Columbia River Project Water Use Plan

Revelstoke Flow Management Plan

CLBMON-18 Middle Columbia River Adult Fish Habitat use Monitoring Program

Implementation Year 4

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LGL Limited environmental research associates
Sidney, BC

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Modelling the Influence of Hydrodynamics on Bull Trout (*Salvelinus confluentus*) and Mountain Whitefish (*Prosopium williamsoni*) Bioenergetics Downstream of Revelstoke Dam

FINAL REPORT

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Executive Summary[1]

The CLBMON-18 Middle Columbia River Adult Fish Habitat Use Monitoring Program was designed to assess the effects of variations in discharge and reservoir elevations on habitat use and daily activity of fish species downstream of Revelstoke Dam. A second objective was to assess if their pattern of habitat use was influenced by minimum flow releases and the joint entry in operations of Revelstoke Unit 5 (REV5; both started in December, 2010).

In the first three years of the program (fall 2008 to fall 2010; pre-REV5), Bull Trout (*Salvelinus confluentus*) and Mountain Whitefish (*Prosopium williamsoni*) were tracked through radio tags and coded electromyogram (EMG) radio tags in Reaches 3 and 4 (the region from immediately downstream of Revelstoke Dam to the confluence of the Illecillewaet River, approximately 7 km downstream as the crow flies, or 11 km of shoreline).

Radio tags. During the Fall 2009, 12 Mountain Whitefish were implanted with conventional radio tags specially programmed to transmit intermittently over multiple seasons - fall 2009, winter 2010 (February) and in spring 2010 (June). During the fall 2010, 20 Bull Trout were also implanted with similar, larger, radio tags. Bull Trout and Mountain Whitefish were tracked every 12 hours along Reaches 3 and 4 of the MCR during the fall . Daily fish tracking occurred at noon and midnight with the exception of surgery nights (cf. EMG section below).

Each session lasted approximately three hours to develop a time series of fish locations. The two daily tracking times were chosen to represent the approximate time of daily discharge peak and nightly low flows.

Fish tracking was conducted from shore using various access points to cover the entire study area. Fish locations (longitudinal position in the river) were used to determine patterns of distribution and estimate movements across a range of operational flows. Bull Trout movements were analyzed for trends amongst sex and sizes of fish. Bull Trout movements patterns were also related to river hydrology parameters associated with hydropeaking at the twelve-hour scale.

EMG tags. Adult Bull Trout and Mountain Whitefish were captured at night in late September and October and surgically implanted with coded electromyogram (EMG) radio tags (which measure the frequency of tail beats in their dorsal muscles) and tracked. The procedure necessitated specialized surgical skills and a lengthy recovery and tag calibration time (> 12 hrs per fish). Over the duration of three years (Fall 2008 to Fall 2010), a total of 88 Bull Trout and 33 Mountain Whitefish were implanted with coded EMG tags. Catching Mountain Whitefish

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[1] The first part of this ES was written by BC Hydro to reflect the work done in the first three years of the program. It is solely based on the report from the third year of the program (Taylor and Lewis 2011), available at *https://www.bchydro.com/content/dam/hydro/medialib/internet/documents/planning_regulatory/wup/southern_interior/2011q3/clbmon-18_yr3_2011-06-10.pdf*

large enough for EMG tagging was a challenge and Mountain Whitefish movement data from this project were scarce compared to Bull Trout movement data.

Hydrological variables tested were hourly discharge magnitude and within-hour discharge change (defined as the difference between the within-hour maximum and minimum instantaneous discharges).

Small thermal loggers were attached to 18 large Bull Trout EMG tags to document fine-scale temperatures at fish locations and to compare these temperatures to the river temperature recorded approximately 7km downstream of REV. The intent was to determine if these fish showed behavioural thermoregulation (choosing positions in the river that offer refuge from ambient river temperatures).

Blood cortisol. Blood samples were also collected from Mountain Whitefish and analyzed for the glucocorticoid hormone. Cortisol is the primary stress hormone in fish.

The electromyogram telemetry studies on fish populations in the area found inconclusive results for the biological significance of flow regimes changes. With the addition REV 5 in 2010 a minimum discharge of 142 cms was implemented, with flow velocities expected to be similar to the pre-flow phase, but with maximum predicted discharges resulting in flow velocities rarely experienced by the fishes during the pre-flow change phase. Concern over the energetic consequences of increased maximum discharge magnitude lead to a literature review assessing the feasibility of building fish bioenergetic models to predict these energetic consequences. The review suggested that currently available data should be sufficient to allow this modelling exercise to proceed.

The study herein focuses on the development of empirically based bioenergetics models for Bull Trout and the Mountain Whitefish. The goal of the bioenergetics models was to be able to predict the respiration costs associated with a hydrology regime downstream of Revelstoke Dam. Bioenergetics models provide a theoretical approach for estimating the energy budget in animals. Typically three main components may be considered: metabolism, waste, and growth. The current study focuses on the two primary components of metabolism: standard and active metabolic rates. These two components are often of interest to ecologists as they provide the floor and ceiling for aerobic energy metabolism. Both components are also expected to be directly affected by flow regime changes.

The afore-mentioned three-year telemetry tagging study conducted under CLBMON-18 was used as a basis to predict fish behaviour under varying environmental conditions of discharge and temperature. Linear mixed effect models were fit to predict behavioural components such as the propensity to swim, swim speed, and movements. These separate components were combined to make predictions about hourly activity of fish under novel flow regimes. Activity estimates were then paired with estimates of standard metabolism, which is largely driven by temperature changes, to predict hourly respiration rates under a novel flow regime. Uncertainty in these estimates was determined using a Monte Carlo approach (i.e., computer experiment), which assessed the impact of individual and hourly stochasticity in fish behaviour on calculated respiration rates.

A complete bioenergetics model was developed for Bull Trout; however, a lack of calibration data for tagged Mountain Whitefish prevented completion of a similar model for this species. Male and female Bull Trout appeared to behave quite differently to hydrological conditions, which may have been the result of the spawning period overlapping with the commencement of the telemetry study. Male Bull Trout showed good swim performance, including similar estimates of maximally sustained swim speeds. The performance of the bioenergetics model for male Bull Trout was therefore assessed by comparing predicted respiration for two months in 2010; one representing a lower flow, higher temperature regime and the other a higher flow, lower temperature regime. Comparisons of the two months indicated differing predicted swim behaviours, but overall similar respiration profiles across the month suggesting behavioural changes can compensate for energetic demands caused by temperature differences. This emergent model behaviour was unexpected and may represent an adaptive mechanism for "economizing" respiration energetics under variable environmental conditions.

The linear regression predictions associated with flow showed consistent responses to river discharge, suggesting that extrapolations outside of the observed maximum discharge of 1,765 cms should be possible within reason (e.g., 2,200 cms). When such flow conditions were tested, the bioenergetics model produced plausible energetics estimates, suggesting that it should be possible to use the model to assess altered flow regimes expected under REV 5. Additional observations during higher periods of flow are therefore not required.

Using the male Bull Trout energetics model as a surrogate for both sexes during non-reproductive period, daily energy expenditures under REV 5 were compared to base conditions across all seasons and within reproductive and non-reproductive periods. Overall, daily energetic expenditures were found to be similar with difference in the uncertainty associated with the calculation. Given that the range of energetic demands under REV 5 flows were also found to be well within the biological range we do not find evidence for a sustained impact on Bull Trout energetics assuming water management practices remain similar to the practices observed during the study period. While this assessment included short-term behavioural changes, long-term foraging trade-offs could not be considered because effects are unknown and difficult to estimate in a field environment.

Finally, further field work would be required to develop an equivalent Mountain Whitefish bioenergetic model. For Mountain Whitefish, this could potentially be completed in a single year if a sufficient range of hydrological conditions were available and a sample size of approximately 98-150 individuals could be collected and equipped with accelerometer tags.

Objective	Management Question (MQ)	Summary of Key Results¹
Assess how movement patterns and activities (and hence habitat use) of Bull Trout (Salvelinus confluentus) and Mountain Whitefish (Prosopium williamsoni) are affected by flow releases from Revelstoke Dam.	What are the movement patterns of selected resident fish species in the Middle Columbia River?	Bull Trout and Mountain Whitefish occupied similar locations in both spring and fall: the Big Eddy, the area immediately upstream of the Jordan River, the area downstream of Scales Creek and a two kilometre section of the MCR downstream of REV. Mountain Whitefish did exhibit some localized movements, but there were no clear pattern. Large Bull Trout did not move more frequently than small ones; however, they did move greater distances and had larger linear home ranges. There was no effect of flow magnitude on the proportion of Bull Trout which moved between tracking periods. ("It was assumed that the proportion of bull trout that move between tracking periods may increase with declining flows; however, we found no significant effect that suggests this to be true"; Taylor and Lewis 2011, p. 64).

	How do fishes in the Middle Columbia respond to diel variations in flow from Revelstoke Dam?	**Movements**. The magnitude of discharge change had no effect on the probability of movement, nor did the minimum discharge during the same period. **Muscle activity**. The correlation between hourly mean discharge magnitude and Bull Trout muscle activity was statistically significant (r= 0.56). Bull Trout closer to REV showed more muscle activity than fish located at stations further downstream. Hourly mean discharge had a medium effect (r = .36) on Whitefish swimming activity. There were large variations in within-hour changes in discharge (range = 0-1045 m^3 /s), which are characteristic of hydropeaking systems. However, activity in either species was not correlated with the within-hour changes in discharge. The diel effect on Bull Trout activity was very small and not a significant predictor of activity. Mountain Whitefish were more active during the day than at night. Mountain Whitefish blood cortisol concentrations were higher during periods of high discharge, but the highest cortisol values were very low and corresponded to values of unstressed fish. The differences between Bull Trout body and ambient temperature were small and did not show any evidence of these fish seeking a temperature refuge. The largest heterogeneities were around the Revelstoke golf course and Big Eddy, where the river depth is least homogenous.

	Does the implementation of the 142cms minimum flow affect the energy expenditure of resident fishes from the Middle Columbia, and does this affect their growth or survival?	The study ending in 2010 included the minimum discharge from REV during the 12 hours between tracking locations as a predictor in Bull Trout movement models to test for potential effects of minimum flows on movement parameters. The minimum discharge between tracking locations was never a significant effect in any Bull Trout movement model of the five seasons tested. Mountain Whitefish movement models were not developed due to the small sample size. An empirically based bioenergetics model was built for Bull Trout to predict daily energy expenditures associated with flow regimes. The model incorporated behavioural components and produced plausible energetics estimates, well within the biological range for the species, across the range of flow rates under the 142 cms minimum flow regime. Comparisons of daily energy expenditures before and after the minimum flow regime did not find significant changes to daily energetics across the seasons, nor during the reproductive period. Taken together, modelling results did not find evidence for a sustained impact on daily energy expenditures. Finally, long-term behavioural trade-offs such as foraging were not considered as part of the assessment due to their unknown nature.

1 The MQ table format originated after the original contractors (Golder and U. of Carleton) had completed the first three years of the study. The answers to the first two MQ above, and part of MQ 3 are based on the report from the third year of the program (Taylor and Lewis 2011).

Acknowledgments

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Abbreviations and Acronyms

Abbreviation or Acronym	Definition
AICc	Akaike information criterion (AIC), that has a correction for small sample sizes
AMR	Active metabolic rate
BL	Body lengths
CLB-MON	CLBMON-18 Middle Columbia River Adult Fish Habitat Use Monitoring Program
cms	Measure of discharge volume, cubic meter per second or *cms* (m^3/s)
CMR	Capture-mark-recapture
DMR	Digestion metabolic rate
HEC-RAS	Hydrological model
EMG	Electromyography or Electromyogram
FL	Fork length
TBF	Tail beat frequency
SEMG	Standardized electromyography
SMR	Standard metabolic Rate
SS	Swim speed

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1 Introduction

The CLBMON-18 Middle Columbia River Adult Fish Habitat Use Monitoring Program (CLBMON-18 hereafter) was designed to assess the effects of variations in discharge and reservoir elevations (i.e., hydroelectric dam operations) on the habitat use and daily activity of selected fish species using the Middle Columbia River (MCR) downstream of Revelstoke Dam. Two species targeted in CLBMON-18 are Bull Trout (*Salvelinus confluentus*) and Mountain Whitefish (*Prosopium williamsoni*).

Studies on the Bull Trout and Mountain Whitefish populations downstream of Revelstoke Dam were conducted using electromyogram (EMG) telemetry (Taylor and Lewis 2009, 2010, 2011, Taylor et al. 2013, 2014). EMG techniques allow for direct measurement of axial swimming muscle activity, and when combined with remote telemetry allow for the remote monitoring of locomotor activity and activity related energetics (Cooke 2001, Cooke et al. 2004, Brown et al. 2007). Generally, fish activity levels are thought to be influenced by patterns of flow change by events such as pulse flows during hydroelectric operations (Murchie and Smokorowski 2004, Cocherell et al. 2011); although activity changes are not always the case (Geist and Brown 2005). Initial results from earlier CLBMON-18 EMG telemetry studies found associations between activity and discharge, but the biological significance of these effects were inconclusive.

In 2011, a fifth turbine unit was installed in Revelstoke Dam (REV 5), followed by the implementation of a minimum discharge of 142 cms. While, the range of discharges experienced by the two species during the pre-flow change are expected to be similar to the water velocities encountered under the new flow regime, the maximum predicted discharges resulting from REV 5 (i.e., 2124 cms and higher) would have rarely been experienced by the fishes during the pre-flow change phase. Taylor et al. (2014) highlighted the need to focus on the effects of maximum discharge magnitude when considering the energetic consequences of altered flow regimes on these species. A subsequent literature review of energetics models by Guénard and Boisclair (2015) suggested that, based on the available data, it was feasible to model the effects of the new flow regime on Bull Trout energetics, but that Mountain Whitefish may be a more difficult task.

This study attempts to build bioenergetic models to assess novel flow regime effects on respiration of Bull Trout and Mountain Whitefish downstream of Revelstoke Dam using data from previous sampling programs (Taylor and Lewis 2009, 2010, 2011). Bioenergetics models provide a theoretical approach for estimating the energy budget in animals into three main components: metabolism, waste, and growth (Winberg 1956; Chipps and Wahl 2008). Depending on the goal, these components can be regrouped or studied separately. The current study focuses on predicting energy expenditure (i.e., respiration), rather predicting the full energy budget. Fish energy expenditure is the result of three components: the energy required for basic functioning and maintenance (termed standard metabolic rate; SMR), the energy required for activity (active metabolic rate; AMR) and the energy required for digestion (digestive metabolic rate; DMR). SMR and AMR are typically the two physiological parameters of most interest to ecologists as they represent the floor and ceiling in aerobic energy metabolism (Norin and Malte 2011). These two components are also expected to be directly affected by changes to flow regimes resulting from REV 5. Because direct estimation of these quantities in the field is not currently practical, the current modelling exercise looks to build empirical models for predicting SMR and AMR expenditures related to changes in flow regimes based on data from the available EMG telemetry studies.

2 Study Site

The current study relies on data collected during previous EMG telemetry studies (Taylor and Lewis 2009, 2010, 2011). The study area was situated downstream of Revelstoke Dam, which is located in the Middle Columbia River approximately 8 km upstream from the Trans-Canada Highway bridge just outside of the City of Revelstoke (Figure 1). As such, the study sites were defined as Reaches 3 and 4 as the river from Revelstoke Dam to the Illecillewaet River, which is the only permanently flowing river habitat in the Middle Columbia River (Taylor and Lewis 2010).

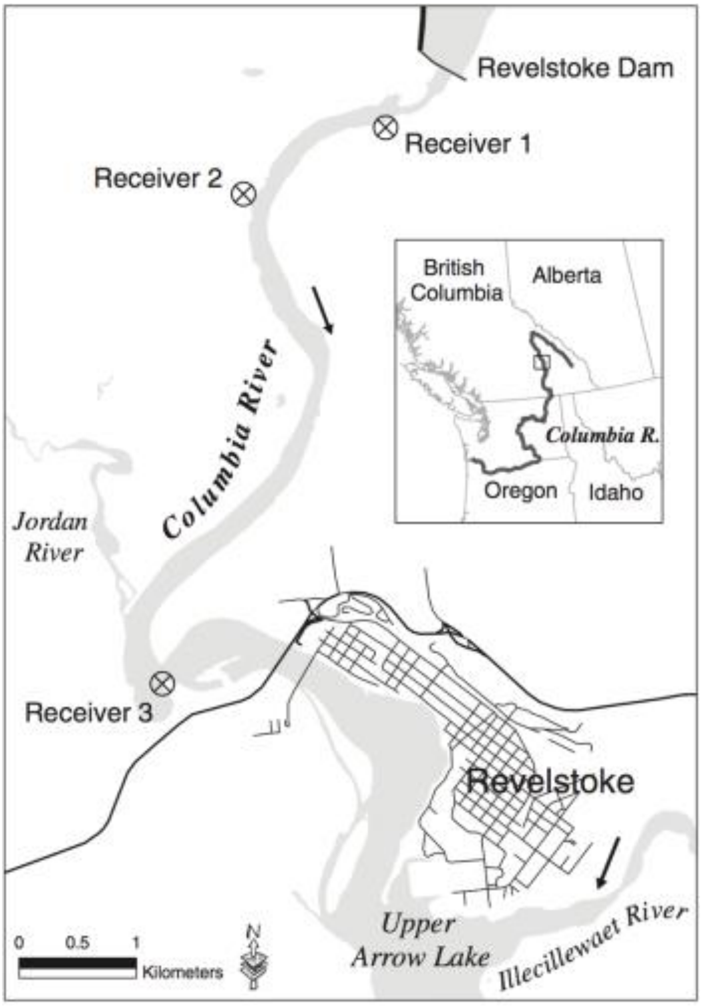

Figure 1. **Map of the study area located in the Middle Columbia River downstream of Revelstoke Dam, Revelstoke, British Columbia, Canada.** Circle with X represents the fixed receiver locations: Receiver 1 = Revelstoke Dam; Receiver 2 = Scales Creek; Receiver 3 = Skull Point. Figure from Taylor et al. 2014.

3 Methods

An energetics model was developed to assess the effects of hydrological characteristics (i.e., temperature and flow) on standard and active metabolic rates of individual Bull Trout (*Salvelinus confluentus*) and available information was assessed for Mountain Whitefish (*Prosopium williamsoni*).

3.1 Energetics Simulator Overview

An individual-based energetics simulator was developed. The simulator operated on an hourly timestep, was based on attributes observed in the tagged population, and featured three main classes of predictors: environmental, temporal, and individual characteristics. The simulator was used to predict individual behaviour, where the behaviours affected standard and active metabolic rates within a given hour (Figure 2).

For the individual-based simulations, a population of fish was created at the initialization step, and each individual in the simulated population was tracked over the duration of the simulation period. Different simulation runs were conducted under a variety of hydrological conditions. At each hourly time step, individuals were moved, and their hourly swim speed was determined (as a combination of the time spent swimming within that hour and the predicted swim speed when actively swimming; Figure 2). The realized hourly swim speeds, along with environmental (i.e., temperature) and individual characteristics (i.e., weight) were used to predict the standard and active metabolic rates (thus we could measure energetic expenditure) during that hour. The simulator then repeated these steps (i.e., calculations of movement, realized swim speed, and energy expenditure) for each hour under a variety of hydrological conditions. The result was a distribution of simulated energetic values, which could be summarized to derive performance metrics on which to compare the hydrological scenarios.

The structure of the simulator model was based on patterns observed within field data. The simulator's parameter values were based on estimates from statistical models which were fit to the observed field data. Linear mixed effects models were used to estimate general average behaviour with respect to predictors (Figure 2), and variance component estimates were used for among-individual and hour-to-hour variations in the simulated individual's response (i.e., residual error). An observation-weighting scheme was used in model fitting to account for the differing number of detections per individual, and the affected variance components estimates (i.e., residual error) were adjusted to represent variability under a scenario of 'complete data collection', which would better reflect behavioural variability rather than variability associated with data collection.

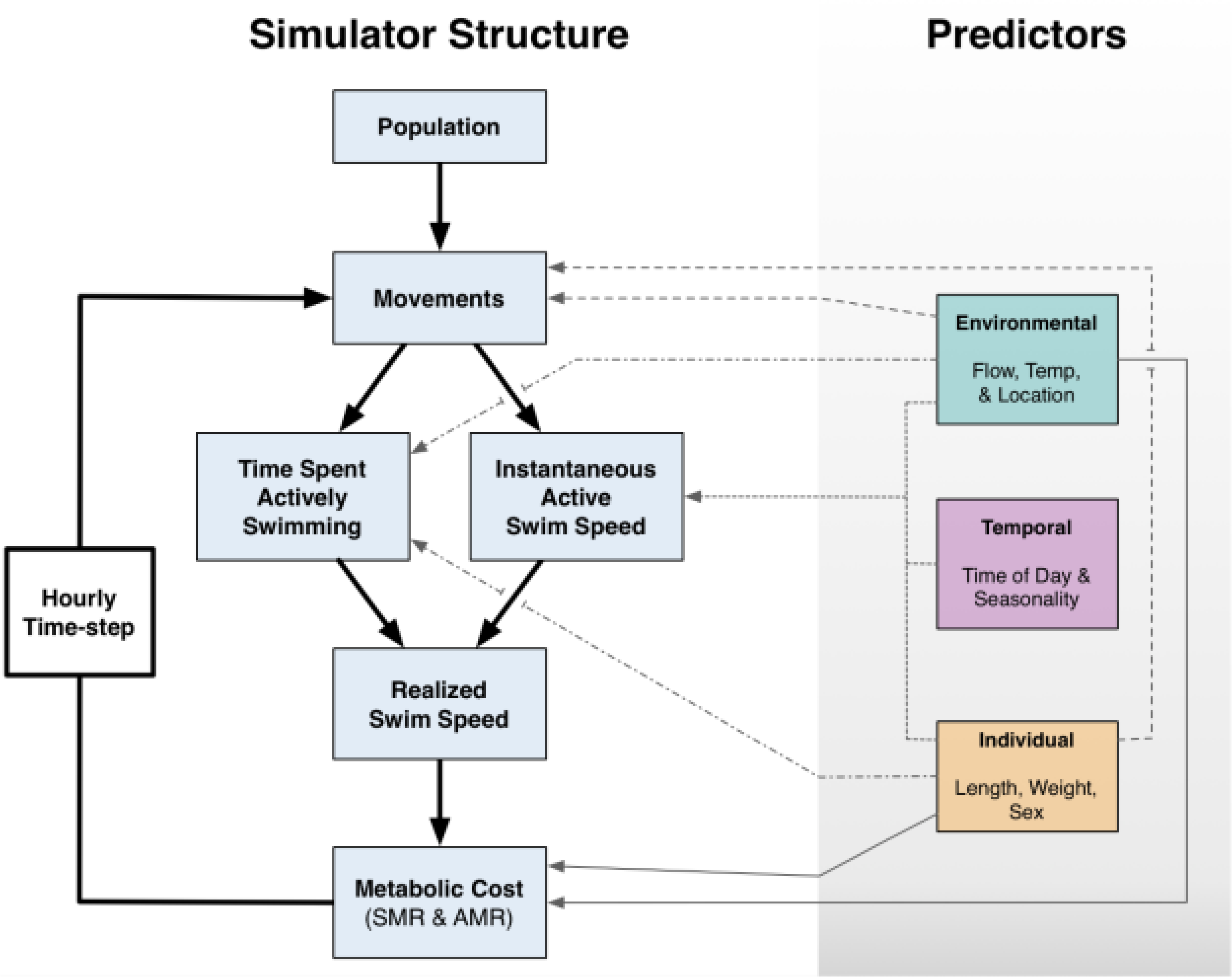

Figure 2. **Flow diagram illustrating simulator structure (blue) and environmental (teal), temporal (mauve) and individual (orange) predictors of simulated fish behaviour.** The bioenergetics simulator operates on an hourly time step to assess respiration costs associated with a hydrology regime.

3.2 Field Data

Field observations were collected in previous EMG telemetry (Taylor and Lewis 2009, 2010, 2011). A total of 5,208,838 receiver detections (Bull Trout: 4,490,278; Mountain Whitefish: 718,560) were available over three study years (i.e., 2008-2010) (Appendix A). The three fixed-station receiver locations were in areas where most of the tagged fish were found to congregate, and the recorded detections should therefore be generally representative of movements of fish in the population at large (Taylor et al. 2014). A total of 88 Bull Trout and 33 Mountain Whitefish were surgically implanted with a coded EMG transmitter (Lotek Wireless, New Market, ON). Full details of surgeries can be found in Taylor et al. (2014) and Cooke et al. (2004).

3.3 Hydrological Data

Hourly averages of predicted hydrodynamic flow at each of the three fixed receiver locations were determined by averaging predicted flow from the BC Hydro HEC-RAS model (NHC 2016) of the Middle Columbia River downstream of Revelstoke Dam (Figure 1). Generally, receivers were believed to record fish within 400 m of their locations (Taylor et al. 2014). As such, predicted flows at corresponding HEC-RAS river cross-sections were averaged together on an hourly basis to determine the average hourly flow (Table 1). Water temperature at each of the three fixed receivers were assumed to be the same and was based on hourly-averaged temperature readings from measurement station 2 approximately 1 km downstream of the 2nd fixed telemetry receiver.

Table 1. Model cross-sections from NHC (2016) HEC-RAS model used when deriving the average hourly flow conditions for each fixed receiver location (Figure 1).

		Cross Section		Data Summary
Receiver	Name	Start	End	
1	Revelstoke Dam	242	225	Hour Average
2	Scales Creek	218	212	Hour Average
3	Skull Point	182	175	Hour Average

3.4 Standardized Length to Weight Relationships

Estimates of weight were required as part of the AMR calculations. Existing standardized-weight equations for Bull Trout (see Hyatt and Hubert 2000) were found to under-predict weights (as compared to those observed in the our Bull Trout field data), and did not distinguish between sexes. Standardized-weight equations for Mountain Whitefish were not available. As such, standardized-weight equations were derived for each species based on the available field data (a subset of our sampled fish were weighed, including 28 Bull Trout and 12 Mountain Whitefish) using a linear regression. Log-transformed weight was the response variable and fork length and sex (Bull Trout only) were used as potential predictors, with AICc model selection used to choose among potential prediction models (Appendix B). Sex-specific standardized-weight equations were not possible for Mountain Whitefish due to the lack of sample size.

3.5 Standardizing EMG values based on field observations

Electromyogram (EMG) acoustic tags provided real time estimates of axial swimming muscle activity. The EMG (muscle activation) data could then be converted into tail beat frequency (TBF), and, by extension, into swim speeds (SS) if the body length was known (see Section 3.7). However, raw EMG values had to first be standardized by subtracting off a baseline value (to produce standardized EMG readings, SEMG). Importantly, EMG readings recorded from fish at rest varied among individuals due to individual differences in tag responses (Brown et al. 2007), thus it was important to determine baseline EMG readings under no visible activity for each fish. In previous field studies, the SEMG values were calibrated to observed TBF for a subset of individual Bull Trout's using swim tunnel tests (Taylor et al. 2014).

Unfortunately, while the SEMG to TBF relationships were readily available from previous work, the baselines EMG values used to derive the SEMG observations were not retained, making field-based TBF predictions problematic. Without a baseline EMG value, only the raw EMG values (i.e., what is transmitted by the inserted tag) was available for field based observations in the Columbia River. Directly using EMG values in place of SEMG values would result in bias for predicted field-based TBF and swim-speed predictions.

To deal with the loss of baseline EMG values, a work-around was developed to derive baseline EMG values based on field observations. Receiver records were queried for observations under low river discharge conditions (i.e., less than 100 cms). Where sufficient records were available (i.e., more than 100 records), the lower 1 % quartiles were used as an estimate of the baseline EMG (Appendix A). The absolute minimum was not chosen to avoid using anomalous tag readings as the baseline EMG value, which could positively bias swim speed predictions. Field-derived baseline EMG values were then used to produce field-based SEMG values, which could then be used in the predictive models of Bull Trout TBF and swim speed.

3.6 Predicting Tail Beat Frequency from SEMG

Tail beat frequency (TBF) was predicted from SEMG values based on swim tunnel trials of Bull Trout performed by Taylor et al. (2014). The relationship between SEMG and TBF were determined using linear mixed effect models based on the results from the calibration experiments, using the `nmle` package (Pinheiro et al. 2018) in the R computing environment (R Core Team, 2018). All models used log transformed SEMG readings, with random effects to describe among-tag differences. Because our data included repeat observations, an auto-regressive structure with lag 1, (i.e., AR(1)) was used to describe model errors for each individual (i.e., individual observations that were closer together in time were expected to be more similar to each other than observations separated widely in time). This structure was determined by preliminary inspection of the SEMG to TBF calibration results using autocorrelational and partial-autocorrelational plots, as well as by inspecting autocorrelation of residuals from initial model fitting.

Two sets of TBF calibration equations were created: 1) one set applied to all tagged Bull Trout based on the subset of individuals that were calibrated; and 2) another set was used to infer TBF for only those individuals that were calibrated (which fit a separate slope for each individual; Appendix C). This was done because only 14 out of the 88 tagged Bull Trout had been calibrated, and only 13 could be used because we could not derive a field-based EMG baselines for the 14th fish (see Table A1). The second calibration set was used to confirm results from swim speed predictive models.

No SEMG to TBF calibration experiments were available for Mountain Whitefish, so TBF could not be determined. By extension, instantaneous swim speeds (see Section 3.7) and proportions of time spent swimming (see Section 3.8) could not be determined for this species.

3.7 Predicted Instantaneous Swim Speeds

Each individual EMG reading was first converted to TBF, then the instantaneous swim speeds were predicted based on the 'TBF to swim speed' relationship that was published by Brett (1995), who demonstrated a strong linear relationship between swim speeds in body lengths per second (BL) and TBF: $BL = 0.023(TBF) - 1.286$ ($P < 0.001$, $r^2 = 0.97$). This conversion equation has also been used by Taylor et al. (2014) to model Bull Trout swim speed, and is used herein. Fork lengths (FL) were converted to body length (BL) based on the conversion factor provided by Hyatt and Hubert (2000) for Bull Trout ($BL = 1.049 \cdot FL$). Therefore, the final TBF to swim speed (SS) conversion used was

$$SS = 1.049 \times FL \times (0.023 \times TBF - 1.286).$$

This equation was used to predict instantaneous swim speeds that corresponded to a given EMG reading recorded during a receiver detection (based on the EMG to TBF conversion; Section 3.6). Instantaneous swim speeds were then used to compute hourly averages of swim speeds (Section 3.9) after adjusting for the periods of time in which fish were not actively swimming (Section 3.8).

