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HYDROLOGIC CORRELATES OF BULL TROUT (*SALVELINUS CONFLUENTUS*) SWIMMING ACTIVITY IN A HYDROPEAKING RIVER

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ABSTRACT

There is a growing need to develop quantitative relationships between specific components of river flow and the behavioural responses of fishes. Given this, we tested for an effect of hydrologic parameters on axial swimming muscle electromyograms of bull trout (*Salvelinus confluentus*) in a large hydropeaking river (river discharge ranging from 0 to 1790 m^3/s) while controlling for other exogenous factors such as temperature and light intensity. Hourly mean discharge had a significant positive effect ($R^2 = 0.13–0.31$; depending on the distance from the dam) on swimming muscle activity. Within-hour changes in river flow from 0 to 1045 m^3/s did not elicit a hyperactive response in bull trout. When a subset of electromyogram transmitters were calibrated to swimming speed, we found there were periods, across a range of river discharges, when bull trout were not actively beating their tails—a behaviour documented in some bottom-dwelling species associated with moving water. Not including these periods of rest, bull trout swam at median hourly speeds of 0.53 body lengths per second. Understanding fish behaviour in the context of their physical environment may help explain population-level responses to hydrologic change. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: swimming speed; bull trout; electromyogram; swimming activity; fish

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INTRODUCTION

Recent meta-analyses (e.g. Haxton and Findlay, 2008) found that fluvial fishes showed consistent negative responses (abundance, demographics and/or diversity) to changes in flow regimes. However, population-level responses cannot be linked to any specific component of flow (magnitude, frequency, timing, rate of change and duration) as these components change at timescales much shorter than population responses. Therefore, there is a need to understand the immediate, sublethal responses of fish to altered flow regimes across a range of flow manipulations under nonforced, volitional conditions (Katopodis, 2005). One such endpoint is locomotor activity, which we define as any external body movement of an animal (e.g. swimming). In fish, locomotor activity has long been used as a proxy for activity metabolism (e.g. Spencer, 1939), a large and variable part of a fishes' energy budget (Boisclair and Leggett, 1989) that can explain significant individual variance in growth rates (Marchand and Boisclair, 1998; Hölker and Breckling, 2002).

For a fluvial species to hold station in a river, it must maintain a constant position relative to the substrate despite the flow of water exerting force to displace the fish downstream (Gee, 1983). This energetic demand of swimming can be substantial and is directly related to the fish's drag and current velocity (Webb, 1988). Lab experiments have found large positive correlations between water flow and swimming activity; in fact, the effect of flow velocity on fish swim speed is evident in all swimming energetic models (Enders *et al*., 2003). However, these were forced swimming experiments whereby fish were confined to a restricted space. Free-swimming fish can use a variety of behavioural tactics to reduce the energetic costs of swimming against flowing water such as using low-flow microhabitats to reduce drag (i.e. flow refuging; Webb, 1998). For example, rainbow trout (*Oncorhynchus mykiss*) and rosyside dace (*Clinostomus funduloids*) typically swim in microhabitats with velocities substantially lower than the mean river velocity (Facey and Grossman, 1992). Furthermore, mottled sculpins (*Cottus bairdii*) and Atlantic salmon (*Salmo salar*) hold position in flow by clinging to substrates with enlarged pectoral fins that generate downward force as water passes over them (Facey and Grossman, 1990; Arnold *et al*., 1991). The inability of fishes to use these

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behaviours in an enclosed chamber has been the main criticism of forced-velocity tests. A more ecologically relevant swimming performance measure is spontaneous swimming activity of fishes in the wild. However, to date, few studies have measured routine swimming activity relative to hydrologic variables in free-swimming fish (but see Murchie and Smokorowski, 2004; Geist *et al*., 2005; Cocherell *et al*., 2011).

When discharge changes in a river, so does the spatial arrangement of energetically favourable positions (Fausch and White, 1981), and fish may shift from one suitable position to another to compensate for the changing quality of the habitat (Kraft, 1972). Despite the potential energetic consequences of this behaviour, the effect of unsteady flow (i.e. water flow varies with respect to time for a given point in space; Liao, 2007) on the behaviour of free-swimming fishes has not been well documented.

