# Reach-scale movements of bull trout (Salvelinus confluentus) relative to hydropeaking operations in the Columbia River, Canada

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# Reach-scale movements of bull trout (*Salvelinus confluentus*) relative to hydropeaking operations in the Columbia River, Canada

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## ABSTRACT

Despite the widespread use of on-demand hydropeaking operations for generating electricity from rivers, relatively little is known about how pulsed flows influence the behaviour of fishes. We studied the movements of bull trout by using radio telemetry in a hydropeaking reach of the upper Columbia River, near Revelstoke, British Columbia, Canada. Fifty-seven bull trout were located every 12 h to evaluate the effects of discharge magnitude and rate of change on the: (1) odds of movement; (2) movement distances; and (3) movement direction. Twelve-hour mean discharge magnitude had a negative effect on the odds of bull movement: for every $100 \, \mathrm{m^3 \, s^{-1}}$ increase in discharge, movement odds decreased by a factor of 0·91. Movement odds were unrelated to 12-h discharge rate of change. Every 1 °C increase in water temperature increased movement odds by a factor of 1·27. Also, bull trout were more likely to move during the AM versus PM by a factor of 1·36. Movement distances were related to diel period, sex and fork length; however, these effects were not very strong. We found no evidence of downstream displacement during periods of high or changing river discharge. In fact, movement direction was unpredictable, which is consistent with the salmonid non-migratory movement literature. Collectively, these findings provide insight into the biology of bull trout during an understudied seasonal life-history period (i.e. autumn). It also informs river managers that bull trout movement can be modulated by operational water release from a dam. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS    fish movement; hydropeaking; bull trout; telemetry

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## INTRODUCTION

There is growing recognition that altered flow regimes threaten the biodiversity and ecosystem functions of rivers on a global scale (Nilsson *et al.*, 2005). Negative effects of river water management practices on fish population abundance and community structure have been identified (e.g. Haxton and Findlay, 2008). However, little is known about the sub-lethal behavioural responses of fishes to short-term changes in river flow (e.g. pulsed flows; Katopodis, 2005; Hasler *et al.*, 2009). Pulsed flows are produced by hydropeaking systems whereby water is held in a reservoir and released according to the demand for electricity, resulting in rapid flow changes that occur on a daily or sub-daily cycle (Cushman, 1985). Pulsed flows can also result from flushing operations which are used to maintain sediment accumulation. Other sources of pulsed flows exist such as recreational flows and emergency spill flows (Young *et al.*, 2011).

Globally, hydropower operations are developing rapidly on rivers of various size (Frey and Linke, 2002; Bratrich *et al.*, 2004), but there is particular interest in hydropeaking systems on medium to large rivers given that power production can occur on demand with little time needed to start or stop production (Yuksel, 2007).

Given the persistence of pulsed flow events around the globe, researchers have been developing an understanding of the biotic response of free-swimming fishes to short-term changes in river flow. Response metrics have included blood physiology (e.g. Flodmark *et al.*, 2002; Taylor *et al.*, 2012), swimming energetics (e.g. Geist *et al.*, 2005;

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Cocherell *et al.*, 2011), habitat use (e.g. Bunt *et al.*, 1999; Dare *et al.*, 2002) and behaviour (e.g. Scruton *et al.*, 2005; Krimmer *et al.*, 2011).

Movement is among the most important of behaviours because it allows animals to respond to changing physical conditions within their environment to maximize growth, survival and reproductive success (Kahler *et al.*, 2001). For example, some evidence suggests that brook trout make large movements to monitor stream habitat conditions at a broad spatial scale to gain access to optimal foraging locations (Gowan and Fausch, 2002). In a dynamic environment such as a hydropeaking river, habitat conditions and foraging potential change rapidly. Given these conditions, one may expect fish to displace themselves often as they continually re-assess habitat quality in their changing environment. The downstream forcing of fishes during periods of high river flow is another concern for river management (e.g. Heggenes and Traaen, 1988; Vehanen *et al.*, 2000). Displacement from habitats with water flows above maximum swimming speeds has resulted in mortality (e.g. Quinn and Peterson, 1996).

