

Columbia River Water Use Plan Lower Columbia River Fish Management Plan

Lower Columbia River Rainbow Trout Spawning Assessment Implementation Year 9 Reference: CLBMON-46 Study Period: January to July 2016

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Prepared for: BC Hydro Castlegar, BC

Final Report

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February 1, 2017





LOWER COLUMBIA RIVER RAINBOW TROUT SPAWNING ASSESSMENT 2016

WLR Monitoring Study CLBMON-46 (Year 9)

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Cover Photos: Lower Columbia River Rainbow Trout Spawning Assessments (DNA sampling, aerial view of the Norn's Fan spawning area, and channel E spawner exclusion fence installation).

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EXECUTIVE SUMMARY

Thousands of Rainbow Trout (*Oncorhynchus mykiss*) spawn each spring in the Lower Columbia River (LCR) below Hugh L. Keenleyside Dam (HLK), and in the Lower Kootenay River (LKR) below Brilliant Dam. The resultant redds have the potential to be dewatered by flow reductions from the dams. To mitigate this risk, BC Hydro has implemented Rainbow Trout Spawning Protection Flows (RTSPF) from April 1-June 30 since 1992.

Rainbow Trout spawn monitoring began in 1999. The current program, which aims to better understand the links between the spring flow regime of the RTSPF and the abundance and trends of the ecologically and recreationally important Rainbow Trout population, commenced in 2008. Based on the absence of a detectable negative population-level effect, the regulatory agencies have granted BC hydro permission to dewater up to 1% of the average estimated annual redd abundance. In 2016, 36 dewatered redds were observed. Further dewatering of approximately 100 redds was probably prevented by the installation of an exclusion fence in channel E.

The Rainbow Trout abundance for 2016 was estimated at 25,740 fish, which was an increase from 2015 and continued the positive trend in Rainbow Trout abundance that has occurred since 1999. The 2016 estimate was highly uncertain due to the lack of reliable data from the latter half of the spawning period. The spatial distribution of fish throughout the river has generally expanded over the study's duration. The mean redd dewatering rate was 1.13% from 1999 to 2016. The conditions that lead to higher rates of dewatering, such as high water levels earlier in the season, appear to be associated with higher incubation success for the remaining embryos and alevins. One explanation is that when water levels are high fish spawn higher in the channel and as result their eggs are not scoured during peak discharge. Experimental flow manipulations are required to confirm this hypothesis and definitively answer the second and third management questions.

Objectives	Management Questions	Year 9 (2016) Status
Assess changes in the	1. Does the implementation of RTSPF over	The number of Rainbow Trout spawners and
relative abundance,	the course of the monitoring period lead to	redds has increased ~15-fold since 1999.
distribution and spawn	an increase in the relative abundance of	RTSPF may be responsible for this increase.
timing of Rainbow Trout	Rainbow Trout spawning in the LCR	
in the lower Columbia	downstream of HLK?	
River		
	2. Does the implementation of RTSPF over	The spatial distribution of Rainbow Trout
	the course of the monitoring period lead to	spawning increased from 1999-2015 and
	an increase in the spatial distribution of	showed a slight decline in 2016. RTSPF may
	locations (and associated habitat area) that	be responsible for this increase.
	Rainbow Trout use for spawning in the LCR	
	downstream of HLK?	
	3. Does the implementation of RTSPF over	Yes. Over all years of analysed data, the
	the course of the monitoring period protect	mean stranding rate of redds has been
	the majority of Rainbow Trout redds (as	1.13%, as compared to the estimated 50-
	estimated from spawning timing) from	75% stranding rate noted in shallow water
	being dewatered in the LCR downstream of	habitat on Norn's Fan in 1990 and 1991
	HLK?	prior to implementation of RTSPF.

A summary of the management questions and status for CLBMON-46 is in the table below.

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Additional Technical Support Clint Tarala, Gary Pavan, and Crystal Lawrence

ABBREVIATIONS

Abbreviations used throughout the report:

Abbreviation	Full Name
2D	Two Dimensional
ALR	Arrow Lakes Reservoir
AUC	Area-Under-the-Curve
BCH	BC Hydro
BRD	Brilliant Dam
HLK	Hugh L. Keenleyside Dam
LCR	Lower Columbia River
LDR	Lower Duncan River
LKR	Lower Kootenay River
RB	Rainbow Trout
RTSPF	Rainbow Trout Spawning Protection Flows
TOR	Terms of Reference
WLR	Water Licence Requirements
WUP	Water Use Plan

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1.0 INTRODUCTION

The Rainbow Trout (*Oncorhynchus mykiss*) population in the Lower Columbia River (LCR) between Hugh L. Keenleyside (HLK) dam and the U.S. border and in the Lower Kootenay River (LKR) below Brilliant Dam (BRD) has been studied extensively since the 1990s. Studies have focused on the assessment of effects of hydro-electric dam operations on life history, genetics, spawn timing, habitat use, and population trends and dynamics. (Heaton and Hildebrand 1997a, 1997b, Arndt 2000, Taylor 2002, Arndt and Klassen 2004, Ford and Hildebrand 2007, Baxter 2011). A brief summary of the previous studies on the Rainbow Trout in this section of the Columbia River can be found in Irvine et al. (2014).

Prior to 1992, HLK discharge typically decreased from March to May resulting in Rainbow Trout redd dewatering and potential population level effects (Hildebrand and McKenzie 1995, Thorley and Baxter 2011). In 1992 BC Hydro altered the spring HLK operations to keep river levels stable or increasing from April 1 to June 30 (BC Hydro 2005, Ford et al. 2008). The Rainbow Trout Spawning Protection Flows (RTSPF), which have occurred annually since 1992 (BC Hydro 2007), have been effective at significantly reducing the cumulative elevational drops in the Lower Columbia River (Larratt et al. 2013).

Various programs have monitored Rainbow Trout redds in shallow water areas since 1992 to identify redds at risk of dewatering. Between 1999 and 2012, dewatered redds were excavated as a matter of course and the salvaged eggs transferred to suitable, wetted gravels to minimize egg mortality (Baxter 2010a, 2010b, 2011). In 2013, the regulatory agencies granted BC hydro permission to annually dewater a maximum of 111 redds (1% of the average redd abundance from 1999 to 2011) before commencing salvage. From 2013 onwards the number of dewatered redds has not exceeded the threshold. Dewatered redds were enumerated by BC Hydro staff in 2014 and 2015 and by Mountain Water Research staff in all other years.

The primary objective of the present program is to monitor the status of the Rainbow Trout population in order to better understand the link between flow management strategy and population abundance and to propose and monitor testing of other flow strategies (BC Hydro 2007). It is important to consider alternatives to the current RTSPF flow regime as its implementation requires ~1 million acre-feet of retained storage in Arrow Lakes Reservoir (ALR) that is released in summer. Minimizing the volume of water stored in ALR, delaying the onset of storage and quickly releasing the additional storage could improve vegetation survival and increase littoral productivity and wildlife habitat (BC Hydro 2007).

Spawner assessments have occurred every year since 1999. The program annually records spawning activity in order to address the primary objective of the program which "*is to continue the collection of annual Rainbow Trout monitoring data to qualitatively and quantitatively assess changes in the relative abundance, distribution and spawn timing of Rainbow Trout in the lower Columbia River*" (BC Hydro 2007 p.3) and to address the specific management questions outlined below.

Long term monitoring of the LCR RB population continues to be of vital importance due to ongoing changes in the river's natural and operationally altered environment. Current questions of relevance to the health and sustainability of the RB population in the LCR include, but are not limited to, the impacts of Northern Pike (*Esox lucius*), Didymo (*Didymosphenia geminata*) and other invasive species introductions, and the ecological consequences of shifts in angler effort, climate change, and the increase in the sub-adult White Sturgeon (*Acipenser transmontanus*) population. While the long term fish indexing study on the LCR provides key data on a number of important parameters including growth rate, body condition, and spatial distribution of Rainbow Trout, Walleye and Mountain Whitefish fish, the low recapture rates may be limiting the program's ability to detect population trends in Rainbow Trout (Ford et al. 2013, 2014).

The following management questions are the focus of the LCR RB spawning assessment program:

- 1) Does the implementation of RTSPF over the course of the monitoring period lead to an increase in the relative abundance of Rainbow Trout spawning in the LCR downstream of HLK?
- 2) Does the implementation of RTSPF over the course of the monitoring period lead to an increase in the spatial distribution of locations (and associated habitat area) that Rainbow Trout use for spawning in the LCR downstream of HLK?
- 3) Does the implementation of RTSPF over the course of the monitoring period protect the majority of Rainbow Trout redds (as estimated from spawning timing) from being dewatered in the LCR downstream of HLK?

The TOR state that these three management questions will be answered by testing three key hypotheses:

 H_{01} : The relative abundance of Rainbow Trout spawners or redds in the Columbia River mainstem does not increase between the baseline period (1999 to 2006) and the WUP monitoring period associated with the continued implementation of RTSPF.

 H_{02} : The spatial distribution of locations and the associated habitat area that Rainbow Trout spawners use in the Columbia River mainstem does not increase between the baseline period (1999 to 2006) and the WUP monitoring period associated with the continued implementation of the RTSPF.

 H_{03} : The proportion of redds dewatered relative to the total redd production for Rainbow Trout spawning in the Columbia River mainstem does not increase between the baseline period (1999 to 2006) and the WUP monitoring period associated with the continued implementation of the RTSPF.