Given this, we used electromyogram (EMG) telemetry to determine if axial swimming muscle activity in free-swimming bull trout (*Salvelinus confluentus*) was correlated to two components of a river's flow regime. River discharge at our study site, the hydropeaking Columbia River, is controlled by the release of water from the Revelstoke Dam (REV). Discharge peaks last less than a day and can occur multiple times per day depending on the demand for electricity. EMGs are bioelectric voltage changes that are proportional to the degree and duration of muscle tension (Sullivan *et al*., 1963). EMGs recorded from electrodes embedded into myotomes of the red oxidative muscles can be used as quantitative indicators of overall fish activity and can be calibrated to kinematics such as tail beats (e.g. Hinch and Rand, 1998; Standen *et al*., 2002) and swimming speed (Booth *et al*., 1997; Thorstad *et al*., 2000).

Our first objective was to determine if bull trout swimming activity was elevated during peaking river flows. We specifically tested for a relationship between hourly river discharge magnitude and axial swimming muscle EMGs while controlling for individual variation in bull trout responses, as well as exogenous factors such as temperature and light. Our second objective was to determine if bull trout demonstrated heightened swimming activity during periods of within-hour fluctuations in river flow (i.e. unsteady flow). Specifically, we sought to determine the relationship between swimming activity and the degree of within-hour change in river discharge. Thirdly, we calibrated EMGs to kinematic variables (tail beats and swimming speed) with a subset of fish to estimate ecologically relevant measures of behaviour that can be compared with laboratory-derived measures of swimming performance from the literature.

METHODS

Study site and fish surgery

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

Eighty-eight bull trout were collected from the entire 10.6-km study area by boat pulsed DC electroshocker during 3 years (year 1, 24 September to 8 October 2008; year 2, 28 September to 7 October 2009; and year 3, 14–26 October 2010). Bull trout were captured at night

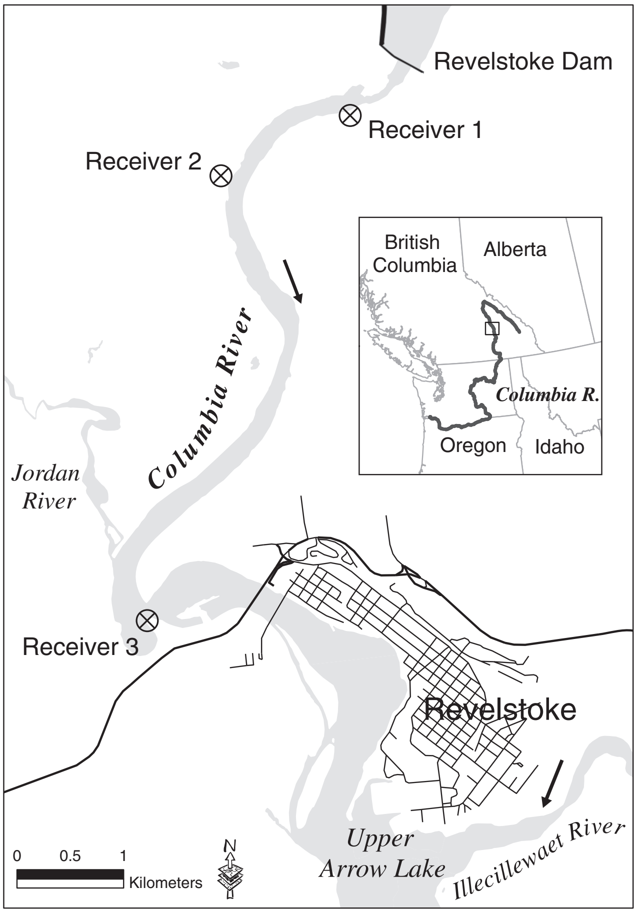

Figure 1. Map of the Columbia River downstream of Revelstoke Dam, Revelstoke, British Columbia, Canada. Study area was a 10.6-km section from Revelstoke Dam downstream to the Illecillewaet River. Circle with X represents the fixed receiver locations

using a large dip net and transferred into an on-board livewell with a recirculation pump while being relocated to the surgery site. Water temperatures at the time of capture ranged from 8°C 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 3–4 anaesthesia (Summerfelt and Smith, 1990) 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 bath of 30 ppm clove oil. By using a scalpel (number 3 blade, rounded cutting point), a ~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, ON; mean tag/body mass ratio = 1.4%, range = 0.4–2.6%). EMG electrodes were inserted ~10 mm apart, in the red axial musculature, using rods and plungers. Electrode placement was standardized at 0.7 body length on the right side of the fish (Beddow and McKinley, 1999). 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). Additional details on surgical procedures can be found in Cooke *et al*. (2004). 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 regained equilibrium and had strong responses to tail grabs, 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; details in the succeeding text).