To address some of these issues, researchers have attempted to explain variation in fish movements using hydrologic metrics at different scales from hourly (e.g. Berland *et al.*, 2004) to seasonally (e.g. Zimmer *et al.*, 2010). However, studies examining fish movement relative to hydropower operations have shown conflicting results; some studies showed an effect of pulsed flows on movement (e.g. Young and Isely, 2007), whereas others showed no effect (e.g. Heggenes *et al.*, 2007). No grand model exists to explain fish movement in regulated rivers. Some knowledge can be gained from fish movement studies in unregulated rivers whereby natural variations in river flow may influence movement at longer time scales (e.g. Clapp *et al.*, 1990; Brown *et al.*, 2001). Temperature has also been shown to effect lotic fish movement (e.g. Popoff and Neumann, 2005), and considering that a river's flow and temperature regimes are often linked (Olden and Naiman, 2010), it is important to consider both parameters in correlative studies.

Bull trout (*Salvelinus confluentus*) are a species of char native to western North America that have received protection in many jurisdictions (IUCN, 2011). Thus, there is interest in identifying the anthropogenic factors that are contributing to declines or impeding recovery. These piscivorious fish are characterized by their diverse life histories which can involve long-distance movements between spawning and overwintering habitat (Swanberg, 1997; Bahr and Shrimpton, 2004; Muhlfeld and Marotz, 2005). Despite the existing literature on migratory movements, an understanding of the timing of movements outside their spawning migration has not developed. Furthermore, previous bull trout telemetry studies located their subjects at a mean frequency of three locations per month (Dare, 2006), yielding movement estimates at time scales that are too coarse to correlate with sub-daily changes in river flow.

Given the previous discussion, the purpose of this study was to determine if bull trout movements were associated with the operational release of water from a hydropeaking dam. We determined if river flow parameters (discharge magnitude and rate of change) had a significant statistical effect on bull trout movements while controlling for other conditions such as temperature and light. Specifically, we tested for an effect of discharge magnitude and rate of change, at a 12-h time scale, on the: (1) odds of movement; (2) distance of movements; and (3) direction of movement.

## METHODS

### Study site and fish surgery

The study site was the Columbia River between the Revelstoke Dam (REV) and the downstream Arrow Lakes Reservoir (Figure 1) in British Columbia, Canada. REV is a hydropeaking power facility: water released through turbines control the increase and decrease in river discharge downstream. These discharge peaks typically last less than a day and can sometimes occur multiple times per day (Figure 2). REV is a barrier to bull trout migrations (McPhail *et al.*, 1996) so these fish are forced to carry out their life history within the confines of REV and the downstream Arrow Lakes reservoir.

Bull trout movements were estimated from manually tracking their location during a companion study of bull trout swimming activity using electromyogram (EMG) radio transmitters. EMGs not only provide a quantitative estimate of axial swimming muscle activity but also emit a radio signal which was tracked using the same methods as regular radio telemetry (EMG data are reported in a separate manuscript; Taylor *et al.*, In press). Eighty-eight bull trout were collected by pulsed DC boat electroshocker during 3 years (Year 1: 24 September to 8 October 2008; Year 2: 28 September to 7 October 2009; Year 3: 14 October to 26 October 2010). Bull trout were captured at night using a large dip net and transferred into an on-board live-well with a recirculation pump while being relocated to the study site. Water temperatures at the time of capture ranged from 8 to 11 °C. All fish were transferred again to a holding tank (diameter = 243 cm, depth = 90 cm and volume = 2839 L) on the shoreline of the Columbia River with aerated continuous flow of river water.