In order to achieve the program's primary objective, the population's response to alternative discharge regimes needs to be understood. The possibility of experimentally manipulating the flows were discussed in 2012, but to date the hydrograph has remained relatively constant between years (Baxter 2012). The experimental approach has been successful at teasing apart mechanisms behind population changes in other systems such as the Colorado (Korman et al. 2011).

2.0 METHODS

2.1 Mainstem Spawner and Redd Surveys

The mainstem portions of the Canadian LCR below HLK and the LKR below BRD (Figure 1) have been surveyed from helicopter approximately weekly during the spawning season (late January to May) since 1999 and the numbers of redds and spawners recorded by location. Prior to the start of helicopter surveys, boat surveys are done to confirm the commencement of spawning.

The major gravel areas are known by name and river kilometre, and are surveyed each flight. Since 2014 the section of river from Genelle to the U.S. border that lacks any major gravel areas has not been surveyed. The helicopter surveys are supplemented by the use of boat surveys, which cover the main spawning areas from Norn's Creek Fan to the lower island at Genelle. The boat surveys allow the identification of redds that are could not be identified with certainty from the air. The boat surveys also allow shallow-water redds to be monitored for dewatering potential (Baxter 2011).

In 2016, nine aerial surveys were completed from a single engine helicopter and each aerial survey was followed by a boat survey (Table 1). As in previous surveys the spawners and redds were enumerated by two experienced observers situated on the same side of the helicopter with one person responsible for counting redds and the other for counting spawners. Boat surveys without aerial surveys were conducted to assess the onset of spawning and/or to assess shallow water redds on January 28, February 18 and February 25 (Table 1). The number of days between helicopter surveys during the 2016 field season ranged from 13 to 6 with 9.3 days on average between surveys. It was an exceptional year with low water levels throughout the survey period.

Date	Survey Type(s)
January 28	Spawner onset and shallow water boat survey
February 18	Spawner onset and shallow water boat survey
February 25	Spawner onset and shallow water boat survey
March 4	Single engine helicopter, Boat survey
March 17	Single engine helicopter, Boat survey
March 25	Single engine helicopter, Boat survey
April 1	Single engine helicopter, Boat survey
April 11	Single engine helicopter, Boat survey
April 19	Single engine helicopter, Boat survey
April 28	Single engine helicopter, Boat survey
May 6	Single engine helicopter, Boat survey
May 18	Single engine helicopter, Boat survey

Table 1. Helicopter and boat based redd surveys and shallow water survey schedule for 2016.

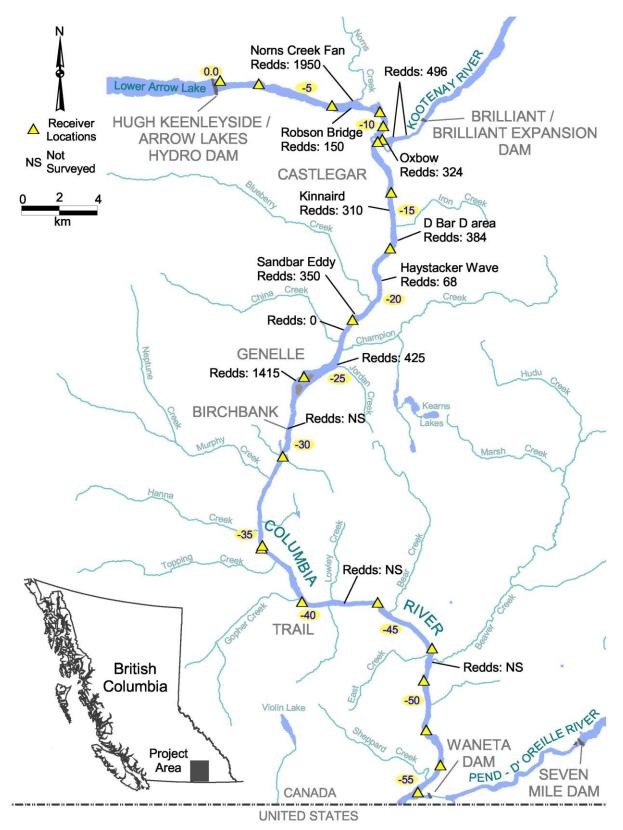


Figure 1. Study area for the Rainbow Trout spawning assessment program within the Lower Columbia and Lower Kootenay Rivers. The yellow numbers indicate river kilometre downstream of HLK dam and NS refers to areas that were not surveyed.

2.2 Norn's Creek Spawner and Redd Surveys

Spawner and redd surveys are conducted in Norn's Creek when time, resources and conditions permit. It is a major spawning tributary and likely a significant contributor to Rainbow Trout recruitment in the LCR. Reconnaissance surveys were completed in April and May, 2016 to assess whether aerial redd or spawner surveys could be done in conjunction with ground and snorkel surveys. Due to the early onset of high water conditions fish or redds could not be successfully enumerated in 2016 in Norn's Creek.

2.3 Redd Dewatering Surveys and Exclusion Fencing

Locations of shallow water redds with the potential to dewater were recorded by crews during 2016 boat surveys. A standard protocol was followed when an operational reduction was predicted by BC Hydro operations. This involved carrying out surveys in several locations with shallow water habitats that were vulnerable to dewatering. The day or two prior to a planned reduction, the areas were surveyed and each shallow water redd (< 1m in depth) marked with a flagged weight so it could be identified when the water levels were altered. The survey was completed by returning to the site after the operational reduction to determine how many redds were exposed by the drop (Table 2).

Reduction Date	HLK Discharge Start (m ³ /s)	HLK Discharge End (m ³ /s)	BRD Discharge Start (m ³ /s)	BRD Discharge Start (m ³ /s)	Dewatered Redds	Location
January 29	1519.9	1310	482	477	12	Kootenay Oxbow
January 30	1310.1	1080.4	477	478	8	Norn's Fan
February 5	1077.7	826.2	457	457	5	Norn's Fan
February 6	826.2	569.9	403	366	3	Genelle Channel E
February 13	567.6	426.2	455	452	4	Norn's Fan
March 4	283.3	284.3	821	745	2	Norn's Fan
March 17	139.2	121.1	784	805	2	Genelle Channel E

Table 2.	Reduction dates.	magnitude of reduction.	number and general locat	tion of dewatered redds.
	neudellon dutes,	indenitate of reduction,	finalliser and general loca	

Early in the spawning season, there were 20 redds constructed in Channel E (Right Downstream Bank of the Genelle area – see map A6, Appendix A). Given the low water levels this year, it was determined that if the area remained accessible to spawners, there was the potential for significant redd construction and subsequent dewatering. To prevent redd construction, an exclusion fence was maintained at Channel E between March 21, 2016 and April 8, 2016. By April 11, just 3 days

after the fence was removed, 102 new redds had been constructed in Channel E. It is estimated that without the exclusion fence, approximately 100 redds may have been dewatered.

2.4 DNA Analysis of Residence Timing and Population Structure

DNA samples (caudal fin clips) were taken at the time of capture in 2012 and were processed in January, 2016 to sex the tagged fish in order to potentially refine residence time estimates in future analyses and assess if they differ between males and females. There were 11 female fish and 9 male fish, approximating a 1:1 sex ratio from the tagged fish (Baxter et al. 2016).

In addition, DNA samples were taken from early spawners, autumnal non-spawners and peak spawners at three locations in the LCR in 2013, 2014 and 2015 and assessed for neutral genetic differentiation evidencing 'isolation by time' (Taylor 2014, 2016). When inter-annual variation was accounted for, there was a lack of significant differentiation among the timing groups showing that there is likely sufficient interbreeding between spawning timing groups to keep them from showing genetic differentiation (Taylor 2016). Rainbow Trout spawning at different times within the LCR may differ with respect to phenology such as behaviour, growth rate or development despite the lack of neutral genetic differentiation (Taylor 2016), but for management purposes, there is no need to manage for preservation of separate genetic stocks.

Spawner and Redd Abundance and Spawn Timing

2.4.1 Data Preparation

The Rainbow Trout fish and redd aerial count data for the LCR and LKR were collected by Mountain Water Research and databased by G. Pavan. Golder Associates provided the age-1 Rainbow Trout abundance estimates from the LCR Fish Population Indexing Program (CLBMON-45). Poisson Consulting Ltd. provided data on discharge and temperature for the study area from the BC Hydro database they maintain on the Columbia Basin flow and temperature data.

For analytic purposes, the study area was divided into three sections: the LCR above the LKR, the LKR and the LCR below the LKR. Redd and spawner counts upstream of Norns Creek Fan and downstream of Genelle were excluded from the section totals because they constitute less than 0.1% of the total count and were not surveyed every year. The redd and spawner counts for the right bank (looking downstream) above Robson Bridge were also excluded as they appear to be primarily driven by viewing conditions (and constitute less than 2.5% of the total). A decline in the redd count of more than one third of the previous maximum count for a particular section was inferred to be caused by poor viewing conditions (turbidity) and the affected spawner and redd section counts were excluded from any subsequent analyses.

The data were prepared for analysis using R version 3.3.1 (R Core Team 2015).

2.4.2 Data Analysis

The spawner residence time in days at Norns Creek Fan was estimated from the acoustic detection data using a Generalised Linear Model. An acoustically tagged fish was considered to be resident on a particular day between March 7th and May 31st if it was detected by the Norns Creek receiver at location 1 for at least three hours (with at least three detections in each hour) between 8:00 and 12:00 (which corresponds to the general timing of the surveys).

