shown in Korman (2015) and Golder (2017), there is a paucity of observations at low stock size (Fig.'s 3 and 4). As a result, we are uncertain about the productivity of the MWF population (the initial slope of the curve and the stock size where the curve flattens). This is a critical uncertainty with respect to evaluating effects of egg loss on recruitment, because declines in recruitment will only occur when stock size is low enough so that the reduction of stock size due dewatering of eggs lies within the steep initial slope. Ideally, to best evaluate effects of egg dewatering on recruitment, we would need repeated observations of high and low egg loss during periods when the mature population of MWF is lower than what has been observed historically, which is unlikely to occur.

An alternate explanation for the flat stock-recruitment curve for LCR MWF is that the large error in stock size estimates results in overestimation of productivity (Hilborn and Walters 1992). This errors-in-variables problem has been shown to produce stock-recruitment curves that have an initial slope that is too steep and a flatter shape of the overall curve. If stock size estimates were corrected, the initial slope would decrease and predicted reductions in recruitment due to egg loss due from dewatering at the lower stock sizes that have been observed would potentially be greater. Ideally, analytical methods that account for uncertainty in stock size should be used in future assessments to avoid this potential bias. The most viable solution to this problem is to explicitly account for uncertainty in stock size in the stock-recruitment analysis. This can be done using a meta-analytical approach where error in stock size is simulated in the Bayesian model used to estimate stock-recruitment parameters. Typically such analyses lead to greater uncertainty in the shape of the stock-recruitment curve which in this case will reduce our ability to evaluate effects of egg dewatering on recruitment. In addition, results will still be limited by the uncertainty in the extent of error in stock sizes that are used as input to the meta-analysis. See Table 5 for a summary of stock-recruitment modelling issues.

Limitations in the stock-recruitment approach do not make the inferences from the analysis useless to decision-makers. If we have even modest confidence in current abundance estimates, we can be fairly certain that there is considerable density-dependent compensation in early survival rates over the adult stock size estimates that have been observed historically, and that the extent of this compensation is sufficient to limit the effects of egg loss on recruitment to relatively low levels (~10% on average). Furthermore, if we trust the existing stock-recruitment relationship, or one in the future generated based on a meta-analytical approach described above, it can be used to implement a stock-size dependent protective flow regime. Here protective flows would only be implemented in years when the stock-recruit model indicates that spawner (stock) abundance is low enough that density-dependent effects would not be great enough to compensate for egg losses. Alternatively, the stock-recruitment model could be used to adjust the protective flow regime to allow higher rates of egg loss up to the point where they cannot be compensated for by density-dependent processes.

3.2. Recruitment Ratio Method

Owing to challenges in estimating Mountain Whitefish recruitment described above, a ratio-method to index annual differences in recruitment has been recommended (Golder 2017). This index is computed based on the ratio of estimated age-1 abundance to the sum of age-1 and-2 abundance. The idea is that this ratio should be variable if recruitment strength varies substantively across adjacent years. A high ratio two years after spawning would indicate high recruitment in that brood year (two years ago) relative to the previous brood year (three years ago). The main advantage of this approach is that it reduces effects of confounding due to long term changes in the ecosystem (higher predation rates due to expanding Walleye, Sturgeon, and Northern Pike populations), as major changes in these confounding factors are less likely to occur over short periods. Golder (2017) related the ratio index of recruitment to the ratio of egg loss in years associated with each index of recruitment (2 and 3 years prior to the year the index was calculated in). There was a weak but insignificant negative relationship between the index of recruitment and the ratio of egg loss. This result supports the stock recruitment analysis which also indicates very limited or no effects of egg loss due to dewatering on recruitment.

I have a number of concerns about the ratio approach:

1. It isn't clear from the description of this method (Golder 2017) whether scale ages and lengths were used to separate the total abundance estimate each year (as determined by mark-recapture) into age-1 and age-2 abundance, or whether the analysis was restricted solely to the proportion of age-1 and age-2 fish from the scale analysis. I believe it is the latter. If that is the case then this approach is not sensitive to uncertainties in abundance estimates but is still dependent on the assumption that relative differences in capture probability of age-1 and age-2 MWF do not change over time. As well, any size-stratified sampling of scales would need to be accounted for in calculating the annual age-1 to age-2 ratio.