3.7.1 Validating Instantaneous Swim Speed Predictions

The predicted instantaneous swim speeds derived from the instantaneous EMG readings (see Section 3.6) provided an estimate of the individual swim speed at a single moment in time (i.e., at the moment the acoustic tag transmitted the EMG reading). With a large number of observations for some individuals (i.e., greater than 100) under varying conditions, we were able to approximate their critical swim speed (U_{crit}) by determining their maximum observed instantaneous swim speeds; and these approximations were compared to the known species-specific values that were determined by Mesa et al. (2004).

3.8 Proportion of the Hour Spent Swimming

In the Bull Trout critical swim speed experiments (i.e., U_{crit} tests) performed by Mesa et al. (2004), it was noted that a high proportion of fish would hold position by using pectoral fins as hydrofoils (i.e., 77.5% of tested Bull Trout held position in higher flows, making U_{crit} determination problematic). Therefore, we assumed that Bull Trout (and potentially Mountain Whitefish) in the natural environment could also be expected to hold stationary without beating their tail fins using a similar technique. The propensity to hold without tail beats could therefore affect our predictions of average hourly swim speeds, and by extension our estimates of associated energetic cost.

The propensity of Bull Trout to hold position in the natural environment was determined by estimating the proportion of receiver detections (i.e., the proportion of instantaneous swim speed measurements) that indicated an individual was swimming under differing environmental conditions. Whether or not an individual was swimming was based on a predicted TBF threshold of 58, which was observed as the cut-off for active swimming in Sockeye (*Oncorhynchus nerka*)(Hinch and Rand 1998) and has been used as the threshold in previous Columbia River Bull Trout work (Taylor et al. 2014). The proportion of the hour spent swimming was determined in a hierarchical manner similar to swim speed (see Section 3.8), where averages of the proportion of the signals indicating active swimming were first determined at the minute, followed by the quarter hour and then finally at the hour level. Only hourly observations that were based on more than 50 receiver detections were retained.

A predictive model for the proportion of the hour spent swimming ($p_{i,h}$) was then determined by modelling the logit of the response using linear mixed effects models. The linear mixed effect models where of the general form:

$$\text{logit}(p_{i,h}) = \sum_{k=1}^{K} \text{Predictor}_\text{k} + \text{Tag}(R)$$

where $\text{Tag}(R)$ was an random variable representing individual based differences in active swim speeds and one or more predictors were included as fixed effects. The set of predictors used to predict logit transformed proportion was the same as the active swim speed analysis (see Section 3.8). Sample size corrected Akaike information criterion (AICc) was used to rank competing models (Burnham and Anderson 2002). A hierarchical approach was used where primary predictors were first determined, followed by the inclusion of additional predictors.

Linear models were fit using the `nmle` package (Pinheiro et al. 2018) in the R computing environment (R Core Team 2018) with a weighting scheme based on the number of minute observations used to derive the individual hourly observation. Residual errors were modeled as having an AR(1) (i.e., autoregressive lag 1) process to account for autocorrelation between observations (i.e., observations of the same individual that were closer in time were expected to be more highly correlated than hourly observations farther apart in time). This step was deemed necessary after inspecting of the hourly proportions using autocorrelational and partial-autocorrelational plots, which indicated that an autoregressive component was present.

Finally, because TBF calibration experiments were not performed on Mountain Whitefish, it was not possible to associate EMG readings with whether or not Mountain Whitefish were actively swimming and as such this analysis could not be performed.

3.9 Computing Average Hourly Active Swim Speeds

Computing the average hourly active swim speeds was complicated by three sources of potential noise and bias:

1. Proportion of time spent swimming;
2. Uneven distribution of samples across an hour; and
3. Differing number of observations.

The first source of potential variation was the frequency with which an individual choses to actively swim within the hour. This may or may not be actively related to the swim speeds chosen when actively swimming. As such, hourly swim speed averages were based on instantaneous observations where the individual was assumed to be swimming (i.e., see Section 3.8), herein referred to as instantaneous “active” swim speeds.

The second and third source of variation related to the passive nature of data collection. EMG and derived SEMG readings were recorded multiple times per hour whenever a tagged fish was within proximity (i.e., roughly 400 m) of a receiver (Taylor et al. 2014). This represented a passive data collection method, which may have been subject to random processes such as the portion of time a tagged fish remained within proximity of the receiver within an hour. As such, raw hourly averages of instantaneous swim speeds (or EMG readings) could misrepresent the true response of an individual to the current environmental conditions. For example, if the environmental condition changed over the course of an hour, and the fish was detected frequently at the start of the hour and less so at the end, a raw average EMG reading for the hour would be biased toward the behaviours that are associated with the first environmental condition. Given that flow conditions can undergo non-trivial changes over the course of an hour, this could add noise when trying to predict how Bull Trout respond to environmental conditions.

To counter these potential issues with passive data collection, average hourly swim speeds were determined in a hierarchical manner based on predicted instantaneous swim speeds (Section 3.7) using the following steps:

1. Compute within-minute averages of instantaneous *active* swim speeds;
2. Compute quarter hour averages for each individual, based on within-minute averages, using a weighted average with a weighting scheme based on the total number minutes observed within the quarter hour.
3. Compute an hourly average for each individual, based on quarter-hour averages, using a weighted average with a weighting scheme based on the total number of available minutes within each quarter hour.

Within-minute active swim speed averages were computed for each individual, based on the proportion of receiver detections that indicated the individual was swimming. Formally, this was computed as:

$$\overline{SS}_{i,m}^{\text{min}} = \frac{\sum_{j=1}^{J} SS_{j,m} \times I(TBF_j \geq 58)}{\sum_{j=1}^{J} I(TBF_j \geq 58)},$$

where J is the total number of receiver detections within minute m for individual i, and $I(TBF_j \geq 58)$ is an indicator function that returns 1 if the TBF is greater than 58 and 0 otherwise. Quarter-hourly averages were calculated as:

$$\overline{SS}_{i,q}^{\,0.25\text{hr}} = \frac{\sum_{m=1}^{M_{i,q}} \overline{SS}_{i,m}^{\text{min}} \times w_{i,m}}{\sum_{j=1}^{M_{i,q}} w_{i,m}},$$

where $M_{i,q}$ is the total number of minute averages available for individual i and quarter hour q, $\overline{SS}_{i,m}^{\text{min}}$ is the average swim speed for minute m and $w_{i,m}$ is the corresponding weight based on the total number of receiver detections within a given minute. The hour average is then computed as

$$\overline{SS}_{i,h}^{\text{hr}} = \frac{\sum_{q=1}^{Q_{i,h}} \overline{SS}_{i,q}^{\,0.25\text{hr}} \times w_{i,q}}{\sum_{q=1}^{Q_{i,h}} w_{i,q}},$$

for individual i and on hour h, where $\overline{SS}_{i,q}^{\,0.25\text{hr}}$ are the available quarter hour averages (with $Q_{i,h}$ total quarter hours estimates) and $w_{i,q}$ are the corresponding weights based on the total number of available minutes for a quarter hour.

This hierarchical approach was developed to provide a temporally balanced estimate of the average hourly active swim speed under variable environmental conditions and passive data collection.

3.10 Predicting Hourly Active Swim Speed

Linear mixed effect models were used to predict the average hourly active swim speeds (i.e., $\overline{SS}_{i,h}^{\text{hr}}$; see Section 3.9) based on a suite of predictor variables that cover environmental, temporal and individual specific variables (Table 2). The linear mixed effect models were of the general form:

$$\log\left(\overline{SS}_{i,h}^{\text{hr}}\right) = \sum_{p=1}^{P} \text{Predictor}_{\text{p}} + \text{Tag}(R),$$

where $\text{Tag}(R)$ was a random effects term representing individual based differences in active swim speeds and one or more predictors were included as fixed effects. Linear models were fit using the `nmle` package (Pinheiro et al. 2018) in the R computing environment (R Core Team 2018) with a weighting scheme based on the number of minute observations used to derive the hour swim speed average and an auto-regressive process with lag 1 (i.e., AR(1)) on the errors. Residual errors were modeled as having an AR(1) process to avoid autocorrelation (observations (i.e., $\overline{SS}_{i,h}^{\mathrm{hr}}$) of the same individual that were closer in time were expected to be more highly correlated than observations that were farther apart in time). This step was deemed necessary after inspecting preliminary hourly active swim speed averages using autocorrelational and partial-autocorrelational plots, as well as the autocorrelation of residuals from initial model fitting.

Support for the pool of proposed predictors were compared using AICc model ranking in a step-wise fashion. In the first step, support for a single predictors was determined, with subsequent steps looking at combination of predictors. Early visualizations revealed clear differences in the distribution of swim speeds by receiver location (Figure 1), so all models estimated predictor related parameters separately for each location.

Table 2. List of covariates investigated as potential predictors of average hourly active swim speed.

Predictor	Type	Scope	Values	Notes
Location	Factor	Environmental	Revelstoke Dam, Scales Creek, and Skull Point	Receiver locations are indicated in Figure 1.
Flow	Continuous	Environmental	0 - 1,765 cms	Location-specific average hourly discharge from river positions within the expected range of each receiver (see Table 1).
Water Temperature	Continuous	Environmental	6.7 – 12.4 °C	Location-specific average hourly temperature from river positions within the expected range of each receiver (see Table 1).
Time of Day	Factor	Temporal	Dawn, Daytime, Dusk, and Night	Dawn and dusk periods were determined using maptools package (Bivand and Lewin-Koh 2018) based on the nautical definition of twilight period (i.e., a sun angle of 12 degrees below the horizon).
Day of Year	Continuous	Temporal	270 - 343	Used to predict systematic changes that may occur.
Year	Continuous	Temporal	2008-2010	See Table A1 for yearly Bull Trout tag releases.
Sex	Factor	Individual	Female, Male	See Table A1 for more details.
Fork Length	Continuous	Individual	Female (455 – 674mm); Male (435 – 830mm)	See Table A1 for more details.
Weight	Continuous	Individual	Female (931 – 3415 g); Male (972 – 10,134 g)	Predicted weights based on measured fork lengths, see Section 3.4 for methodologies and Table A1 for specific values.

3.11 Estimating Markov Movements among Areas

Movements of tagged individuals among the three modeled areas (Figure 1) were assumed to occur in a Markovian manner, with the probability of any transition occurring being independent of any previous transitions. Estimates for the Markov transition probabilities were generated using multi-state capture-mark-recapture (CMR) models available in Program MARK (White and Burnham 1999). Preliminary inspection of the data revealed that most fish remained at one location throughout the day. As such, multi-state CMR models were fit using individual capture histories based on a daily time step, with strata corresponding to the three fixed receiver locations (i.e., Figure 1). Fish were assigned daily to a location based on the receiver at which 75% or more of its detections were recorded. In situations where no receiver met the 75% threshold for a given fish in a given day, a zero (i.e., no detection) was assigned for that day.

3.12 Metabolic Costs

A general model for daily metabolism (R_U) for salmonids was developed by Stewart et al. (1980), which considered contributions from the standard active metabolic components:

$$R_U = \alpha \cdot w^{\beta} \cdot e^{\rho T} \cdot e^{\nu U}$$

where R_U is total daily metabolism (i.e., $g \cdot O_2 \cdot d^{-1}$), and w represents the body weight in grams, T represents the water temperature (°C) and U is the swim speed (cm/sec). Parameters α, β, ρ, and ν represent empirical constants that can be estimated from observed experiments. The standard metabolic rate (SMR) is therefore represented by the terms $\alpha \cdot w^{\beta} \cdot e^{\rho T}$ while the active metabolic rate (AMR) is represented by the term $e^{\nu U}$. The impact of changes to digestion metabolic rate (DMR) were not considered.

Different sized fish can be expected to have differing absolute metabolic rates due to differences in size. This can be normalized by revising parameter values to return mass-specific units (i.e., $g \cdot O_2 g^{-1} \cdot d^{-1}$). Parameter estimates for the SMR component were derived from Mesa et al. (2013), while Lake Trout (*Salvelinus namaycush*) was used as a surrogate for the AMR component (Table 3). Models developed for Lake Trout have previously been used as a surrogate for Bull Trout (Beauchamp and Van Tessell 2001).

Metabolic parameters of Mountain Whitefish were based on estimates from Brook Trout (*Salvelinus fontinalis*), a fluvial salmonidae with similar diet (Tang et al. 2000) and AMR parameters based on Lake Trout as a surrogate (Table 3). Values from Tang et al. (2000) were converted to gram-specific values based on an approach suggested by Stewart et al. (1983). Mountain Whitefish respiration rates were not assessed due to the inability to predict swim speeds (see Section 3.7).

Table 3. Parameter values for standard and active metabolic rate components.

Parameter	**Lake Trout** (*Salvelinus namaycush*)	**Brook Trout** (*Salvelinus fontinalis*)	**Bull Trout** (*Salvelinus confluentus*)		**Mountain Whitefish** (*Prosopium williamsoni*)
	Stewart et al. (1983)	Tang et al. (2000)	Mesa et al. (2013)	Current Study	Current Study
α	0.0100	0.0766	0.0009	0.0009	0.0766
β	− 0.295	-0.250	− 0.1266	− 0.1266	-0.250
ρ	0.059	0.0173	0.0833	0.0833	0.0173
ν	0.0232			0.0232	0.0232

4 Results

4.1 Standardized Weights

A subsample of sampled Bull Trout (Table A1) and Mountain Whitefish (Table A2) had wet mass measured at the time of tagging. In general, log-transformed weights increased as a linear function of length (Figure 3) as expected. The published standardized weight formula for Bull Trout (Hyatt and Hubert 2000) did not adequately predict the mass of males in the Middle Columbia River (Figure 3), and there was no available standardized-weight function for Mountain Whitefish. As such, for this study we derived our own standardized weight formulae based on the observed 'log weight to length' relationships in our sampled data.

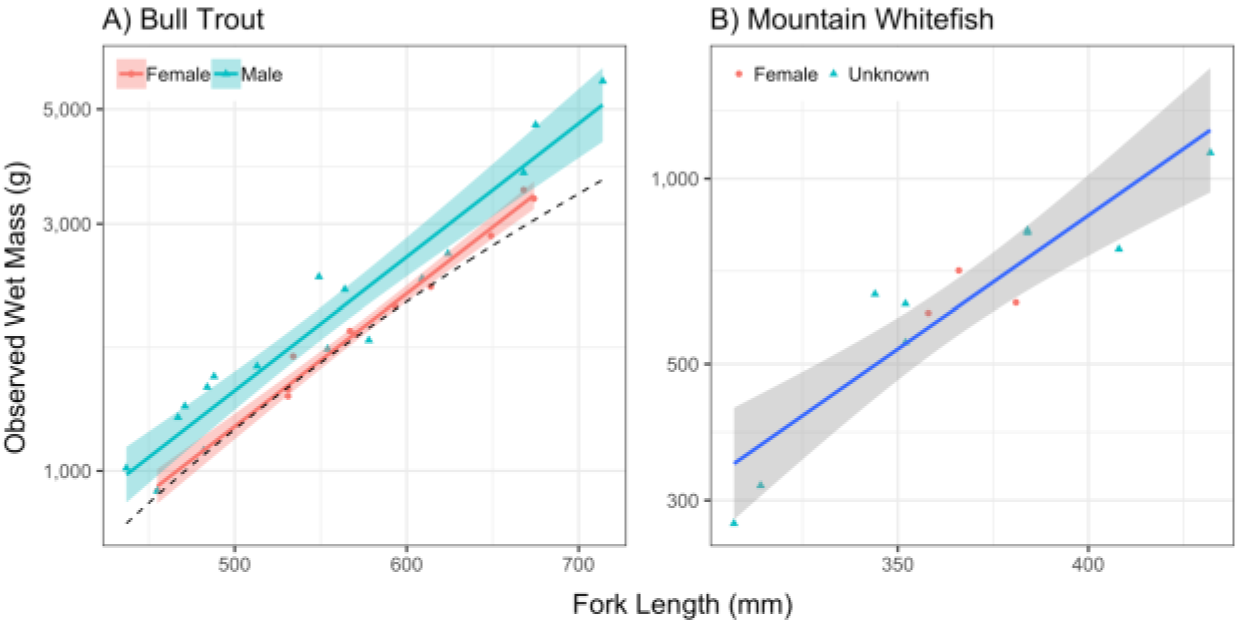

Figure 3. Observed mass to fork length relationship in A) Bull Trout and B) Mountain Whitefish. Dashed line in A) Bull Trout plot indicate the weight predicted by Hyatt and Hubert (2000). The y-axis scaling uses log base 10. Shaded region indicates the 95% confidence region for the regression.

For our Bull Trout standardized weight formula, simple linear regressions were fit to log transformed wet weights, and support was compared using AICc model ranking (Table B1). Four possible models were considered that either forced the intercept through zero, or fit a sex-specific intercept, and either estimated a common slope or separate slopes for each sex. The model that fit a sex-specific intercept, but with a shared slope (i.e., per unit change in log weight as a function of fork length) had the most support (i.e., lowest ΔAICc score). Estimates from the top supported model resulted in the following standardized weight equation for female and male Bull Trout:

$$W_i = \begin{cases} \exp(4.146 + 0.00593 \times FL) & \text{if female,} \\ \exp(4.298 + 0.00593 \times FL) & \text{otherwise} \end{cases}.$$

Insufficient information was available to estimate separate male and female Mountain Whitefish weight equations (in fact, we had no available weight measurements for males; Appendix A, Table A2). As such only two linear regression models were considered, with top support for the model that fit a non-zero intercept (Table B2). Estimates from the top supported model gave a single standardized weight equation for Mountain Whitefish:

$$W_i = \exp(2.774 + 0.00999 \times FL).$$

4.2 Predicting Instantaneous Active Swim Speed

The maximum instantaneous swim speeds (across the whole study area) were determined for each individual that had 1000 or more observations (Figure 4) by querying their instantaneous active swim speeds (see Appendix C). These provided an empirical estimate of critical swim speed (U-crit), where a strong linear relationship was observed between body length and observed maximum swim speeds, especially for observations using the universal calibration equation.

Sex-specific differences were observed in the ‘length to maximum swim speed’ relationships (Table 4), either when determined from directly calibrated individuals (Figure 4a), or when using the universal calibration approach (Figure 4b). Males showed a consistent positive association between maximal swim speed and fork length, while females showed a neutral or potentially negative association. Under the universal calibration approach (Figure 4b) there was little variation among locations in the ‘length to maximum swim speed’ relationship, though the fit was tightest at the Revelstoke Dam receiver location (Figure 1), suggesting that conditions there may be more challenging.

Slope estimates for the fork length to maximum swim speed relationships from the two calibration approaches were also comparable, with higher levels of uncertainty for the individual based calibration approach due to smaller sample sizes (Table 4). This suggests that when applied to natural conditions both approaches were producing similar estimates of swim speed performance.

When the estimated regression relationships were extended outside the range of our observed fork lengths the maximum observed instantaneous swim speeds overlapped with forced critical swim speed experiments by Mesa et al. (2004) on Bull Trout (see Figure 4, star symbols). This was especially true of universally calibrated males near the Revelstoke Dam receiver, which showed the strongest positive association between length and maximum swim speed relationship ($P < 0.001$; $r^2 = 0.96$) and the closest agreement with Mesa et al. (Figure 4b).

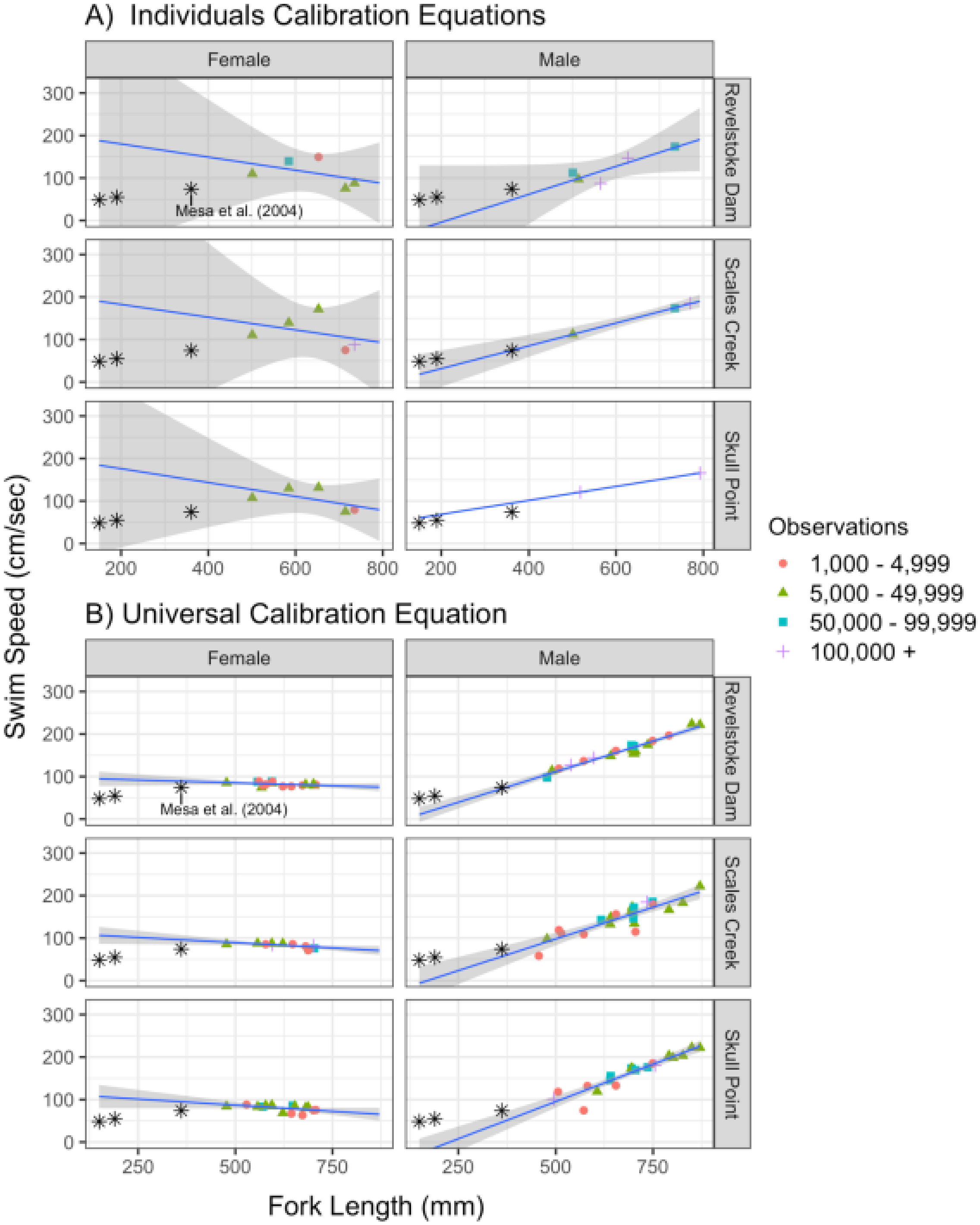

Figure 4. **Maximum observed swim speeds of Bull Trout in the Middle Columbia River using A) individual specific calibration equation and B) a universal TBF calibration equation (Appendix C).** Star symbol indicates independently derived U-crit estimate by Mesa et al. (2004). Shaded region indicates 95% confidence region for the regression line (which excludes the Mesa et al. data).

Table 4. Slope estimates for the fork length to maximum observed swim speed (i.e., U-crit) relationship based on the individual based and universal calibration approaches. 95% confidence interval is indicated in parentheses.

Location	Sex	Sample Size: Individual Calibration	Sample Size: Universal Calibration	Slope Estimate: Individual Calibration	Slope Estimate: Universal Calibration
Revelstoke Dam	Female	5	20	-0.16 (-0.47, 0.15)	-0.04 (-0.15, 0.06)
Scales Creek	Female	5	21	-0.16 (-0.47, 0.15)	-0.05 (-0.15, 0.05)
Skull Point	Female	5	21	-0.17 (-0.48, 0.14)	-0.05 (-0.15, 0.05)
Revelstoke Dam	Male	6	26	0.30 (0.00, 0.59)	0.30 (0.25, 0.36)
Scales Creek	Male	8	32	0.23 (0.04, 0.41)	0.24 (0.19, 0.28)
Skull Point	Male	7	29	0.23 (0.04, 0.41)	0.33 (0.28, 0.37)

The smaller fish tested by Mesa et al. showed the biggest deviation from the extrapolated regression line, which could indicate: 1) a potential bias caused either by the calibration methodology, and/or the use of observed maximum speed as an estimate of critical swim speed; or 2) a potential breakdown of the straight line association between body size and critical swim speed relationship in smaller or younger Bull Trout.

Regardless of calibration technique employed, female Bull Trout displayed a non-significant (P = 0.42) negative association with length and significantly lower maximal swim speeds ($P <$ 0.001). This finding was unexpected and may be related to the fact this population is likely to have spawned prior to or during the September commencement of the EMG tracking period (McPhail and Baxter 1996).

Due to the comparable maximum swim speed relationships and the larger sample sizes, results from universal calibration approach were used for the remainder of the analyses.

4.3 Proportion of Time Spent Swimming

All instantaneous EMG records were summarized on an hourly basis to determine the proportion of the records where Bull Trout were assumed to be swimming (i.e., a TBF value of 58 or greater). This was used as an estimate of the proportion of time spent swimming as previous studies found no association between flow conditions and signal reception (Taylor et al. 2014). The observed proportion of the hour spent actively swimming showed strong associations with flow conditions, sex and length (Figure 5). Box plots showing the distribution of individual responses (for individuals with a total of 100 hours or more of observations) are also available in Appendix D (Figure D1).

Male and female Bull Trout displayed different behaviours under differing flow conditions. Smaller female Bull Trout appear to spend, on average, a larger proportion of time swimming compared to larger females (Figure 5). Across flow conditions, females tended to spend a larger proportion of time swimming as compared to males, although this did not occur for all individuals and locations.

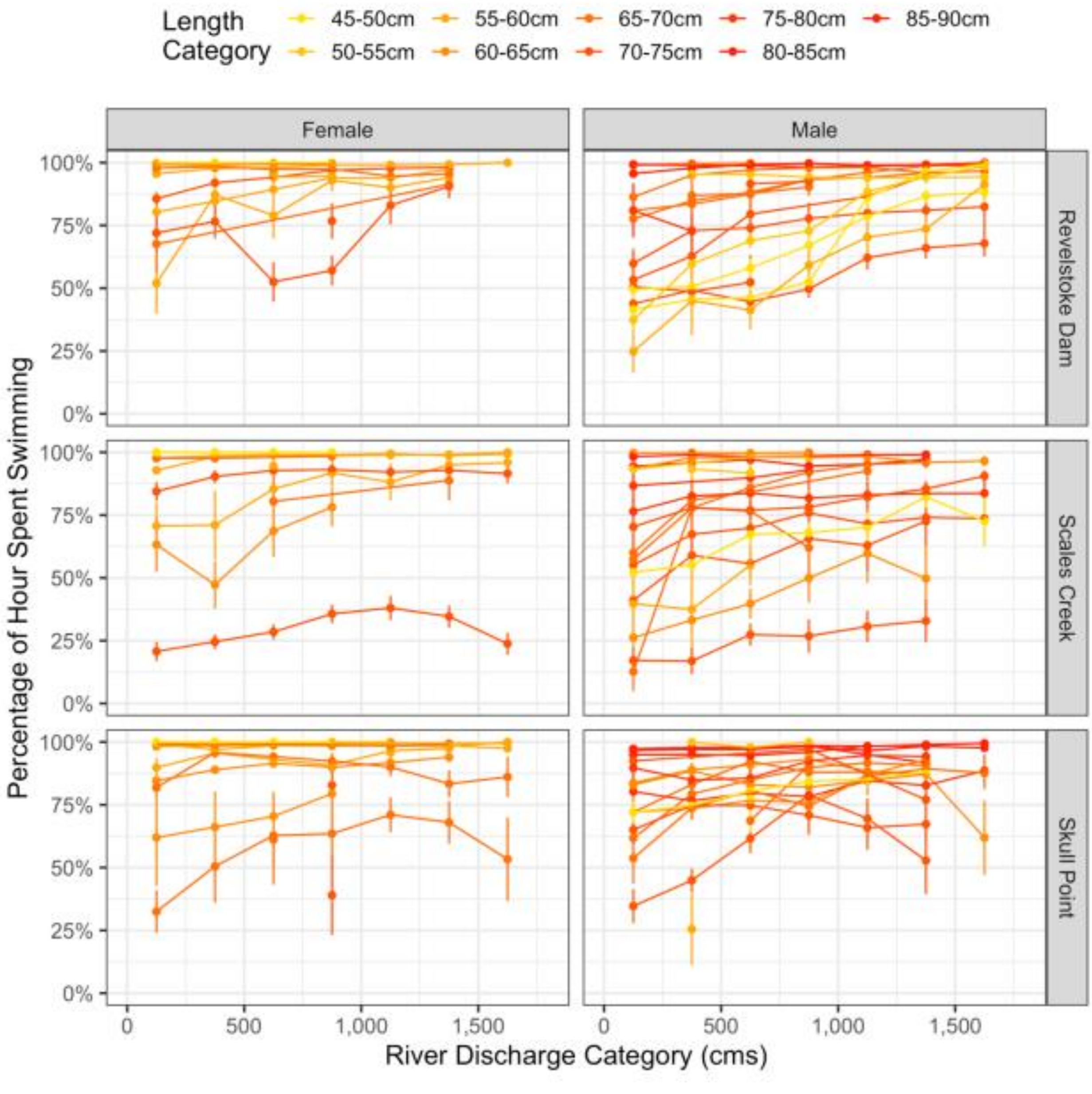

Figure 5. Percentage of hour spent swimming for female (left) and male (right) Bull Trout under varying river discharge conditions, by receiver location (rows). Individual responses are connected by lines, and the color indicates length category. Bars indicate 95% confidence interval for the mean response of individual observations. The same data is shown with logit scaling on the Y-axis in Figure D1.

Compared to female Bull Trout, males showed the inverse body size relationship, with smaller individuals tending to swim less at lower flow conditions than larger individuals (Figure 5). Larger individuals (i.e., those with total body length of 75 cm or larger), tended to spend most of their time swimming regardless of the underlying flow conditions. Compared to larger males, smaller males (i.e., those with a total body length less than 60 cm) tended to swim less under low flow conditions, but spent proportionally more time swimming as discharges increased, especially under higher discharge conditions (i.e., 1,000 cms or greater) at the Revelstoke Dam receiver location (Figure 5). Compared to smaller and larger males, intermediate sized males showed a diversity of responses, with most demonstrating a higher propensity to swim as river discharges increased (Figure 5).