Electromyogram data

Three fixed receiver stations (Lotek SRX600 telemetry receiver, Newmarket, ON) were locked in a weatherproof box and were deployed to log EMG data continuously where most fish were found to congregate (Figure 1), allowing for maximum continuous detections. Two antennas were fixed to a tree, side by side, with one antenna pointing upstream and the other downstream. The receiver at each fixed station scanned every channel (1–8) in succession, 24 h/day, and recorded any fish within range of the station (estimated maximum distance of 400 m upstream and downstream). Coded EMG signals were converted to hourly averages, a timescale that corresponded to a prolonged period of swimming (i.e. 20 s to 200 min; Beamish, 1978). Only hourly averaged EMG values based on at least 100 EMG measurements were used in the model.

Studies have shown that EMG transmitters may behave differently in different fish (Brown *et al*., 2007). Considering this, we tested for individual variation in intercepts and slopes when modelling the effect of discharge on uncalibrated EMGs. Because the intercepts varied across fish (Wald $Z = 3.907$, $p < 0.001$) and the intraclass correlation indicated that 27% of the variation in EMGs was among fish, we controlled for this variation using random factors under the linear mixed model framework (MIXED, SPSS Inc., Version 18, Chicago, IL). We used a reduction in variance estimate (R^2; Heck *et al*., 2010) as the effect size, which is independent of individual differences in slopes and intercepts. Preliminary analyses using ordinary least squares (OLS) regression suggested autocorrelation in the model residuals due to the repeated EMG measurements on the same fish (Durbin–Watson statistic $<< 2$). Autocorrelation plots confirmed this; therefore, we began our mixed-model analysis with an autoregressive (AR1) covariance structure. Our multilevel modelling strategy is based on that of Heck *et al*. (2010). We added predictors using a hierarchical technique, which is the practice of building successive models and assessing the response to each new predictor (Field, 2009). We started with the two main hydrologic variables: hourly discharge magnitude (D_{MAG}, defined as the average instantaneous discharge within any given hour) and within-hour change in discharge (D_{CHANGE}, is the difference between within-hour instantaneous maximum and minimum discharges). Discharge was measured from REV, and although there were periods of zero water release (i.e. $D_{\mathrm{MAG}} = 0$), some water remained in the channel as the result of residual water, leakage from REV and water backed up from the downstream Arrow Lakes reservoir. We controlled for diel period (Diel; day, night and dusk/dawn) and hourly mean water temperature (T_{WATER}). Then, we added subject-level predictors (size and sex), followed by organizational-level predictors such as the year data were logged (Year; 2008, 2009 or 2010). The categorical receiver variable (*Rec*) represented the distance from the source of discharge (three receivers, ~1, 2.5 and 7 km from the dam) from which each fish was logged. We tested for a time-lag effect of the water to reach each receiver and included a 30-min time delay for discharge at receiver 3. As our degrees of freedom were very large, most predictors were statistically significant ($p < 0.05$) in the model, despite having very small effect sizes. Therefore, only those variables that had an R^2 change >0.00 were added to the final model.

Cross-level interactions were added in an attempt to use the variation at one level to account for the variation at another. For example, the interaction between the average discharge magnitude that each fish experienced

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(D_{MAG}_mean; level 2 variable, one value per fish) and hourly discharge magnitude (level 1 variable, multiple values per fish) was added to determine if the average discharge that a bull trout experienced during the study period moderated the slope of the discharge effect. The interaction between the number of EMG observations for each fish (*#observ*) and discharge magnitude was also tested to see if fish that were observed more (or less) often had a stronger (or weaker) relationship with discharge. Following the addition of predictors, the model structure was evaluated in terms of random slopes and covariance structures using Akaike information criteria (AICs; Heck *et al.*, 2010; Field, 2009). A "variance components" covariance type for the random subject coefficients was found to be the best structure.