2. The ratio method only indexes relative variation in recruitment across adjacent years but does not address recruitment variation over longer time scales. In a worst case, say recruitment is high and stable for five years and then very low and stable for the next five years. The only year in this 10 year series that would show recruitment variation based on the ratio method would be in the transition from year 5 to 6. The ratio-based index of relative recruitment strength in all other years would be the same, even though recruitment in the first five years was much higher then in the second. In an attempt to correct for confounding long-term patterns in recruitment (due to factors other than dewatering), the index method may be "throwing the baby out with the bathwater" since it largely eliminates long-term variation that may in part be driven by egg loss.

3. The original idea of the ratio method was that it would be used in conjunction with purposeful manipulation of egg loss rates in alternating years to produce a sequence of low and high egg loss rates. However, the likelihood of obtaining such a sequence is very low due to a number of hydrologic and management constraints. The ratio index is not useful in the absence of substantive manipulation of egg loss rates across adjacent years.

4.0 Management Implications

In a relative sense, the LCR Mountain Whitefish egg loss model is one of the best models in the Province to evaluate effects of flow regimes. The structure of the model is logical and accounts for the key processes affecting the probability of egg dewatering (water level, spawn timing, egg depth distribution, incubation duration). All the relationships describing those processes have been estimated based on field data collected over multiple years. The model has been well documented and has been ported to a flexible modelling environment ('R') that is accessible to a variety of users. This review has identified minor improvements to the model which include a better way of accounting for interannual variation in key relationships and weighting factors leading to more accurate estimates of egg loss and uncertainty. Substantial additional field effort could lead to a reduction in some uncertainties and potential biases, but such investments may be difficult to justify given that current egg loss estimates are relatively low, and due to the extreme challenges of mapping egg depth distributions in a large river.

The utility of the MWF egg loss model for management is limited. In the vast majority of years, there is considerable overlap in credible intervals of egg loss (e.g. Fig. 2 of Korman 2015), indicating that the model is not able to distinguish differences in egg loss among years. The width of the credible intervals is currently inaccurate owing to limitations identified above (but this issue could be addressed). Model improvements suggested in this review would likely increase the extent of uncertainty in egg loss estimates. To date, egg loss tier categorization has only been based on most likely estimates and does not account for uncertainty in annual egg loss estimates. Representing this uncertainty in tier categorization would make it obvious to decision-makers that we are often highly uncertain about the egg loss tier in any year, and this conclusion is not likely to change with further investment.

The biggest uncertainty with respect to MWF egg loss is not however predictions from the ELM, but whether modest amounts of predicted egg loss have an effect on recruitment. Existing assessments of that question indicate the answer is no because the stock-recruitment curve has a relatively steep initial slope and an overall flat shape. This indicates that there is strong density-dependence in survival rates so that egg loss due to dewatering is compensated for by higher survival rates at later early life history stages (prior to age-1). Unfortunately, my review indicates that the stock-recruitment analysis is uncertain due to considerable error in stock and recruit estimates, the lack of low stock size estimates, and a variety of analytical issues of the fish population indexing data (some of which could probably be resolved). These factors result in considerable uncertainty about the initial slope of the curve, which determines the stock size where we would expect egg loss due to dewatering to result in lower recruitment. Thus, even if managers have confidence in egg loss estimates from the ELM and can make use of that information after accounting for large uncertainty in annual estimates, the interpretation of what that loss means to population abundance is uncertain and will likely remain so in the future.

These issues bring into question whether it is worth continuing with the MWF egg loss monitoring program and the protective flow regime. The monitoring and flow regime have substantive costs (monitoring, lost power revenues/flood control, etc.), and managers and biologists spend a considerable amount of time discussing both model results and in-season flow planning. The ELM indicates that egg loss is generally very low. It is likely egg loss is even lower if sampling underestimates the proportion of eggs in deeper water that are less vulnerable to dewatering. The current stock-recruitment analysis, although uncertain, suggests very limited effects on recruitment over the observed range of stock sizes.

Moving forward, it would be useful to continue to run the ELM each year with the suggested changes even if protective flows are discontinued. Stopping the protective flow regime could potentially lead to lower MWF abundance if the benefits of the regime are underestimated by the egg loss and stock-recruit analysis conducted to date. Continuing with the fish population indexing program is therefore essential to determine if the MWF population declines in the absence of protective flows. If this occurs, lower abundance coupled with higher egg loss provides informative data to better define egg loss effects on recruitment. Thus, in addition to economic benefits and simplification of flow planning, temporarily stopping the protective flows will provide better information to evaluate the historic benefit of this regime. The protective regime could be reinstated if a more informed stock-recruitment analysis indicates that it does produce benefits to the MWF population.