Key assumptions of the residence time model include:

• The residual variation in spawner residence time is log-normally distributed.

Preliminary analyses considered sex as a predictor of residence time, but the difference was not significant (p > 0.5).

In order to estimate spawner and redd abundance as well as the spawn timing of Rainbow Trout in the LCR, hierarchical Bayesian Area-Under-the-Curve (AUC) models were fitted to the aerial spawner and redd counts. The prior distribution for the spawner residence time was as estimated by the spawner residence time model.

Key assumptions of the AUC model include:

- Spawner and redd arrival and departure times are normally distributed.
- Spawner abundance varies by river section.
- Spawner abundance varies randomly by year and section within year.
- Spawner observer efficiency is between 0.9 and 1.1 (with values greater than 1 indicating overcounting).
- Peak spawn timing varies randomly by year.
- Spawning duration varies by river section.
- Mean spawner residence time is as determined in by the spawner residence time model.
- Redd observer efficiency is between 0.9 and 1.1 (with values greater than 1 indicating overcounting).
- The number of redds per spawner is a fixed constant.
- The residual variations in the spawner and redd counts are described by separate overdispersed Poisson distributions.

The models' variables, parameters, distributions and assumptions are more fully described in the online analytic report (http://www.poissonconsulting.ca/f/1385788078) and in Appendix C in this document.

2.5 Spatial Distribution of Spawners

The proportions of spawners at each site were used to calculate the Shannon Index, an information-theoretic measure of the diversity in the abundance distribution of a resource (Krebs 1999). In the current context, the Shannon Index takes into account both the number of spawning

sites and how the spawning activity is distributed among these, with a higher index indicating a greater spatial distribution of spawning.

The Shannon Index (H) is given by:

$$H = -\sum p_i log(p_i)$$

Where, p_i is the proportion of the spawning activity at the i^{th} location.

2.6 Fry Emergence Timing

The expected annual emergence timing was calculated from the estimated spawn timing and the mean daily surface water temperature at Norn's Creek Fan and Birchbank under the assumption that Rainbow Trout embryos require 480 accumulated thermal units (ATUs) to reach the emergence stage at approximately 10°C (K. Scheer and O. Schoenberger, Freshwater Fisheries Society of BC, pers. comm., 2010). Water temperature data have been collected at the gauging station on Norn's Creek Fan since 1999 and consistently throughout the year since 2000 though in some years there are missing data. In 2009, temperature loggers were buried in the gravels at depths of 0.15 m and 0.30 m from May to August at the Norn's Creek Fan site. Comparison of these two hyporheic temperatures with the surface water temperature suggested that surface water temperatures approximate the ATUs experienced by the developing embryos. In 2016 Golder Associates deployed a temperature logger in the LKR for CLBMON-45, which will be in place for the next 5 years and will help inform on temperatures encountered by fish in the Kootenay River.

2.7 Stock-Recruitment Relationship

The spawner estimates were combined with the following years boat electrofishing based estimates of age-1 RB abundance for the LCR from HLK dam to the U.S. Border and in the ~1.8 km of the lower Kootenay River below Brilliant Dam (Ford et al. 2012) to estimate the stock-recruitment relationship. Previous genetic work shows that the fish in the Kootenay and the Columbia interbreed readily so they are considered the same population for the purposes of assessment (Taylor 2002).

The relationship between the adults and the resultant number of age-1 subadults was estimated using a Bayesian Beverton-Holt stock-recruitment model (Walters and Martell 2004):

$$R = \frac{\alpha.S}{1+\beta.S}$$

Where, S is the adults (stock), R is the subadults (recruits), α is the recruits per spawner at low density and β determines the density-dependence.

Key assumptions of the Beverton-Holt stock-recruitment model include:

• The prior probability distribution for the maximum number of recruits per spawner (R0) is normally distributed with a mean of 90 and a SD of 50.

- The density-dependence varies with the proportional egg loss.
- The residual variation in the number of age-1 recruits is log-normally distributed.
- The prior probability distribution mean of 90 for R0 was based on an average of 2,900 eggs per female spawner, a 50:50 sex ratio, 50% egg survival, 50% post-emergence fall survival, 50% overwintering survival and 50% summer survival (Allen and Sanger 1960, Hildebrand and McKenzie 1995, Thorley 2009).

Models were fitted to the data using R version 3.2.2 (R Core Team 2015) and JAGS 4.2.0 (Plummer and Northcott 2013) which interfaced with each other via jaggernaut (Thorley 2013). For additional information on hierarchical Bayesian modelling in the BUGS language, of which JAGS uses a dialect, the reader is referred to Kéry and Schaub (Kéry and Schaub 2011).

2.8 General Analytic Approach

Unless indicated otherwise, the models used prior distributions that were vague in the sense that they did not affect the posterior distributions (Kéry and Schaub 2011). The posterior distributions were estimated from a minimum of 1,000 Markov Chain Monte Carlo (MCMC) samples thinned from the second halves of three chains. Model convergence was confirmed by ensuring that Rhat was less than 1.1 for each of the parameters in the model (Kéry and Schaub 2011).

The posterior distributions of the fixed parameters are summarised in terms of a point estimate (mean), lower and upper 95% credible limits (2.5th and 97.5th percentiles), the standard deviation (SD), percent relative error (half the 95% credible interval as a percent of the point estimate) and significance (Kéry and Schaub 2011). Variable selection was achieved by dropping insignificant fixed variables and uninformative random variables. A fixed variable was considered to be insignificant if its significance was 0.05, while a random variable was considered to be uninformative if its percent relative error was 80%. The Deviance Information Criterion (DIC) was not used because of its questionable validity when applied to hierarchical models (Kéry and Schaub 2011).

Results are displayed graphically by plotting the modeled relationships between particular variables and the response with 95% credible intervals (CRIs) with the remaining variables held constant. In general, continuous and discrete fixed variables are held constant at their mean and first level values respectively, while random variables are held constant at their typical values (expected values of the underlying hyperdistributions) (Kéry and Schaub 2011). Where informative the influence of particular variables is expressed in terms of the effect size (i.e., percent change in the response variable) with 95% CRIs(Bradford et al. 2005).

3.0 RESULTS

3.1 Mainstem LCR and LKR Spawner and Redd Abundance and Spawn Timing

The spawner and redd counts from the aerial surveys were analyzed together to produce annual abundance (Figure 2) and annual spawn timing estimates (Figure 3). The estimated abundance of

Rainbow Trout for 2016 was 25,740 fish (95% CI 13,950 – 48,480). This is an increase of ~10,000 fish from the 2015 estimate of abundance and an increase of 12,000 from the 2014 estimate (Figure 2).

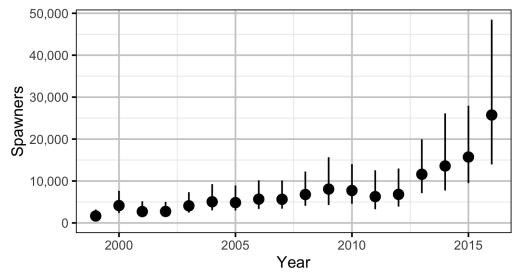


Figure 2. Annual estimates of abundance of Rainbow Trout spawners in the LCR below HLK dam and the LKR below Brilliant Dam from 1999-2016 with 95% credible intervals.

The spawn timing for three stages of spawning within the spawning period were estimated with 95% credibility intervals for each period (start, peak, end) from spawner and redd surveys for 2016. The start of spawning was estimated to be on March 9, 2016 (95% CI March 2, 2016 - March 16, 2016), the peak spawning had an estimated mean date of May 9, 2016 (95% CI May 1, 2016 – May 16, 2016), and the end of spawning had an estimated mean date of June 25, 2016 (95% CI June 13, – July 6, 2016) (Figure 3). The spawner and redd counts for 2016 are mapped in Appendix A. The spawner and redd counts for the study area's three sections, their AUC estimates and inferred viewing conditions are plotted in Appendix B.

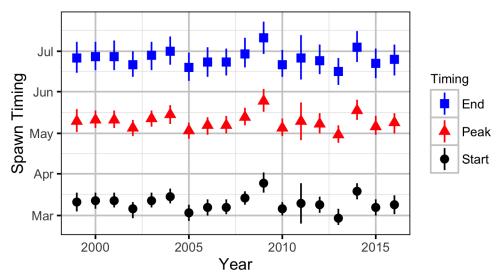


Figure 3. Annual estimates of peak, start and end of spawn timing of Rainbow Trout in the LCR below HLK dam and the LKR below Brilliant Dam from 1999-2016 with 95% credible intervals plotted for each timing category.

3.2 Spatial Distribution of Spawners

The percent of the peak spawner count by river kilometre shows relatively similar distributions among years with the exception of a spike in the percentage of fish in the river section of the Columbia above the Kootenay confluence in 2001, 2004 and 2012 (Figure 4).