Linear mixed effect models were developed to predict the percentage of time spent swimming. Models used a logit transformation of the hourly proportions as a response variable (see Figure D1) and used a multi-step approach. In the first step, there was strong support for river discharge as a primary explanatory factor (Table D1). Because of this, and due to observed differences in behaviour by sex (e.g., Figure D1), the second model ranking step included sex as an additional predictor, along with the environmental factors that we considered in the first step. Two versions of each of seven models were considered during step two: one version pooled across sex, and the others included sex-specific parameterizations (Table D2). Of the seven models considered, two models had the majority of support (i.e., ΔAICc < 2) when pooling across sex, while only one model had virtually all the support (i.e., AICc weight of one) in the sex-specific formulation. The top sex-specific model also had much more support (i.e., AICc score that was 76 AICc units lower) than the top model that pooled across sex, indicating virtually all support is for a sex-specific approach. As such, the top sex-specific model (one that included sex, flow and temperature) was used as a baseline model in the final model ranking step.

In the final step, additional predictors were considered alongside the sex-specific flow and temperature model selected in the previous step (Table D3). Of the nine models considered, one model had the majority of support (i.e., AICc weight of one) and included location-specific size responses with a size and temperature interaction on top of the factors from step two. The predicted mean responses from the top model, without individual variation, were visualized as a function of discharge and fish size under three temperatures (Figure 6; this can also be viewed on the original logit scale in Figure D3). Extrapolations for river discharges up to 2,200 cms were also included and showed a small increase in the predicted value relative to predictions under the maximum observed discharge of 1,765 cms.

Compared to raw responses (Figure 5), the mean response showed much less variability, indicating that there is a large degree of individual variability in behavioural responses to environmental conditions. Estimates of individual variability ($\hat{\sigma}_{\text{tag}}^{\text{swim}}$=1.35; 95% CI: 1.10, 1.67) were roughly equivalent to the residual variation ($\hat{\sigma}_{\text{resid}}^{\text{swim}}$=0.91; 95% CI: 0.89, 0.93), which represented how variable the response was on an hourly basis within individuals (assuming 60 minutes of observations). Both estimates of variability represent the response on the logit scale. Finally, the estimated autoregressive correlation coefficient ($\widehat{\Phi}_1^{\text{swim}}$= 0.71, 95% CI: 0.70, 0.72) indicated a strong correlation among the observed individual responses (i.e., logit-transformed hourly proportion spent swimming) after controlling for environmental predictors and individual specific effects. The autoregressive component of the model assumed a time-step lag of one.

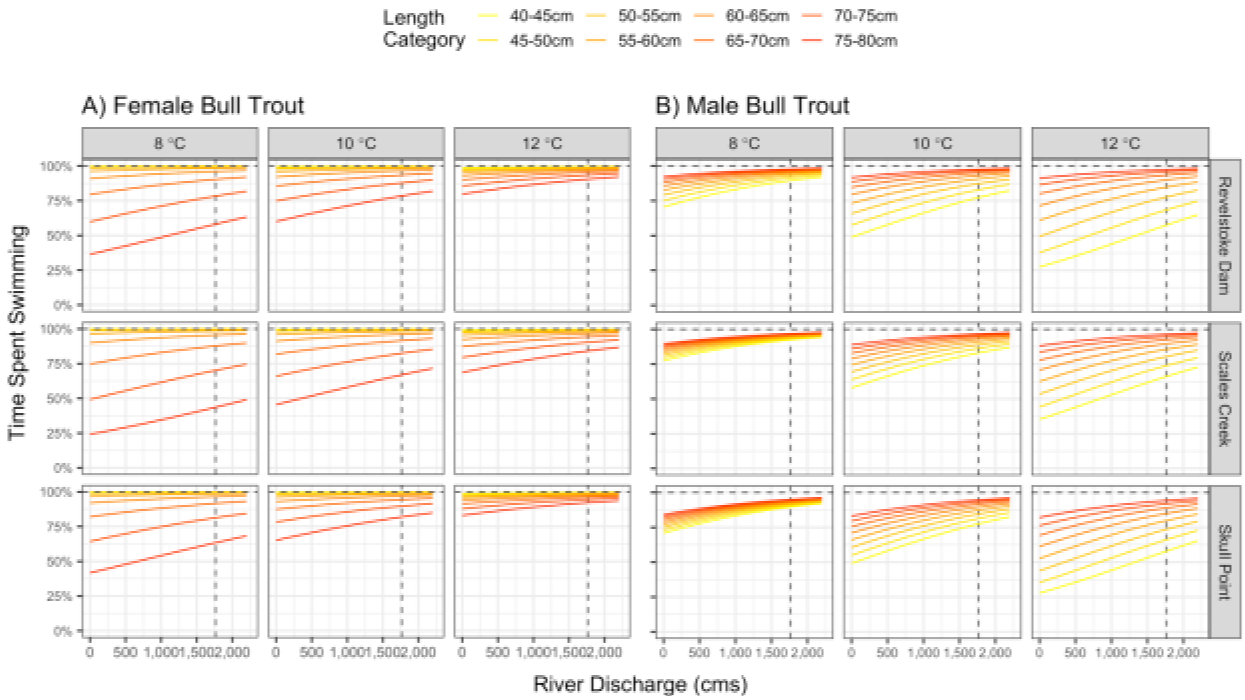

Figure 6. **Predicted mean percentage of an hour spent swimming by temperature (panel columns), location (panel rows), and size (line colour) for A) female and B) male Bull Trout, based on the top supported model (Table D3).** Vertical dashed line indicates highest observed river discharge conditions (i.e., 1765 cms), with predictions to the right representing extrapolations.

4.3.1 Simulator Formulation

As part of the pre-computation step (see Section 4.6), the energetics simulator used the top-supported model (Table D3) to predict logit-transformed mean response values (i.e., $\text{logit}\left(\widehat{p_{i,h}^{\text{swim}}}\right)$) under a variety of simulation scenarios. Individual and temporal variability in the proportion of an hour spent swimming was added at each time step (Figure 2) based on the estimate $\sigma_{\text{tag}}^{\text{swim}}$ for individual variation, and on estimates of $\sigma_{\text{resid}}^{\text{swim}}$ and Φ_1^{swim} (individual-specific temporal variability based on an AR(1) process). For individual i in hour h, the proportion of the hour spent swimming was determined as:

$$p_{i,h}^{\text{swim}} = \text{expit}\left(\text{logit}\left(\widehat{p_{i,h}^{\text{swim}}}\right) + \omega_h^{\text{swim}} + \delta_i^{\text{swim}} + \zeta_{i,h}^{\text{swim}}\right).$$

Prediction uncertainty associated with the linear mixed effect model were represented by the ω_h^{swim} error term $\left(\text{i.e., } \omega_{i,h}^{\text{swim}} \sim N\left(0, \text{SE}\left[\text{logit}\left(\widehat{p_{i,h}^{\text{swim}}}\right)\right]\right)\right)$. Individual differences were represented by the random variable δ_i^{swim}, which was a normally distributed random variable $\left(\text{i.e., } \delta_i^{\text{swim}} \sim N\left(0, \hat{\sigma}_{\text{tag}}^{\text{swim}}\right)\right)$. Temporal variation in time spent swimming was represented by the random variable $\zeta_{i,h}^{\text{swim}}$ which followed an AR(1) process, where the size of an individual's hourly deviation depended on the deviation in the previous hour $\left(\text{i.e., } \zeta_{i,h}^{\text{swim}} = \hat{\Phi}_1^{\text{swim}} \cdot \zeta_{i,h-1}^{\text{speed}} + \epsilon_{i,h}^{\text{swim}}\right)$ and $\epsilon_{i,h}^{\text{swim}}$ represents white noise in the logit-transformed response on the hourly time scale $\left(\text{i.e., } \epsilon_{i,h}^{\text{swim}} \sim N\left(0, \hat{\sigma}_{\text{resid}}^{\text{swim}}\right)\right)$. The expit function converts logit-transformed values from logit space to anti-logit space (i.e., $\text{expit}(\mu) = (1/e^{\mu} + 1)^{-1}$).

4.4 Active Hourly Swim Speeds

Active hourly swim speeds were calculated based on nested hourly averages of instantaneous swim speeds when Bull Trout were actively swimming (see Section 3.9). Average hourly swim speeds were log transformed in order to stabilize variability and skew (Figure E1). Observed average hourly active swim speeds showed a positive association with river discharge for both female and male Bull Trout and potentially area-specific responses to discharge (Figure 7).

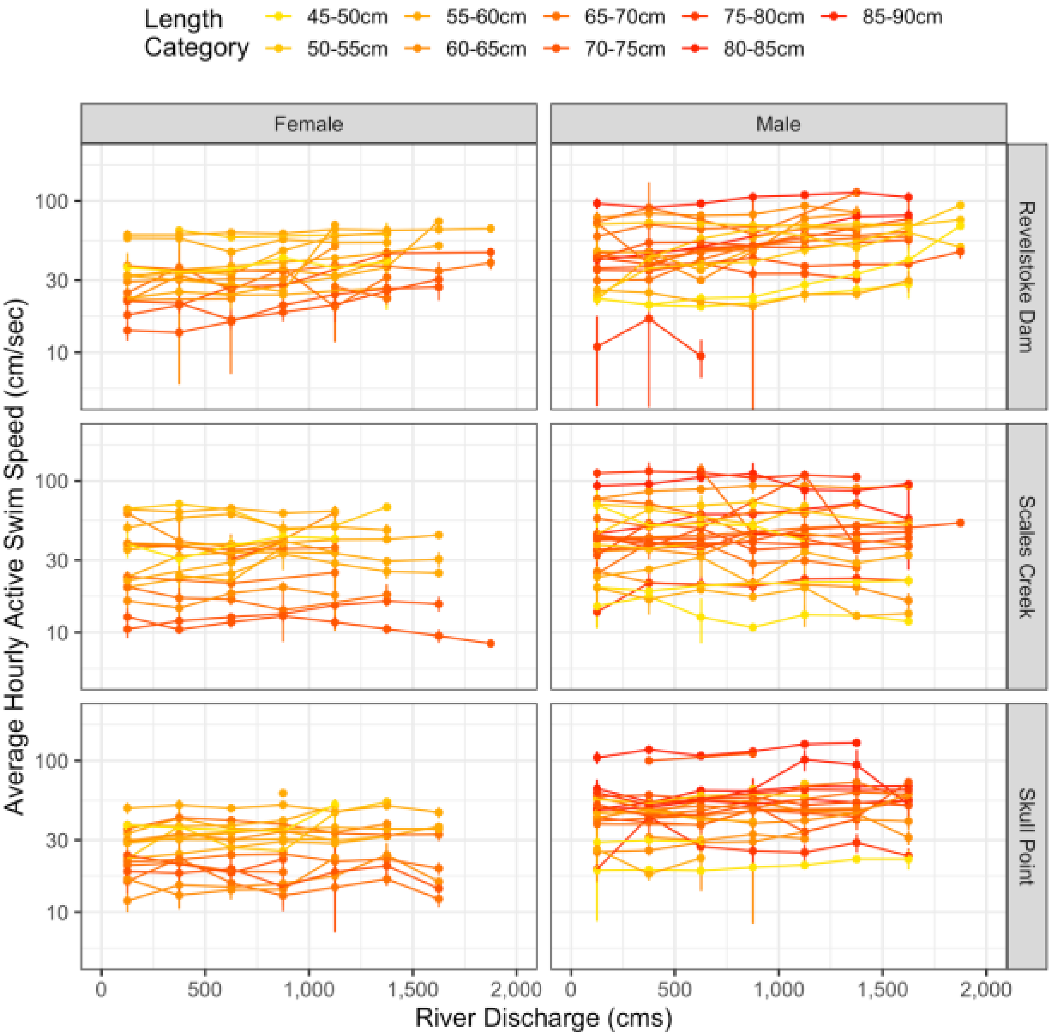

Figure 7. Average female (left) and male (right) Bull Trout swim speeds by river discharge, receiver location (rows) (Figure 1) and body length category. Individual responses are connected by lines. Error bars indicate 95% confidence intervals.

Active hourly swim speeds also appeared to show some signs of a second order polynomial response to discharge in some locations that was shared between female and male Bull Trout (Figure E2). Differing study years generally followed the same trends with potentially some differences by size category.

Due to the differing observed relationships between average hourly active swim speeds and discharge by location and sex, a baseline linear mixed effect model was fit with the following fixed effect structure:

$$\log(SS) = Location{:}Sex + Location{:}Sex{:}Flow + Location{:}Flow^2$$

where the $Location\!:\!Sex + Location\!:\!Sex\!:\!Flow$ term represented a separate linear regression of log-transformed hourly swim speed against river discharges for each combination of sex and location. The $Location\!:\!Flow^2$ term represented a second order polynomial that was independently estimated by area (i.e., allowing for different 2nd order curvatures by location) but shared across sex. Sex was not included in the second order polynomial effects because these effects are typically difficult to estimate, and the raw data plots showed similar 2nd order curvatures by area for both sexes.

Support for additional predictors not in the baseline model were assessed using AICc model ranking (Table E1). Similar to the baseline, each additional predictor was modeled as having a location-specific effect. The model that included a location-specific light effect (i.e., dawn, daytime, dusk, and night; see Table 2) had virtually all the support (i.e., AICc weight of one), so it was added to the baseline model and support for the remaining predictors was assessed in the final model ranking step (Table E2).

Similarly to the first model ranking step, a single model, which considered day of year and temperature (along with the interaction), held the vast majority of support. The mean response, without individual variation, was visualized as a function of discharge, temperature, location and sex (Figure 8). Swim speeds in both Revelstoke Dam and Skull Point increased under the observed discharged conditions (i.e., 0 to 1,765 cms), but an inverted “U” shape was indicated for Scales Creek. Mean active hourly swim speeds were well below critical swim speeds (Figure 4), indicating capacity for increased speeds. Estimated mean active swim speeds were also slightly lower for female Bull Trout as compared to males. Extrapolations for mean active swim speeds up to 2,200 cms were also included (Figure 8) and showed predicted values well below the maximum observed swim speeds, which were typically close to or greater than 100 cm/sec (Figure 4).

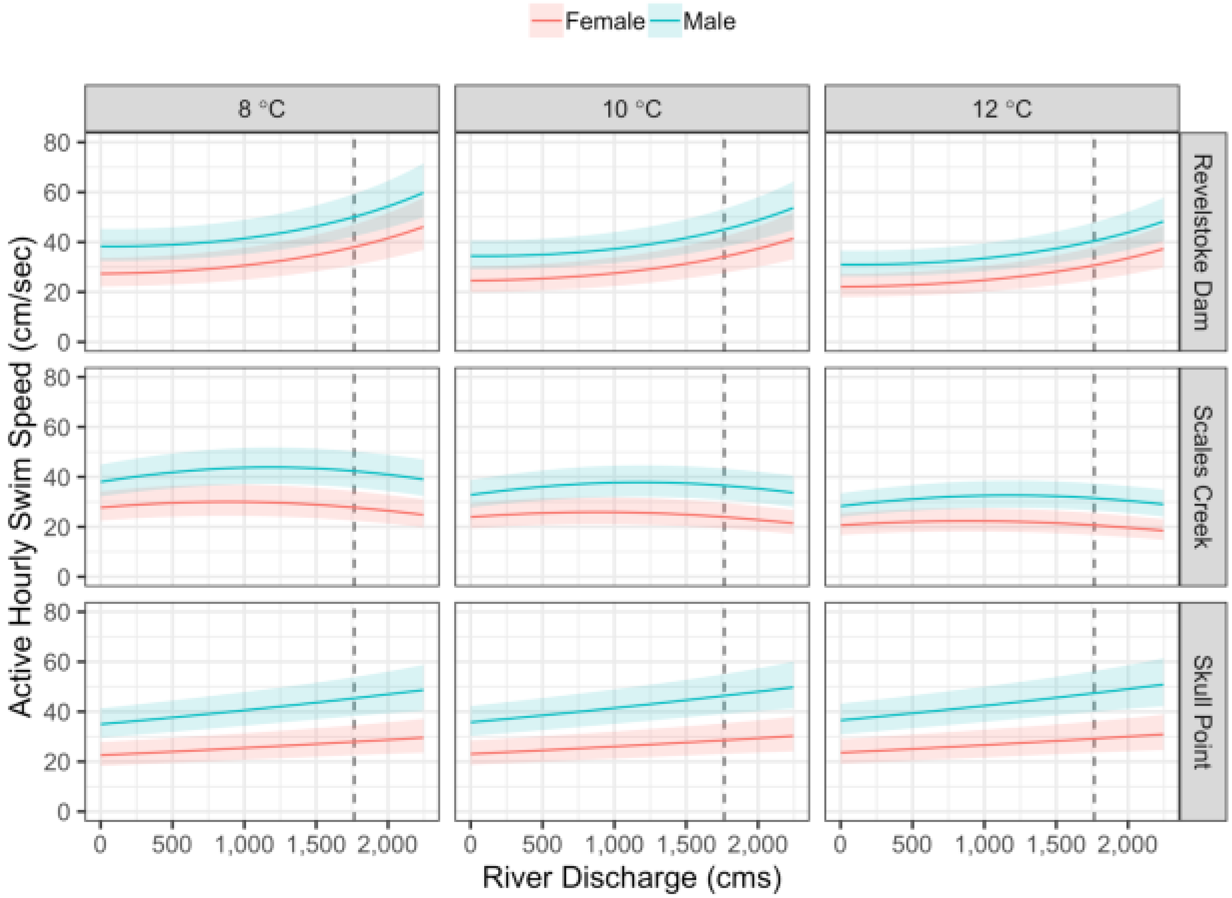

Figure 8. **Predicted Bull Trout mean active hourly swim speed response as a function of river discharge, by sex (color), temperature (panel columns), and fixed receiver location (panel rows).** Shaded region indicates 95% confidence region for the mean response. Vertical dashed line indicates highest observed river discharge conditions (i.e., 1765 cms), with predictions to the right representing extrapolations.

The top model was also used to estimate an autoregressive correlation coefficient on the residual error ($\widehat{\Phi}_1^{\text{speed}}$ = 0.68, 95% CI: 0.67, 0.69), which indicated a strong correlation among observed log-transformed hourly individual swim speeds after controlling for environmental predictors and individual specific effects. Variance component estimates from the top model also indicated that the among individual variation in swim speeds (i.e., $\hat{\sigma}_{\text{tag}}^{\text{speed}}$ = 0.48; 95% CI: 0.39, 0.58) was similar, but higher than the hour-to-hour individual variation ($\hat{\sigma}_{\text{resid}}^{\text{speed}}$ = 0.196; 95% CI: 0.193, 0.200), which we assumed was the variation associated with 60 minutes of observations. Fewer observations within a minute would be expected to have greater residual variation, given that an observation weighting scheme was used.

4.4.1 Simulator Formulation

As part of the pre-computation step (see Section 4.6), the Bull Trout energetics simulator used the top supported model (Table E2) to predict the mean log-transformed active hourly swim speeds (i.e., $\log(\widehat{SS}_{i,h})$) under novel hydrological scenarios. Individual and temporal variability in hourly active swim speeds was added at each time step (Figure 2) based on the estimates of $\sigma_{\text{tag}}^{\text{speed}}$ and individual-specific temporal variability (based on an AR(1) process using the estimates for Φ_1 and $\sigma_{\text{resid}}^{\text{speed}}$). For individual i the swim speed in hour h was determined as,

$$SS_{i,h}^{\text{active}} = \exp\left(\log(\widehat{SS}_{i,h}) + \omega_h^{\text{speed}} + \delta_i^{\text{speed}} + \zeta_{i,h}^{\text{speed}}\right),$$

where ω_h^{speed} represented prediction uncertainty associated with the linear mixed effect model $\left(\text{i.e., } \omega_{i,h}^{\text{speed}} \sim N\left(0, \text{SE}\left[\log(\widehat{SS}_{i,h})\right]\right)\right)$ and δ_i^{speed} represented inter-individual variation was a normally distributed random variable representing average differences in log transformed active hourly swim speeds between individuals $\left(\text{i.e., } \delta_i^{\text{speed}} \sim N\left(0, \hat{\sigma}_{\text{tag}}^{\text{speed}}\right)\right)$. Temporal variation in log transformed active swim speeds was represented by the random variable $\zeta_{i,h}^{\text{speed}}$ which followed an AR(1) process, where the size of an individual hourly swim speed deviation depended on the deviation in the previous hour $\left(\text{i.e., } \zeta_{i,h}^{\text{speed}} = \widehat{\Phi}_1^{\text{speed}} \cdot \zeta_{i,h-1}^{\text{speed}} + \epsilon_{i,h}\right)$, and $\epsilon_{i,h}$ represented white noise in hourly swim speeds $\left(\text{i.e., } \epsilon_{i,h}^{\text{speed}} \sim N\left(0, \hat{\sigma}_{\text{resid}}^{\text{speed}}\right)\right)$.

The final realized hourly swim speed is then the product of the proportion of the hour spent swimming ($p_{i,h}^{\text{swim}}$) and the active hourly swim speed ($SS_{i,h}^{\text{active}}$), that is

$$SS_{i,h}^{\text{realized}} = p_{i,h}^{\text{swim}} \times SS_{i,h}^{\text{active}}$$

for individual i in hour h.

4.5 Site Selection and Movements

The simulator handled site selection and movements in two steps:

1. Individuals were randomly assigned to a starting location based on predicted site preference probabilities; and
2. Individuals were moved at the start of each day based on the estimated movement probabilities.

Each was estimated separately for Bull Trout and Mountain Whitefish based on receiver detection records.

4.5.1 Site Selection

Movements between locations were determined by analyzing the number of receiver detections that occurred at a single location over differing time scales for both species (Figure 9). At shorter time scales (i.e., hourly or daily) most individuals, regardless of species or sex, spent the vast majority of time at a single location. As time scales were extended (i.e., weekly or monthly), a large proportion of time was still spent at a single location, but to a lesser degree than the shorter time scales.

Site selection, as measured by proportion of time spent at a site, appeared to be related to body size for male Bull Trout but less so for female Bull Trout (Figure 10a). Smaller male Bull Trout appeared to spend proportionately more time at Revelstoke Dam, while larger male Bull Trout spent more time at Skull Point. Preference for Scales Creek appeared to be largely neutral across the range of tagged male body sizes. By contrast, female Bull Trout appeared to show neutral preferences for all three sites across all of the tagged body sizes (Figure 10a). Mountain whitefish also showed some indication that site preference was related to body size, but sex-specific responses were unclear due incomplete sexing of tagged fish, and to a lack of confirmed males among the tagged fish (Figure 10b).

The proportion of time spent at each location by Bull Trout and Mountain Whitefish was also assessed under differing river discharge conditions (i.e., low discharge: <500 cms, medium discharge: 500-1000; high discharge: > 1000 cms for Bull Trout (Figure F1) and Mountain Whitefish (Figure F2). Both species showed similar site selection preferences as they did when discharge was ignored (Figure 10). Female Bull Trout again showed a fairly equal preference for the three sites across body sizes and discharge conditions (Figure F1a), while male Bull Trout exhibited a similar size-based preference, with smaller-sized fish preferring Revelstoke Dam and larger-sized individuals preferring Skull Point, and with no discernable differences among discharge condition (Figure F1b). Finally, for Mountain Whitefish there was insufficient data to

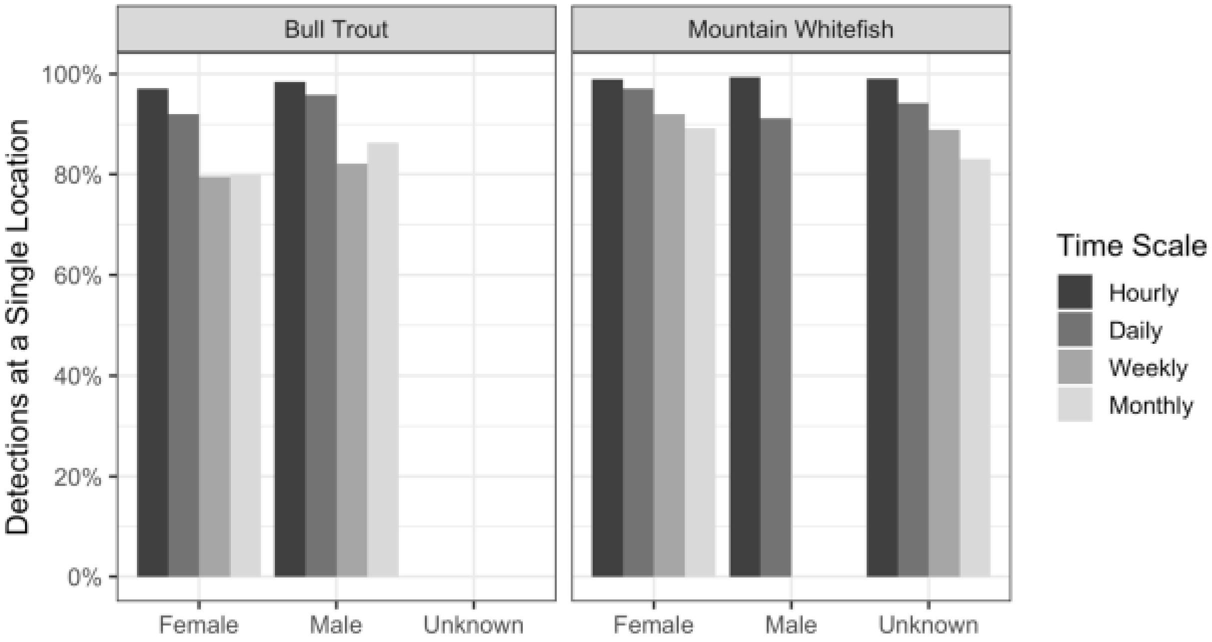

Figure 9. Percentage of receiver detections occurring at one location within a day for Bull Trout and Mountain Whitefish.

draw any conclusions about sex-specific location preferences, but there were potentially some body-sized preferences under lower discharge conditions (Figure F2).

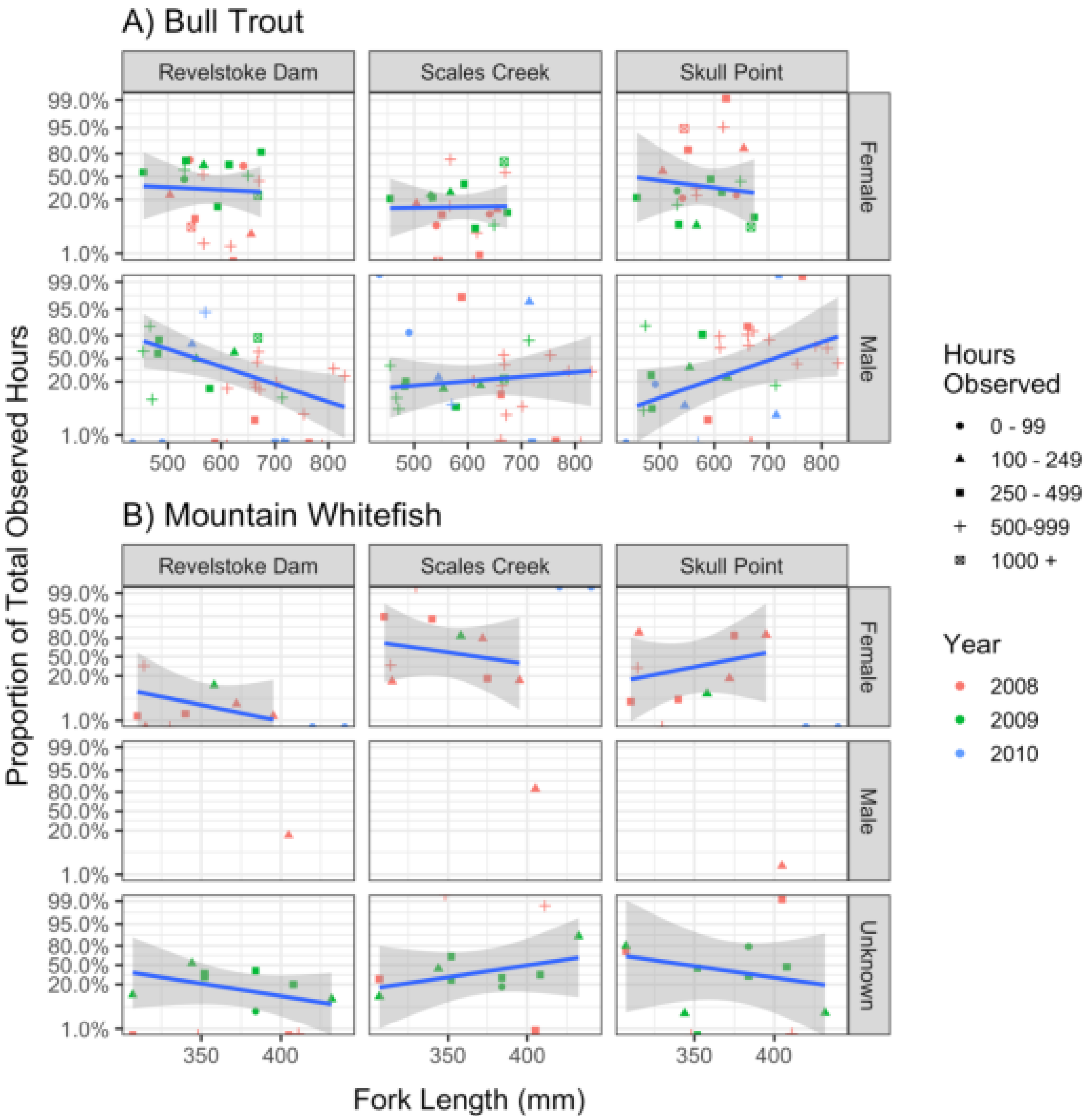

Figure 10. **Proportion of observed time spent in each location by body size for A) Bull Trout and B) Mountain Whitefish.** Shading indicates 95% confidence bands, y-axis is displayed on the logit scale.

4.5.1.1 Simulator Formulation

Predictions of site preference in the simulator were therefore based on patterns observed in proportion of time spent at each location (ρ_i^a) for Bull Trout. A separate linear mixed effect model was fit for male (length by location) and female (length only) Bull Trout, using logit transformation of the observed proportion of time spent at each location (ρ_i^a) as the response variable. The fixed effect portion of the model included a full factorial length by location relationship for males, that is,

$$\operatorname{logit}(\rho_i^a) = Location * Length + Tag(R)$$

while for females only length was considered:

$$\operatorname{logit}(\rho_i^a) = Location + Tag(R).$$

In these models $Location$ and $Length$ represented fixed effects, while $Tag(R)$ was a random effect. The $Location * Length$ fixed effect term represented a full factorial design where a separate intercept and slope was fit for each location.