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Table 1. Summary of Mountain Whitefish predictions of egg loss for Columbia (CPR island) and Kootenay areas based on the original formulation (Old, Golder 2014a) and a revised model that accounts for differences in cell (node) area (New).

	Columbia		**Kootenay**		**% Difference**	
Year	**Old**	**New**	**Old**	**New**	**Columbia**	**Kootenay**
1992	59%	32%	39%	38%	-46%	-3%
1993	44%	30%	17%	16%	-32%	-6%
1994	23%	8%	8%	9%	-65%	13%
1995	48%	22%	32%	35%	-54%	9%
1996	35%	16%	20%	24%	-54%	20%
1997	23%	11%	7%	8%	-52%	14%
1998	28%	11%	15%	16%	-61%	7%
1999	34%	19%	25%	29%	-44%	16%
2000	12%	5%	7%	6%	-58%	-14%
2001	12%	4%	4%	5%	-67%	25%
2002	50%	24%	25%	27%	-52%	8%
2003	25%	10%	17%	19%	-60%	12%
2004	30%	12%	25%	25%	-60%	0%
2005	28%	12%	18%	19%	-57%	6%
2006	27%	11%	14%	15%	-59%	7%
2007	27%	10%	11%	12%	-63%	9%
2008	43%	19%	30%	24%	-56%	-20%
2009	32%	15%	31%	35%	-53%	13%
2010	22%	7%	4%	5%	-68%	25%
2011	29%	13%	9%	10%	-55%	11%
2012	45%	25%	32%	50%	-44%	56%
2013	36%	14%	16%	17%	-61%	6%
2014	31%	15%	12%	14%	-52%	17%
Average	32%	15%	18%	20%	-55%	10%

Table 2. Frequency of years in egg loss tiers 1 (0-20%), 2 (20-40%), and 3 (40-60%) predicted by the new egg loss model (Realized ('92-'14)) in comparison to the desired (Planned) percentage of years in each category.

	Realized ('92-'14)		**Planned**
ELM Range	**# Yrs**	**% Yrs**	**% Yrs**
0-20%	14	60.9%	60%
20-40%	8	34.8%	30%
40-60%	1	4.3%	10%
Total	23	100.0%	100.0%

Table 3. Summary of Lower Columbia River Mountain Whitefish egg loss modelling issues.

Modelling or Data Issue	Effects on Prediction of Egg Loss
Account for cell (node) area	Older model versions, which did not account for differences in cell area, overestimated egg loss by 55% at CPR Island
Uncertainty in CPR:Kootenay weights not accounted for	Underestimation of uncertainty in system-wide estimate of egg loss proportions
Variation in amount of information on spawn timing and egg depth distribution among years not accounted for	Underestimation of uncertainty in egg loss proportions and possible modest bias in mean estimates
Correlation among parameter estimates not accounted for	Overestimation of uncertainty in egg loss proportions and possible modest bias in mean estimates
Censoring of random sampling of parameter values	Underestimation of uncertainty in egg loss proportions and possible modest bias in mean estimates
Extrapolation of site-specific spawn timing and egg depths to broader areas	Underestimation of uncertainty in egg loss proportions and possible bias in mean estimates
Possible under-estimation of egg deposition at greater depths	Overestimation of egg loss proportions

Table 4. Summary of Lower Columbia River Mountain Whitefish stock assessment issues.

Modelling or Data Issue	Effects
Low and variable capture probability	Large uncertainty in abundance estimates
Sensitivity of MWF to electrofishing	High post-release mortality rate leading to underestimation of capture probability and overestimation of abundance
Highly aggregated MWF distribution	Underestimation of uncertainty in abundance estimates if not accounted for in estimation procedure
Error in assigning age from scale reads	Error in age-1 and age-2 recruitment estimates
Inconsistency in age estimates from length frequency analysis and scale reads	Error in age-1 and age-2 recruitment estimates
Unconventional and poorly integrated approaches to estimate abundance and age structure	Error in uncertainty and bias in abundance estimates

Table 5. Summary of Lower Columbia River Mountain Whitefish stock-recruitment modelling issues.