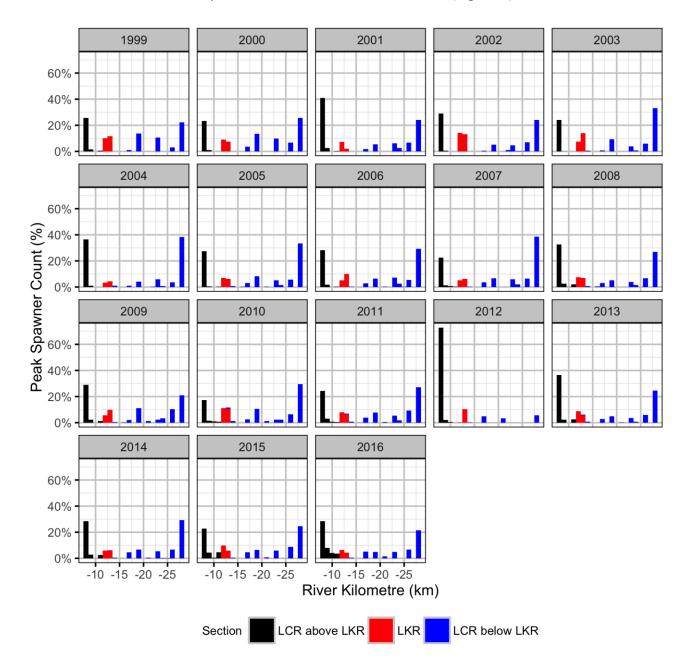
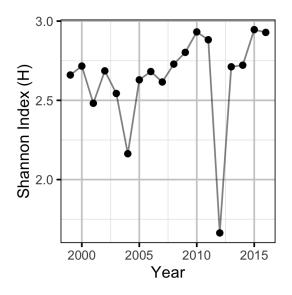
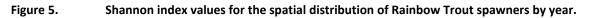


Figure 4. Percent of peak spawner counts by river kilometre and year and coded by river section with the mainstem Columbia above the Kootenay confluence in black, the Kootenay River in red and the Columbia below the Kootenay confluence in blue.

A higher Shannon index value indicates a greater spatial distribution of the spawning Rainbow Trout throughout the sites in the river. The general pattern through time has been for a gradual increase in the spatial distribution of the spawners since 1999. The lowest index value of 1.66 in 2012 corresponded to a very high water year with the vast majority of the counts occurring at Norn's Creek Fan (Figure 5).





3.3 Redd Dewatering

In 2013, based on the absence of a detectable negative population level response the regulatory agencies granted BC Hydro permission to dewater 111 redds each year (1% of the mean annual redd abundance from 1999 to 2011). In 2016, 36 redds were dewatered which corresponds to 0.2 % of the total for that year (Table 3). When the annual dewatering rate is averaged over the entire dataset the mean percentage of dewatered redds is 1.13% with a maximum of 3.8% (Figure 6). Part of the low redd dewatering numbers in 2016 was due to the exclusion fence at Channel E. It was estimated, given use of the channel before and after the fencing period, that approximately 100 redds might have been dewatered had the fencing not been erected.

Year	Number of Dewatered Redds	Observer
2013	97	MWR
2014	77	BCH
2015	52	BCH
2016	36	MWR

Table 3. Dewatered redd abundance from 201
--

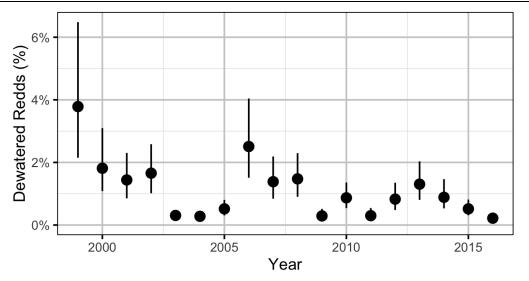


Figure 6. Percentage of redds dewatered in the Lower Columbia River below Hugh L. Keenleyside Dam and the Kootenay River below Brilliant Dam by year from 1999 to 2016. The bars represent 95% credible intervals.

3.4 Fry Emergence Timing

The fry emergence timing estimates combine the spawn timing estimates from the AUC model (Section 3.1) with the water temperature. The water temperature was the average at Norn's Creek Fan and Birchbank. In 2016 Golder Associates began collecting water temperature data from the LKR. The water temperatures at Norn's Creek Fan, Birchbank and the LKR throughout the spawning and emergence periods are plotted in Figure 7. Water temperatures higher than 17°C are associated with increased embryonic mortality (Humpesch 1985)

The mean estimate of peak fry emergence for the 2016 spawn year was June 18 (95% CI June 13 – June 24) (Figure 8). The mean estimate for the start of fry emergence was May 15 (95% CI May 12 - May 19), which is the earliest it has ever been (Figure 8). The end period of fry emergence was estimated at July 28 (95% CI July 17 – August 6). It is important to note that the last fry may not emerge until mid-August as the upper 95% credibility interval for 2009 was August 18th and for 2011 was August 12th (Figure 8, Irvine et al. 2014).

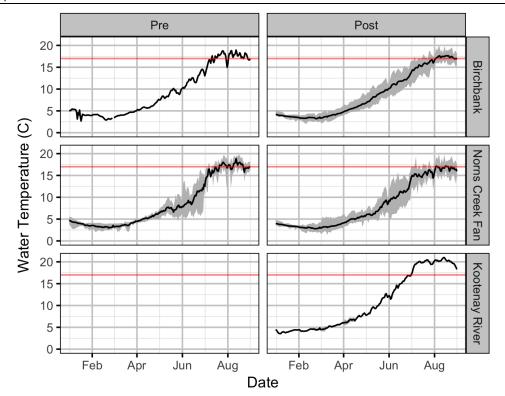


Figure 7. Mean daily surface water temperature at Birchbank, Norn's Creek Fan and in the Kootenay River from January to September for the pre (1999-2006) versus post (2007-) period (as defined in the management questions). The time series were incomplete. The black line indicates the average temperature, while the grey band indicates the range. The red horizontal lines indicate the lower range of the temperatures associated with increased embryonic mortality.

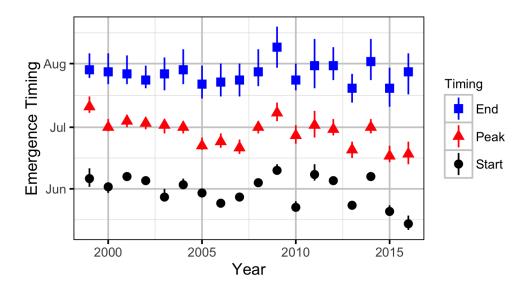


Figure 8. Annual estimates of the timing of emergence of Rainbow Trout fry from 2000 to 2016 in the Lower Columbia River below Hugh L. Keenleyside dam and the Lower Kootenay River below Brilliant Dam. The bars indicate the 95% credibility intervals for each estimated timing point. The estimates are derived from the spawner and redd counts and the mean surface water temperature at Norn's Creek Fan and Birchbank.

3.5 Stock-Recruitment Relationship

The Beverton-Holt stock-recruitment model lacked data informing the slope of the line through the origin (Figure 9). Consequently, the lower part of the stock-recruitment curve reflects the prior distribution for the maximum number of age-1 recruits per spawner. The prior distribution was based on the biology of the species including information on the number of eggs, survival of eggs and survival of 1-year-old fish (Figure 9). The carrying capacity was allowed to vary with the proportional egg loss as a significant positive correlation between age-1 abundance and egg loss was detected in 2015 (Baxter et al. 2016). Even after taking the stock size into account in the stock-recruitment model the significant positive correlation remained (p=0.016; Figure 11).

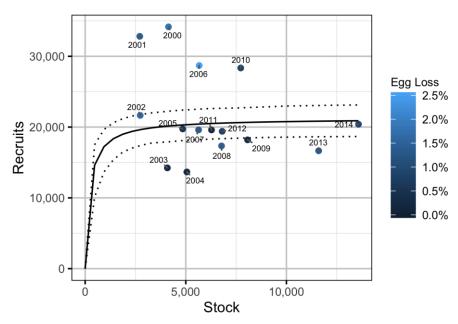


Figure 9. Beverton-Holt stock recruitment curve including prior information for estimating the starting slope of the curve for Rainbow Trout in the Lower Columbia River below Hugh L. Keenleyside Dam and the Kootenay River below Brilliant Dam for the spawn years from 1999 to 2014.

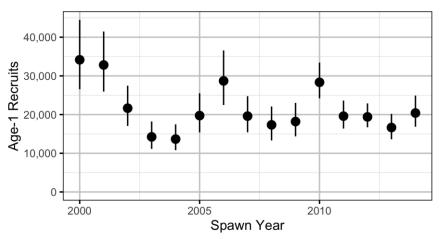


Figure 10. Number of age-1 Rainbow Trout vs. the spawn year for the Lower Columbia River below Hugh L. Keenleyside Dam and the Kootenay River below Brilliant Dam from 1999 to 2014. The vertical and horizontal bars represent 95% credible intervals.

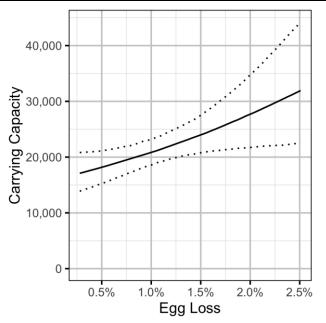


Figure 11. Relationship between carrying capacity and percentage egg loss estimated from the stock recruitment model based on the number of age-1 Rainbow Trout and the percentage of dewatered redds by year for the Lower Columbia River below Hugh L. Keenleyside Dam and the Kootenay River below Brilliant Dam from 2000 to 2014.