Because multilevel models are an extension of regression, we tested all of the assumptions of OLS regression as well as some additional assumptions pertaining to the random coefficients. We visually inspected scatter plots of all combinations of predictors to find correlations that may affect our ability to address the main hypothesis (i.e. collinearity). There was a significant correlation between hourly mean discharge magnitude and within-hour discharge rate of change ($r = 0.30$); therefore, we added these predictors to the model both alone and together so as to look for suppressor/synergistic effects (Grafen and Hails, 2002). EMG values were positively skewed; therefore, EMGs (+1) and continuous predictors were log transformed. Residuals were plotted across the range of predicted values to assess homoscedasticity, and a histogram of residuals was used to assess normality. The random intercepts and slopes were normal about their means.

Data were unbalanced for each fish owing to different levels of missing EMG data because of the detection ability of the receivers. For this reason, we tested for covariant-dependent dropout (Singer and Willett, 2003) using a generalized estimating equation (GEE) in SPSS with the binary response (detected/not detected) for every hourly averaged period. We fitted a model using a logit link with a binary distribution. The fitted GEE demonstrated that the hourly discharge rate of change did not have an effect on the odds of detection (GEE, Wald $\chi^2(1) < 0.001$, $p = 0.99$). The hourly averaged discharge magnitude did have a significant effect on the odds of receiver detection (GEE, Wald $\chi^2(1) = 15.41$, $p < 0.001$). However, the odds ratio for this effect was very small, indicating that our ability to test the effect of discharge on swimming muscle activity was not compromised by missing receiver detections.

Estimating swim speed

Because bull trout perform poorly in swim tunnels (Mesa *et al.*, 2004), we used an alternate approach previously employed for early EMG work on migrating salmon (e.g. Hinch and Rand, 1998; Standen *et al.*, 2002). We constructed a spontaneous swim chamber consisting of a 1.8-m-diameter circular polyethylene aquaculture tank with a video camera (Sony HDD 2000, Tokyo, Japan) mounted above the water surface. A submersible pump was used to create flow in a circular direction to stimulate spontaneous swimming. Each fish was held for approximately 12 h following surgery and then placed in the swim chamber. Bull trout usually faced the direction of the current and held station in one position by beating their tail at a frequency proportional to the current speed. Current speeds were adjusted randomly at a range from the minimum to maximum outputs of the pump. We did not measure actual swimming speeds; our goal was simply to record bull trout swimming at a range of EMG values and, therefore, tail beat frequencies (TBFs). The time counter on the video camera was synchronized to the counter on the EMG receiver, and fish were videotaped swimming while EMG values were recorded. Fish were monitored in the chamber for ~20 min until a range of EMGs were recorded. Upon completing swim trials, the fish were dip-netted out of the chamber and released back into the river at the surgery site (~2 km downstream from REV).

Fish swimming videos were reviewed one frame at a time, and the number of frames per tail beat (i.e. one complete oscillation of the caudal peduncle) was recorded for those periods when the fish exhibited approximately steady-state swimming. The TBF (tail beats per minute) was transcribed relative to synchronized EMG readings. We regressed TBF on EMG with, on average, 44 ± 20 (mean ± *SD*) tail beat/EMG observations for each fish. EMGs showed a different range for different fish, for example, a resting EMG (lowest EMG value) for one fish may be '12', whereas for another fish, a resting EMG may be '5'. Standardized EMGs (SEMG) were then calculated by subtracting the resting value from observed EMGs. TBF was converted to swimming speed [body lengths per second (BL/s)] using the relationship between TBF and swimming speed developed for sockeye salmon by Brett (1995). Brett (1995) let adult sockeye salmon swim in an open flume, which demonstrated a strong linear relationship between swim speeds and TBF: $BL = 0.023(TBF) - 1.286$ ($R^2 = 0.97$). For SEMG values that were less than the minimum TBF (i.e. no visible movement of the caudal peduncle), we set swimming speed to 0 BL/s. Swimming speeds were only estimated for those fish from which we had generated an individual EMG/TBF relationship. For those fish without an individual EMG/TBF relationship (i.e. subjects from 2008), uncalibrated EMGs were modelled as an indicator of relative activity.