Bull trout were individually anaesthetized to stage 5 anesthesia in 60-ppm clove oil (emulsified in ETOH at a ratio of 1 part clove oil to 10 parts ETOH; Anderson *et al.*, 1997). Fish were then transferred to a v-shaped plastic surgery trough in a supine position. Water was continuously pumped across their gills with a maintenance
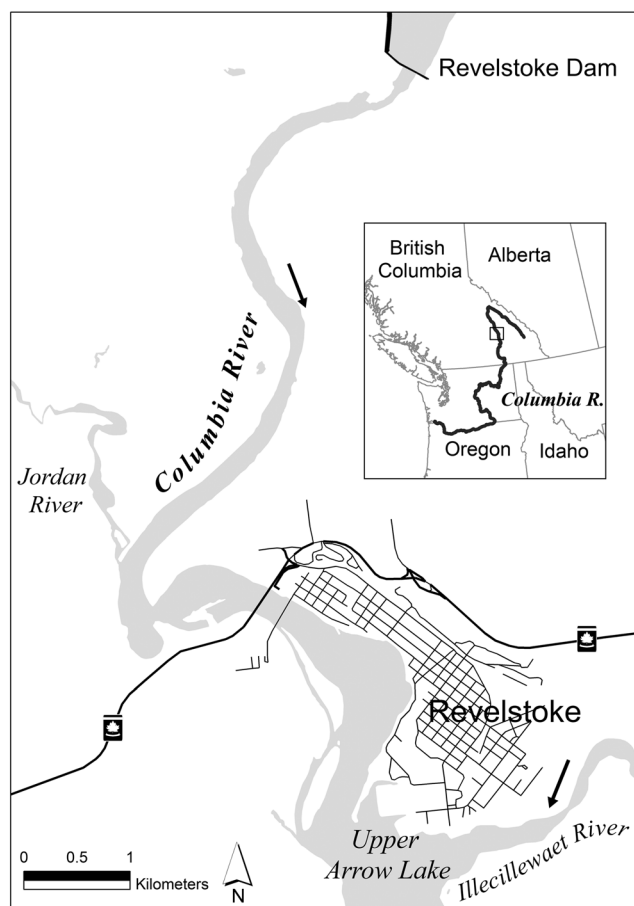
Figure 1. Map of the Columbia River downstream of Revelstoke Dam, Revelstoke, British Columbia, Canada. Study area was 10·6-km section from Revelstoke Dam downstream to the Illecillewaet River.



Figure 2. Twelve-hour mean discharge (m³ s⁻¹; shaded), 12-h mean water temperature (°C; black) for the Columbia River downstream of REV. Discharge was measured from the dam. Some periods of zero discharge occur when the dam does not release any water and the only water in the channel is residual flow, dam leakage and backfill from the downstream reservoir. These periods are not evident on the figure as discharge was averaged every 12 h. Water temperature was measured from gauging station 7 km downstream of the dam. Tracking session is the numbered sequence of tracking sessions every 12 h. Panel 1 is 16 October to 3 December 2008. Panel 2 is 15 October to 5 December 2009. Panel 3 is 14 November to 14 December 2010.