4.0 **DISCUSSION**

4.1 Management Question 1

The first management question asks whether RTSPF are linked to an increase in the number of spawners. The AUC-based estimates showed ~25,000 spawners in 2016 in comparison to ~1,600 in 1999 which is an approximately 15-fold increase of RB in the Lower Columbia and Lower Kootenay Rivers since the study program commenced. However, it is unknown whether this increase is due to the RTSPF, as a number of environmental and biological factors have also changed including the opening of 26 km of Blueberry Creek for Rainbow Trout spawners between 1998 and 2001 (Arndt and Klassen 2004), and the fertilization programs in Kootenay Lake and Arrow Lakes Reservoir. It is also likely that some of the spawning population in the study area is coming up from the United States portion of the Columbia River so some of the increase may be due to management strategies undertaken in the U.S. Nonetheless it is an impressive increase in Rainbow Trout abundance.

The accuracy and magnitude of the abundance estimates depend on the extent to which the assumptions of the model are met. In 2016, the estimate was highly uncertain due to the absence of data from the second half of the spawning period. The current rule is that if redd numbers decline by more than one third from an earlier peak for the year, the observation data are considered unreliable and are excluded from the AUC analysis. Field observations in 2016 noted an earlier end of spawning than the model predicted. In order to reduce the uncertainty in the annual abundance estimates it is recommended that: 1) the historical visibility estimates be reviewed and QA/QC'd, 2) the estimates of visibility be incorporated into the analyses, 3) the spawn timing in

years with few reliable counts data be fixed as the expected value for a typical year, 4) the LCR River above the LKR be further subdivided into Norn's Creek Fan and all other areas. The peak spawn timing date, the start date and end date vary by year but are fixed relative to each other. In a year with few reliable counts, these will be fixed to the expected value for a typical year. Norn's Creek Fan should be analysed separately because it is a large area of relatively shallow gravels that has been surveyed in all years and often retains good visibility longer than other areas.

In order to carry out these improvements under the current program budget, a reallocation of effort will have to occur with less flights occurring at the start of the spawning season, where the shape of the AUC curve is well parameterized. More resources will be required for assessing and defining visibility, improving the database, and refining the model to incorporate visibility, fixed spawn timing and four sections.

The positive correlation between the number of age-1 recruits and the percentage of dewatered redds was statistically significant. The stock-recruitment model allowed carrying capacity to vary with levels of egg loss and higher rates of egg loss were significantly correlated with increased recruitment. One hypothesis behind this surprising pattern is that the conditions that lead to higher rates of dewatering are coincident with higher survival in the remaining embryos and alevins. Experimental flow manipulations are required to test this hypothesis as well as definitely answer the first management question.

It is also important to be aware that the AUC-based estimates exclude fish spawning in tributaries (other than the Lower Kootenay River below Brilliant Dam), at deep-water sites, downstream of Genelle including below the US Border and upstream of Norn's Creek fan. The current state of knowledge regarding the numbers of fish spawning in tributaries, deep-water sites and in the US, is summarized in Thorley and Baxter (2011, 2012). In brief, tributaries to the LCR may provide habitat for over 3,000 spawners, fish are likely spawning unrecorded in the deeper parts of the Lower Columbia and Lower Kootenay Rivers (based on deep water observations on an exceptionally clear viewing day in 2010) and Rainbow Trout in the U.S. spawning locations may contribute to the LCR Canadian population. As part of their early 1990s Lower Columbia River fisheries inventory Hildebrand et al. (Hildebrand et al. 1995) radio-tagged 34 Rainbow Trout, 15 (44%) of which moved downstream into the U.S.; moreover, acoustically tagged fish were observed to undertake 50 km spawning migrations.

4.2 Management Question 2

The second management question concerns the spatial distribution and associated habitat area of spawning Rainbow Trout within the study area. As discussed by Thorley & Baxter (2011) the spawner and redd count data indicate that the spatial distribution and habitat area of spawning have moderately increased over the last decade. As spawner abundance has increased, particular areas may have saturated with fish and as a result fish have begun to utilize additional locations.

Field crews have noted over the years that the locations available for spawning Rainbow Trout vary considerably with the river stage and the discharge levels provided from HLK and BRD. Rainbow Trout spawning in the LCR and LKR select habitats where velocities range from 0 to 1.4 m/s with

peak spawning activity at a velocity of ~0.6 m/s and depth ranges from 1 to 1.5 m with peak habitat suitability curve values at ~1.1 m (Thorley and Baxter 2012). Therefore, although there are some spawning areas that are used every year, there are locations and habitats that are used sporadically depending on their suitability. In 2012, which was a very high water year, the percentage of fish observed above the Kootenay confluence was higher which may have been habitat or food related as much of the low-lying riparian area was inundated that spring.

4.3 Management Question 3

The third and final management question asks whether RTSPF protect the majority of redds from dewatering. This management question can be answered positively. In 2016, 36 Rainbow Trout redds were estimated to have dewatered during the spawning season. Using the redd dewatering estimates from the hierarchical model, the calculations suggest that the mean dewatering rate between 1999 and 2016 was 1.13%. There are no good, continuous data on the level of redd dewatering prior to the protection flows, but in a study done in 1990-1991 approximately 50-75% of the redds observed during field surveys were exposed by ensuing flow reductions (Hildebrand and McKenzie 1995).

Each year the vast majority of dewatering occurs during the early spawning period (beginning of January to the end of March). Fish were sampled from early and late spawners in the LCR study area to determine whether the early spawners are genetically unique from the peak spawners. The assessment of neutral genetic differentiation found that there was no statistically significant isolation by timing occurring (Taylor 2016).

4.4 Recommendations

The first recommendation is to review and QA/QC the historical visibility estimates and incorporate them into the AUC analysis. This task would likely take several days but is expected to noticeably reduce the uncertainty around the abundance estimates (MQ 1). The second recommendation is to assume a constant spawn timing for years with few reliable counts. It would likely take one to two days to implement but is also expected to noticeably reduce the uncertainty around the abundance estimates (MQ 1). The next recommendation is to estimate emergence timing separately for each river section. It would take a couple of days of coding and may provide further insights into dewatering (MQ 3). The final recommendation is to conduct experimental flow manipulations to better understand the effects of flow on the stock-recruitment relationship. Although this would require BC Hydro to alter flows it is required to definitively answer MQ 1.

5.0 CONCLUSIONS

To date, the program has conclusively answered the last of the three management questions. The first two management questions have been partially answered by documenting the increasing trends in RB abundance and spatial distribution. However, these increases cannot be attributed solely to the RTSPF without further research. In particular, experimental manipulations of flow are required to test the relationship between discharge and RB abundance.

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APPENDIX A

2016 Spawner and Redd Count Maps

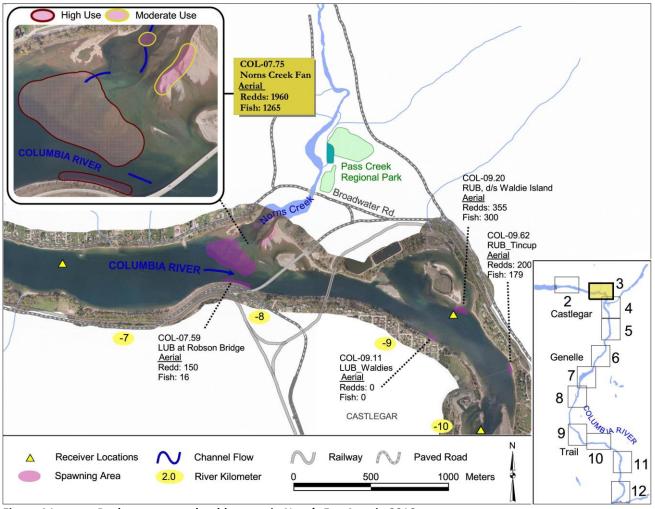


Figure A1. Peak spawner and redd counts in Norn's Fan Area in 2016.

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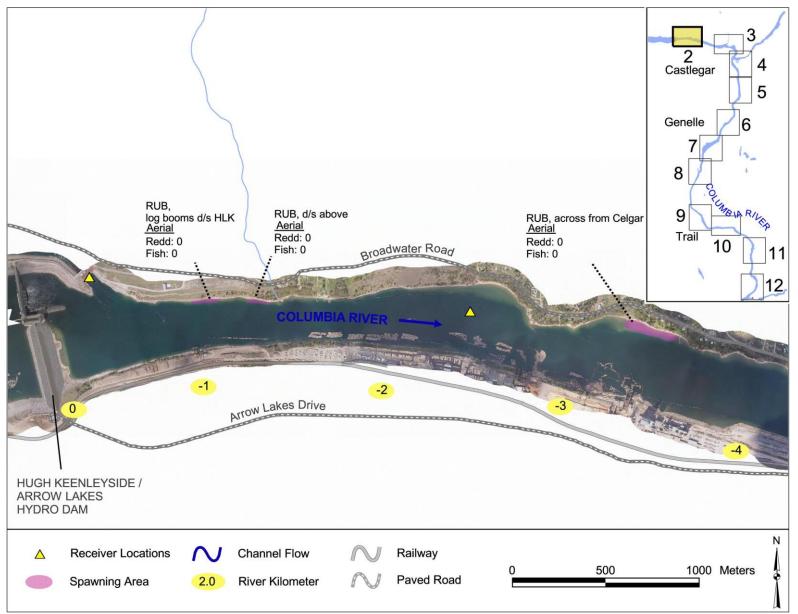
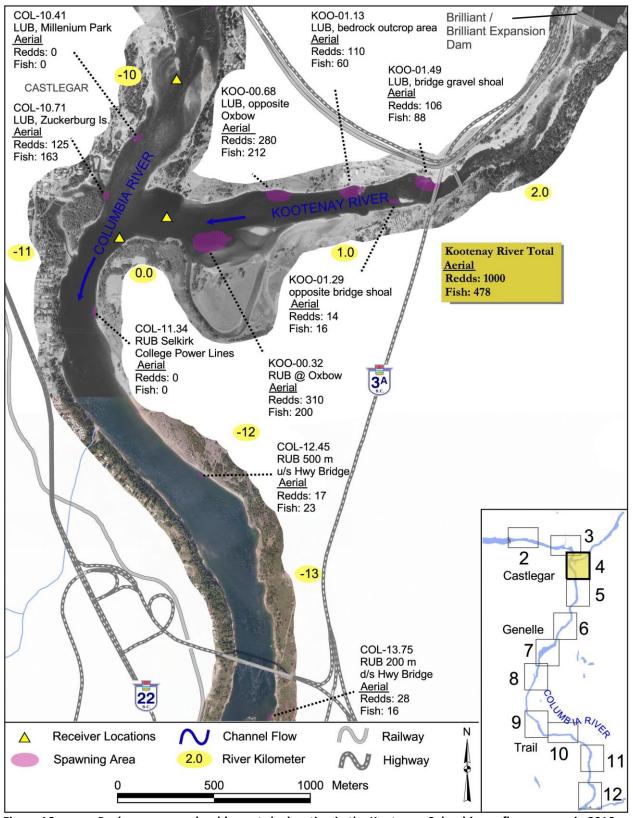