RESULTS

Electromyogram data collection

Of eighty-eight fish tagged over 3 years, 24 male and 12 female fish (36 total; fork length = 628 ± 104 mm) yielded at least 100 hourly- averaged EMG values with each hourly average comprised of 100 instantaneous EMGs. The remainder (i) were never located in the 10.6-km study area; (ii) were located in the study area, but were not located near the three fixed receivers; or (iii) were located within range of the receivers, but for a shorter time (i.e. <100 h). We logged 378 ± 231 (mean ± *SD*) hourly mean EMG values for each fish over the course of 44 ± 17 (mean ± *SD*) days. EMGs were logged during a mean discharge of 614 m^3/s (range = 0–1790 m^3/s). The mean within-hour change in discharge was 162 m^3/s (range = 0–1045 m^3/s). The mean temperature was 9.1°C (range = 6.6–12.2°C). Ten fish were recorded from one receiver only, 17 bull trout were recorded at two receivers and nine were recorded at all three receivers.

Modelling axial swimming muscle activity

D_{MAG} had a is significant positive effect on swimming muscle activity (MIXED, $F_{(1,\ 13\,560)} = 1706.88$, $p < 0.001$). D_{CHANGE} was also a significant predictor (MIXED, $F_{(1,\ 11\,789)} = 16.45$, $p < 0.001$); however, because of the small effect (Table I), D_{CHANGE} was not added to the model. In the preceding steps, only T_{WATER} (MIXED, $F_{(1,\ 1971)} = 12.52$, $p < 0.001$) and the interaction between D_{MAG} and *Rec* were significant predictors (MIXED, $F_{(2,\ 13\,441)} = 26.55$, $p < 0.001$) and explained at least 1% of the variance of swimming muscle activity. Finally, the D_{MAG} slope varied among individual fish (Wald $Z = 3.76$, $p < 0.001$) and significantly improved AICs ($\chi^2(1) = -220$, $p < 0.001$). In the final model (Table II), D_{MAG} had the following effect (R^2) at each receiver: receiver 1 = 0.31, receiver 2 = 0.13 and receiver 3 = 0.25. Pairwise comparisons, based on estimated marginal means of log (SEMG + 1), suggest that muscle activity just downstream of REV (i.e. receiver 1) is 1.2 and 1.08 times that of muscle activity at receiver 2 (~2.5 km from REV) and receiver 3 (~7 km from REV), respectively (both comparisons $p < 0.001$).

Estimating swimming speed

During the second 2 years of the study, we successfully calibrated 27 out of a possible 56 fish. Calibrations were successful when fish were swimming consistently for a period long enough to record at least 10 tail beats/EMG data points. Of those calibrations, we consistently found a positive linear relationship between SEMG and TBF. There was a significant difference in bull trout fork lengths between sexes (GLM, $F_{(1,\ 1170)} = 6.65$, $p = 0.01$). Therefore, male and female bull trout were considered in separate

Table I. Summary steps for fitting bull trout log (EMG + 1) model

Model	Fixed effect	ΔR^2	*p*
Level 1 hydrologic predictors			
1	D_{MAG}	0.17	<0.001
2	D_{MAG}, D_{CHANGE}	0.00	<0.001
Level 1 environmental controls			
3	D_{MAG}, T_{WATER}	0.01	<0.001
4	D_{MAG}, T_{WATER}, Diel	0.00	<0.001
Level 2 subjects			
5	D_{MAG}, T_{WATER}, Size	0.00	0.04
6	D_{MAG}, T_{WATER}, Sex	0.00	0.09
Level 3 organizational			
7	D_{MAG}, T_{WATER}, Year	0.00	0.38
8	D_{MAG}, T_{WATER}, *Rec*	0.00	<0.001
Cross-level interactions			
10	D_{MAG}, T_{WATER}, *Rec*, D_{MAG} * *Rec*	0.01	<0.001
11	D_{MAG}, T_{WATER}, *Rec*, D_{MAG} * *Rec*, D_{MAG} * D_{MAG}_mean	0.00	<0.001
12	D_{MAG}, T_{WATER}, *Rec*, D_{MAG} * *Rec*, D_{MAG} * *#observ*	0.00	0.26

D_{MAG} is the hourly average discharge measured from REV; D_{CHANGE} is the difference between the within-hour instantaneous maximum and minimum discharges; T_{WATER} is the hourly average temperature; Diel is a categorical value of daytime, night time and dusk/dawn; Size is the fork length of each individual fish; Sex is male or female for each individual; Year is the year in which data were collected (2008, 2009 or 2010); *Rec* is one of three radio receivers that remotely logged fish; D_{MAG}_mean is average of all D_{MAG} within each fish; *#observ* was the total number of observations for that individual. One new predictor was added to each successive model to evaluate its individual effect size. ΔR^2 is the change in effect size from the previous model. All continuous predictors were log transformed.