Predictions from these linear mixed effect models $\left(\text{i.e., } \operatorname{logit}(\widehat{\rho_i^a})\right)$ were used estimate multinomial selection probabilities at the start of the simulation experiment, by normalizing the predicted values to ensure they summed to unity, that is

$$\widehat{\Psi_0^a} = \frac{\operatorname{expit}\left(\operatorname{logit}(\widehat{\rho_i^a})\right)}{\sum_{a=1}^{3} \operatorname{expit}\left(\operatorname{logit}(\widehat{\rho_i^a})\right)}.$$

Here $\widehat{\Psi_0^a}$ represented the probability of individual i selecting location a at the start of the experiment (i.e., $\sum_{a=1}^{3} \widehat{\Psi_0^a} = 1$) and $\operatorname{logit}(\widehat{\rho_i^a})$ was the predicted average from the linear mixed effect models. Initial locations at the start of the experiment (L_i) were then selected from a multinomial distribution $\left(\text{i.e., } L_i \sim \text{Multinomial}\left(\widehat{\Psi_i^a}\right)\right)$.

4.5.2 Movements

Once individuals were assigned to an initial location, the energetics simulator would also need to consider how and when individuals transition between the three receiver locations (Figure 1). First-order Markovian transitions were assumed and estimated using the multi-strata model in Program MARK (White and Burnham 1999). Estimating hourly transitions was not computationally feasible due to the size of the hourly capture histories and the number of transitions modeled. Instead, daily transition probabilities were estimated, further justified based on the similarity in movement behaviours compared to longer durations such as weekly or monthly movement patterns (Figure 9). First order Markov transition probabilities were estimated based on a multi-strata CMR model using daily transitions (Table 5).

Table 5. Estimated daily Markov transition probabilities for Bull Trout and Mountain Whitefish. Rows represent current location and columns represent transition probabilities for the three receiver locations (Figure 1). RD = Revelstoke Dam; SC = Scales Creek; SP = Skull Point.

	Bull Trout						Mountain Whitefish		
	Female			Male			Pooled Across Sex		
	RD	SC	SP	RD	SC	SP	RD	SC	SP
RD	0.88	0.05	0.08	0.85	0.08	0.07			
SC	0.12	0.77	0.11	0.10	0.83	0.07			
SP	0.03	0.05	0.91	0.03	0.03	0.94			

4.5.2.1 Simulator Formulation

Transition probabilities were based on estimated transition probabilities from Table 5. For example, male Bull Trout have the following daily transition probabilities,

$$\Psi_{Male} = \begin{bmatrix} 0.85 & 0.08 & 0.07 \\ 0.10 & 0.83 & 0.07 \\ 0.03 & 0.03 & 0.94 \end{bmatrix},$$

where rows represented the current location ($a = \{1,2,3\}$) and columns represented the transition probabilities for the next time step. Movements between hour $h-1$ and hour h were restricted to the start of each day, if available in the test hydrology scenario, based on the following multinomial draw,

$$L_{i,h} \sim \begin{cases} \text{Multinomial}\left(\Psi_{\text{sex}_\text{i}}\left(L_{i,h-1}\right)\right) & \text{if } h \text{ is midnight} \\ L_{i,h-1} & \text{otherwise} \end{cases},$$

where $\Psi_{\text{sex}_\text{i}}\left(L_{i,h-1}\right)$ represented the transition probabilities associated with being in location $L_{i,h-1}$ in the previous hour, otherwise individuals remained at their previous hourly location (i.e., $L_{i,h-1}$).

4.6 Example Energetics Comparison

An energetics simulator could only be built for Bull Trout due to a lack of EMG calibration experiments available for tagged Mountain Whitefish. While both female and male Bull Trout EMG signals could be calibrated for swim speed estimates, females at times also showed different swimming behaviours, especially with regards to critical swim speeds (Section 4.2) and the proportion of time spent swimming (Section 4.3). Because there were concerns that female swim behaviour was affected by the proximity to spawning, the simulator example analysis has focused on male Bull Trout.

The simulated male Bull Trout respiration energetics were compared under months with low and high discharge as a demonstration of the simulator (Figure 11). These two months contrast a low discharge, high temperature hydrology regime with a higher flow, lower temperature regime. September 2010 had a lower average hourly discharge rate of 429 cms, but a higher average hourly temperature of 11.8 °C. In comparison, November 2010 had an average hourly discharge rate of 968 cms and average hourly temperature of 9.4 °C.

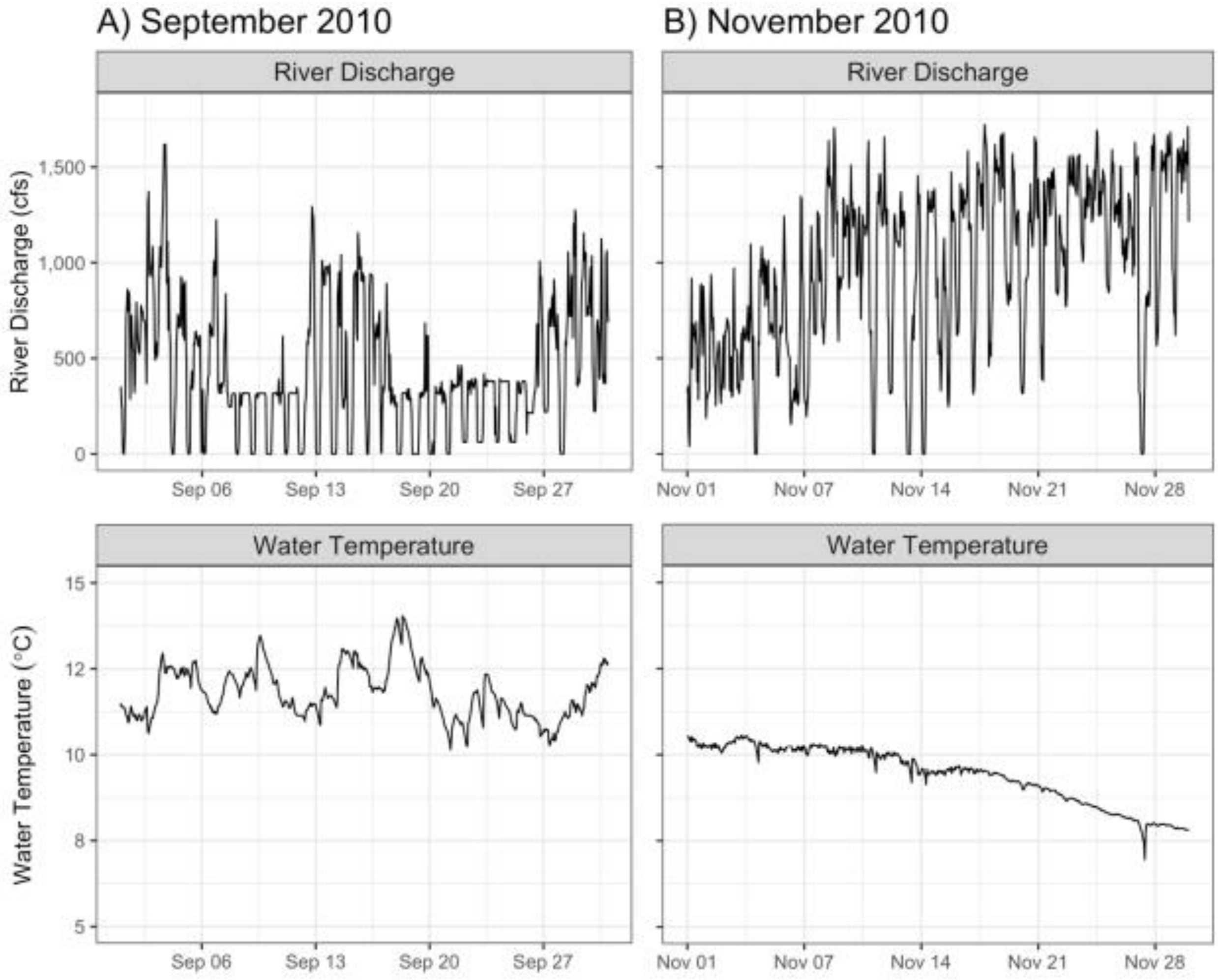

Figure 11. Hourly river discharge and water temperature at the Revelstoke Dam receiver in A) September and B) November 2010. The two regimes were used to represent a lower discharge, higher temperature and a higher discharge, lower temperature scenarios.

The respiration energetics of 500 male Bull Trout were simulated over 719 hours using the two example hydrology regimes (Figure 11). Estimates of the average daily respiration load was determined by first averaging daily respiration energetics for each individual, then averaging for the population each day. Simulations were repeated 1,000 times to determine the variability in the average daily population respiration rate for each hydrology regime.

Within a given iteration simulated male Bull Trout showed both hourly variability within an individual as well as between individual variation, with simulated individuals showing a diversity of emergent behaviors (i.e., active metabolism row; Figure 12). The two main components of respiration are standard and active metabolism (see Section 3.12) which are broken out for each example individual. The active metabolic rate component reflects average daily swim speeds, which is the combination of behaviour decisions in response to environmental conditions (e.g., discharge, temperature, time of day), individual variation, and stochasticity. The standard metabolic rate is the minimum metabolic rate needed to sustain life at a given temperature, whereas the active metabolic rate acts as a multiplier against the standard metabolic rate to determine the respiration rate (see Section 3.12).

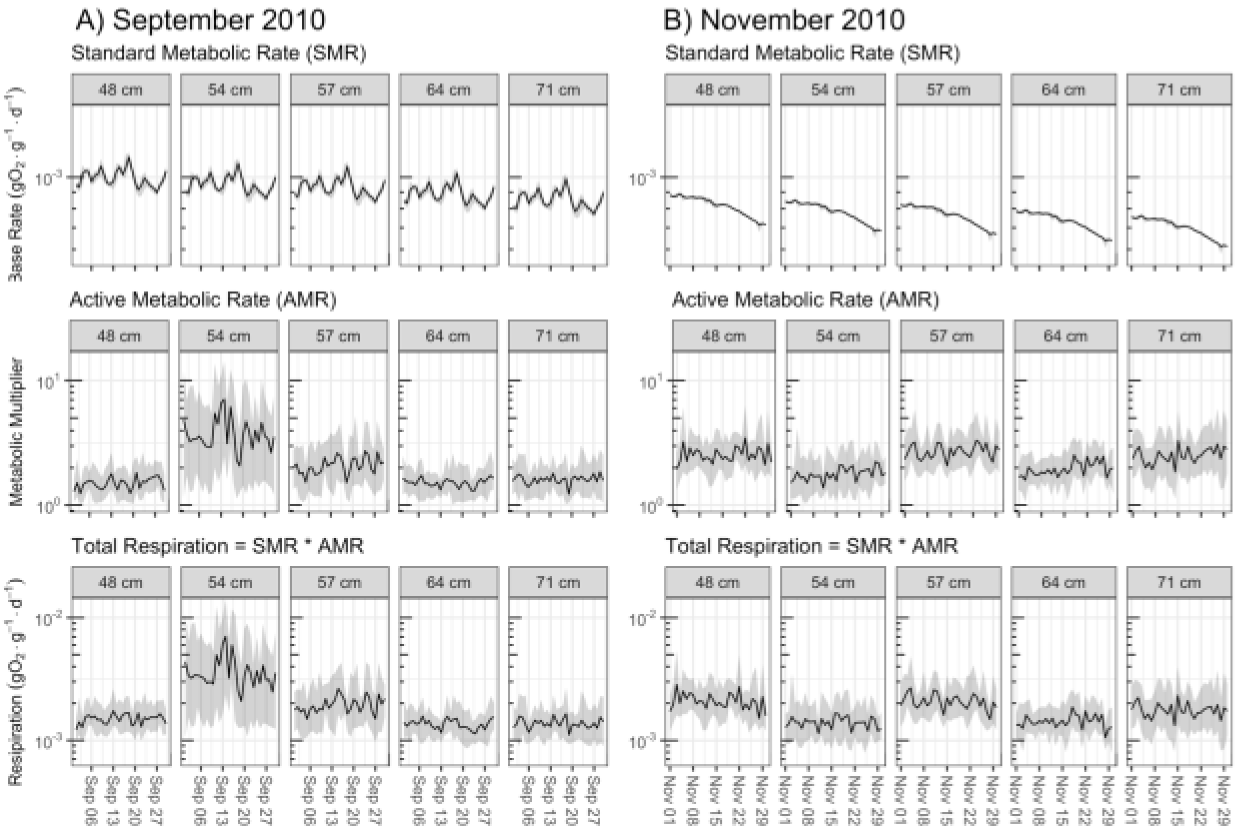

Figure 12. Daily respiration rates for five randomly selected individuals with a range of body sizes from the simulated population based on the September (A) and November (B) hydrological regimes (see Figure 11). Respiration has been broken down into the two primary component pieces (first two rows) as well as final respiration values (bottom row). Line indicates the daily average and shading indicate the 2.5 and 97.5 percentiles of the simulated hourly values from a single simulation run. Size of the simulated male Bull Trout is indicated in the panel strip text.

Individual variability in active metabolic rate relates to differing activity levels, which can be seen as a shifting up or down of the active metabolism multiplier value in similar sized individuals (active metabolism row; Figure 12). Individuals with higher activity levels also showed higher variation in hourly metabolic rates than less active individuals (range indicated by shading; Figure 12).

Estimates of average daily respiration for the population was determined from the simulated hourly individual energetics in a hierarchical manner:

1. Estimates of daily individual energetic rates by averaging individual hourly energetic rates for each day and simulation iterations; and
2. Estimates of population daily averages for each simulation iteration, by averaging the individual daily averages.

This provided a distribution of daily population averages, which can be directly (Figure 13), or estimates of a cumulative metabolism under each hydrology regime (Figure 14). Average daily respiration estimates (i.e., Figure 13a) are presented on a gram specific basis (i.e., per gram of fish) and provide a way to determine which days produced significant differences in either standard metabolic rate (i.e., first row; Figure 13a), active metabolic rate (i.e., second row; Figure 13a) or respiration (i.e., combination of standard and active, third row; Figure 13a). Shading indicates the 2.5 and 97.5 percentiles from the 1,000 simulation runs. This indicates the range of daily values a simulated population of 500 Bull Trout can be expected to exhibit (i.e., 95% of simulated population realizations). A confidence band was not included in the standard metabolism estimates as temperature was only known at a single location, and all individuals were assumed to experience the same hourly temperature, and as such uncertainty in standard metabolic rate could not be included. In contrast, active metabolic rate showed a high degree of day-to-day variability within a regime and between regimes with November 2010 tending towards higher rates (i.e., second row; Figure 13a). Differences in average daily active metabolism between regimes was largely the result of differences in the proportion of each hour spent swimming (i.e., top row; Figure G1), rather than substantive differences in the average hourly swim speed (i.e., middle row; Figure G1).

The percent differences in metabolic components were also compared (Figure 13b). These showed a much smaller degree of uncertainty as prediction errors will cancel on any given simulation iteration when making a comparison between two hydrology scenarios. As with the daily values, shading indicates the 2.5 and 97.5 percentiles for the 1,000 simulation runs. Days where the confidence band does not overlap zero (i.e., no average difference) can be interpreted as a “significant” differences. While there were significant daily differences in standard and metabolic rates (i.e., first two rows; Figure 13b), total respiration tended to over close to zero (i.e., bottom row; Figure 13a). This indicates that male Bull Trout may be making a potential trade-off between standard and active metabolic rates, where conditions that result in a higher standard metabolism may be offset with a reduction in active metabolism, through less time spent active swimming.

Finally, the total respiration load of the two hydrology regimes can be determined by comparing the cumulative respiration (Figure 14). As before shading indicates the 2.5 and 97.5 percentiles from the 1,000 simulation runs. Percent difference comparison (Figure 14b) again indicated that both regimes produced similar respiration demands, despite large differences in flow and temperature, with the November 2010 regime showing marginally significant difference by the end of the 30 day period (Figure 14b; mean: 9.7% reduction; 95% CI: -0.9%, 19.6% reduction).

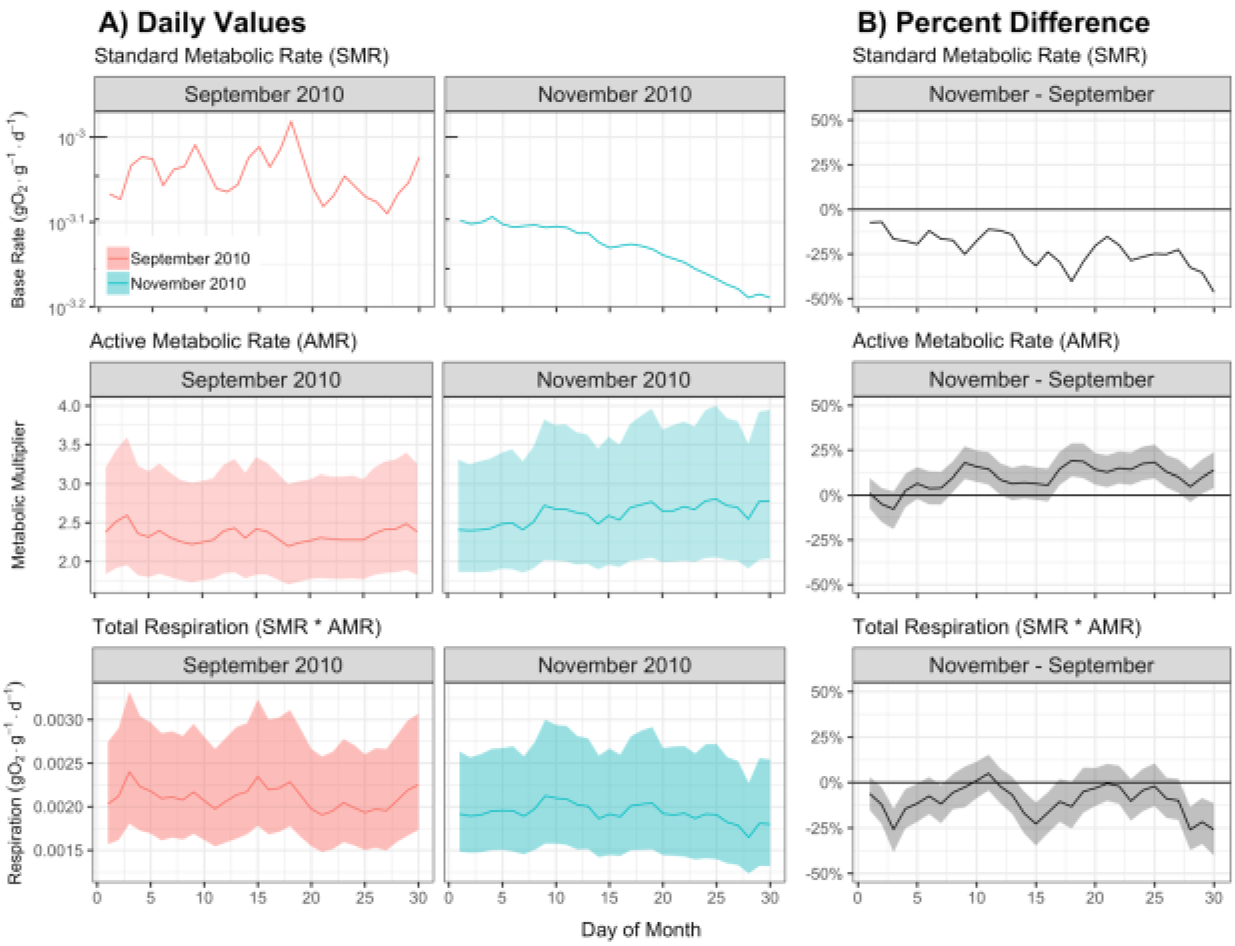

Figure 13. Comparison of the population daily respiration rates for the September and November 2010 hydrological regimes (A) and the percent differences (B). Respiration has been broken down into the two primary component pieces (first two rows) as well as final respiration values (bottom row). Solid lines indicates the daily average and the shading indicates the 2.5 and 97.5 percentiles from 1,000 simulations.

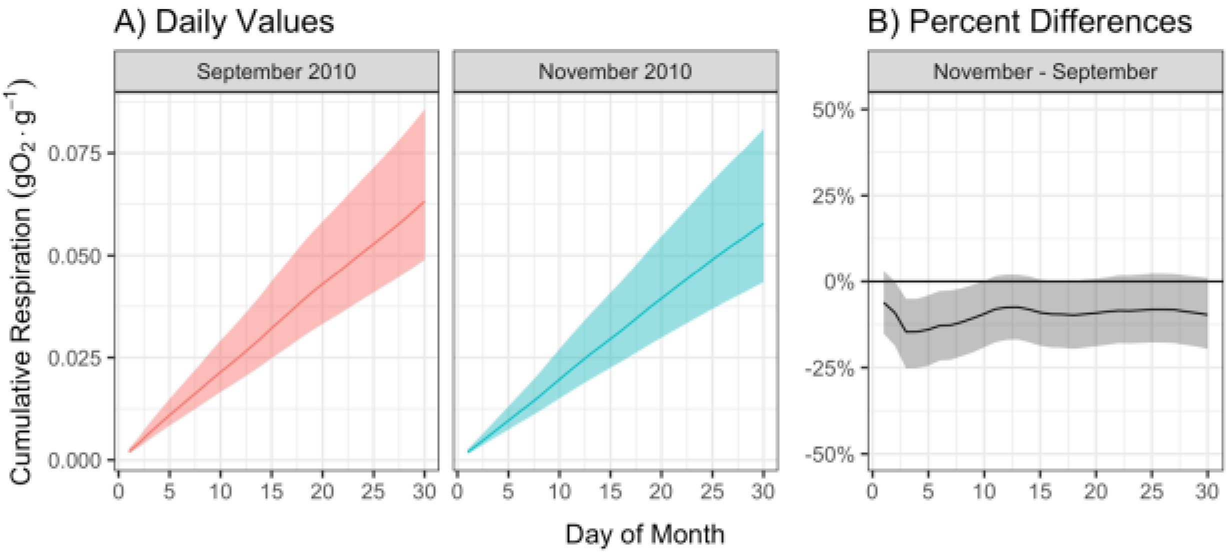

Figure 14. Per capita cumulative metabolism per gram of fish over the September and November 2010 hydrological scenarios (A) and the percent differences (B). Solid lines indicates the daily average and the shading indicates the 2.5 and 97.5 percentiles from 1,000 simulations.

4.7 High Discharge Extrapolations

The current EMG telemetry component of the study encountered a maximum river discharge of 1,765 cms, but there is concern over energetic consequences of potentially higher maximum discharge magnitudes. Predicted average daily energetic values were calculated for a range of temperatures and river discharges up to 2,200 cms (Figure 15). As expected, standard metabolic rate was a function of temperature, and was not sensitive to river discharge values. Active metabolic rates indicated a curvilinear increase and higher variability with higher discharge. Predicted active metabolic rates were also quite similar under different temperature conditions, largely due to differences in percentage of time spent swimming balancing differences in active swim speeds (Figure H1). Explorations beyond 1,765 cms showed averages within the range of daily activity rates observed in the example hydrology comparison (Figure 13, middle row), but with higher extreme values (Figure 15, middle row). These values were also well within biologically plausible values, which can be as high as seven (7) times SMR under routine activities (Tang and Boisclair 1995). Extrapolations also showed uncertainty range (shading, Figure 15), which was the result of higher prediction errors. Finally, total respiration showed a similar curvilinear increase as active metabolism (bottom row, Figure 15) with the average value within example hydrology (middle row, Figure 13), but with higher extreme values. Overall, the tested discharge extrapolations that went up to 2,200 cms appeared to produce plausible results.

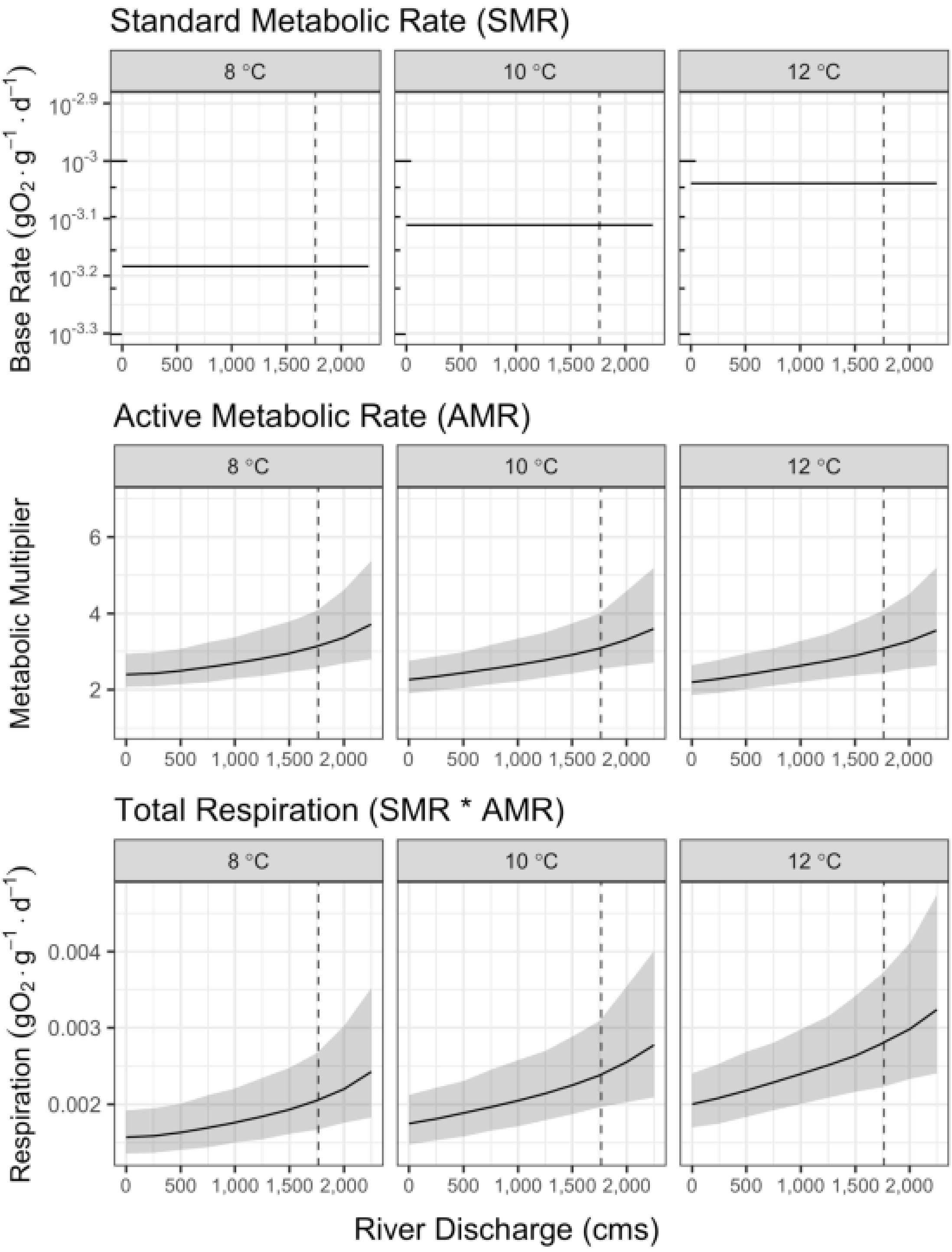

Figure 15. Comparison of respiration rates across a variety of river discharge and temperature (panel columns) values. Respiration has been broken down into the two primary component pieces (first two rows) as well as final respiration values (bottom row). Solid lines indicates average and the shading indicates the 2.5 and 97.5 percentiles from 1,000 simulations. Vertical dashed line indicates highest observed river discharge conditions (i.e., 1765 cms), with predictions to the right representing extrapolations.

4.8 Pre/Post Rev 5 Comparison

Average daily energetics in a population of 500 Bull Trout were compared across four seasons and under base and peak flow conditions based on 14 days randomly chosen from the median conditions or days with peak flow conditions (Appendix I).

Overall, the energetics results indicated a larger inter-season difference in respiration than across REV 5 periods within a season for both baseline conditions and peak flow conditions (Figure 16). The uncertainty ranges, which capture individual variation in behaviour as well as estimate uncertainty, showed a range comparable to the inter-seasonal differences. Average gram specific per capita respiration between the pre- and post REV 5 periods was very similar with the post period showing similar or slightly higher values for most seasons, except for summer and fall under base conditions. These differences were small compared to the inter-seasonal differences and instances of lower average per capita respiration under REV 5 may be related to large variation in hour-to-hour flow often observed within a day (Figure 11). That is, peak energy expenditure associated with short-term peak flows under REV 5 conditions may by offset by other parts of the day that may exhibit lower flow conditions.

Male energetics were considered to be representative of female energetics for all seasons except fall, when spawning occurs. In this case the female-specific energetics model was used, as empirical data used in this model is likely reflective of the spawning period and female-specific behavior differed during this period. Female specific respiration estimates in fall showed a similar pattern to male-specific patterns except at a slightly lower rate, which is not surprising given that females tended to exhibit slower average hourly active swim speeds during this period, especially larger females (Figure 8).

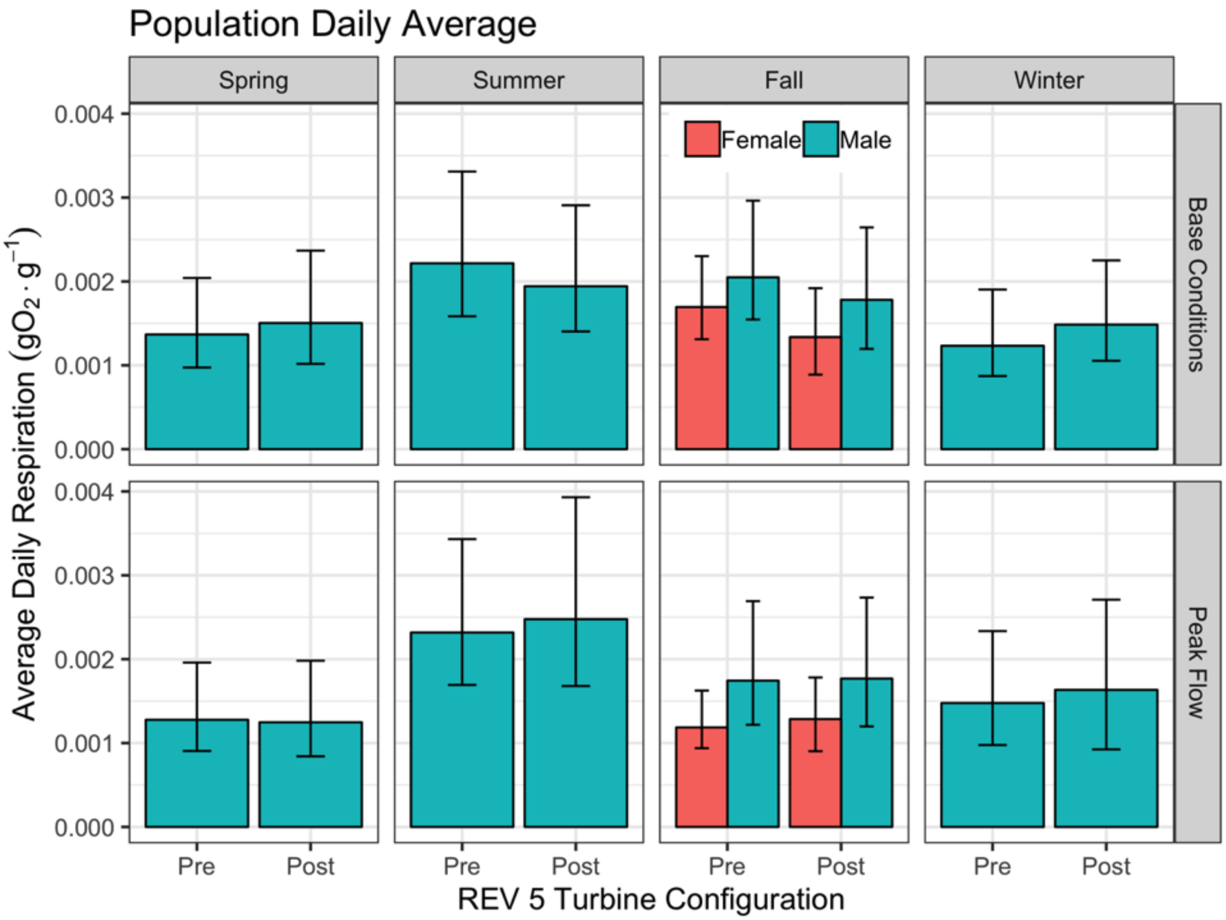

Figure 16. Comparison of the per capita average daily metabolism per gram of male Bull Trout between pre and post REV 5 conditions. Error bars indicates the 2.5 and 97.5 percentiles from 1,000 simulations.