bath of 30-ppm clove oil. By using a scalpel (number 3 blade, rounded cutting point), an approximately 30-mm incision was made in the ventral body surface, posterior to the pelvic girdle, slightly off midline. Via the incision, sex was visually determined using forceps and white LED lights, and a coded EMG transmitter was inserted (CEMG2-R16-25; dimensions: 16 × 62 mm, weight: 25 g in air; Lotek Wireless, New Market, Ontario). EMG electrodes were inserted in the red axial musculature by using rods and plungers (Taylor *et al*., In press). A 16·5 gauge hypodermic needle was pushed through the body cavity wall, and the antenna wire passed through to the outside. The incision was closed using four independent sutures (PDS II absorbable monofilament, 3/0, FSL needle). The entire procedure took approximately 5 min per fish and the same surgeon performed all surgeries. Fish were then placed back into a holding tank until they recovered and exhibited 'normal' swimming behaviour (i.e. demonstrated exploratory activity and maintained equilibrium) at which time they were released back into the river (Year 1) or were held overnight in the tank to await calibrations (Years 2 and 3; Taylor *et al*., In press).
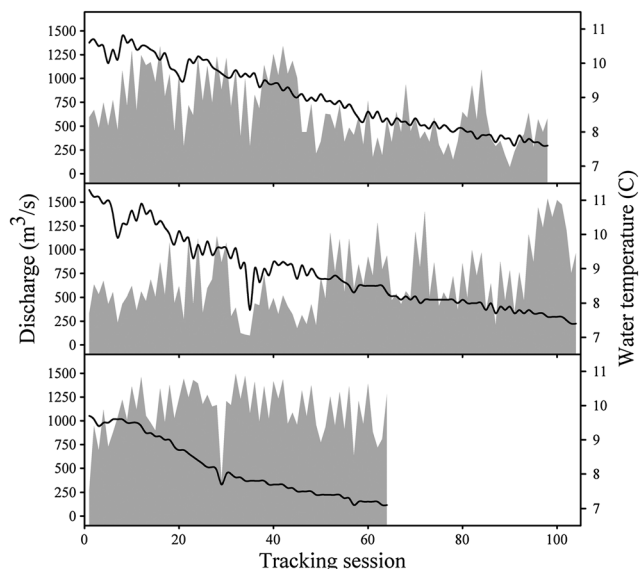
Daily fish tracking sessions occurred at noon and midnight with the exception of some days (approximately one session/week) to allow for the rest of researchers. Each session lasted approximately 3 h to scan the entire study area. Tracking was conducted on foot, from shore, by a two-person team equipped with a three-element Yagi antenna and a Lotek SRX600 receiver. Successive gain reduction techniques (i.e. zero point tracking) were used whereby fish position was identified by successively reducing the gain until one was as close to the fish as possible, while on shore. Once directly adjacent to the fish (distance from the fish depended on the width of the river at each specific location), the longitudinal location was determined by standing on shore at 90° to the thalweg and recording the location by storing a waypoint into the GPS (Garmin 60CS).

Tracker location error was estimated to range from 1 to 50 m, depending on water depth and safe access to shoreline. In order to ensure that movement estimates represented true movements and not artifacts of location error, fish were only considered to have moved if re-locations were at least 100 m apart. A map was created whereby the study area was divided into 100-m river sections, as measured along the thalweg using GIS (ArcView 3.2), and fish were assigned to these 100-m longitudinal positions. The locational error was considered

too large to reliably detect lateral positions in river cross-section; therefore, movements were longitudinal only. Each fish location corresponded to a river section number representing the fish's distance from REV (e.g. section 26 is 2600 m downstream of REV).

*Data analysis*

When multiple measurements are generated on the same individuals, the data are not independent (Heck *et al.*, 2010) and may be autocorrelated (Swihart and Slade, 1985). While there is advice on designing tracking schedules to ensure that locations are independent of one another (e.g. Hodder *et al.*, 2007), relocating fish at finer time scales better describes what the animal is doing (Aebischer *et al.*, 1993). This presumably allows for a finer-scale understanding of the environment correlates of movement. A second source of non-independence in telemetry data is that the response variable (i.e. fish location) is hierarchically organized, with individual locations being organized within subjects (individual fish) and those subjects being organized at higher levels (e.g. sex and species). Such issues violate key assumptions of single-level multiple regression models (independent errors) and will lead to underestimated variances and standard errors that may, in turn, lead to false conclusions (Heck *et al.*, 2010). We modeled the movement parameters using generalized estimating equations (GEEs). GEEs can model correlated data with continuous, dichotomous, polychotomous, ordinal and event-count response variables (Zorn, 2001). GEEs allowed us to account for the correlations within individuals but are a 'population-averaged' approach rather than the 'subject-specific' approach of mixed models (Zorn, 2001).

A second challenge we had with data analysis was that fish were often relocated in the same location as the previous tracking session. Therefore, movements were 'zero-inflated' and could not be described with a single distribution. Thus, we built three different GEE models to predict different aspects of fish movement. Despite many periods of zero movement, each fish did occasionally move to a new position and absolute distances where right-skewed owing to the infrequent flarge movements. However, we considered the timing of departure to be as informative as movement distance. Therefore, binary-logistic models were used to predict the odds that a bull trout moved (probability of movement/ probability of no movement) and movement direction (upstream or downstream). Secondly, we modeled all non-zero movements as the number of 100-m quadrants (i.e. counts) the fish traversed in a fixed period (i.e. 12 h), using a negative binomial model. The negative binomial distribution is similar to the Poisson distribution but is used when the variance is larger than the mean. This multi-step approach has been used by other animal movement studies with similarly constraining movement distributions (e.g. Veysey *et al.*, 2009).