Modelling or Data Issue	Effects on Prediction of Egg Loss
Uncertainty in MWF stock abundance	Overestimation of productivity, leading to potential underestimation of egg loss on recruitment
Uncertainty in age-1 abundance due to error in total abundance or proportion of total abundance that is age-1	Reduced ability to evaluate stock-recruitment relationship and therefore evaluate effect of egg loss on recruitment
No observations at low stock size	Uncertainty in productivity estimate, leading to uncertainty in effect of egg loss on recruitment

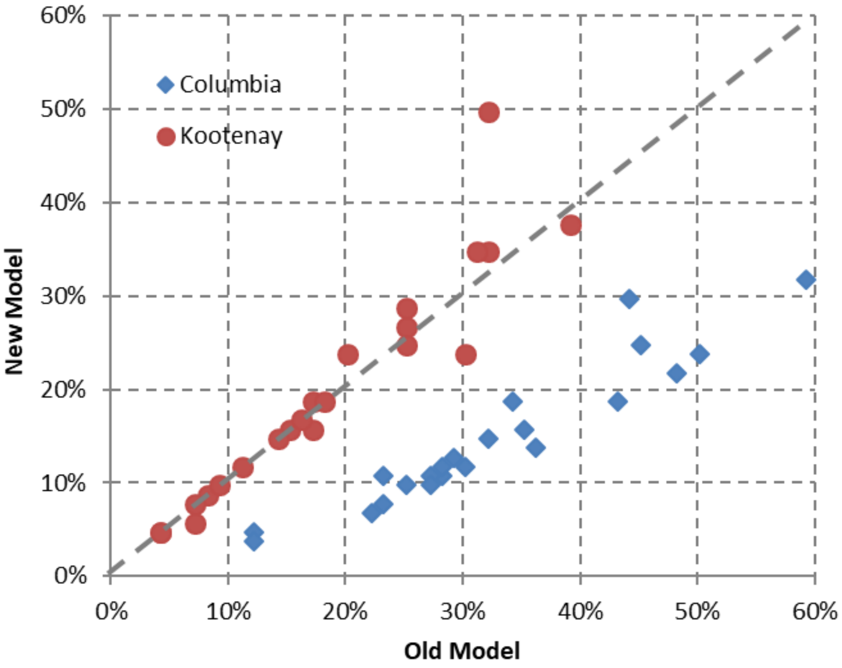

Figure 1. Comparison of egg loss predictions at CPR island (Columiba) and Kootenay spawning areas based on old (<April 2015) and new (April 2015) versions of the MWF egg loss model (1992-2014).