5 Discussion

The primary focus of the study was the development of a model to assess Bull Trout and Mountain Whitefish energetics under altered Middle Columbia hydrological flow regimes. A further goal of these models was to assess the energetics requirements under maximum discharge magnitudes greater than what has been explicitly studied to date. An energetics model predicting respiration metabolism associated with novel hydrological regimes was successfully built for Bull Trout, but currently could not be built for Mountain Whitefish due to lack of data. Furthermore, when the Bull Trout energetics model was tested under discharge conditions, greater than the maximum observed river discharge of 1,765 cms predictions were found to be biological plausible suggesting that the developed model will be useful in assessing the energetic impacts of higher maximum predicted discharges resulting from REV 5.

The bioenergetics model considered the effect of hydrology regimes on metabolism (i.e., respiration) by considering the impact on standard and active metabolic components, rather predicting the full energy budget. Fish energy expenditure is the result of three components: the energy required for basic functioning and maintenance (termed standard metabolic rate), the energy required for activity (active metabolic rate) and the energy required for digestion (digestive metabolic rate). The effects of digestion were not directly considered as standard and active metabolic rates were the two components most likely to be affected by altered hydrological regime (Guénard and Boisclair 2015). Furthermore, these two physiological parameters are typically of most interest to ecologists as they represent the floor and ceiling in aerobic energy metabolism (Norin and Malte 2011).

Temperature alterations under new hydrology regimes affected the standard metabolic component of the developed model, while temperature and discharge impacted predicted behavioural traits, which was then used to model changes in active metabolism. For the active metabolic component of the model, a key partitioning was the division between swim behavior (i.e., periods of inactivity) and active swim speed, which was estimated from the EMG telemetry data. Predictions of active swim speed generally increased with river discharge (Figure 8), but swim behaviour (i.e., the decision to actively swim) arguably showed a stronger response to discharge especially when considering extremes of body size and temperature (Figure 6). Within the Bull Trout energetics model these two components were combined to produce estimates of realized hourly swim speeds, which was then used to determine active energetic costs.

Of these two activity components there was less uncertainty associated with predictions of how often an individual will be swimming, as opposed to the swim speed which had higher uncertainty (Figure G1). The strength of the propensity to swim model component, may indicate the importance of this behaviour in the natural environment, a trait that is known to show a large degree of individual variability even under routine swimming conditions (Tang et al. 2000). Bull Trout also have an innate ability to hold position at the bottom of channels using pectoral fins as hydrofoils under elevated flow conditions (Mesa et al. 2004). Other behaviours that may be associated with this component include potentially adaptive behaviours such as hiding in the velocity refuges downstream of rocks where eddies and slower velocities existed (Gido et al. 2012) or deeper pools (Bunt et al. 1999). Taken together, these behaviours likely represent a suite of adaptations for minimizing energy expenditure during unfavourable swimming conditions. As such, these represent an important behavioural component to include in an energetics model designed to assess water management strategies.

To date, investigating activity costs associated with hydroelectric river flow have tended to look at EMG or swim speed responses as a whole, rather than partitioning activity into different categories (Murchie and Smokorowski 2004, Cocherell et al. 2011, Taylor et al. 2012). Some have even noted that there was a high degree of muscle activity unexplained by discharge, and proposed behaviour traits such as ‘flow refuging’ could be used to economize energy expenditures (Taylor et al. 2012). Other species, such as juvenile White Sturgeon (*Acipenser transmontanus*), did not exhibit swim speed responses to altered discharge, but rather opt to hold station at the cost of feeding opportunities (Geist and Brown 2005). As such, to our best knowledge this is the first study using EMG to first predict when an individual will be swimming, rather than simply predicting the average swim speed. We believe this represents a more realistic behavioural model than using aggregate measures of swim speed.

Interestingly, when we combined the separate model components, and assessed the example hydrology regimes, an emergent behaviour of the model was one of a potential energetic trade-off, where the lower discharge, higher temperature regime resulted in similar respiration rates as the higher discharge, lower temperature hydrology regime. Under the colder hydrology regime the standard metabolic rate was predicted to be lower, but active metabolism was predicted to be higher. Combined, this produced a total respiration value similar to the higher temperature hydrology regime, which had a higher predicted standard metabolism rate, but a lower predicted active metabolism rates. The fact that these two differing hydrology regimes resulted in similar total respiration rates is suggestive of a trade-off. Furthermore, the majority of this trade-off can be attributed to differences in the predicted propensity to swim, as the active swim speed predictions were very similar for the two hydrology regimes. This emergent property of the model suggests that Bull Trout may have the behavioural capacity to economize energy expenditure under a variety of environmental conditions by altering the frequency of swimming bouts, as has been suggested as a possible coping mechanism for other fluvial species such as Mountain Whitefish (Taylor et al. 2012). This potential activity trade-off would also seem appropriate for Bull Trout, which are a cold water specialist and are seldom found in systems above 15°C (McPhail and Baxter 1996). The propensity to hold position without actively swimming could also have important consequences for important life history behaviours such as foraging, a component not considered in the current modelling exercise. For example, predictions assume that the lengths of unfavourable hydrology conditions will be similar to the lengths observed during the EMG study. Extended periods of unfavourable hydrological conditions could leave fish in a food deficit, which may eventually force individuals to increase activity levels in energetically unfavourable conditions in order to forage for food. Higher order behavioural trade-offs, such as foraging, were not considered in the proposed model.

We also found that it should be possible to determine energetic requirements under altered flow regimes with higher maximum flows like those expected under REV 5. While the maximum observed discharge during the study period was 1,765 cms extrapolations outside this range (e.g., 2,200 cms) produced biologically plausible results, suggesting that the extrapolations may be valid. This was largely due to predictions being well behaved and within biological ranges under observed discharge rates, such that prediction under higher discharge rates (greater than 1,765 cms) still remained biologically plausible. That said, as with all extrapolations the farther the extrapolation is outside the observed range, the less reliable the predictions are likely to be. Some of this was captured with higher prediction uncertainties included in the model, but predictions also relied on the assumption that the underlying Bull Trout behaviours (e.g., propensity to swim) will continue to respond in a similar fashion as has occurred in the observed hydrology conditions.

Given that extrapolations to higher flow conditions appeared to be plausible, the average respiration was compared between base conditions and under REV 5. Only small differences were found in average daily energetics across the four seasons with male energetics model being used as a surrogate for female energetics during non-reproductive periods. The comparison was careful not to compare all available days as environmental and water management responses may have differed in this period, which would have confounded the comparison. Rather, base conditions were compared by selecting days representative of "median conditions" of discharge and reservoir level shared across both periods, while peak conditions represented the upper end of discharge within each period. In both cases, energetics were largely similar with a difference that was much smaller than the uncertainty related to variation in individual behaviour and uncertainty in parameter estimates. This is likely the result of higher peak energetic demands under REV 5 being offset in other parts of the day where lower flow occurs. Given that extrapolated energetic demands under peak REV 5 flows appear to be well within the biological range, we do not find evidence for a sustained impact on Bull Trout energetics under REV 5 if overall water management practices remain similar to the practices during the study period (e.g., the duration of peak flows).

Further refinements of the male Bull Trout bioenergetics model could include sensitivity analyses of the regression relationships. Of prime interest is the sensitivity of the emergent energetic trade-offs to analysis model structure. This could be assessed by considering a suite of potential linear model structures for predicting the propensity to swim and active swim speeds. The structure of the proposed model could be expanded further by considering other swimming behavioral traits such as sustained bursts of speed or the energetics of cost of non-swimming behaviour. The proposed energetics model also used a hard threshold for determining active swimming behaviour and therefore a contribution to the active metabolism component. Higher order behavioural trade-offs, such as foraging trade-offs, could also affect when active swimming occurs and could be included in the model, however, these costs are unknown, would are likely difficult to estimate in a field environment.

Where possible we tried to ground truth components of the analysis. A number of extrapolations were required to infer swim speeds from EMG readings for the study population. Some of these include: 1) using field based observations to standardized EMG readings; 2) basing tail beat frequency predictions for the study population of 88 tagged fish on the results of 13 calibrated individuals, which exhibited EMG readings about one third the range observed under natural conditions; 3) using models developed for sockeye (*Oncorhynchus nerka*)(Brett 1995) to predict relative swim speeds; and 4) body length scaling conversions from a study that was found to under predict the weight of the study population (Hyatt and Hubert 2000). Despite these potential draw backs, empirical estimates of male Bull Trout critical swim speed (i.e., observed maximal instantaneous swim speed) were regressed against body length and predictions for smaller sizes roughly match critical swim speeds independently measured by Mesa et al. (2004), who also found a significant positive associations between critical swim speed and body size.

We also found that our universal calibration approach provided good performance when compared to the subset of Bull Trout that were individually calibrated. Slope estimates of the 'length to maximum swim speed` relationship were statistically indistinguishable when estimated using the 13 fish that were individually calibrated, versus the 88 fish that used a universal calibration equation to predict tail beat frequency. The relationship between size and observed maximal swim speed for male Bull Trout was also strongest near the Revelstoke Dam fixed receiver location, an area in closest proximity to the dam tailrace and one that likely contained the most challenging swim conditions. Here body size accounted for roughly 96% of the variation in observed maximal swim speed, an incredibly strong association for a field study. Our findings also contradicts the generally accepted perspective that EMG transmitters are expected to behave differently in different individuals, requiring approaches that focus on calibrating each individual separately (Brown et al. 2007), which can be difficult in practice due to the difficulties and stress in transporting live fish (Cooke et al. 2004).

The largest deviations between the extrapolated 'length to maximum swim speed` regression line were for the smallest sizes tested by Mesa et al.(2004), which were nearly half the size of the study population. These differences could be caused by a number of factors such as a breakdown of a straight line relationship between body size and critical swim speed, bias in the methods, or the fact that critical swim speed is often considered to be a measure of maximum aerobic capacity during steady state swimming (Hammer 1995, Gregory and Wood 1998). Maximum observed swim speeds may relate to unsteady swim performance which can differ from steady state performance (Fu et al. 2013).

While male Bull Trout showed a strong linear relationship between maximal swim speed and body size, female Bull Trout showed non-significant negative relationship and significantly lower maximal swim speeds. This result was unexpected and may suggest compromised swim performance in the female study population. One possible explanation is that spawning would have occurred just prior to or during the September commencement of the tracking period for this study (McPhail and Baxter 1996) and post-spawn females are known to behave different from males (Fraley and Shepard 1989). Swim behavior also differed between the two sexes. While the propensity to swim generally increased as a function of discharge, size- and temperature-specific responses differed greatly between sex, with larger females tending to swim less frequently during colder conditions than smaller females. Generally, the opposite was true for males, and may be the result of larger females bearing a larger energetic cost during spawning than smaller females. As such, we suspect female Bull Trout may be actively trying to conserve more energy, although we did not directly test this hypothesis. This is also consistent with other work which found a larger decline in female condition during the spawning period, but with a recovery in condition by spring (Nitychoruk et al. 2013). As such, we suggest using the male Bull Trout energetics model as a surrogate for both sexes when assessing energetic costs of altered flow regimes outside the reproductive period and male- and female-specific models during the reproductive period.

We were not able to develop a complete energetics model for Mountain Whitefish, due to a number of missing components. Probably the most critical hinderance was the lack of calibration experiments for Mountain Whitefish, as such it was not possible to predict tail fin beat frequency from the available EMG telemetry data. This made it problematic to predict either the propensity to swim or swim speeds, which are required for the active metabolic component. Given the success of deriving a universal calibration equation for Bull Trout, a small addendum study to derive this calibration relationship and apply it to data from previously tagged Mountain Whitefish data may be viewed as a possible approach. However, the current lack of available small EMG tags is considered a major drawback to this approach (see Appendix J). A further hindrance to the use of existing EMG Mountain Whitefish data is the lack of sexing for most of the sampled individuals. The Mountain Whitefish spawning period occurs in late fall, which likely have coincided with the telemetry studies (Roberge et al. 2002). If post-spawning female Mountain Whitefish behaviour differed from male behaviour, as it did with Bull Trout, then the previous tagging study may be of limited utility as few tagged fish were successfully identified as male. As such, sex-specific post-spawning behaviour could affect parameter estimates if sexes were pooled together, as would be required if the original EMG data was to be employed. Other components that would need to be determined in a future field study include the tail beat frequency threshold for active swimming, and a standardized length equation for converting fork length measurements to total length.

It was determined that a future study using accelerometer tags could address all these issues at the cost of discarding most of the EMG Mountain Whitefish data. No year-specific effects were noted in the Bull Trout responses, suggesting a future field study with accelerometer tags could potentially be completed in a single year if a sufficient range of hydrological conditions were available during the study period. Future studies may also consider avoiding the spawning period to avoid potential sex-specific post-spawning behavioural differences, or have observations both before and during spawning, if energetics during spawning is a goal. Mountain Whitefish will also need to be successfully sexed if sex-specific differences are to be modelled.

Finally, any future telemetry studies may also wish to consider the use of accelerometry tags as an alternative to EMG tags as these could provide an easier surgical option (Metcalfe et al. 2015). While promising, care should be taken to confirm that behavioural components, such as the propensity to swim, can still be accurately estimated. Furthermore, the change in methodology could negate the ability to include previous field data involving EMG telemetry due to potential response differences between the two tagging technologies.

6 Conclusions

Bull Trout – A bioenergetics model successfully produced realistic biological behaviours that included activity trade-offs under differing environmental conditions. When the model was used to predict energetic demands under peak REV 5 flows the extrapolation appeared to be well within the biological range and daily energy expenditures compared to base conditions and were found to be similar across the seasons and during reproductive and non-reproductive periods. As such, we do not find evidence for a sustained impact on Bull Trout energetics under REV 5, compared to base conditions, if overall water management practices remain similar to the current practices (e.g., duration of peak flows). While the model makes predictions about holding behaviours under differing environmental and hydrological conditions, foraging trade-offs associated with holding were not considered because costs are unknown and would be otherwise difficult to estimate in a field environment.

Mountain Whitefish – It was not possible to develop bioenergetic model based on currently available field data, as no EMG calibration data was collected for Mountain Whitefish during the study. This prevented EMG from being used in the energetics equations. Further field study options were considered including:

1. A follow-up EMG telemetry study designed to build off the original study. ***Drawbacks:*** Current available EMG tag have a larger tag burden than in the original EMG study. Furthermore, the original EMG study often lacked sex determination for Mountain Whitefish making reuse of previously collected data problematic, given that the original study likely occurred during reproductions which could have resulted in sex-specific swimming behaviour as was observed in Bull Trout. ***Suggestion*****:** Not recommended primarily due to the tag burden associated with available EMG tags. Furthermore, the original study lacked EMG calibration data for Mountain Whitefish, so it is unclear whether calibration experiments with new larger EMG tags would even be applicable to the original study.

2. Repeat Mountain Whitefish study using accelerometer tags as an alternative to EMG tags as these could provide an easier surgical option with lower tag burdens and less handling. ***Drawbacks*****:** previous EMG data cannot be used and a shorter tag life could mean a less diverse set of natural conditions are sampled. That said, shorter tag life can be mitigated by decreasing tag pulse rate, which is expected to have a minimal effect on study precision and therefore sample sizes. **Suggestion:** recommended approach, assuming this sample size is attainable.

Any follow-up Mountain Whitefish study will require swim tunnel calibration experiments to ensure that the data collected from the tag can be converted to predict energetic expenditures. The number and types of calibration experiment required will depend on the approach used to predict energetic expenditures. All approaches should attempt to validate the threshold for active swimming as this was a key behavioural component in the Bull Trout model. A study sample size of 98-150 individuals would be required to produce a precision similar to that of the Bull Trout study.

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Appendices

Appendix A: Tagged Fish Metrics

Table A1. Characteristics associated with tagged Bull Trout. Missing information is indicated with a dash.

				Length (mm)		Weight (g)			Total	Baseline EMG (flow < 100 cms)	
Season	Tag ID	Tag Code	Sex	Fork	Total	Observed	Predicted	TBF Calibration	EMG Readings	n	1% Quartile
Fall 2008	3	13	Female	541	568	–	1,551	–	12,842	3,009	3
Fall 2008	5	15	Female	504	529	–	1,245	–	5,976	870	2
Fall 2008	6	16	Female	617	647	–	2,435	–	107,766	18,025	2
Fall 2008	9	21	Female	615	645	–	2,406	–	1,061	11	–
Fall 2008	11	23	Female	567	595	–	1,810	–	188,045	29,631	8
Fall 2008	12	24	Female	566	594	–	1,799	–	142,123	30,690	1
Fall 2008	21	40	Female	670	703	–	3,335	–	120,197	24,337	7
Fall 2008	22	42	Female	530	556	–	1,453	–	361	1	–
Fall 2008	23	43	Female	641	672	–	2,808	–	7,302	2,824	10
Fall 2008	24	44	Female	610	640	–	2,336	–	814	31	–
Fall 2008	26	48	Female	655	687	–	3,051	–	20,297	3,443	1
Fall 2008	29	55	Female	622	652	–	2,509	–	28,866	5,471	2
Fall 2008	30	57	Female	544	571	–	1,579	–	108,991	25,338	8
Fall 2008	32	59	Female	551	578	–	1,646	–	25,541	5,895	4
Fall 2008	2	12	Male	611	641	–	2,763	–	84,092	12,801	3
Fall 2008	4	14	Male	669	702	–	3,898	–	100,483	22,878	8
Fall 2008	7	19	Male	793	832	–	8,136	–	110	2	–
Fall 2008	8	20	Male	588	617	–	2,410	–	69,640	14,137	8
Fall 2008	10	22	Male	830	871	–	10,134	–	102,257	17,253	6
Fall 2008	13	25	Male	788	827	–	7,898	–	55,651	12,327	1
Fall 2008	14	26	Male	610	640	–	2,747	–	118,126	22,216	8
Fall 2008	15	29	Male	662	694	–	3,739	–	120,498	17,506	1
Fall 2008	16	32	Male	667	700	–	3,852	–	93,338	22,048	8
Fall 2008	17	33	Male	702	736	–	4,741	–	88,985	17,852	9
Fall 2008	18	35	Male	664	697	–	3,784	–	79,888	16,751	2
Fall 2008	19	36	Male	705	740	–	4,826	–	520	–	–
Fall 2008	20	39	Male	764	801	–	6,850	–	53,335	8,613	7
Fall 2008	25	47	Male	810	850	–	9,000	–	49,112	6,619	0
Fall 2008	27	49	Male	592	621	–	2,468	–	1,168	51	–
Fall 2008	28	52	Male	754	791	–	6,455	–	78,192	14,824	1
Fall 2008	31	58	Male	662	694	–	3,739	–	47,942	4,409	1
Fall 2008	33	60	Male	672	705	–	3,968	–	113,536	35,036	3
Fall 2009	51	30	Female	531	557	1,440	1,462	Yes	121,785	27,403	3
Fall 2009	52	31	Female	534	560	1,666	1,488	–	2,267	356	1
Fall 2009	55	17	Female	674	707	3,357	3,415	–	5,852	2,156	3
Fall 2009	56	46	Female	649	681	2,845	2,944	Yes	55,788	11,713	6
Fall 2009	62	56	Female	593	622	2,086	2,112	Yes	19,759	3,648	2
Fall 2009	65	90	Female	455	477	914	931	Yes	26,216	5,823	3
Fall 2009	66	41	Female	570	598	1,839	1,842	–	138	10	–
Fall 2009	73	85	Female	614	644	2,268	2,392	–	9,661	2,738	8
Fall 2009	74	87	Female	–	–	–	–	–	8,251	2,757	3
Fall 2009	75	97	Female	–	–	–	–	–	4,199	1,101	10

				Length (mm)		Weight (g)				Baseline EMG (flow < 100 cms)	
Season	**Tag ID**	**Tag Code**	**Sex**	**Fork**	**Total**	**Observed**	**Predicted**	**TBF Calibration**	**Total EMG Readings**	**n**	**1% Quartile**
Fall 2009	76	93	Female	567	595	1,864	1,810	–	3,129	705	2
Fall 2009	78	86	Female	668	701	3,490	3,296	Yes	180,619	29,897	2
Fall 2009	81	95	Female	531	557	1,395	1,462	–	1,211	364	9.63
Fall 2009	53	50	Male	578	606	1,789	2,272	–	19,486	5,084	9
Fall 2009	54	18	Male	484	508	1,452	1,300	–	7,014	753	2
Fall 2009	57	38	Male	554	581	1,721	1,970	–	3,393	1,109	7
Fall 2009	58	27	Male	675	708	4,663	4,039	–	71	8	–
Fall 2009	59	11	Male	564	592	2,241	2,090	–	162	23	–
Fall 2009	60	51	Male	437	458	1,012	984	–	190	19	–
Fall 2009	61	28	Male	609	639	2,352	2,730	–	36	4	–
Fall 2009	63	88	Male	488	512	1,523	1,332	–	182	32	–
Fall 2009	64	37	Male	624	655	2,628	2,985	–	9,290	1,932	2
Fall 2009	67	54	Male	549	576	2,370	1,912	–	122	22	–
Fall 2009	68	89	Male	482	506	1,095	1,285	–	3,919	290	2
Fall 2009	69	34	Male	668	701	3,768	3,875	Yes	175,710	35,896	4
Fall 2009	70	53	Male	471	494	1,334	1,204	Yes	107,865	25,983	8
Fall 2009	71	92	Male	467	490	1,269	1,176	Yes	51,889	14,811	2
Fall 2009	72	91	Male	455	477	914	1,095	Yes	126,475	26,067	3
Fall 2009	79	96	Male	714	749	5,667	5,091	–	85,358	5,812	3
Fall 2009	80	94	Male	513	538	1,595	1,545	Yes	119,907	24,550	2
Fall 2010	96	28	Female	532	558	–	1,471	–	36	4	–
Fall 2010	108	36	Female	548	575	–	1,617	–	–	–	–
Fall 2010	117	27	Female	522	548	–	1,386	–	2,015	1	–
Fall 2010	93	11	Male	505	530	–	1,473	–	–	–	–
Fall 2010	94	17	Male	560	587	–	2,041	–	18	–	–
Fall 2010	95	20	Male	720	755	–	5,276	Yes	304,345	5,021	10
Fall 2010	97	29	Male	715	750	–	5,121	–	1,920	217	10
Fall 2010	98	32	Male	760	797	–	6,689	–	1	1	–
Fall 2010	99	12	Male	515	540	–	1,563	–	1	–	–
Fall 2010	100	14	Male	435	456	–	972	–	1,386	300	10
Fall 2010	101	16	Male	490	514	–	1,348	–	1,083	241	6
Fall 2010	102	23	Male	755	792	–	6,494	–	871	1	–
Fall 2010	103	24	Male	545	572	–	1,868	–	9,999	268	2
Fall 2010	104	25	Male	805	844	–	8,737	–	251	–	–
Fall 2010	105	31	Male	486	510	–	1,316	–	12	1	–
Fall 2010	106	34	Male	617	647	–	2,863	–	3	1	–
Fall 2010	107	35	Male	605	635	–	2,666	–	5	–	–
Fall 2010	109	13	Male	565	593	–	2,103	–	–	–	–
Fall 2010	110	15	Male	595	624	–	2,513	–	17	–	–
Fall 2010	111	19	Male	580	608	–	2,299	–	199	9	–
Fall 2010	112	33	Male	467	490	–	1,176	–	2	–	–
Fall 2010	113	18	Male	520	545	–	1,610	–	193	3	–
Fall 2010	114	21	Male	510	535	–	1,517	–	797	2	–
Fall 2010	115	22	Male	570	598	–	2,166	Yes	667,667	30,922	2
Fall 2010	116	26	Male	780	818	–	7,532	Yes	49,416	9	–
Fall 2010	118	30	Male	700	734	–	4,685	Yes	273,042	23,113	2

Table A2. Characteristics associated with tagged Mountain Whitefish. Missing information is indicated with a dash.

				Length (mm)		Weight (g)			Total EMG	Baseline EMG (flow < 100 cms)	
Season	Tag ID	Tag Code	Sex	Fork	Total	Observed	Predicted	TBF Calibration	Readings	n	1 % Quartile
Fall 2008	38	65	Unknown	307	322	–	450	–	46,740	6,784	0.0
Fall 2008	40	68	Unknown	405	425	–	788	–	37,980	4,460	7.0
Fall 2008	43	73	Unknown	305	320	–	444	–	1,038	71	–
Fall 2008	44	74	Unknown	411	431	–	816	–	29,894	879	7.0
Fall 2008	45	75	Unknown	348	365	–	569	–	196,278	12,197	3.0
Fall 2008	34	61	Female	372	390	–	652	–	15,363	2,107	2.0
Fall 2008	35	62	Female	340	357	–	543	–	54,147	7,664	9.0
Fall 2008	36	63	Female	314	329	–	468	–	109,599	19,147	8.0
Fall 2008	37	64	Female	375	393	–	664	–	4,288	702	1.0
Fall 2008	39	66	Female	375	393	–	664	–	793	6	–
Fall 2008	41	71	Female	330	346	–	513	–	19,113	2,810	10.0
Fall 2008	46	76	Female	310	325	–	457	–	48,565	2,005	1.0
Fall 2008	47	77	Female	395	414	–	744	–	16,646	1,778	1.0
Fall 2008	49	83	Female	315	330	–	471	–	8,430	799	5.0
Fall 2008	42	72	Male	405	425	–	788	–	11,474	1,775	11.0
Fall 2008	48	82	Male	311	326	–	460	–	2,865	1	–
Fall 2009	82	67	Unknown	307	322	275	450	–	16,615	5,709	14.0
Fall 2009	83	103	Unknown	314	329	317	468	–	64	11	–
Fall 2009	86	81	Unknown	384	403	817	699	–	6,722	2,908	11.0
Fall 2009	87	100	Unknown	344	361	649	556	–	1,598	558	3.0
Fall 2009	88	102	Unknown	408	428	768	802	–	15,509	2,226	6.0
Fall 2009	89	69	Unknown	432	453	1,102	920	–	19,566	6,442	1.0
Fall 2009	90	84	Unknown	352	369	542	582	–	11,070	4,219	2.0
Fall 2009	91	80	Unknown	352	369	626	582	–	9,115	3,079	2.0
Fall 2009	92	101	Unknown	384	403	824	699	–	8,215	2,295	3.0
Fall 2009	77	79	Female	358	376	605	602	–	4,567	306	1.0
Fall 2009	84	78	Female	366	384	709	630	–	445	62	–
Fall 2009	85	70	Female	381	400	629	687	–	1,744	4	–
Fall 2010	119	42	Female	420	441	–	859	–	10,244	1,240	2.0
Fall 2010	120	47	Female	420	441	–	859	–	1	–	–
Fall 2010	121	37	Female	440	462	–	963	–	9,872	556	3.0

Appendix B: Standardized Weights

Table B1. AICc model ranking results for proposed Bull Trout standardized weight equations fit to log-transformed observed wet weights.

Model		K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
(3)	Sex-specific intercept, same slope	4	-35.3	0	0.82	0.82	22.52
(4)	Sex-specific intercept, separate slopes	5	-32.31	2.98	0.18	1	22.52
(2)	Zero intercept, separate slopes	3	20.75	56.05	0	1	-6.88
(1)	Zero intercept, same slope	3	56.29	91.59	0	1	-24.65

Table B2. AICc model ranking results for proposed Mountain Whitefish standardized weight equations fit to log-transformed observed wet weights.

Model		K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
(2)	Non-zero intercept, separate slopes	3	-2.27	0	1	1	5.64
(1)	Zero intercept, same slope	2	10.51	12.78	0	1	-2.59

Appendix C: Predicting Tail Beat Frequency from SEMG Readings

Approach 1: Individual Calibration Equations

Taylor et al. (2014) calibrated the standardized EMG (SEMG) response of subset of tagged Bull Trout (Table A1). We developed two calibration approaches, to predict tail beat frequency (TBF) from SEMG readings (see Section 3.5 for a description). As suggested by Brown et al. (2007), the first approach developed individual calibration equations for the 14 calibrated individuals (Figure C1), which would only make 13 individuals available for the *in situ* portion of the study due to lack of data (see Table A1). Linear mixed effect models were using the `nmle` package (Pinheiro et al. 2018) in the R computing environment (R Core Team, 2018). All models used log transformed SEMG readings, with random effects to describe among-tag differences, but with separate slopes for each individual. Because our data included repeat observations, an auto-regressive error structure was used (i.e., AR(1)) was used because individual SEMG observations closer together in time were expected to be more similar to each other than those separately widely in time. This structure was determined by preliminary inspection of the SEMG to TBF calibration results using autocorrelational and partial-autocorrelational plots, as well as by inspecting autocorrelation of residuals from initial model fitting. In all cases, SEMG values were log transformed before being regressed against observed TBF.