For each model, we started with the same list of a potential six continuous and two categorical fixed effects (Table I). We had an *a priori* prediction that river discharge and temperature were related to fish movement based on previous research (Taylor and Cooke, 2012). Therefore, these variables were added to the models first. We reported on the significance of all effects using the forced entry method (all predictors at once). No strong collinearity was evident among predictors (no correlations were $>r = 0.33$); however, any predictors that were correlated with one another were added alone and together to check for synergistic/suppressor effects (Grafen and Hails, 2002). We tested only those fixed-effects interactions that seemed biologically plausible. Then we refined the correlation matrix, comparing models using the quasi likelihood under independence model criterion (QIC).

We suspected that individual repeated measures were not independent such that fish locations closer in time would be most similar to each other. Autocorrelation plots confirmed this. Therefore, we used an AR1 within-subject correlation structure in all models. No Pearson residuals were $>2$ in

Table I. Summary of tracking statistics of bull trout in the Columbia River, Revelstoke, British Columbia, Canada.

| Term | 2008 | | 2009 | | 2010 | |
|---|---|---|---|---|---|---|
| | Mean | Range | Mean | Range | Mean | Range |
| #Locations (count) | 64 | 29–73 | 67 | 6–80 | 49 | 32–50 |
| $D_{MAG}$ (m$^3$ s$^{-1}$) | 639 | 68–1337 | 654 | 9–1534 | 1104 | 360–1494 |
| $D_{CHANGE}$ (m$^3$ s$^{-1}$) | 984 | 55–1650 | 828 | 178–1589 | 475 | 0–1375 |
| $T_{WATER}$ (°C) | 8·9 | 7·6–10·8 | 8·8 | 7·4–11·3 | 8·3 | 7·1–9·6 |
| Visibility (km) | 11·6 | 5·0–15·0 | 12·2 | 2·70–15·0 | 9·7 | 1·0–15·0 |
| Length (mm) | 669 | 544–830 | 562 | 455–714 | 635 | 467–830 |

#Locations is the number of times an individual fish was located (i.e. one value per fish); $D_{MAG}$ is the 12-h mean discharge during the period of movement; $D_{CHANGE}$ is the difference between the 12-h maximum and minimum discharges; $T_{WATER}$ is the 12-h mean water temperature; Visibility is the number of kilometres of visible automatically measured from the Revelstoke airport (1–15 km); Length is the fork length of the fish. The sex of the fish (sex; M or F) and diel period (diel period; AM or PM) were also included as categorical predictors.

the logistic models. Residuals for the movement distance model were plotted across the range of predictors and predicted values to assess homoscedasticity and linearity; some degree of imbalance was evident because of the skewed movement distribution. Therefore, despite using a model intended for overdispersed data, fitted movement distances were underestimates of the true distances for long range movements (>500 m).