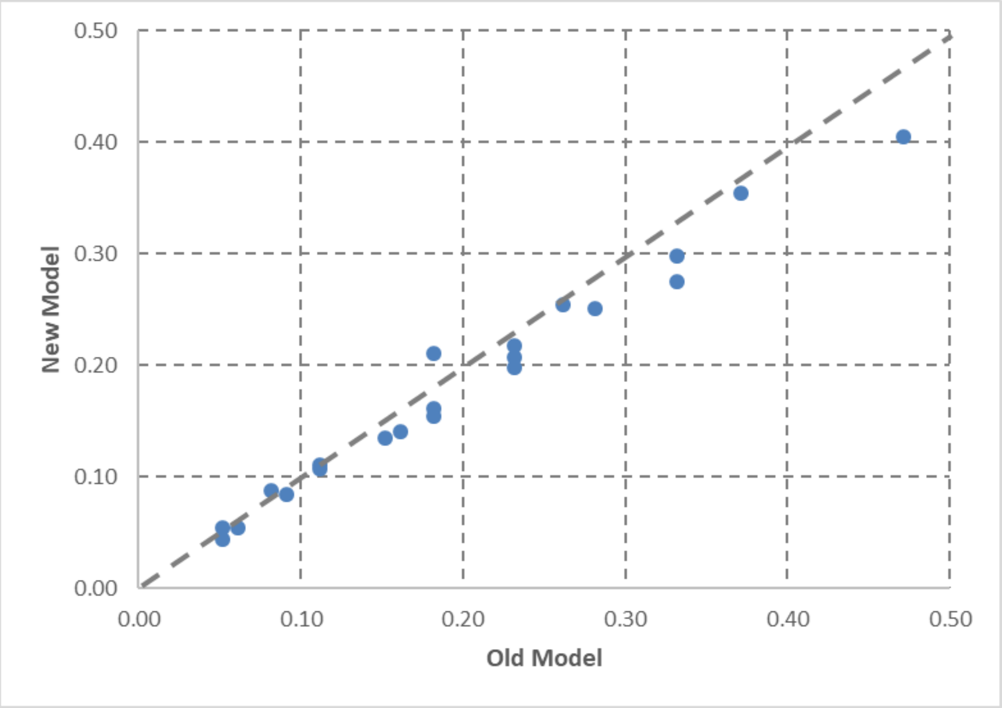

Figure 2. Comparison of weighted-average egg loss predictions across CPR island and Kootenay spawning areas based on old and new versions of the MWF egg loss model (1992-2012).