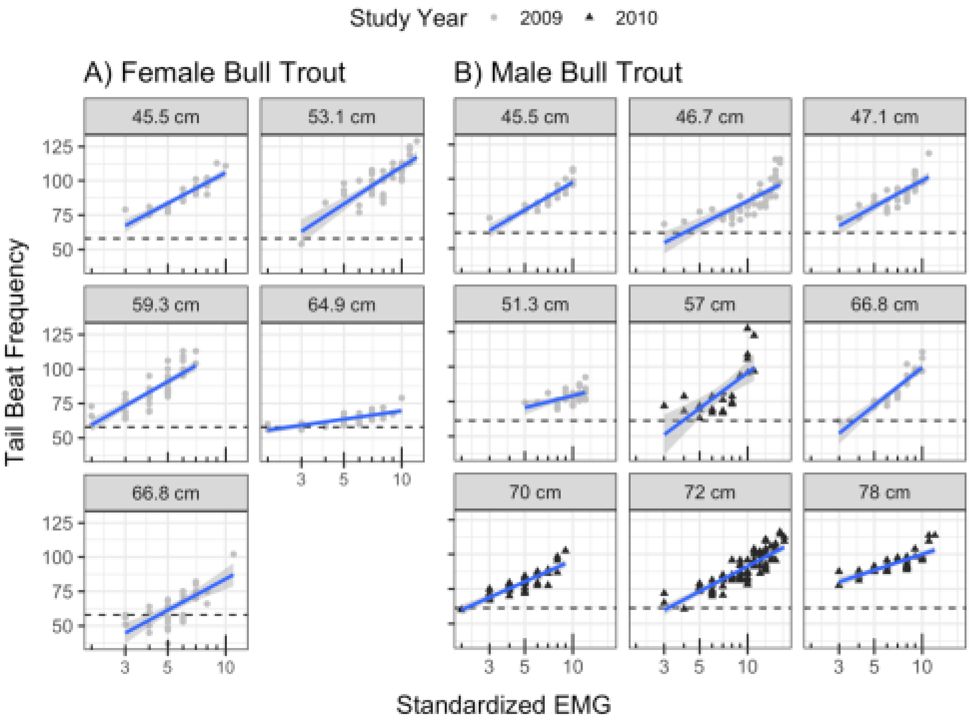


Figure C1. **Standardized EMG (SEMG) to tail beat frequency relationships for individually calibrated Bull Trout.** Solid lines indicate simple linear regression line against log transformed SEMG readings, shading indicated 95% confidence region for the regression line. Horizontal dashed line indicates a tail beat frequency of 58, which was assumed to be the cut-off for active swimming. Fork length is indicated in the panel strip text.

Approach 2: Universal Calibration Equation

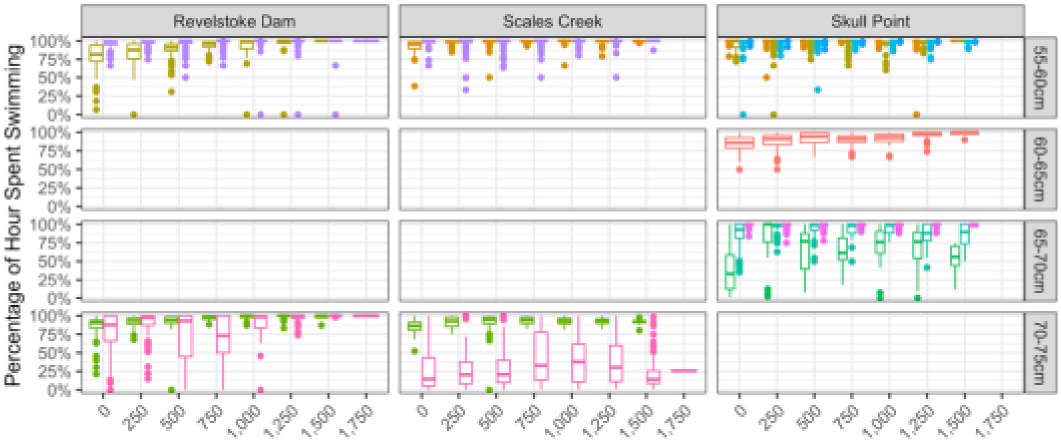
The second approach attempted to build a universal calibration equation using AICc model ranking to select between competing models (Burnham and Anderson 2002). 12 candidate models were considered in addition to a null, intercept only, model (Table C1). Sex-specific and sex neutral models were considered in addition to body length (and potential two-way interactions). All SEMG values were log transformed. The all supported models (i.e., ΔAICc values from 0-7) were sex-specific, implying differing swim performance. The top supported model had most of the support (i.e., AICc weight over 50%) and considered sex-specific SEMG responses as well as sex-specific body size effects. The top model was then used as the universal calibration model when predicting TBF for male and female Bull Trout study population (Table A1).

Table C1. AICc model ranking results for the candidate universal calibration equations for male and female Bull trout.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
SEMG + Sex + Length + SEMG:Sex + Sex:Length	9	4268.2	0.0	0.58	0.58	-2124.9
SEMG + Sex + Length + SEMG:Sex + SEMG:Length + Sex:Length	10	4270.1	2.0	0.22	0.80	-2124.9
SEMG + Sex + SEMG:Sex	7	4271.1	3.0	0.13	0.93	-2128.5
SEMG + Sex + Length + SEMG:Sex	8	4273.2	5.0	0.05	0.97	-2128.5
SEMG + Sex + Length + SEMG:Sex + SEMG:Length	9	4275.2	7.0	0.02	0.99	-2128.4
SEMG + Sex + Length + Sex:Length	8	4278.8	10.6	0.00	1.00	-2131.3
SEMG + Sex + Length + SEMG:Length + Sex:Length	9	4280.7	12.5	0.00	1.00	-2131.2
SEMG	5	4280.8	12.6	0.00	1.00	-2135.3
SEMG + Sex	6	4280.9	12.7	0.00	1.00	-2134.4
SEMG + Length + SEMG:Length	7	4281.9	13.7	0.00	1.00	-2133.8
SEMG + Length	6	4282.8	14.6	0.00	1.00	-2135.3
SEMG + Sex + Length	7	4282.9	14.7	0.00	1.00	-2134.4
SEMG + Sex + Length + SEMG:Length	8	4284.8	16.6	0.00	1.00	-2134.3
Null	4	4351.9	83.7	0.00	1.00	-2171.9

Appendix D: Proportion of Hour Spent Swimming

A) Female Bull Trout



B) Male Bull Trout

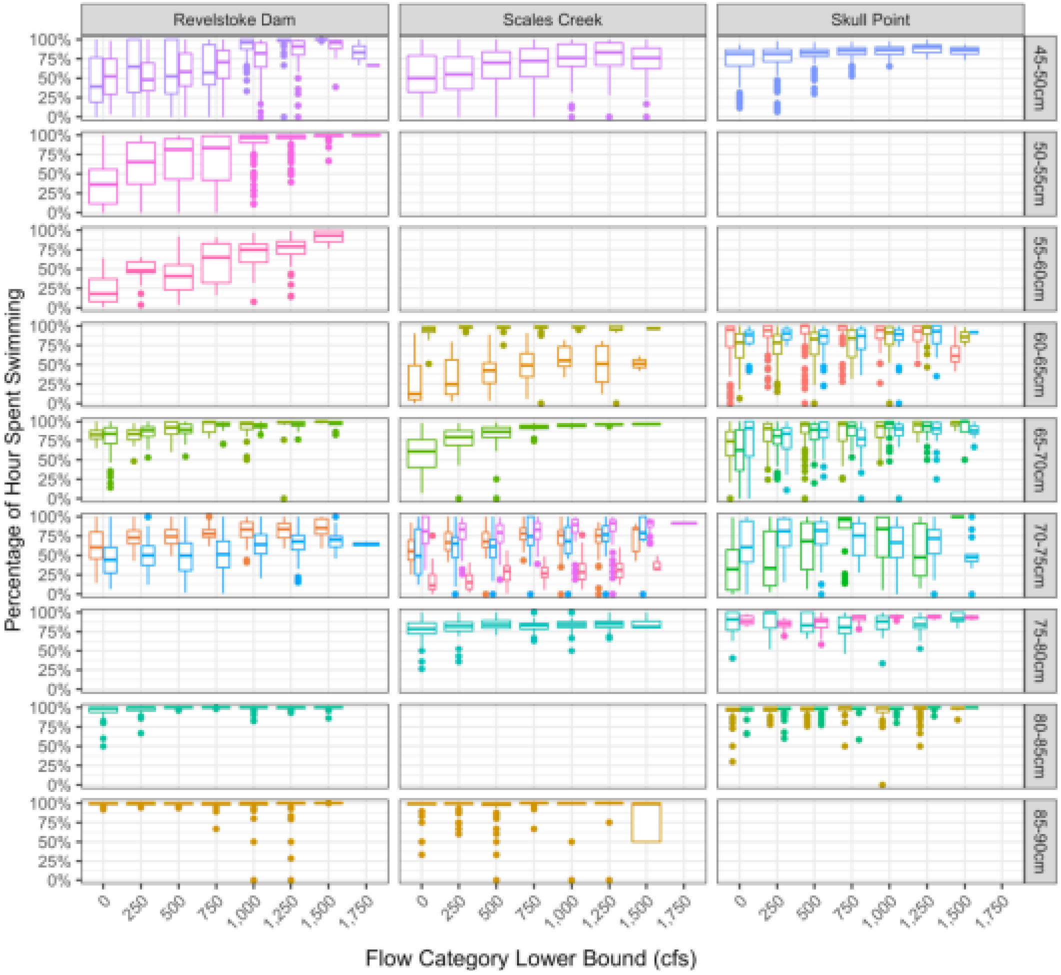


Figure D1. **Distribution of the percentage of an hour spent swimming for A) female and B) male Bull Trout under varying flow conditions.** Color indicates different individuals. Panels text indicate either receiver location (see Figure 1) or total body length.

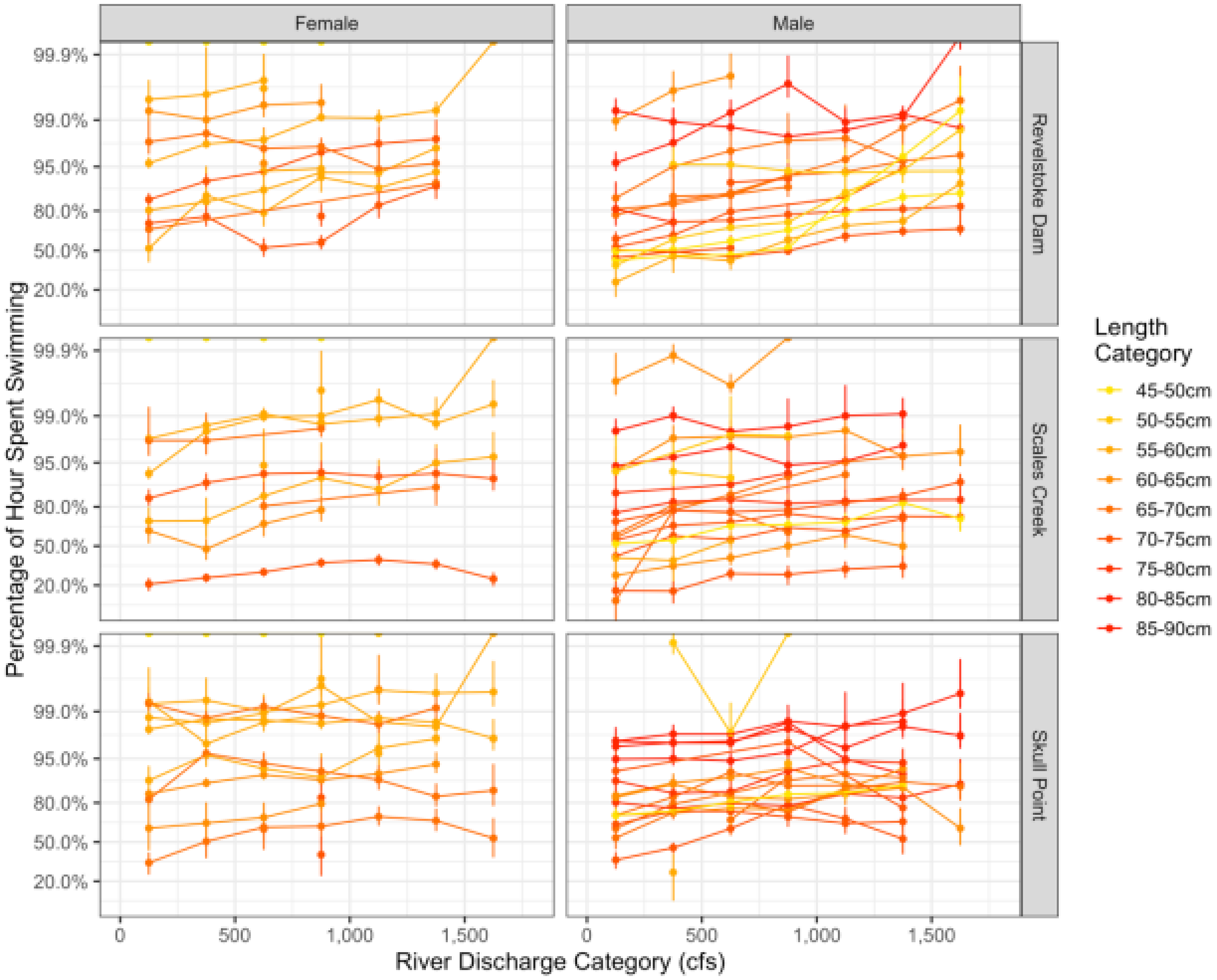


Figure D2. **Percentage of hour spent swimming for female (left) and male (right) Bull Trout under varying river discharge conditions at the three receiver locations (rows; Table 1).** Individual responses are connected by lines, and colors indicate length category. Panels text indicate either receiver location (see Figure 1) and sex. Bars indicate 95% confidence interval for the mean response of individual observations. A logit transformation has been applied to the y-axis scaling.

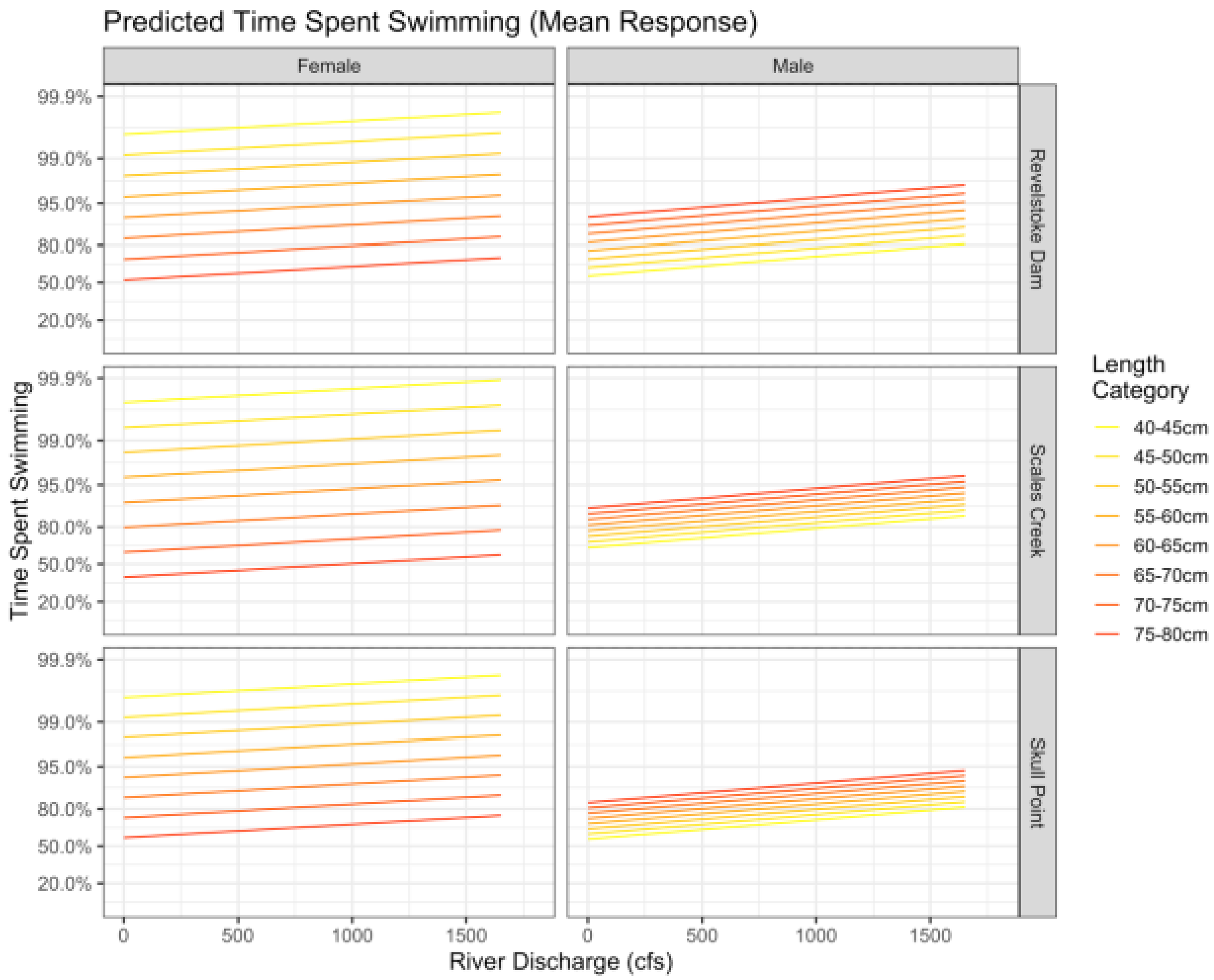


Figure D3. **Predicted mean percentage (logit scale) of an hour spent swimming under average temperature conditions based on the top supported model (Table D3).**

Table D1. **AICc model ranking results for predicting the proportion of an hour that Bull Trout spend swimming as a function of a single environmental predictor.**

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
River Discharge (cms)	5	50428.9	0.0	1.00	1.00	-25209.4
Receiver Location	6	50857.2	428.3	0.00	1.00	-25422.6
Sex	5	50873.0	444.1	0.00	1.00	-25431.5
Water Temperature (°C)	5	50873.4	444.6	0.00	1.00	-25431.7
Null (Intercept only)	4	50875.1	446.2	0.00	1.00	-25433.6
Size	5	50876.1	447.2	0.00	1.00	-25433.1

Table D2. **AICc model ranking results for predicting the proportion of an hour that Bull Trout spend swimming as a function of a secondary environmental predictor in combination with discharge for models that either pool across sex or model sex-specific responses. Flow = River Discharge (cms); Loc = Receiver Location (see Figure 1); Temp = Water Temperature (°C)**

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Pooling Across Sex						
Flow*Loc	9	50393.8	0.0	0.80	0.80	-25187.9
Flow*Size	7	50396.6	2.8	0.20	1.00	-25191.3
Flow + Loc	7	50408.2	14.4	0.00	1.00	-25197.1
Flow*Temp	7	50425.0	31.2	0.00	1.00	-25205.5
Flow	5	50428.9	35.0	0.00	1.00	-25209.4
Flow + Temp	7	50855.4	461.6	0.00	1.00	-25420.7
Flow + Size	7	50858.0	464.2	0.00	1.00	-25422.0
Sex-specific						
(Flow + Temp)*Sex	13	50317.8	0.0	1.00	1.00	-25145.9
(Flow*Loc)*Sex	15	50354.8	37.0	0.00	1.00	-25162.4
(Flow + Size)*Sex	13	50358.5	40.7	0.00	1.00	-25166.3
(Flow*Size)*Sex	11	50364.5	46.7	0.00	1.00	-25171.2
(Flow + Loc)*Sex	11	50364.5	46.7	0.00	1.00	-25171.3
(Flow*Temp)*Sex	11	50369.1	51.3	0.00	1.00	-25173.6
Flow	7	50416.2	98.4	0.00	1.00	-25201.1

Table D3. **AICc model ranking results for predicting the proportion of an hour that Bull Trout spend swimming as a function of a secondary environmental predictor in combination with sex- and area-specific discharge relationship. Flow = River Discharge (cms); Loc = Receiver Location (see Figure 1); Temp = Water Temperature (°C). Baseline model was the top sex-specific model from the previous ranking exercise (Table D2).**

Sex-specific Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
baseline + Size*Loc + Size*Temp	21	50199.0	0.0	1.00	1.00	-25078.5
baseline + Temp*Loc + Size*Temp	21	50222.6	23.6	0.00	1.00	-25090.3
baseline + Size*Loc + Temp	19	50252.4	53.4	0.00	1.00	-25107.2
baseline + Size*Loc	19	50252.4	53.4	0.00	1.00	-25107.2
baseline + Temp*Loc + Size	19	50285.4	86.4	0.00	1.00	-25123.7
baseline + Temp*Loc	17	50291.3	92.3	0.00	1.00	-25128.7
baseline + Size	15	50312.2	113.2	0.00	1.00	-25141.1
baseline + Temp	13	50317.8	118.8	0.00	1.00	-25145.9
baseline	13	50317.8	118.8	0.00	1.00	-25145.9

Appendix E: Active Hourly Swim Speeds

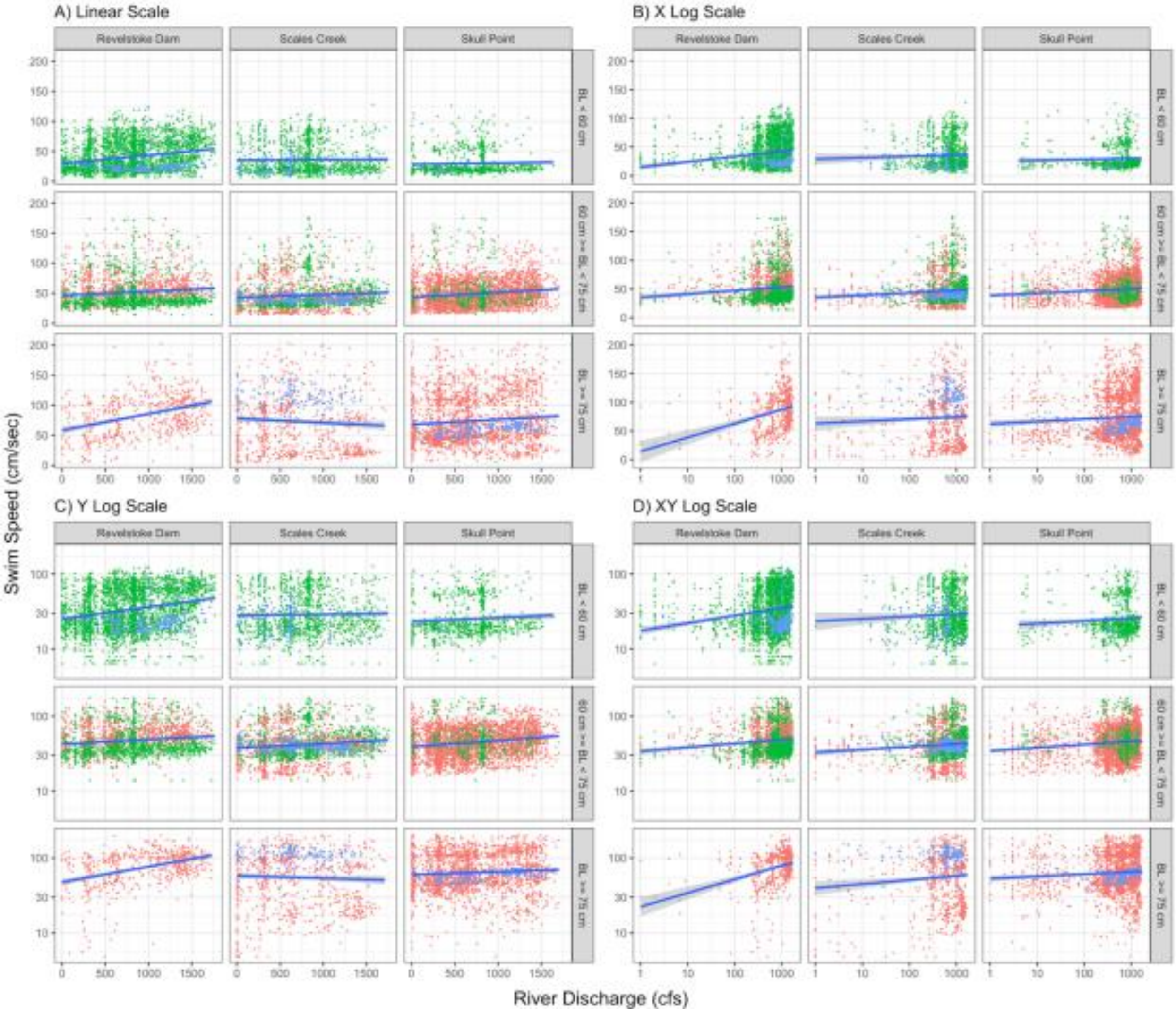


Figure E1. Observed male Bull Trout swim speeds under different river discharge conditions using A) no transformation, B) log transformed discharge, C) log transformed swim speed, and D) log transformed discharge and swim speed.

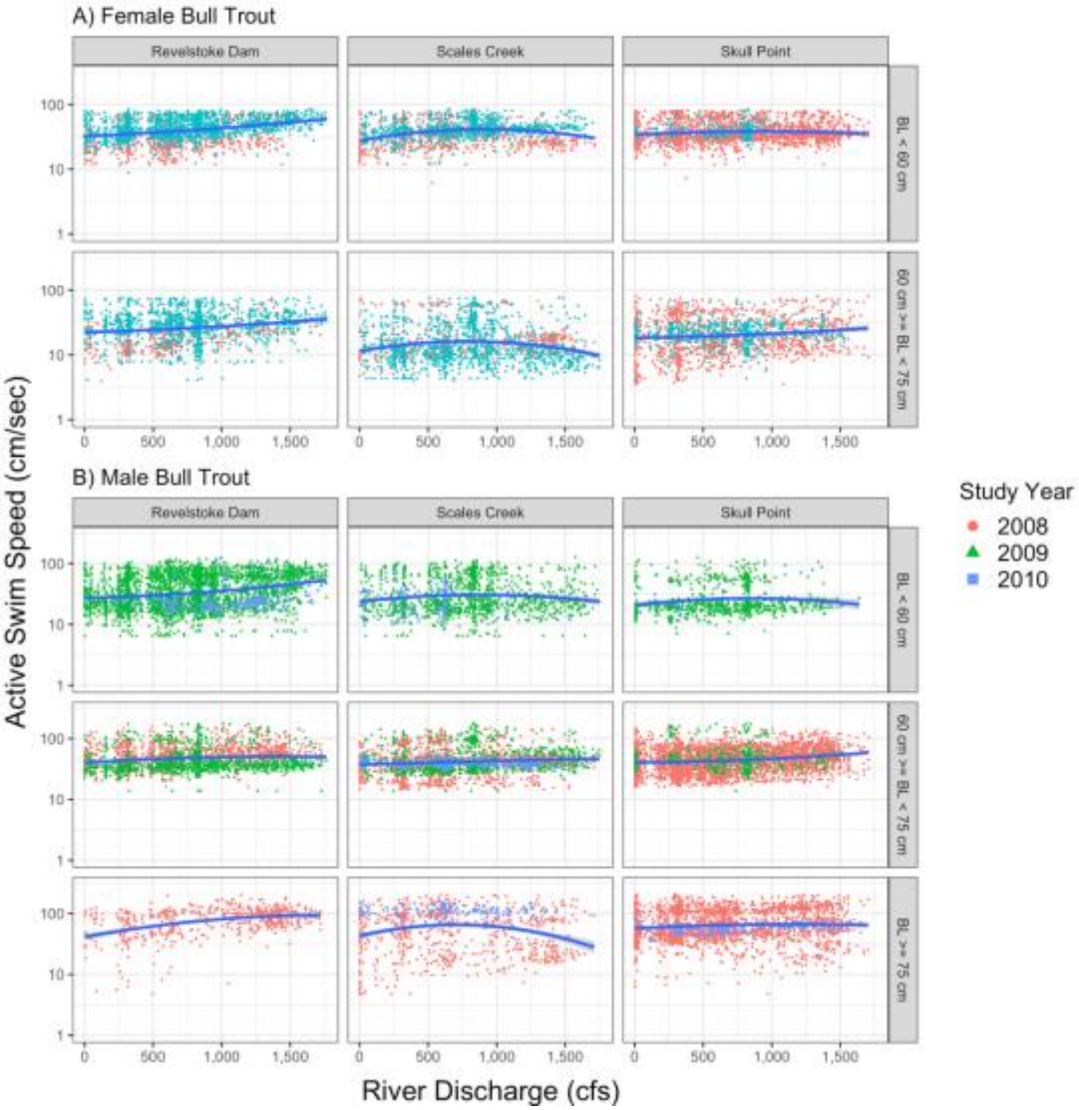


Figure E2. Female (A) and male (B) Bull Trout swim speeds by river discharge, receiver location (Figure 1) and body length category. Regression line is from a second order polynomial regression.