## RESULTS

### Movement odds

Bull trout displaced themselves at least 100 m once every 3 days. Movement odds were negatively related to 12-h mean discharge (GEE, Wald $\chi = 23 \cdot 639$, $p < 0 \cdot 001$; Figure 3) and positively related to water temperature (GEE, Wald $\chi = 13 \cdot 564$, $p < 0 \cdot 001$; Figure 4). For every $100 \, m^3 \, s^{-1}$ increase in river discharge, movement odds decreased by a factor of $0 \cdot 91$. For every 1 °C increase in water temperature, movement odds increased by a factor of $1 \cdot 27$. Day period also had a significant effect (GEE, Wald $\chi = 18 \cdot 130$, $p < 0 \cdot 001$); the odds of movement were greater in the AM (midnight – noon) than PM (noon – midnight) by a factor of $1 \cdot 36$. These three variables comprised the final model (Table II). Twelve-hour change in discharge had no significant effect on movement odds (GEE, Wald $\chi = 2 \cdot 965$, $p = 0 \cdot 085$), nor did visibility (GEE, Wald $\chi = 0 \cdot 340$, $p = 0 \cdot 560$), sex (GEE, Wald $\chi = 0 \cdot 751$, $p = 0 \cdot 386$) or size (GEE, Wald $\chi = 0 \cdot 244$, $p = 0 \cdot 621$).
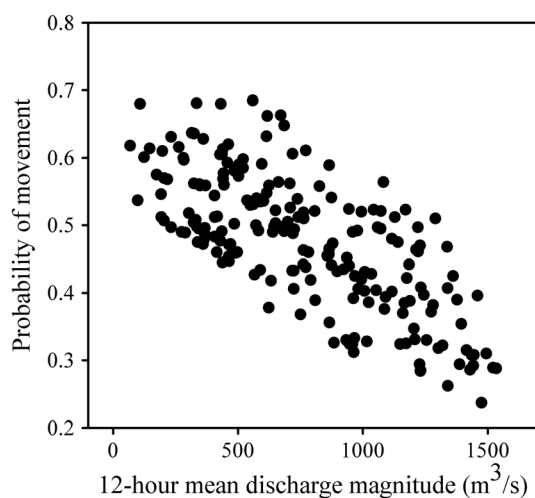


Figure 3. The predicted probability of bull trout movement (>100 m) in relation to the 12-h mean discharge magnitude ($m^3 \, s^{-1}$) in the Columbia River downstream of REV. The relationship between odds and probability: Odds = (probability of an event occurring/the probability of an event not occurring).



Figure 4. The predicted probabilities of bull trout movement (>100 m) in relation to the seasonal decline in water temperature (°C) in the Columbia River downstream of REV. The relationship between odds and probability: Odds = (probability of an event occurring/the probability of an event not occurring).
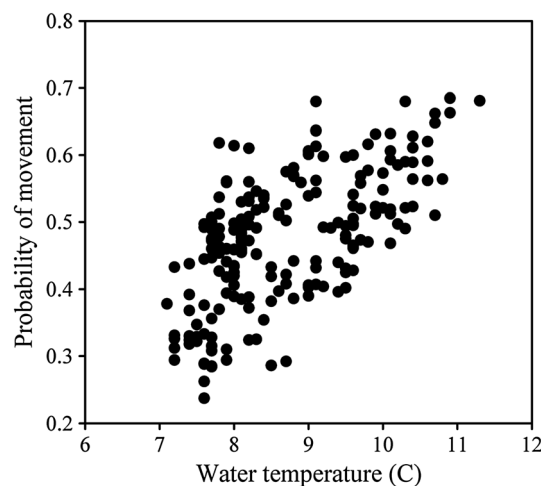
### Movement distance

Twelve-hour mean discharge magnitude had a significant effect on movement distance (GEE, Wald $\chi = 6 \cdot 325$, $p = 0 \cdot 012$) as did 12-h change in discharge (GEE, Wald $\chi = 17 \cdot 548$, $p < 0 \cdot 001$), but with very small effects sizes. For example, movement distances decreased by a factor of $0 \cdot 995$ and increased by a factor of $1 \cdot 007$ for every $100 \, m^3 \, s^{-1}$ increase in discharge magnitude and change in discharge, respectively. Distances bull trout moved were not related to 12-h mean water temperature (GEE, Wald $\chi = 1 \cdot 629$, $p = 0 \cdot 202$) or visibility (GEE, Wald $\chi = 0 \cdot 812$, $p = 0 \cdot 368$). However, Diel period (GEE, Wald $\chi = 6 \cdot 649$, $p = 0 \cdot 010$), sex (GEE, Wald $\chi = 14 \cdot 987$, $p < 0 \cdot 000$) and size (GEE, Wald $\chi = 4 \cdot 247$, $p = 0 \cdot 039$) remained in the final model (Table II). Females made larger movements than males, by a factor of $1 \cdot 05$. Every 10-cm increase in fork length was related to an increase in bull trout movement distance by a factor of $1 \cdot 02$. Movement distances were larger during the AM versus the PM by a factor of $1 \cdot 02$. When bull trout did move, they displaced themselves an average of $400 \pm 730$ m (mean ± SD) during 12 h. However, we documented some displacements up to 7·4 km in 12 h.