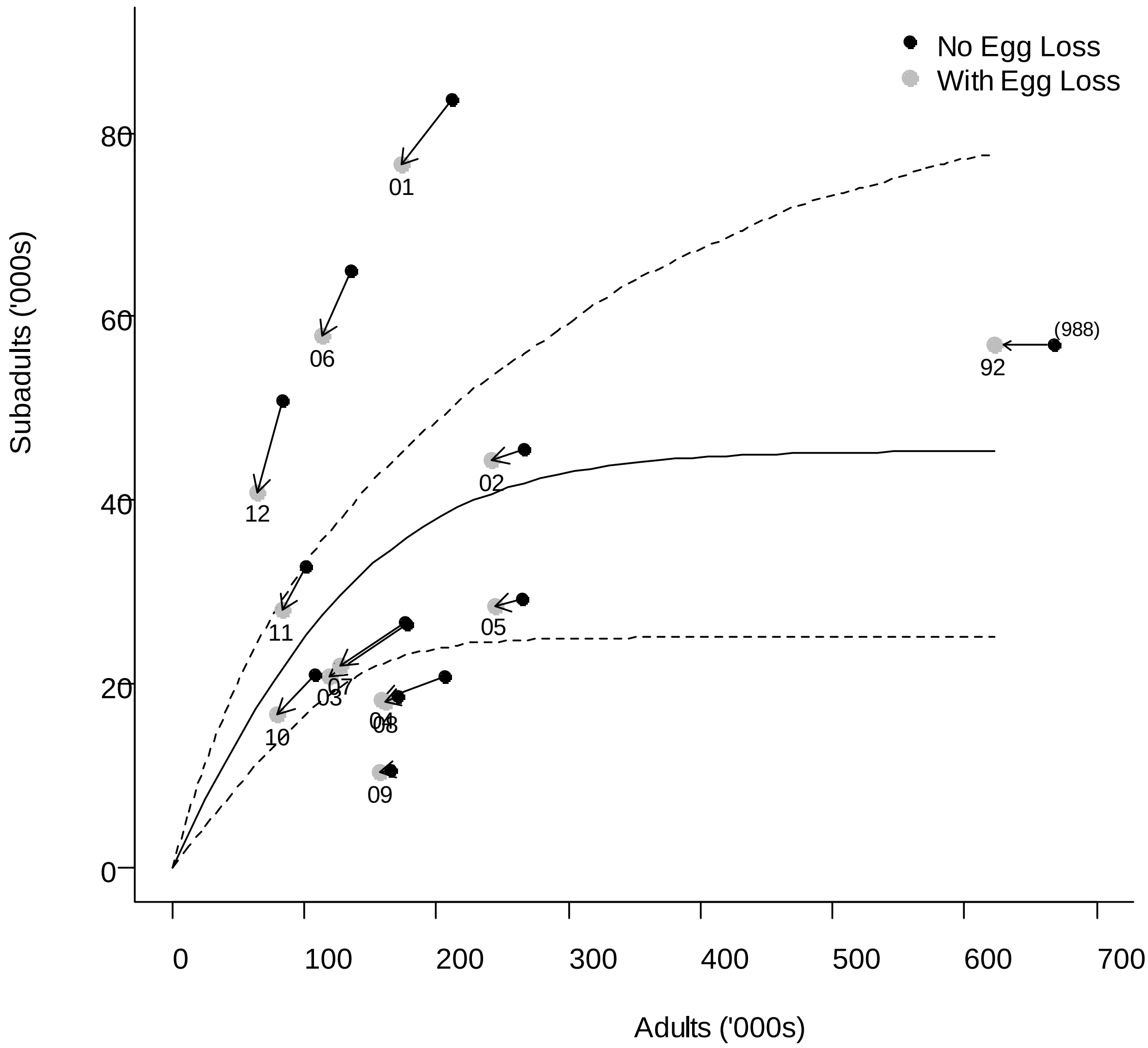

Figure 3. Predicted change in effective adult abundance and resulting recruitment (subadults in the following year) for Mountain Whitefish in the Lower Columbia River based on the logistic hockey stick stock-recruitment model (from Korman 2015). The gray points represent adult abundance adjusted for egg loss, and unadjusted recruitment (unadjusted subadult estimates). The black points show adult abundance unadjusted for egg loss and the back-calculated recruitment resulting from that abundance. The year labels beside each point denote the year associated with adult abundance and proportional egg loss estimates. The solid and dashed black lines represent the mean and 95% credible interval of the logistic hockey stick stock-recruitment model. The black point for brood year 1992 (unadjusted adult abundance) has a value that is off the x-axis scale and is shown in the parentheses above the point.

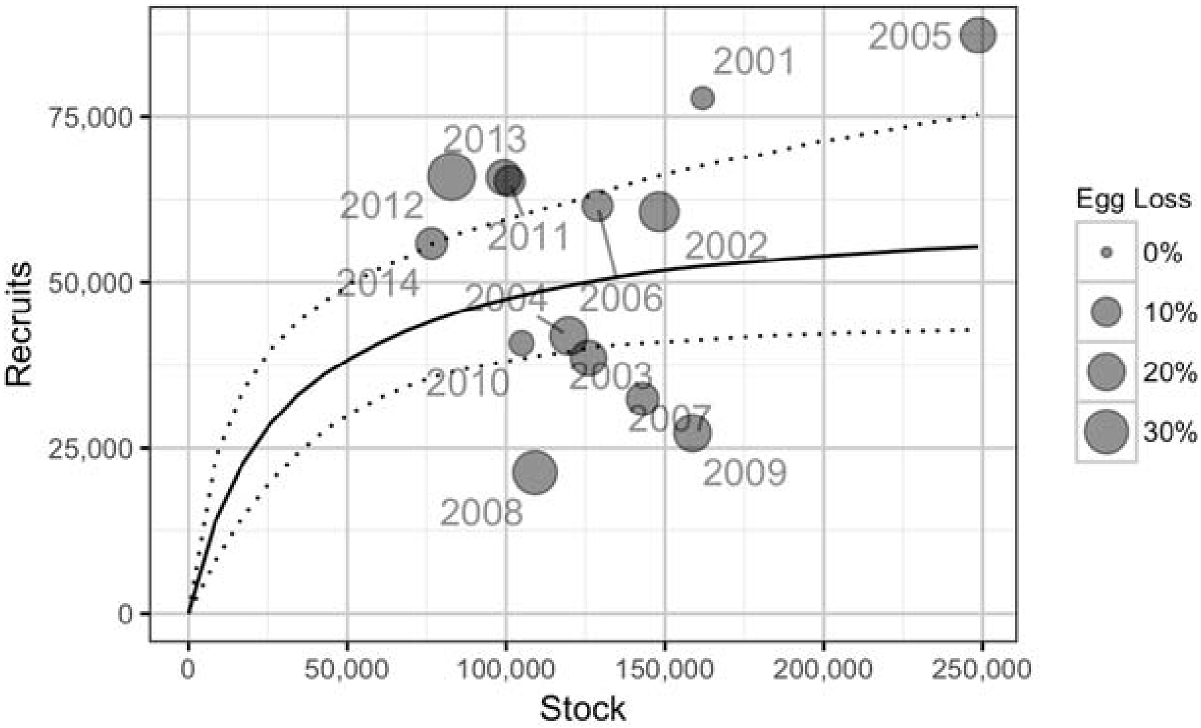

Figure 4. Predicted stock-recruitment relationship between age-2+ spawners ("Stock") and subsequent age-1 Mountain Whitefish ("Recruits") by spawn year (with 95% credible intervals). Estimated proportion of egg loss due to dewatering for each spawning year is shown by the size of shaded circles (reproduced from Golder 2017).