Figure A2. Peak spawner and redd counts by location in the HLK Dam area in 2016.





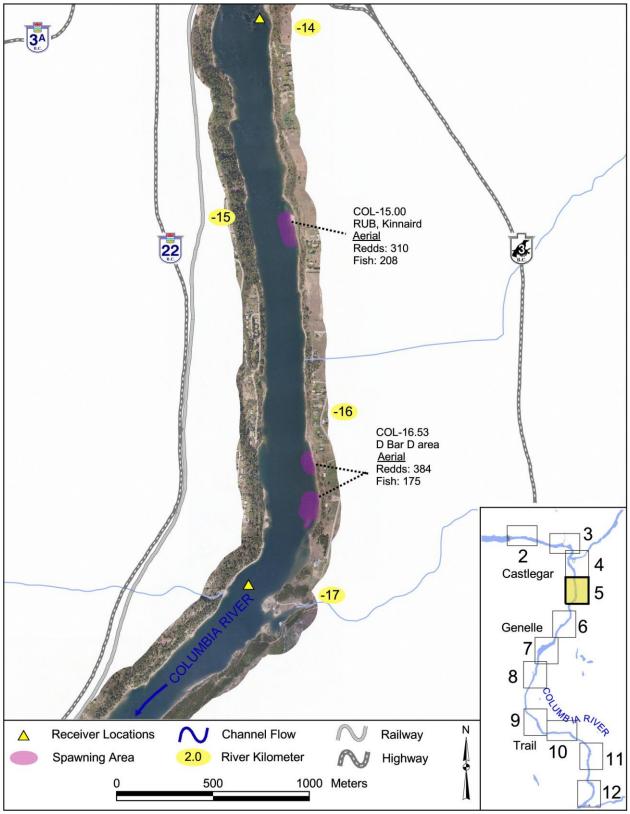


Figure A4. Peak spawner and redd counts by location in the D-Bar-D area in 2016.

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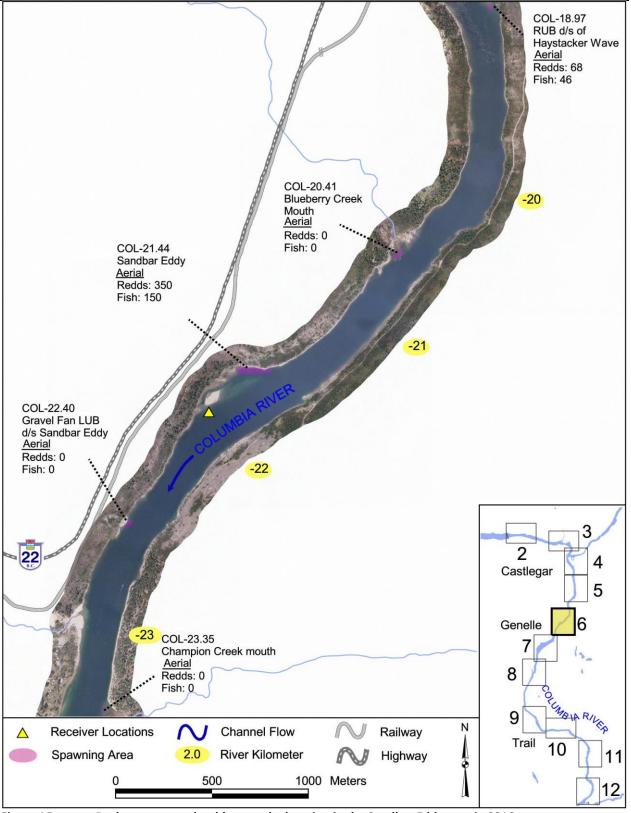


Figure A5. Peak spawner and redd counts by location in the Sandbar Eddy area in 2016.

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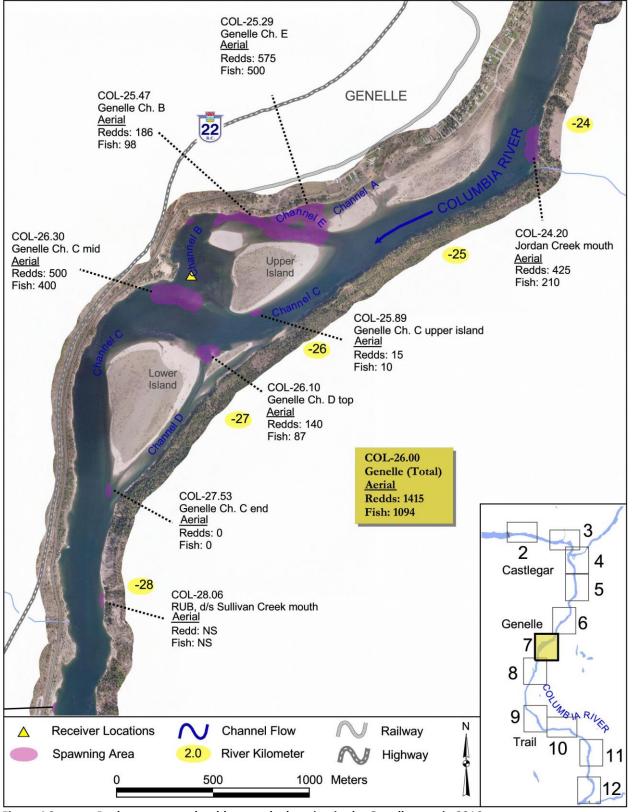


Figure A6. Peak spawner and redd counts by location in the Genelle area in 2016.

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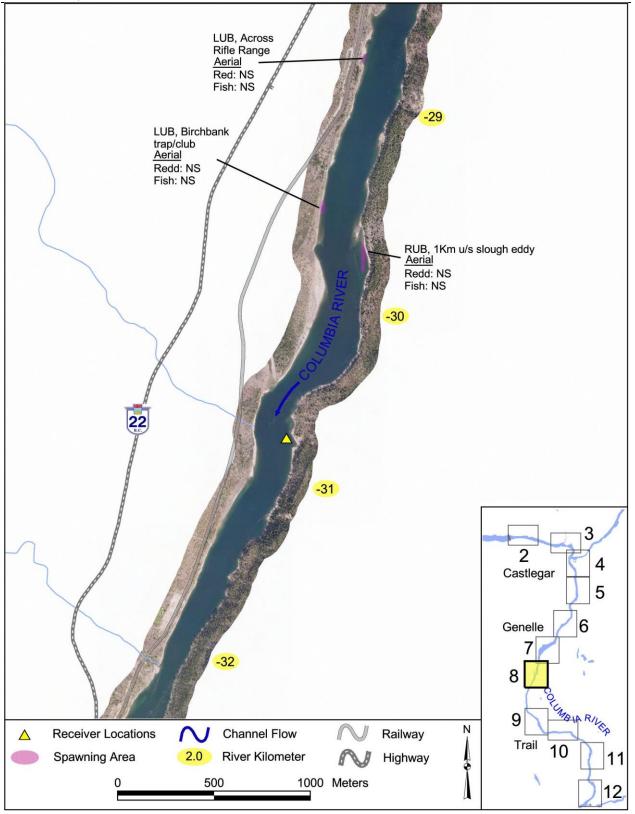


Figure A7. Peak spawner and redd counts by location in the Birchbank area in 2016.