### Movement direction

None of the variables were significant predictors of movement direction. Twelve-hour mean discharge magnitude did have a significant effect on the odds of moving downstream (GEE, Wald $\chi = 5 \cdot 500$, $p = 0 \cdot 019$), but only when controlling for every other candidate variable which themselves were not significant. Twelve-hour change in discharge (GEE, Wald $\chi = 0 \cdot 088$, $p = 0 \cdot 766$), water temperature (GEE, Wald $\chi = 1 \cdot 896$, $p = 0 \cdot 169$), visibility

Table II. Summary of GEE logistic regression predicting logit of odds of bull trout movement.

| Parameter | Mean ± SE | Wald $\chi$ | $p$ | 95% CI Lower | 95% CI Upper |
|---|---|---|---|---|---|
| | | | | Lower | Upper |
| *Movement odds* | | | | | |
| Intercept | −1·627 (0·599) | 7·356 | 0·007 | −2·803 | −0·451 |
| $D_{MEAN}$ | −0·092 (0·019) | 23·356 | <0·001 | −0·129 | −0·055 |
| $T_{WATER}$ | 0·239 (0·065) | 13·564 | <0·001 | 0·112 | 0·366 |
| Diel period = AM | 0·307 (0·072) | 18·130 | <0·001 | 0·166 | 0·449 |
| Diel period = PM | Ref | – | – | – | – |
| *Movement distance* | | | | | |
| Intercept | −0·287 (0·072) | 15·830 | <0·001 | −0·428 | −0·145 |
| Diel period = AM | 0·020 (0·008) | 6·649 | 0·010 | 0·005 | 0·035 |
| Diel period = PM | Ref | – | – | – | – |
| Sex = F | 0·051 | 14·987 | <0·001 | 0·025 | 0·076 |
| Sex = M | Ref | – | – | – | – |
| Length | 0·022 | 4·247 | 0·039 | 0·001 | 0·043 |

Generalized estimating equation (GEE) Negative Binomial movement distance model are summarized. Parameter estimates for movement direction were not included as no variables were significant predictors. 'Ref' refers to the level of categorical predictor used as the reference category (i.e. coded as '0'); these parameter estimates are redundant in the presence of the intercept parameter.

(GEE, Wald $\chi$ = 0·357, $p$ = 0·550), diel period (GEE, Wald $\chi$ = 3·041, $p$ = 0·081), sex (GEE, Wald $\chi$ = 1·719, $p$ = 0·190) and size (GEE, Wald $\chi$ = 0·835, $p$ = 0·361) were not significant predictors of movement direction.

## DISCUSSION

Given that the rate of energy loss for a fish to hold station against flowing water is directly proportional to water velocity, one might expect that fishes change locations during relatively higher water flows if the cost of holding station is greater than the benefit of staying.

However, we found that bull trout movements were significantly depressed at relatively higher 12-h mean discharge magnitudes. The change in discharge during the same period had no effect on movement. This suggested that maintaining position within a 100-m reach (even during maximum discharges) was within the boundaries of their swimming capacities. In fact, a companion study using EMG transmitters to measure swimming muscle activity (Taylor *et al.*, In press) found that bull trout were capable of maintaining position in a reach, across various discharge magnitudes, without beating their tail. When these fish were swimming, their swim speeds were not anywhere close to bull trout critical swimming speeds in the literature.

The fact that bull trout were stationary in a reach and did not displaced downstream during the highest magnitude flows suggested to hydropower producers that maximum discharge magnitude in the Columbia River did not exclude bull trout from their macro-scale (i.e. 100 m) habitat.

However, bull trout movements may have been depressed because their perceived cost of transport during relatively higher river flows was greater than their perceived benefit to foraging in new locations.

The effect of river flow on fish movement is inconsistent among past studies. For example, DeGrandchamp *et al.* (2008) found that monthly movements of bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. Molitrix*) were positively correlated to discharge in a hydrologically flashy tributary of the Mississippi River. Young and Isely (2007) found that striped bass movements (sampled every 2 h) in a tail race increased during daily hypolimnetic release from a dam. However, a number of other studies have found no effect of river flow on fish movement when locating fish at weekly (e.g. Cocherell *et al.*, 2010), daily (e.g. Broadhurst *et al.*, 2011) and sub-daily scales (e.g. Heggenes *et al.*, 2007).