Table II. Parameter estimates for linear mixed model predicting bull trout axial swimming muscle activity [log (SEMG + 1)] based on D_{MAG}, T_{WATER} and *Rec* in the Columbia River, British Columbia, Canada

Parameter	Estimate (*SE*)	*df*	*t*	95% Confidence Lower	95% Confidence Upper	*p*
Intercept	0.637 (0.069)	1005.255	9.233	0.502	0.772	<0.001
D_{MAG}	0.081 (0.008)	48.629	9.761	0.065	0.098	<0.001
T_{WATER}	−0.212 (0.061)	1931.400	−3.438	−0.332	−0.091	<0.001
*Rec*1	Reference	—	—	—	—	—
*Rec*2	0.133 (0.022)	2392.163	−5.810	−0.178	−0.088	<0.001
*Rec*3	−0.001 (0.014)	7580.376	−0.093	−0.029	−0.026	0.926
D_{MAG} * *Rec*1	Reference	—	—	—	—	—
D_{MAG} * *Rec*2	0.020 (0.008)	2391.077	2.592	−0.005	0.036	0.010
D_{MAG} * *Rec*3	−0.010 (0.005)	8892.026	−2.048	−0.019	0.000	<0.041

All continuous predictors were log transformed.

models. For male bull trout, SEMGs could significantly predict TBF (MIXED, $F_{(1,\ 813)} = 1693.58$, $p < 0.001$). The length of the fish was not significant (MIXED, $F_{(1,\ 19)} = 2.16$, $p = 0.16$), nor was the interaction between length and SEMG (MIXED, $F_{(1,\ 811)} = 0.03$, $p = 0.86$). Furthermore, the relationship between SEMG and TBF showed a significant variance in intercepts (Wald $Z = 2.632$, $p = 0.01$) and slopes (Wald $Z = 2.604$, $p = 0.01$) among fish, demonstrating that a group model to estimate TBF from all fish would not be appropriate.

For female bull trout, SEMGs could significantly predict TBF (MIXED, $F_{(1,\ 352)} = 116.22$, $p < 0.001$). The length of the fish was not significant (MIXED, $F_{(1,\ 8)} = 2.00$, $p = 0.19$), nor was the interaction between length and SEMG (MIXED, $F_{(1,\ 349)} = 0.35$, $p = 0.55$). Although the relationship between SEMG and TBF did not show significant variance in intercepts (Wald $Z = 1.54$, $p = 0.12$) and slopes (Wald $Z = 1.35$, $p = 0.18$), a grouped calibration model could only explain 43% of the variance in TBF. On average, a fish's individual relationship between TBF and SEMG was more accurate (mean $R^2 = 0.68$) than the group calibration model. Therefore, we estimated swim speeds using individual TBF/SEMG relationships only for those individuals that were successfully calibrated and for which we recorded EMG values in the field ($N = 14$; Figure 2).