Table E1. **AICc model ranking results for predicting Bull Trout active hourly swim speed as a function of the baseline model combined with an additional location specific predictors. Light = Dawn, Daylight, Dusk, Night; DOY = Day of Year; Size = Body length (mm); Temp = Water Temperature (°C); Year = Study year.**

Location-Specific Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Baseline + Light	27	13742.5	0.0	1	1	-6844.2
Baseline + Temp	21	14018.7	276.2	0	1	-6988.3
Baseline + Size	24	14077.0	334.5	0	1	-7014.5
Baseline + DOY	21	14087.0	344.6	0	1	-7022.5
Baseline + Year	21	14296.2	553.8	0	1	-7127.1
Baseline	18	14318.8	576.3	0	1	-7141.4

Table E2. **AICc model ranking results for predicting Bull Trout active hourly swim speed as a function tertiary effects based on top model from the previous step (Table E1). Light = Dawn, Daylight, Dusk, Night; DOY = Day of Year; Size = Body length (mm); Temp = Water Temperature (°C).**

Location-Specific Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Baseline + Light + Temp*DOY	36	13357.1	0.0	1	1	-6642.5
Baseline + Light + Temp	30	13438.7	81.6	0	1	-6689.3
Baseline + Light + DOY	30	13490.6	133.5	0	1	-6715.3
Baseline + Light + Size	33	13504.3	147.2	0	1	-6719.1
Baseline + Light + Year	30	13717.7	360.6	0	1	-6828.8
Baseline + Light	27	13742.5	385.4	0	1	-6844.2

Appendix F: Site Selection

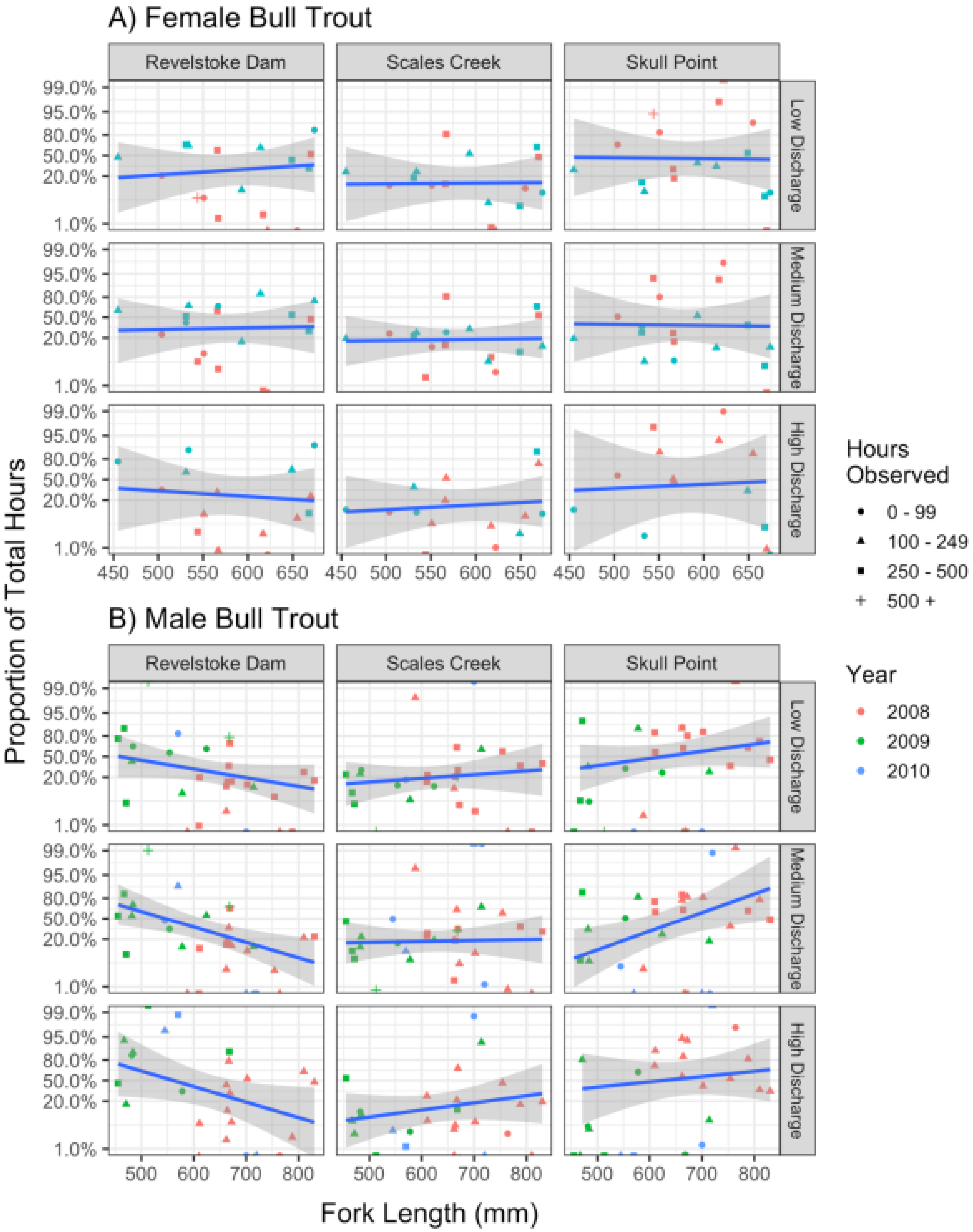


Figure F1. **Percentage of hours spent at the three receiver locations (Figure 1) for female (A) and male (B) Bull Trout under low (<500 cms) medium (500-1000 cms) and high (> 1000 cms) flows, by size.**

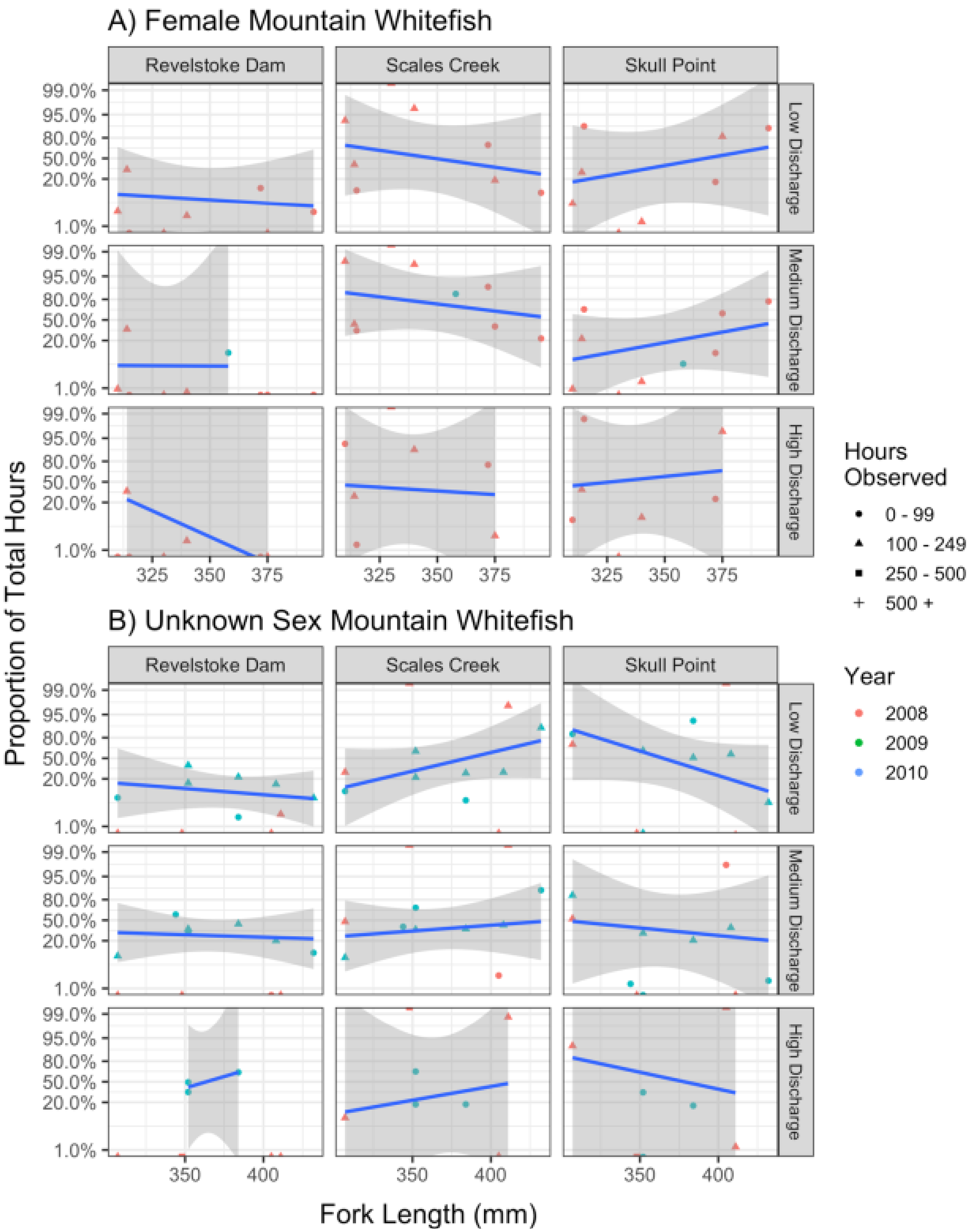


Figure F2. **Percentage of hours spent at the three receiver locations (Figure 1) for female (A) and unknown sex (B) Mountain Whitefish under low (<500 cms) medium (500-1000 cms) and high (> 1000 cms) flows, by size.**

Appendix G: Example Bioenergetics Comparison

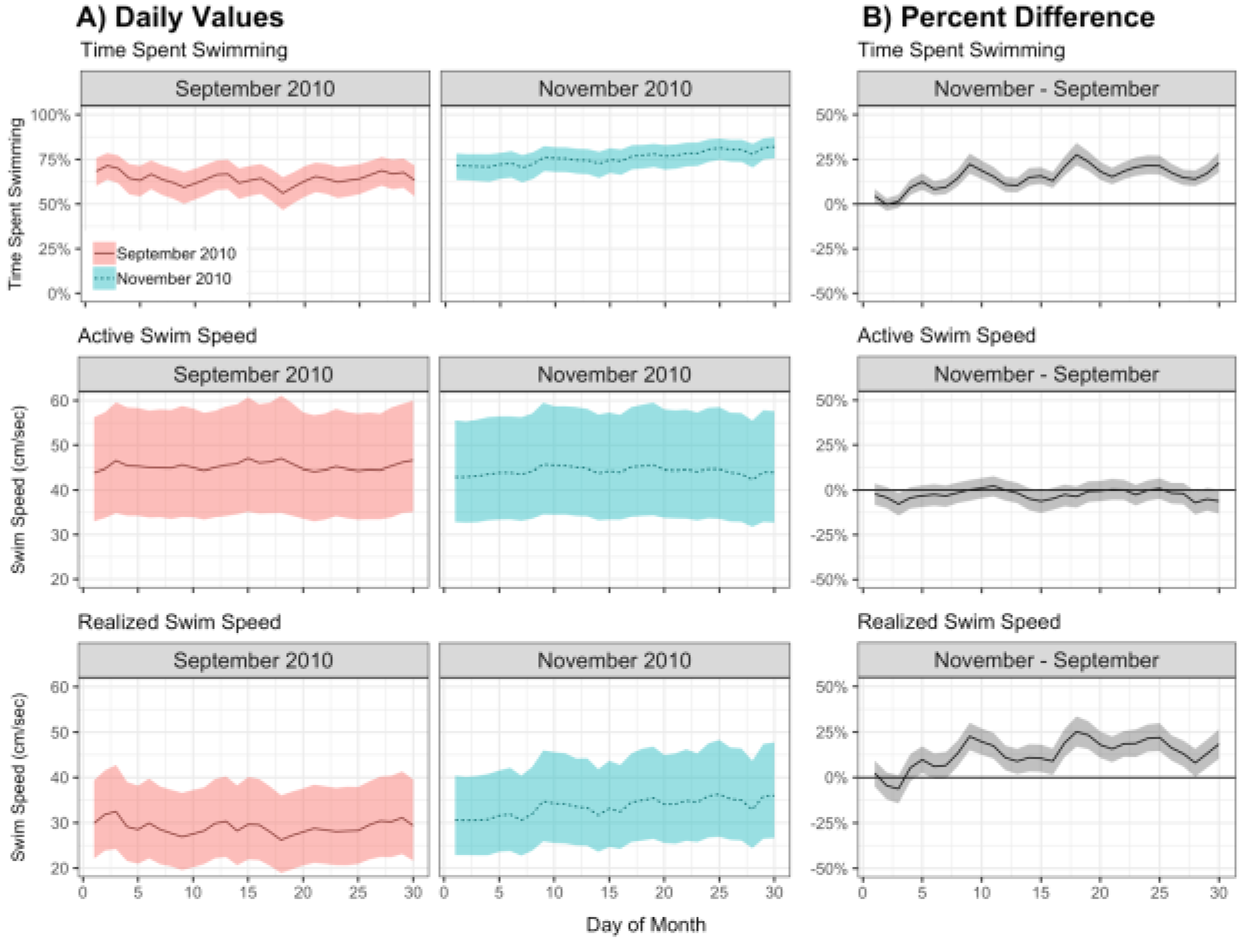


Figure G1. **Comparison of activity metabolism components (i.e., time spent swimming, active swim speed and realized swim speed) on a daily basis for the September and November 2010 hydrological regimes (A) and the percent differences (B).** The proportion of the hour spent swimming (top panel) and the active speed when swimming (middle panel) are combined to produce the realized hourly speed (bottom panel). Solid lines indicates the daily average and the shading indicates the 2.5 and 97.5 percentiles from 1,000 simulations.

Appendix H: High Discharge Extrapolations

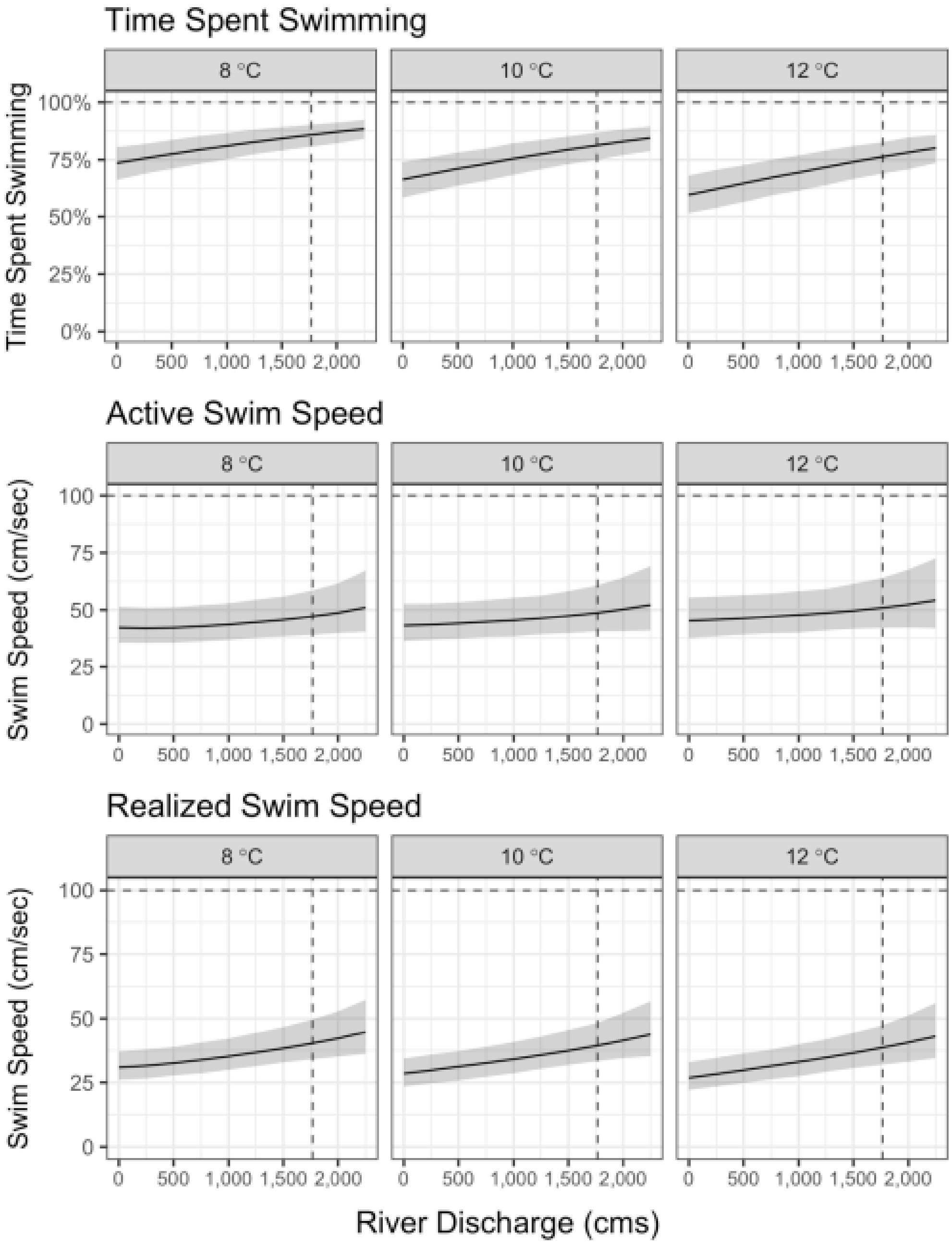


Figure H1. **Predicted Comparison of activity metabolism components (i.e., time spent swimming, active swim speed and realized swim speed) across a variety of river discharge and temperature (panel columns) values.** The proportion of the hour spent swimming (top panel) and the active speed when swimming (middle panel) are combined to produce the realized hourly speed (bottom panel). Solid lines indicates average and the shading indicates the 2.5 and 97.5 percentiles from 1,000 simulations. Vertical dashed line indicates highest observed river discharge conditions (i.e., 1765 cms), with predictions to the right representing extrapolations. Horizontal dashed lines indicate either maximum possible time spent swimming or the lower bound for the observed maximum swim speeds (see Figure 4).

Appendix I: Pre-Post REV 5 Comparison

Daily energetics before and after the addition of fifth turbine unit in Revelstoke Dam (i.e., REV 5) was compared by running the energetics model on hourly hydrology data from select days in both periods across all four seasons (Table I 1).

Hourly temperature data was only available from 2008 onwards, 2008 to Dec 21, 2010 was used as the before period (i.e., pre REV 5), and 2011 to 2018 was used as the after period (i.e., post REV 5). Within the full time span (i.e., 2008-2018) water input into the system and as a result and water management was not identical throughout the period or within seasons (Figure I1). This made direct comparisons between the pre/post Rev 5 periods by season problematic as environmental and water management differences were also confounded with changes to the turbine setup. As such, comparisons using all the data from each period would be as much a test of general water management changes over time as it would be an assessment of the effect of the REV5 addition on bull trout energetics.

Scenarios from the CLBMON-17 project, which considered flow and reservoir level scenarios separately (Table I2), were also considered as guidelines for selecting applicable days for the comparison, but were found not to be fully compatible with observed reservoir operations across all four seasons (Figure I2). As such, any pre/post REV 5 comparison across all seasons based on these scenarios would not be possible as the energetics model requires real operational data summarized on an hourly time step and some seasons had few or no applicable days that matching the CLBMON-17 comparison conditions (i.e., intersection between the vertical and horizontal lines; Figure I2).

To deal with the problem that flow and reservoir level often relate to conditions and water management decisions applicable ranges corresponding “typical” common base and peak flow conditions within each season were determined. For base conditions, the range of conditions around the seasonal median was determined as smallest region captured by the 25th and 75th percentiles across period (i.e., largest pre/post 25th percentile and smallest pre/post 75th percentile) (Figure I3). This was determined separately for reservoir level and average daily discharge. Together these metrics define a region representing seasonal “median conditions” where days could be selected in order compared energetic differences associated with turbine configurations (highlighted area; Figure I4a). Within the sampling there were generally small differences that may be reflective of some seasonal water management differences between periods as well as natural variation (Table I3).

For peak conditions, days with peak hourly flow in the 95th percentile within each period were chosen (Figure I4b). This typically featured higher peak flows for Post REV 5 turbine configuration ((Table I3).

Table I 1. Date range associated each seasonal designation.

Season	Date Start	Date End
Spring	March 19	June 20
Summer	June 21	September 22
Fall	September 23	December 21
Winter	December 21	March 18 (following year)

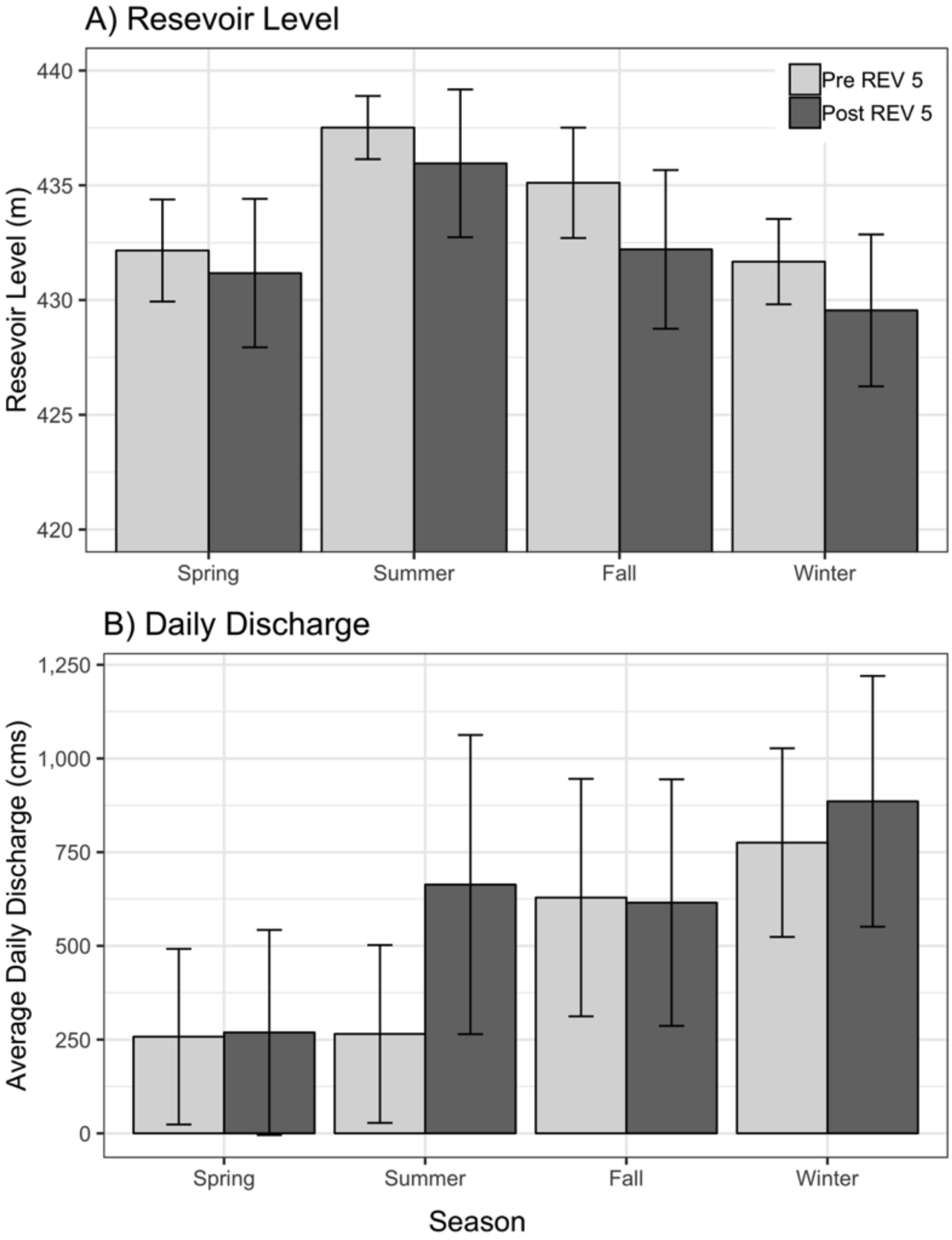


Figure I1. Average reservoir level (A) and daily discharge (B) across four seasons in the pre/post REV 5 periods. Error bars indicate the standard deviation.

Table I2. CLBMON-17 suggested base and peak flow scenarios.

Scenario	Rev Output (m^3/s)	Jordan Flow (m^3/s)	Illecillewaet Flow (m^3/s)	ALR Level (m)
Base #1 – Low	8.5	22	49	427.3
Base #2 – Low	142	22	49	427.3
Base #3 – Low	296	22	49	427.3
Peak #1 – Low	1603	22	49	427.3
Peak #1 – Low	2057	22	49	427.3
Base #1 – High	8.5	22	49	437.1
Base #2 – High	142	22	49	437.1
Base #3 – High	296	22	49	437.1
Peak #1 – High	1603	22	49	437.1
Peak #1 – High	2057	22	49	437.1

Figure I2. Revelstoke Dam average daily discharge with CLBMON-17 flow scenarios (horizontal lines; blue = base conditions, orange = peak conditions) and Arrow Lakes Reservoir level (horizontal lines).

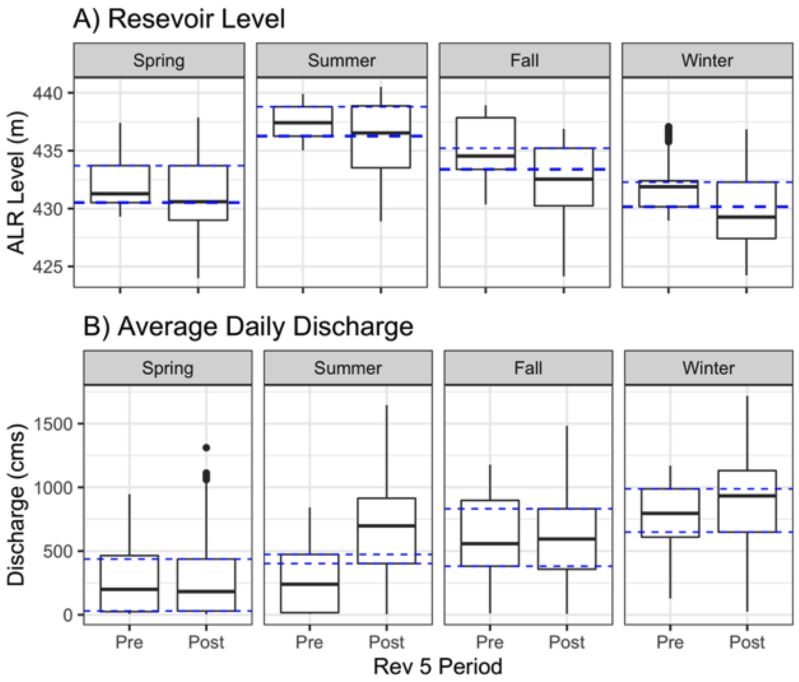


Figure I3. Box plot of season specific daily reservoir (A) and average daily discharge (B) in the pre and post REV 5 periods. Horizontal dashed lines indicate the maximum of the lower 25th percentile and the minimum of the 75th percentile across the pre/post periods.

Table I3. Sample size available, and the corresponding summaries of discharge and Arrow Lake Reservoir elevations for the proposed base and peak conditions comparisons (Figure I4).

	Season	Days Available		Years Available		Daily Discharge (cms)				Peak Discharge (cms)		ALR Level (m)
						Inter Quartile Range		Average				
		Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	
Base Conditions	Spring	67	101	3	7	30 - 429	32 - 430	215	212	753	1,374	429 - 432
	Summer	15	14	3	5	419 - 474	402 - 471	442	442	1,178	1,130	435 - 438
	Fall	41	67	2	3	386 - 740	383 - 828	520	659	1,212	1,132	430 - 434
	Winter	45	9	3	3	662 - 984	649 - 977	803	868	1,219	1,425	427 - 431
Peak Conditions	Spring	28	66	2	5	611 - 830	542-924	725	763	1,148	1,452	424 - 434
	Summer	29	67	2	4	586 - 684	1365-1593	649	1435	1,154	1,983	429 - 440
	Fall	27	64	2	4	1133-1174	1011-1263	1137	1134	1,188	1,820	424 - 436
	Winter	26	69	3	4	1029-1146	1257-1558	1029	1146	1,176	1,804	424 - 436

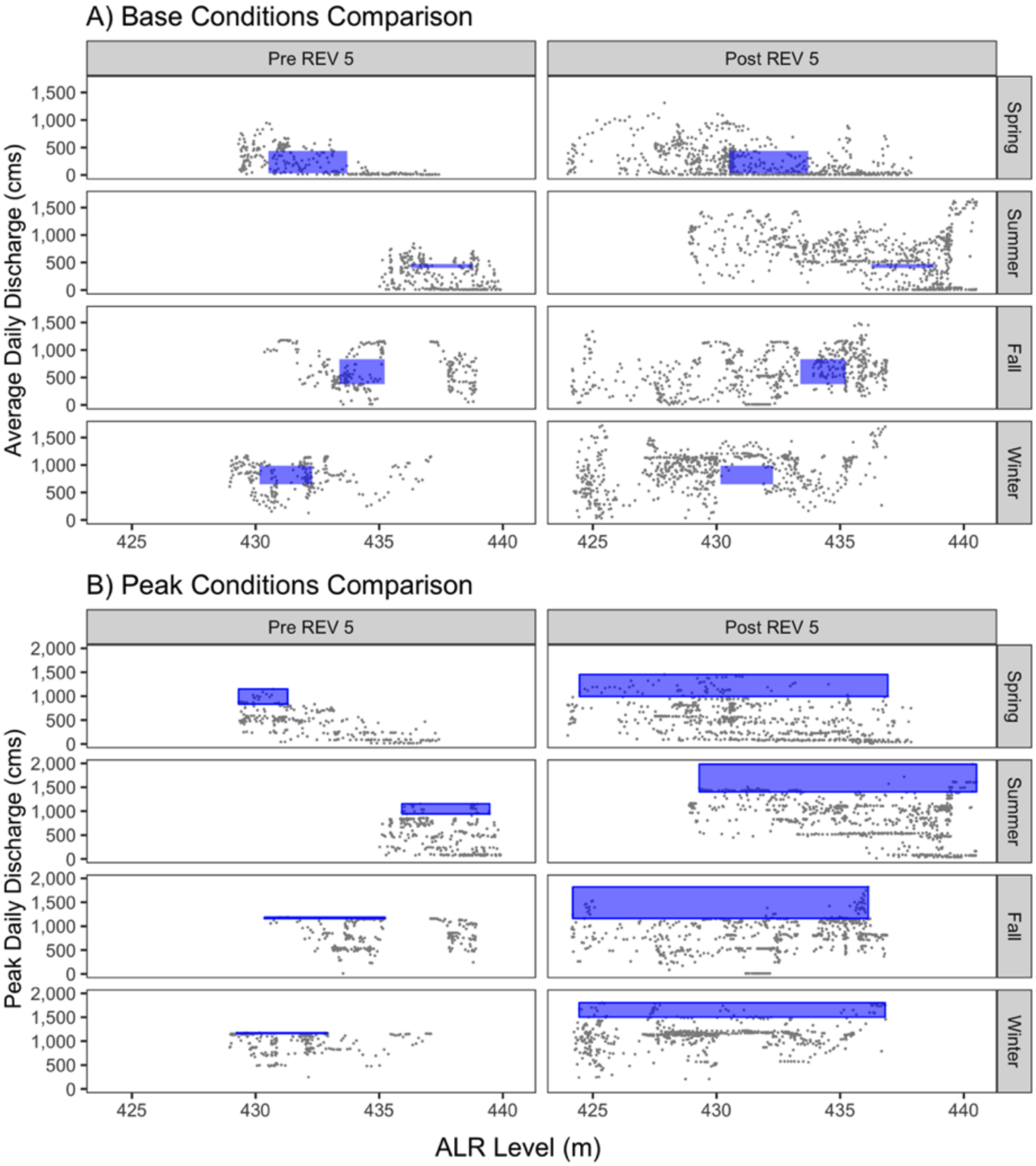


Figure I4. **2-way scatter plot of Revelstoke Dam discharge and Arrow Lakes Reservoir level with highlighting indicating proposed sampling region for base conditions (A) and peak conditions (B).**

Appendix J: Mountain Whitefish Feasibility Assessment

An energetics model predicting respiration metabolism associated with novel hydrological regimes was successfully built for Bull Trout. However, an energetics model could not be built for Mountain Whitefish due to a number of missing components from the field study. The most critical component missing from the field study was the lack of calibration experiments required to convert the electromyogram (EMG) signal to tail fin beat frequency (TBF). The critical calibration experiment that was missing would have allowed tail beat frequency to be used to predict swim speed (SS). The Bull Trout energetic model relied on a TBF to SS relationship derived for Sockeye Salmon (Brett 1995), which had been used before for other Bull Trout studies (e.g., Taylor et al. 2014). While Bull Trout and Sockeye Salmon (both subfamily Salmoninae) have the classic robust salmonid body shape, Mountain Whitefish are more distantly related (subfamily Coregoninae), are more slender, elongate, and smaller-bodied (Scott and Crossman, 1973), and therefore may not follow the Brett (1995) relationship. This made it problematic to predict Mountain Whitefish swim speed, which is a critical input variable for computing the active metabolic component of respiration. Given that the energetic models were intended to assess the energetic impact of changes in hydrology regimes, this was a major shortcoming.