We found evidence that water temperature was a significant predictor of movement odds. Temperature is the most significant abiotic environmental factor for fish as it controls all aspects of physiology and metabolism (Fry, 1971). Given the reduced swimming ability of fish at temperatures below a species-specific optimum (Brett, 1971; Bennett, 1990), it is no surprise that trout are less active during relatively colder temperatures. Ontogenic changes in physiology and seasonal changes in forage prey density were not investigated in this study and may also be reasons for the apparent relationship between temperature and movement. Regardless of the mechanism, our results generally corroborate past telemetry studies regarding temperature and movement. For example, Enders *et al.* (2008) found that the radial distance moved by PIT-tagged Atlantic salmon parr in a small, steep, non-regulated river

was less at low temperatures (0·0–0·9 °C) in comparison with higher temperatures (1·0–4·9 °C). Zimmer *et al.* (2010) found that cumulative upstream movement of brown trout in a temperate, urbanized watershed was positively correlated with mean weekly temperature. Temperature can presumably have the opposite effect on fish movement if it is above the optimal temperature for swimming performance. For example, Young *et al.* (2010) found that the percentage of fish moving >15 m between tracking periods (every 4 days) was negatively related to average daily water temperatures and concluded that very few fish moved when temperatures were above the thermal limit for brown trout (19 °C). The current study did not examine bull trout movements near their upper lethal thermal range (20·9 °C on the basis of acclimated chronic exposure method; Selong *et al.*, 2001).

We were surprised that visibility had no effect on movement considering that bull trout may be less at risk from predators when the ambient light levels are obscured by valley fog and clouds. This strategy would provide protection from avian and mammalian predators. Osprey, eagles, mink and otters have all been observed on the Columbia River in Revelstoke.

Knowledge of the timing of fish movements relative to changes in their environment is largely accomplished by correlative studies. Experimental manipulations of the riverine environment (e.g. flow regime and temperature) seldom occur because of the practical, logistical and financial costs. The relative contribution of each environmental driver of fish movement is difficult to assess because of the collinearity among predictors (e.g. Swanberg, 1997), the large variation in behaviour of individual fish (e.g. Scruton *et al.*, 2003) and the fact that movement response data are most often non-independent in time and space.

Traditionally, radio telemetry data were analysed using ordinary least-squares regression, ANOVA and their non-parametric counterparts (e.g. Brown *et al.*, 2001; Berland *et al.*, 2004) with little regard for issues of collinearity. We showed that GEEs are a statistical technique that can be used to control for the non-independence of observations typically found in telemetry data. Furthermore, discharge and temperature were only mildly correlated in this study ($r = 0·22$), and we specifically tested for suppressor/synergistic effects (Grafen and Hails, 2002) as a consequence of collinearity. We used odds ratios as effect sizes which are easy to understand and report on the relative contributions of predictors. Yet, we were not able to resolve all challenges using GEEs. Our movement distance model underrepresented the infrequent, long-distance movements of bull trout. Veysey *et al.* (2009) had similar challenges when modelling spotted salamander (*Ambystoma maculatum*) movement rates using mixed-effects Poisson regression.

The purpose of the study was to determine if the operational release of water from a hydropeaking dam was associated with bull trout movements. This study is one of the few examples of a study whereby fish were located at a time scale that resembles the scale of hydrologic change (see also Berland *et al.*, 2004; Scruton *et al.*, 2005; Heggenes *et al.*, 2007). Hydropeaking does have an effect on bull trout movement behaviour. From a management perspective, hydropeaking researchers may need to focus on the effects of maximum discharge magnitude, rather than rates of change, when considering the energetic consequences of altered flow regimes. Furthermore, understanding the direct consequences of movement (e.g. stationary or hyperactive) on fish fitness would increase our mechanistic understanding of population changes over time.

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