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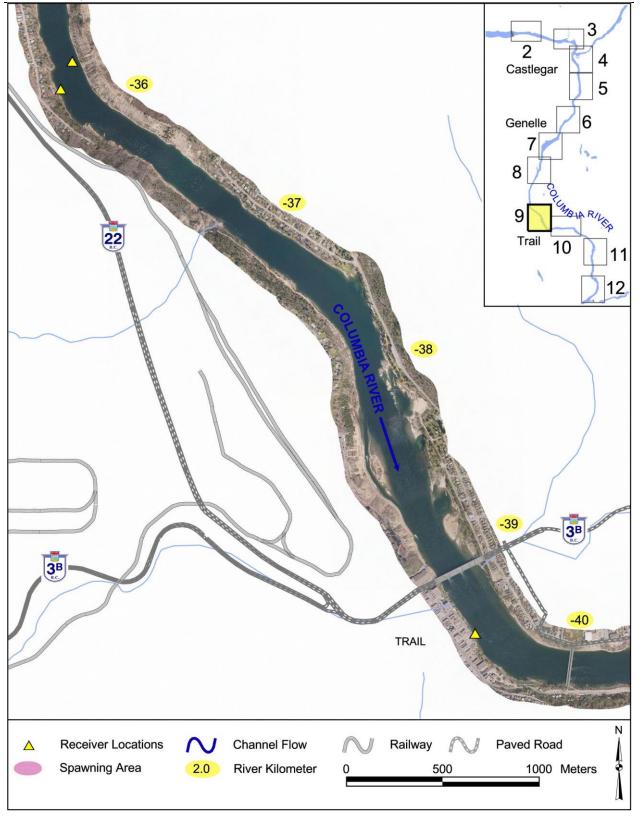


Figure A8. Peak spawner and redd counts by location in the Trail area in 2016.

APPENDIX B

2016 Spawner and Redd Counts with AUC Estimates and Viewing Conditions

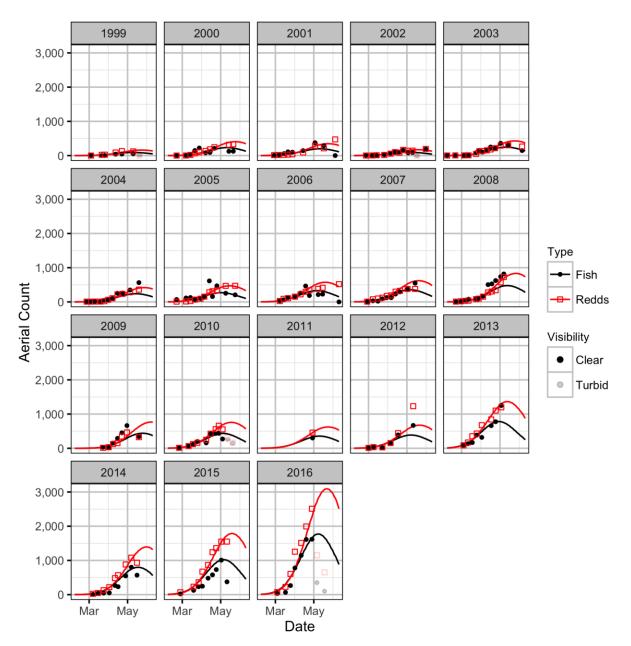


Figure B1. The spawner and redd counts for the Lower Columbia River above the Kootenay River with the AUC-based estimates of the expected counts 1999-2016.

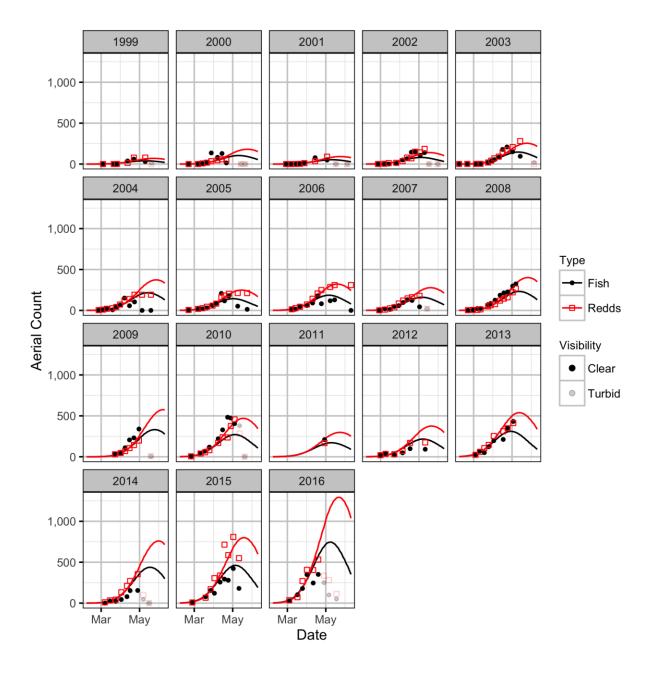


Figure B2. The spawner and redd counts for the Kootenay River below Brilliant Dam with the AUC-based estimates of the expected counts 1999-2016.

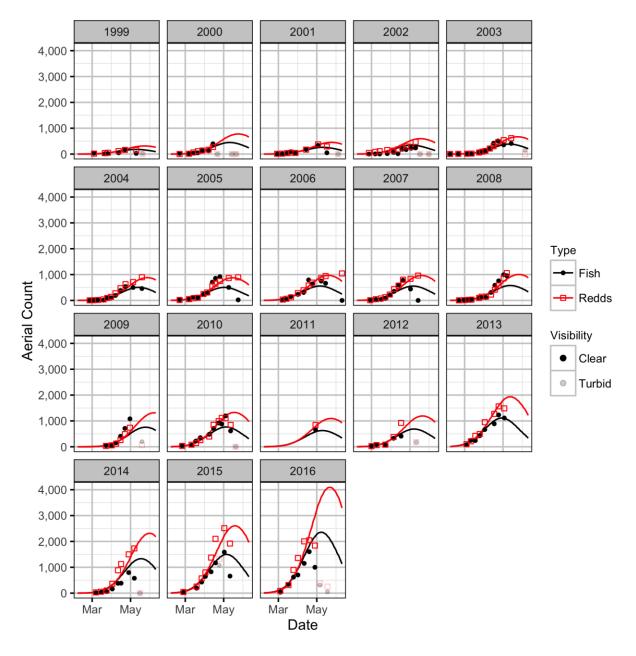


Figure B3. The spawner and redd counts for the Lower Columbia River below the Kootenay River with the AUC-based estimates of the expected counts 1999-2016.

Model Code

The JAGS model code, which uses a series of naming conventions, is presented below.

Area-Under-The-Curve Variable/Parameter bRdObsEfficiency bRdResidence bReddPerSpawner **bSpAbundance** bSpAbundanceSite[i] bSpAbundanceSiteYear[i, j] bSpAbundanceYear[i] **bSpArrivalPeak** bSpArrivalPeakYear[i] bSpArrivalWidthSite[i] **bSpObsEfficiency b**SpResidence Dayte[i] eFishDispersion eRdAbundance[i] eReddDispersion eSpAbundance[i] eSpArrivalPeak[i] eSpArrivalWidth[i] Fish[i] Redds[i] sFishDispersion Site[i] sReddDispersion sSpAbundanceSiteYear sSpAbundanceYear sSpArrivalPeakYear sSpArrivalWidth Year[i] Area-Under-The-Curve - Model1 model{ bSpAbundance \sim dnorm(5, 5^-2)

bSpArrivalPeak ~ dnorm(0, 14^-2) sSpArrivalWidth ~ dunif(log(14), log(42)) bSpResidence ~ dnorm(11, 3.07^-2) T(6.31, 18.16)

bSpObsEfficiency ~ dunif(0.9, 1.1)

Description

Redd observer efficiency Redd residence time Number of redds per spawner Intercept of log(eSpAbundance) Effect of ith site on log(eSpAbundance) Effect of ith site within jth year on log(eSpAbundance) Effect of ith year on log(eSpAbundance) Intercept of eSpArrivalPeak Effect of ith year on eSpArrivalPeak Effect of ith site on log(eSpArrivalWidth) Spawner observer efficiency Spawner residence time Day of the year on ith count **Overdispersion of Fish** Expected redd abundance on ith count Overdispersion of Redds Expected spawner abundance on ith count Expected peak of spawner arrival timing on ith count Expected SD of spawner arrival timing on ith count Observed number of fish on ith count Observed number of redds on ith count SD of overdispersion for Fish Site of ith count SD of overdispersion for Redds SD of effect of site within year on log(eSpAbundance) SD of effect of year on log(eSpAbundance) SD of effect of year on eSpArrivalPeak Intercept of log(eSpArrivalWidth) Year of ith count

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```
bSpAbundanceSite[1] <- 0
for (i in 2:nSite) {
 bSpAbundanceSite[i] ~ dnorm(0, 2^-2)
}
sSpAbundanceYear ~ dunif(0, 2)
for (i in 1:nYear) {
 bSpAbundanceYear[i] ~ dnorm(0, sSpAbundanceYear^-2)
}
sSpAbundanceSiteYear ~ dunif(0, 2)
for (i in 1:nSite) {
 for (j in 1:nYear) {
  bSpAbundanceSiteYear[i, j] ~ dnorm(0, sSpAbundanceSiteYear^-2)
}
}
sSpArrivalPeakYear ~ dunif(0, 28)
for (i in 1:nYear) {
 bSpArrivalPeakYear[i] ~ dnorm(0, sSpArrivalPeakYear^-2)
}
bSpArrivalWidthSite[1] <- 0
for(i in 2:nSite){
 bSpArrivalWidthSite[i] ~ dnorm(0, 1^-2)
}
bReddPerSpawner ~ dunif(0, 4)
bRdResidence ~ dnorm(100, 50^-2)
bRdObsEfficiency \sim dunif(0.9, 1.1)
sFishDispersion \sim dunif(0, 2)
sReddDispersion \sim dunif(0, 2)
for (i in 1:length(Fish)) {
 log(eSpAbundance[i]) <- bSpAbundance +</pre>
              bSpAbundanceSite[Site[i]] +
              bSpAbundanceYear[Year[i]] +
              bSpAbundanceSiteYear[Site[i], Year[i]]
```