A secondary drawback of the original investigation was the partial sexing of sampled Mountain Whitefish. Nearly half (i.e., 45%) of samples were not sexed, and the majority of sexed individuals were female (Table A2). The Bull Trout investigation found that females exhibited different swim behaviours than males during the study period. The study period also overlapped with Bull Trout spawning period, and it was hypothesized that differences in post-spawn behaviour were responsible for the observed differences. Similar to Bull Trout, the Mountain Whitefish spawning period occurs in late fall and likely coincided with the telemetry studies (Roberge et al. 2002). Post-spawning female Mountain Whitefish swimming behaviour and energetics may have differed from male behaviour (as it did with Bull Trout). Given that in the Bull Trout studies male behaviour was used to represent more “typical” swimming patterns, the almost complete lack of confirmed male Mountain Whitefish represents another significant stumbling block.

Finally, Mountain Whitefish are purported to be a species that are sensitive to capture (Taylor et al. 2011), and while radio-tagging of Mountain Whitefish has been successful under certain conditions (e.g., Hildebrand 2009; Table J1), the invasive EMG tagging procedure may have been stressful resulting in a low success rate. This was supported to some degree by the CLBMON-18 EMG studies where only 19 of 31 (62%) of released Mountain Whitefish produced useful information (Taylor et al. 2012). That said, nearly all of the released Mountain Whitefish were detected at some point in the study (Table A2). It is unclear whether individuals with fewer detections had left the detection area or expressed post-tagging effects such as mortality.

Potential Methodologies

Moving forward, there are a number of available methodologies for estimating Mountain Whitefish energy expenditure in the natural environment, including the use of heart rate monitors, doubly-labelled methods, and tagging methodologies such as EMG or accelerometer tags. Of these options, the EMG and accelerometer tag approaches appear to be the most appropriate for aquatic species, as the doubly-labelled water method has limited applicability in fish due to water flux (Nagy and Costa, 1980; Speakman 1997), and heart rate methods are problematic due to variable cardiac stroke volume in fishes (Thorarensen et al., 1996).

This leaves either attempting a second EMG study on Mountain Whitefish, with the potential to reuse some of the previously collected data, or a switch to accelerometer tags, which have their own advantages.

EMG Tagging Approaches

Further deployment of EMG tags could leverage previous work (e.g., Table A2) if a universal EMG to TBF calibration equation can be derived from newly tagged individuals. However, only a subset of individuals in the previous study were sexed or had sufficient information to be used in an energetics model, making the utility of this approach unclear. For example, if it is assumed or found that Mountain Whitefish do not display sex-specific post-spawn swimming behaviours then more of the previously collected data could be leveraged than if sex-specific post-spawn differences are found. EMG tag deployments represent a potentially invasive surgery, given larger incision sizes than for standard tags, and the need to implant and connect electrodes to the axial swim muscle. Furthermore, Mountain Whitefish are smaller on average than Bull Trout (Hugg 1996), thus the relatively higher tag burdens may have contributed to the low success rate of Mountain Whitefish deployments. The key to successful tagging operations with Mountain Whitefish may be to minimize both handling time and the tag burden (Taylor et al. 2011).

Further complicating EMG tags deployments is that the tag model (Lotek CEMG2-R11-12; weight in air: 8.8g) originally used in Taylor and Lewis (2009, 2010, 2011) and Taylor et al. (2012, 2013, 2014) are no longer available. This tag was discontinued due to difficulties in stocking the specialized high-performance battery that was required for the small tag size (Peter Davis, Lotek, personal communication, January 22, 2020). As such any new EMG studies would need to make use of larger tags, which will have a relatively higher tag burden than was used in the previous Mountain Whitefish study. Furthermore, the use of EMG tags in Mountain Whitefish will require two calibration experiments so that energetics calculations can be performed: one to map EMG signals to tail beat frequency, and a second to compare tail beat frequency to swim speeds. This will result in longer handling times, which, due to the sensitivity of Mountain Whitefish to handling stress (Taylor et al. 2011), may require sampling additional individuals (some fish for calibration experiments and additional fish for free-swimming observations). For these reasons, the EMG tagging approach is not suggested, which leaves accelerometer tags as the remaining option. That said, while Mountain Whitefish are typically understudied, successful tagging studies are non-uncommon (Table J1).

Table J1. Summary of Mountain Whitefish tagging studies

Authors	Year	Success Rate	Fishing Method	Tag Burden
Bégout Anras et al.	1994	44%	Net (trap nets or gill nets)	< 2.5%
Reid et al.	2002	Unknown	Electrofishing	~0.5%
Hildebrand	2009	96%	Electrofishing	<2.5%
Taylor et al.	2011	Variable	Electrofishing	< 3 %
Taylor et al.	2012	62%	Electrofishing	1-3%
Boyer et al.	2017	83%	Electrofishing and angling	< 2%
Winkowski et al.	2018	92%*	Electrofishing, hook and line, seining, and snorkel	< 2%

* Initial success rate as part of preliminary finding.

Accelerometer Approaches

Tags with built-in accelerometers measure acceleration in 3D space and have been successfully used to measure free-swimming energetics in salmonids (Wilson et al. 2013). This type of telemetry tag can be used in energetics calculations and should present a lower level of invasiveness relative to EMG type tags which require electrodes to be attached in addition to implantation of the tag. There are two main approaches that could be taken to estimate free-swimming energetics using accelerometer tags:

1. Use accelerometer tags to predict tail beat frequency through a calibration relationship, which can then be used to predict swim speed and energetic expenditure; or
2. Use accelerometer tags to directly predict mass-specific respiration rates (mg O_2 kg^{-1} min^{-1}).

Both approaches will require calibration experiments that will need to be performed in a swim tunnel or swim chamber.

Approach (1) will require three observational experiments to be completed. The first two will be used to map accelerometer tag readings to tail beat frequencies and tail beat frequencies to swim speeds. The third provides a baseline for active swimming. All experiments should be reasonably straightforward to carry out in a field setting. Generally, for EMG tagging applications it was believed that the slope and intercept of the EMG-to-tail-beat-frequency regression line could differ among individuals (Brown et al. 2007). However, the Bull Trout studied showed that most among-individual differences were in the intercepts, which could be estimated from field observations. Similarly, accelerometer tags appear to have a fairly stable relationship with tail beat frequency (see Wilson et al. 2013), so a single calibration equation developed from a subset of individuals is possible, as it was with the EMG study on Bull Trout. A second experiment will be required to develop an equation to predict swim speed based on observed the tail beat frequency. This relationship will be critical for predicting energetics as energetics equations require swim speeds and a model to predict swim speed does not currently exist for Mountain Whitefish. Finally, the current energetic modeling framework predicts the probability of swimming, based on a baseline for active swimming. The Bull Trout analysis estimated this from field data (i.e., lower 1st percentile of activity), which could potentially also be done with accelerometer tags. That said, if swimming experiments were conducted it would be helpful to confirm the threshold for active swimming observed in the swim tunnel roughly matches the estimated threshold for active swimming in the lower levels of activity observed in the natural. This could entail releasing a subset of fish that have been used in the swim tunnel experiments, and it may therefore be appropriate to exclude the swim-tunnel individuals from the main field study. On the other hand, releasing these individuals could be useful for validating the lower baseline threshold for active swimming observed in the swimming experiments. Finally, a sex-specific standardized mass equation may also need to be developed unless the mass of each tagged individual is measured.

Approach (2) will require fewer calibration experiments, but may be more problematic to implement in a field setting. In this approach a swim tunnel can be used to directly measure mass-specific respiration rates under a variety of flows and temperatures (Metcalfe et al. 2015). However, respirometer experiments in this context can be difficult to perform due to the difficulty of transporting respirometer equipment to the field and the handling stress caused by transporting live fish to the lab (Cooke et al. 2004). That said, Wilson et al. (2011) showed very stable relationships between accelerometer readings and aerobic metabolism (i.e., combined digestive, active and standard metabolic rates). If this approach was taken, the relationship between tail beat frequency and swim speed is not needed, but the experiment may need to be executed across a variety of temperatures to either account for temperature differences experienced in the natural environment or to demonstrate that the standard metabolic rate (SMR) can be accurately accounted for (the energetics model predicts periods during which only SMR apply). This can be determined by looking at oxygen consumption when the baseline for active swimming has not been met. Finally, similar to approach (1) it would be helpful to confirm that observed baseline accelerometer readings (associated with active swimming thresholds in swimming experiments) do indeed match lower quartile estimates from the natural environment.

Sample Size Calculations for Accelerometer-based Studies

Moving away from EMG tags towards accelerometer tags with a lower tag burden will require sample size adjustments to achieve precision parity with the Bull Trout study. Electronic tags that actively broadcast information have attributes such as how frequently they broadcast IDs and accelerometer measurements (pulse rate) and the length of time over which the tag can remain active (tag life). Because batteries have limited power, one setting impacts the other (i.e., more frequent pulsing reduces tag life). The longer tags remain active, the greater the total number of hourly bins with at least one detection (Figure J1a), yet the average number of observations per day remains reasonably stable (Figure J1b) during the detection period regardless. Smaller tags, which have a lower tag burden, also tend to have shorter life spans due to reduced battery capacity, which will result in fewer total detections of each individual (hence less information about each individual). While true, the amount of information lost with shorter tag life may not be as large as first expected since repeat observations of the same individual are not independent (i.e., repeated measures) and there are diminishing returns whereby each additional observation provides relatively less new information.

To extend tag life, practitioners may consider changing how frequently tags transmit information. For example, the EMG study used a 2 second pulse rate, which provided a maximum tag life of about 65 days[2]. An accelerometer tag with a lower tag burden from the same company will only have a maximum tag life of 19 days at a 2 second pulse rate, but a 45 day tag life at a 5 second pulse rate. The slower pulse rate could however decrease overall detections and impact the effective number of hours with an observation.

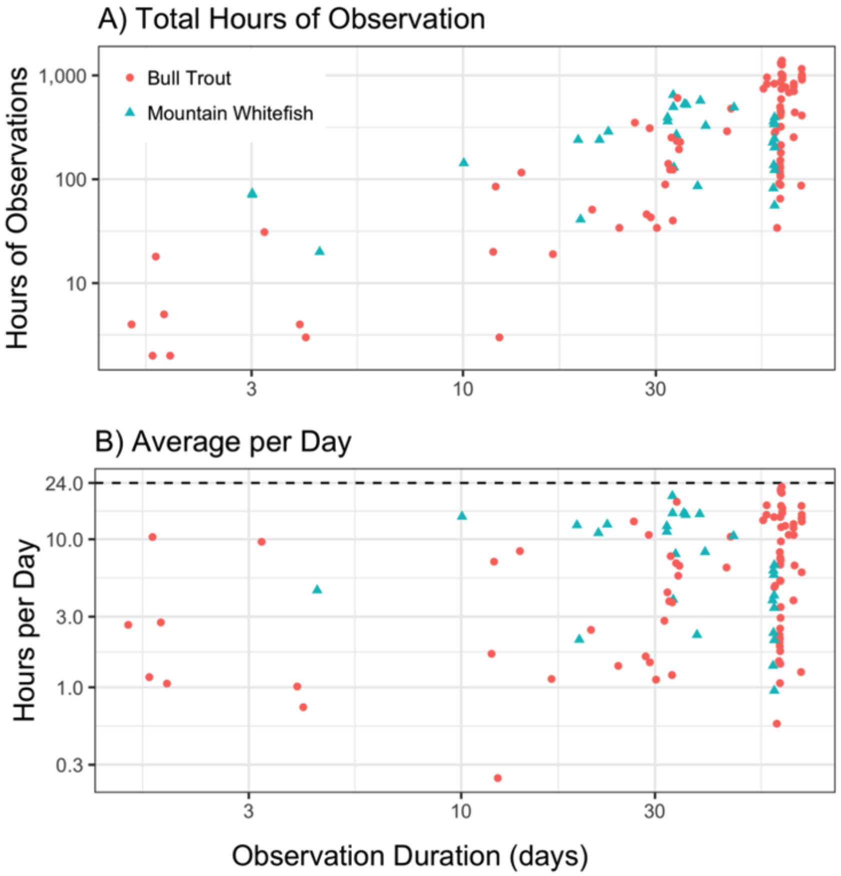


Figure J1. **Scatterplots of the observed number of hours with a detection by the observed duration (i.e., length of time between first and last detection) for Bull Trout and Mountain Whitefish EMG**

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[2] Note that observation duration (i.e., the time between the first and last detection; Figure J1) will be shorter than manufacturer's expected tag life due to processes such as mortality and movement out of the effective study area.

studies (A) and hours per observed day (B). All axes are displayed using logarithmic scaling. The vertical dashed line in in panel B indicates 24 hours.

Reductions in both the tag life and the probability of detections could result in smaller effective sample sizes relative to the Bull Trout study, which would likely reduce the precision of energetic calculations. Hence, we've made calculations to determine sample sizes that would be needed to put the precision of an accelerometer tag study on par with that of the previous Bull Trout study.

Sample Size Adjustment for Tag Life

As outlined in Section 3.6, the energetics model operates on an hourly timestep where raw activity records (i.e., activity logged during each unique detections) are first averaged to the minute level, then the minute averages are averaged to the quarter hour, and the quarter hour averages are finally averaged to the hourly level. Because the energetic model uses hourly activity levels, reduced tag life will reduce the total number of hours observed for each individual (Figure J1a). Furthermore, while the total number of hours observed is positively correlated with the Observation Duration, the average number of hours per day remained reasonably constant (Figure J1b), averaging roughly 8-9 hours per day depending on the species (Table J2).

The question then becomes how many additional tags are required to accommodate for the reduction in tag life. This adjustment is complicated by the fact the reduction in the total number of observed hours was for repeated measures rather than independent measurements (see Hurlbert 1984). Repeated measures of the same individual generally do not provide the same degree of information about a population parameter as observations from new individuals, given that repeat observations are often correlated. If the correlation coefficient is known, then it is possible to calculate the effective sample size using the formula,

$$n_{\mathrm{eff}} = \frac{n}{1 + (n - 1)\rho}$$

where n represents the number of hours and ρ represent the correlation coefficient between hourly observations. This formula would apply to the number of effective hourly observations we would have on an individual but can be used to understand the impact of tag life. Generally, individuals provided 8-9 hours of observation for each day with a correlation of 0.44-0.48 (Table J2).

Table J2. Median and average hours of observations per day by species.

Species	Median (hrs day^{-1})	Average (hrs day^{-1})	SD (hrs day^{-1})	Correlation (ρ)
Bull Trout	6.65	7.86	6.19	0.44
Mountain Whitefish	8.08	9.23	6.50	0.48

If the effective sample size of each individual could be computed, then the total effective sample size can be determined, however not all observations occur under the same environmental conditions and as such are equivalent. Therefore, it is not clear how many hours were observed under a particular set of conditions. That said, if we assumed conditions are randomly distributed across we can assume 45-day tag will capture 69% fewer hours of observations (i.e., 45/65) under any given unique set of environmental conditions than a 65-day tag. Given that we can compute the effective sample size over a range of possible sample sizes, and compare the relative precision of a tag with 65 day tag-life against one with only 45-days of tag life (Figure J2). We can see that by about 10 total hours, the 45-day tag-life will produce an estimate that has a relative error within 3% of the 65-day tag-life. That is, if a unique set of conditions is observed for 10 total hours using a tag with a 65-day tag-life, we can expect about 6.9 hours under the 45-day tag. The fewer observations will mean higher uncertainty, but the realized difference in precision is less than 3% relative to a 65-day tag-life. This is due to the fact each additional repeat observation adds relatively less new information about the population response. As the total numbers of hours of observations increases, the reduction in total observed hours has a relatively smaller effect, which can be seen in Figure J2, where the difference in precision asymptotically approaches zero with larger sample sizes. Therefore, depending on how many unique conditions are sampled, there is a good possibility that a 45-day tag life will provide sufficient information relative to the 65-day tag life.

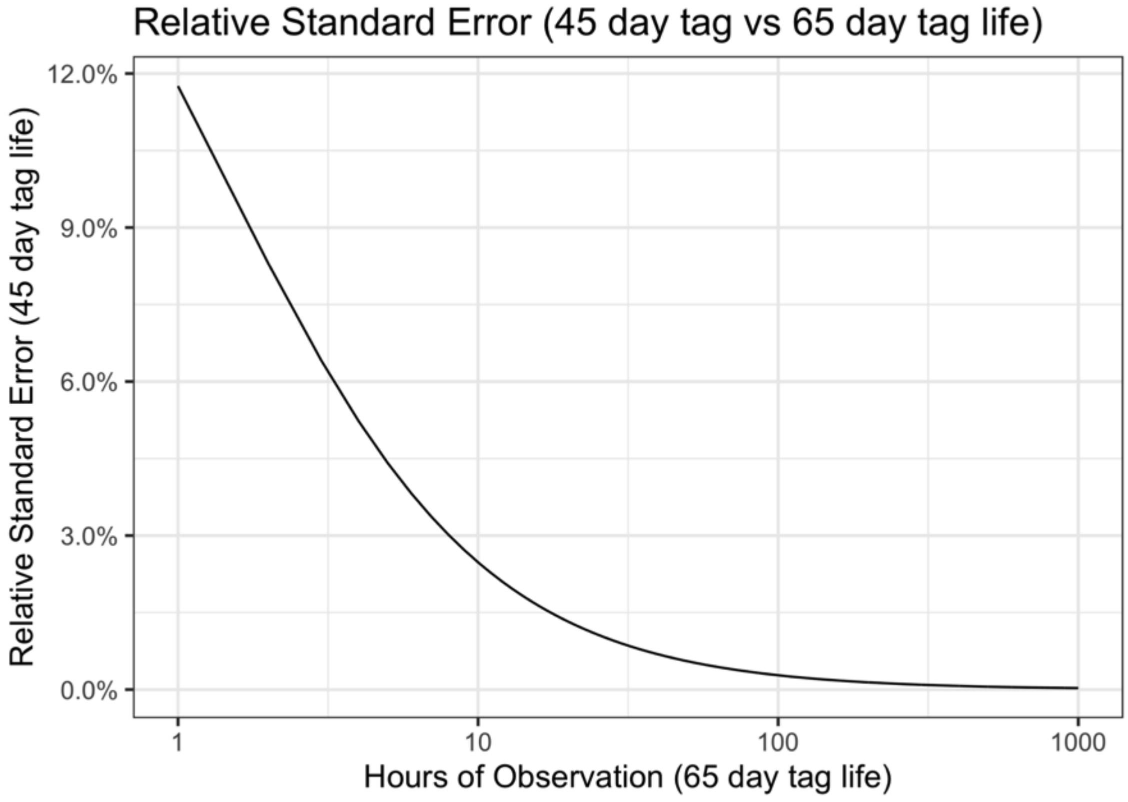

Figure J2. **Expected standard error for estimates derived from observations generated by a 45-day tag relative to a 65-day tag as a function of the total number of hours observed under a given set of**

conditions. The relationship assumes the 45-day tag will observed only 69% (i.e., 45/65) of the total hours under a given set of environmental conditions as the 65-day tag.

To test this assumption that a 45-day tag life could provide a similar amount of information as the 65-day tags, we re-fit the empirical relationships from the Bull Trout energetics model after truncating the data to exclude any observation after 45 days. The Bull Trout model was then reapplied to the selected days from the pre-REV 5 analysis (see Section 4.8) and the relative error between the two analyses was compared. It was found that both produced the same results, and that there was only a marginal difference in the relative precision (i.e., less than 1%) between them. As such, the extended tag-life over 45 days did not appear to add significant amounts of new information, and we do not believe a 45-day tag-life for an accelerometer tag will significantly impact the results relative to the 65-day tag-life used in the EMG study.

Sample Size Adjustment for Pulse Rates

The second suggested change for an accelerometer tag study was to increase the time between tag pulses (i.e., when the tag transmits information) in order to extend the tag life. This can be accomplished by reducing tag pulse rate, which can be expected to impact the total number of receiver detections that occur in the experiment, and therefore the effective sample size. This will occur through two main mechanisms:

1. Reduced precision of averages (e.g., minute-to-minute averages of activity level); and
2. Reduced number of unique minutes or hours during which a detection occurs.

Potential sample sizes adjustments can be considered for both mechanisms. Because the energetics model operates on an hourly timestep raw activity records (i.e., unique detections) are first averaged to the minute level, then the minute averages are averaged to the quarter hour, and the quarter hour averages are then averaged to the hourly level (see Section 3.9). The lower tag pulse rate will reduce the number of observations received each minute, and as a result the minute averages of the activity level will be less precise relative to an experiment that uses a tag with a faster tag pulse rate. The lower precision of the minute averages will also reduce the precision of the quarter-hourly and hourly averages, as these averages are a function of the minute averages. Probabilistically, the lower tag pulse rate will result in fewer unique minutes with an observation, which will further reduce the precision of the quarterly and hourly averages. The question then remains whether these changes will have a meaningful impact on overall precision of the experiment, and whether sample size adjustments need to be made to match the precision of the successful Bull Trout experiment.

As a first step, the detection rates from the original EMG experiment were determined across differing time scales, of which it was clear that average receiver detection rates differed on a short and longer time horizon (Figure J3). The short-term trend likely reflected the frequency of detections when a tagged fish was within the vicinity of the receiver and was under the influence of environmental factors (such as turbulence) and short-term movement behaviours (e.g., foraging) within the vicinity of the receiver. Here there is a much higher probability of detection as the micro-conditions that lead to a successful receiver detection event were much more likely to still exist. On the longer time scale, fish may be moving into and out of the vicinity of the receiver, combined with imperfect detection probabilities, the result was overall lower detection rates.

As observations were first averaged to the minute level, we can consider the effects of changes to the pulse rate on the subsequent detection rates on this time scale. With a 2 second pulse rate, there were roughly 4 receiver detections recorded every minute (i.e., 3.97 detections per minute). Given that there are 30 possible 2-second intervals during which these four detections could have occurred, this gives a probability of detection of $3.97/30 \cong 0.132$ in any 2-second interval. For a fish that remains in the area, this translates a probability of roughly 0.99 of being detected within the minute (i.e., $1-(1-0.132)^{30} \cong 0.986$). Assuming that the probability a tag pulse is detected remains the same, under a 5 second pulse rate there are only 12 windows were a tag pulse can be detected ,and as such the probability of detection within a minute drops to 0.82 (i.e., $1-(1-0.132)^{12} \cong 0.817$), and the average number of detections events are expected to drop from 4 to 1.6.

The models predicting tail fin beats used log transformed values of the SEMG signal (i.e., log(SEMG)), so we can look at the potential impact of fewer observations per minute on the standard error for log(SEMG) minute averages. Across the 965,738 minute averages, the average standard error was about 0.09, which implies a minute-to-minute standard deviation of $\sigma = 0.09\sqrt{4} = 0.18$. With only 1.6 observations per minute, the expected standard error for the minute averages will be $0.18/\sqrt{1.6} \cong 0.142$, an increase of about 58% in minute-to-minute measurement error over a 2-second tag pulse rate.

The next step is to consider how the revised precision of the minute averages will impact the quarter-hourly and hourly averages. These averages are done hierarchically, with the quarter hour averages performed first, then the hourly average afterwards. This was done largely to reduce the impact of outliers or anomalous conditions that could occur throughout the hour rather than to optimize precision of the hourly estimate. However, if conditions are relatively uniform this step is not required and will produce identical answers as just taking the hourly average directly from the minute averages. Therefore, to keep calculations as straightforward as possible, we will simply consider the impact on precision of generating hourly averages directly from the minute averages.

Generally, under constant conditions one can expect the hourly averages to be more precise than the minute averages as the hourly averages will be made up of more underlying observations than any minute average. However, the observed average standard error across all the hour averages was $\widehat{SE(\bar{x}_h)} = 0.8188$, which is larger than the average standard error for minute averages (i.e., 0.09). On average, there were 22 minute averages available for each hour average, thus the expected hourly standard error would have been $0.09/\sqrt{(22)} \cong 0.019$ if only measurement error was considered. This suggests that another source of variation affects the hourly estimates (e.g., Figure J3). Likely this represents variation in the flow conditions within the hour, which we can assume is independent of measurement uncertainty. More formally we can write this as,

$$\mathrm{Var}(\text{hour average}) = \mathrm{Var}(\text{environment}) + \mathrm{Var}(\text{measure})$$

where the observed variation in hourly estimates is a linear function of the environmental uncertainty and the measurement error (covariance is not considered due to the assumption of independence). Given that we had determined the variance of the hourly measurements (i.e., 0.019^2), this suggest that the variance of $\mathrm{Var}(\text{environment}) = 0.819^2 - 0.019^2 \cong 0.670$.

Under a 5 second tag pulse rate we can determine the expected measurement error to be larger due to fewer and less precise minute averages. As indicated in Figure J3, detection rates on the longer time scale appear to operate differently compared to the shorter time scale. Based on the short-term detection rates (i.e., detection rate within a minute), tags with a 2-second pulse rate would have had an expected $60 \times 0.986 \cong 59$ minutes with an activity reading if individuals remained in the area, whereas an average of 22 readings were observed. This suggests that individuals were only in the area for 37% of the time (i.e., $22/59 \cong 0.373$). Therefore, tags with 5-second tag pulse rate can be expected to have $60 \times 0.817 \times 0.373 \cong 18.3$ minutes with observations per hour. This would result in a revised measurement error of

$$\mathrm{Var}(\text{measure})^{5\,\text{sec}} = \left(0.142/\sqrt{18.3}\right)^2 \cong 0.033^2$$

While error associated with the measurement process showed a large increase (0.019 versus 0.33, a 73% increase), the increase in the measurement error associated final hourly average was relatively small. This would imply an expected standard error of

$$\mathrm{SE}(\bar{x}_h)^{5\,\text{sec}} = \sqrt{0.670 + 0.033^2} \cong 0.8192$$

which is less than a 1% increase relative to the 2-second pulse rate (due to the overwhelming impact of environmental variability). Equal precision could be attained by increasing the sample size by roughly 2%, which would translate to about 1 extra fish relative to the Bull Trout study.

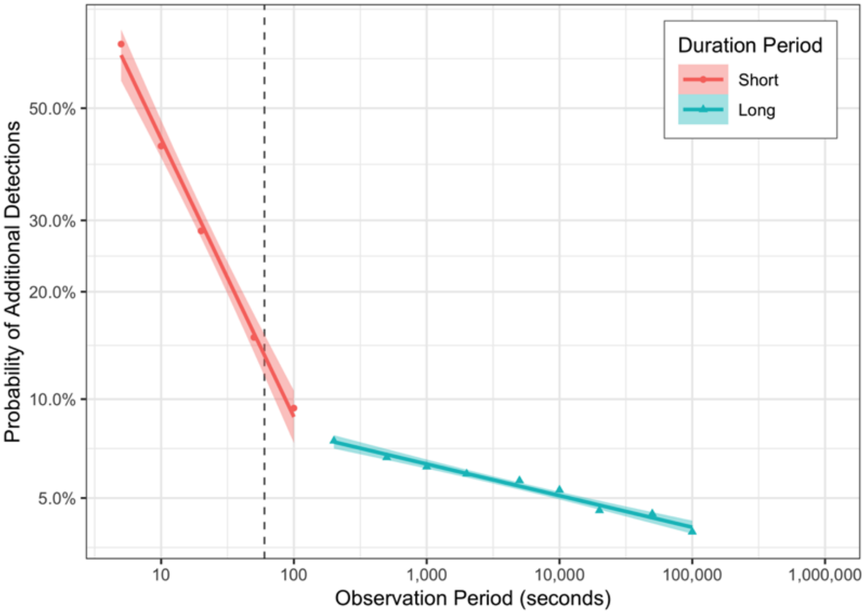

Figure J3. The empirical probability of observing an additional detection by the length of time from the initial detection for short (i.e., under 2 minutes) and observation periods. The y-axis is displayed on the logit scale, while the x-axis using logarithmic scaling. Solid lines indicate linear regression lines with the shading indicating the 95% confidence region. Vertical dashed line indicates one minute.

Final Sample Sizes

Although the tag life and pulse rate issues appear to be largely resolved, Mountain Whitefish tag deployments may not be as successful as Bull Trout. A success rate of 19 out of 30 (i.e., 63%) was originally reported by Taylor et al. (2012), which would suggest 141 tagged individuals would need to be released (i.e., 89/0.63). However, not all of the 88 tagged Bull Trout release should be viewed as successful, many had under 100 total detections, and 32 did not produce enough data to allow a baseline EMG value to be determined (Appendix A). By this measure the Bull Trout study had a similar success rate (i.e., 56 out of 88 or 64%) and therefore further adjusts may not be warranted. Accelerometer tags should have both a lower tag burden and reduced handling stress than the EMG tags, which should further assist the success rate. Finally sample size allocations will also need to consider any calibration experiments. Ideally, these fish should not be included when tallying the sample size of the main study. For example, Wilson et al (2013) required about 9 individuals to successfully build accelerometer calibration equations for energetic estimation. This would bring the total sample size to approximately 98-150, depending on the anticipated success rate.

Summary

Relative to the successful EMG study carried out on Bull Trout, it should be feasible to execute a similarly successful study on Mountain Whitefish by switching to accelerometer tags which feature lower tag burden and less complicated surgeries. One of the primary concerns with the switch was the shorter tag-life, which could reduce the variety of environmental conditions energetic measurements are captured. This could be abated to some degree by increasing the time between tag pulses (i.e., reducing the tag pulse rate). Both changes could however affect precision of the study and therefore the require sample sizes. When this trade-off was investigated further we found no evidence that such changes would meaningfully impact the precision of the energetics calculations relative to the Bull Trout study. In fact, only one additional fish would need to be added to make up for the difference in precision (i.e., n=89), if Mountain Whitefish tag deployments are as successful as Bull Trout deployments.

There has been concern about the poor success of Whitefish studies, suggesting a larger sample size, but we found mixed evidence to support this position, with approximately 60% of Mountain Whitefish and Bull Trout releases producing useful results in the previous EMG study. As accelerometer tags should provide a lower tag burden and less handling stress, we would anticipate an equal or better success rates.

Taken together, along with allowances for calibrations, a total sample size of approximately 98-150 Mountain Whitefish would be needed to produce an energetics model of similar precision to the Bull Trout energetics model.

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