```
eSpArrivalPeak[i] <- bSpArrivalPeak + bSpArrivalPeakYear[Year[i]]
log(eSpArrivalWidth[i]) <- sSpArrivalWidth + bSpArrivalWidthSite[Site[i]]
```

```
eSpFracArrived[i] <- pnorm(
               Dayte[i],
               (eSpArrivalPeak[i] - bSpResidence/2),
               eSpArrivalWidth[i]^-2
              )
  eSpFracDeparted[i] <- pnorm(
               Dayte[i],
               (eSpArrivalPeak[i] + bSpResidence/2),
               eSpArrivalWidth[i]^-2
              )
  eFish[i] <- (eSpFracArrived[i] - eSpFracDeparted[i])
         * eSpAbundance[i]
         * bSpObsEfficiency
  eFishDispersion[i] ~ dgamma(1/sFishDispersion^2, 1/sFishDispersion^2)
  Fish[i] ~ dpois(eFish[i] * eFishDispersion[i])
  eRdAbundance[i] <- eSpAbundance[i] * bReddPerSpawner
  eRdFracArrived[i] <- pnorm(
               Dayte[i],
               (eSpArrivalPeak[i] - bSpResidence/2),
              eSpArrivalWidth[i]^-2
             )
  eRdFracDeparted[i] <- pnorm(
               Dayte[i],
               (eSpArrivalPeak[i] + bRdResidence/2),
               eSpArrivalWidth[i]^-2
              )
  eRedds[i] <- (eRdFracArrived[i] - eRdFracDeparted[i])</pre>
         * eRdAbundance[i]
         * bRdObsEfficiency
  eReddDispersion[i] ~ dgamma(1/sReddDispersion^2, 1/sReddDispersion^2)
  Redds[i] ~ dpois(eRedds[i] * eReddDispersion[i])
 }
}
Stock-Recruitment
Variable/Parameter
                           Description
                           Maximum number of recruits per spawner
alpha
eRecruits[i]
                           Expected number of recruits in ith year
k
                           Maximum number of recruits
                           Observed number of age-1 fish in (i+1)th year
Recruits[i]
sRecruits
                           SD of residual variation about log(eRecruits)
```

```
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                           Observed number of spawners in ith year
Stock[i]
Stock-Recruitment - Model1
model{
 alpha ~ dnorm(90, 50^-2) T(1, )
 k ~ dnorm(2*10^4, (2*10^3)^-2) T(0, )
 sRecruits \sim dunif(0, 5)
 bBetaEggLoss ~ dnorm(0, 2^-2)
 for(i in 1:length(Stock)){
  log(eBeta[i]) <- log(alpha / k) + bBetaEggLoss * EggLoss[i]</pre>
  eRecruits[i] <- alpha * Stock[i] / (1 + Stock[i] * eBeta[i])</pre>
  Recruits[i] ~ dlnorm(log(eRecruits[i]), sRecruits^-2)
 }
}
Acoustic
Variable/Parameter
                              Description
bResidenceTime
                              Intercept of log(eResidenceTime)
eResidenceTime[i]
                              Expected residence time of ith spawner
ResidenceTime[i]
                              Observed residence time of ith spawner
sResidenceTime
                              SD of residual variation about log(eResidenceTime)
Acoustic - Model1
model{
 bResidenceTime \sim dnorm(0, 5^-2)
 sResidenceTime \sim dunif(0, 5)
 for(i in 1:length(ResidenceTime)){
  log(eResidenceTime[i]) <- bResidenceTime
  ResidenceTime[i] ~ dlnorm(log(eResidenceTime[i]), sResidenceTime^-2)
 }
}
Results
Model Parameters
The posterior distributions for the fixed (Kéry and Schaub 2011 p. 75) parameters in each model
are summarised below.
Area-Under-The-Curve
Parameter
                               Estimate
                                                         Upper
                                                                        SD
                                                                                             Significance
                                            Lower
                                                                                     Error
bRdObsEfficiency
                               1.00130
                                            0.90350
                                                         1.09650
                                                                        0.05930
                                                                                     10
                                                                                             0.0010
bRdResidence
                                            36.60000
                                                         110.17000
                                                                        19.44000
                                                                                     54
                                                                                             0.0010
                               67.78000
bReddPerSpawner
                               0.65420
                                            0.48100
                                                         0.82590
                                                                        0.08870
                                                                                     26
                                                                                             0.0010
bSpAbundance
                               7.55800
                                            6.90100
                                                         8.53300
                                                                        0.38400
                                                                                     11
                                                                                             0.0010
bSpAbundanceSite[2]
                               -0.69820
                                            -0.86060
                                                         -0.53130
                                                                        0.08500
                                                                                     24
                                                                                             0.0010
bSpAbundanceSite[3]
                               0.50130
                                            0.34830
                                                         0.66160
                                                                        0.08170
                                                                                     31
                                                                                             0.0010
bSpArrivalPeak
                               33.97000
                                            27.38000
                                                         40.55000
                                                                        3.31000
                                                                                     19
                                                                                             0.0010
bSpArrivalWidthSite[2]
                                            -0.07912
                                                                                     93
                                                                                             0.0260
                               -0.04075
                                                         -0.00368
                                                                        0.01899
```

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	[0]							
bSpArrivalWidthSit		0.02593	-0.06117			0.01737	130	0.1298
bSpObsEfficiency		.00140	0.90710			0.05690	9	0.0010
bSpResidence	1	3.75600	7.90800	17.8840	00	2.61600	36	0.0010
sFishDispersion	0	.74570	0.69400	0.80160	כ	0.02770	7	0.0010
sReddDispersion		.29899	0.27278	0.32763	3	0.01376	9	0.0010
sSpAbundanceSiteYear		.20910	0.14900	0.28720)	0.03430	33	0.0010
sSpAbundanceYear		.76710	0.51840	1.17330)	0.16610	43	0.0010
sSpArrivalPeakYear		.85100	4.40500	10.7110	00	1.56900	46	0.0010
sSpArrivalWidth		.31130	3.24550	3.37410	C	0.03330	2	0.0010
Convergence				Iteratio	ns			
1.07				1e+06				
Stock-Recruitment								
Parameter	Estimate	Lower		Upper	SD		Error	Significance
								•
alpha	111.4000	41.2000		197.8000	40.2	2000	70	0.001
		41.2000 -0.3262	כ		40.2 0.0		70 78	-
alpha	111.4000)	197.8000	0.0		-	0.001
alpha bBetaEggLoss	111.4000 -0.1866	-0.3262)	197.8000 -0.0352	0.0	743 57.0000	78	0.001 0.016
alpha bBetaEggLoss k	111.4000 -0.1866 21239.0000	-0.3262 18993.0)	197.8000 -0.0352 23552.0000	0.0 ⁻ 116	743 57.0000	78 11	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits	111.4000 -0.1866 21239.0000	-0.3262 18993.0)))))))))))))))))))	197.8000 -0.0352 23552.0000 0.3813	0.0 ⁻ 116	743 57.0000	78 11	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits Convergence	111.4000 -0.1866 21239.0000	-0.3262 18993.0)))))))))))))))))))	197.8000 -0.0352 23552.0000 0.3813 Iterations	0.0 ⁻ 116	743 57.0000	78 11	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits Convergence 1	111.4000 -0.1866 21239.0000	-0.3262 18993.0)))))))))))))))))))	197.8000 -0.0352 23552.0000 0.3813 Iterations	0.0 ⁻ 116	743 57.0000	78 11 40	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits Convergence 1 Acoustic	111.4000 -0.1866 21239.0000 0.2532	-0.3262 18993.(0.1774	0000	197.8000 -0.0352 23552.0000 0.3813 Iterations 10000 SD	0.0 116 0.0	743 57.0000 571	78 11 40	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits Convergence 1 Acoustic Parameter	111.4000 -0.1866 21239.0000 0.2532 Estimate	-0.3262 18993.0 0.1774 Lower	0 0000 Upper	197.8000 -0.0352 23552.0000 0.3813 Iterations 10000 SD 0.2740	0.0 ⁷ 116 0.09 Error	743 57.0000 571 Significa	78 11 40	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits Convergence 1 Acoustic Parameter bResidenceTime sResidenceTime	111.4000 -0.1866 21239.0000 0.2532 Estimate 2.3570	-0.3262 18993.0 0.1774 Lower 1.823	0 0000 Upper 2.8980	197.8000 -0.0352 23552.0000 0.3813 Iterations 10000 SD 0.2740 0.2253	0.0 [°] 116 0.09 Error 23	743 57.0000 571 Significa 7e-04	78 11 40	0.001 0.016 0.001
alpha bBetaEggLoss k sRecruits Convergence 1 Acoustic Parameter bResidenceTime	111.4000 -0.1866 21239.0000 0.2532 Estimate 2.3570	-0.3262 18993.0 0.1774 Lower 1.823	0 0000 Upper 2.8980 1.5362	197.8000 -0.0352 23552.0000 0.3813 Iterations 10000 SD 0.2740 0.2253	0.0 [°] 116 0.09 Error 23	743 57.0000 571 Significa 7e-04	78 11 40	0.001 0.016 0.001