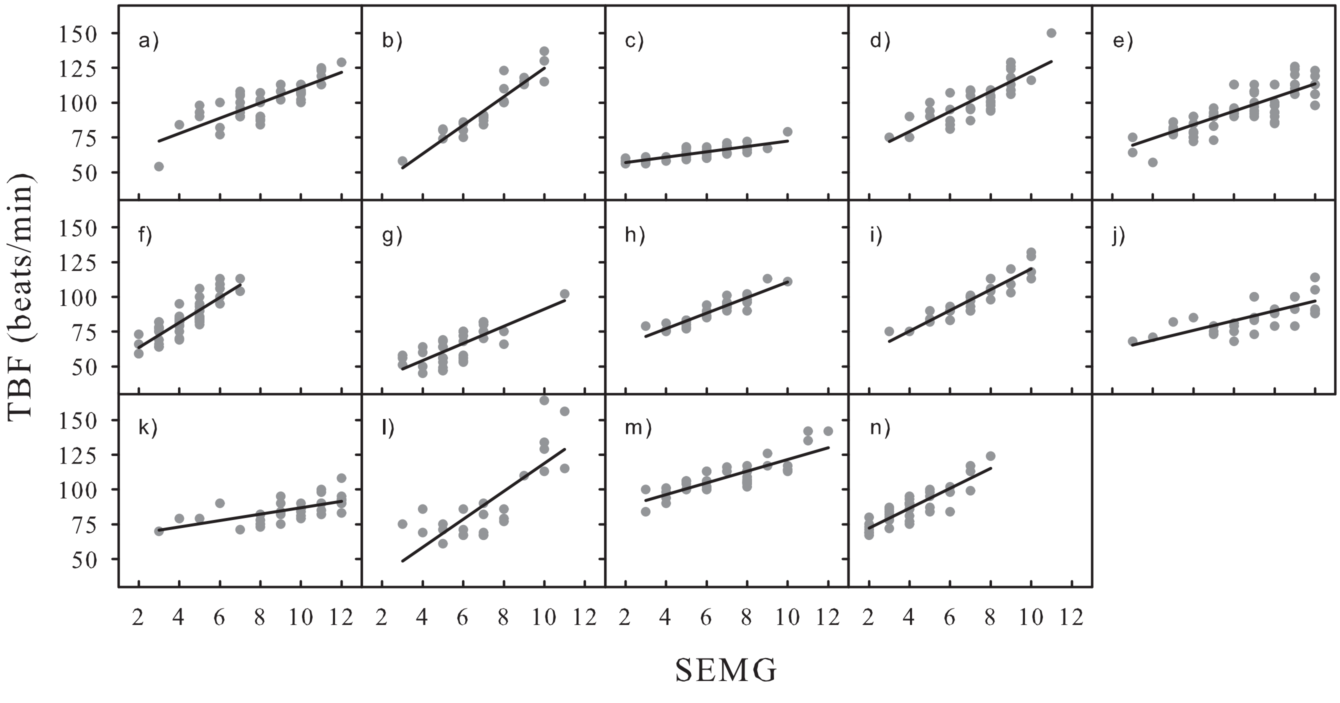

Figure 2. Scatter plot of the relationship between bull trout SEMG and tail beat frequency (TBF; beats/min). Mean R^2 ($\pm SD$) $= 0.68 \pm 0.14$

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Many of the SEMG values recorded from the field (64%) were of a low range (1–3; depending on the fish) that corresponded to a value below the minimum axial muscle activity needed to power a tail beat and initiate undulatory swimming. Not including zero tail beats, the median [±interquartile range (IQR)] TBF was 74 ± 18 beats/min. Correspondingly, estimated swimming speeds were zero inflated (large peak at 0 BL/s) and showed a right-skewed distribution. Not including the zero swimming speeds, on an hourly scale, bull trout swam at a preferred swim speed of 0.53 ± 0.27 BL/s (median, ±IQR).

DISCUSSION

Our first objective was to determine if bull trout swimming activity was elevated during peaking river flows. There was a significant positive relationship between river discharge magnitude and axial swimming muscle activity. Given that the rate of energy loss for a fish to hold station is directly proportional to water velocity, one might expect that fish may increase swimming activity at higher river discharges. Lab experiments have found large positive correlations between water velocities and swimming activity. In fact, the effect of flow velocity on fish swim speed is evident in all swimming energetic models (Enders *et al*., 2003).

However, a large amount of variance in bull trout muscle activity was left unexplained by discharge. And, when muscle activity was related to swimming speeds, these fish were most often not beating their tail. This suggested that they were able to maintain position in the river with smaller energetic costs compared to using the undulatory motion of their swimming muscles. Although we did not make direct observations on the fish, there are a number of behaviours that could allow fishes to maintain position in flowing water without beating their tail. For example, ‘flow refuging’ (Webb, 1998) allows fish to avoid the high costs of swimming by positioning themselves in low-flow microhabitats. Bull trout may have been station holding against the substrate or behind physical obstructions whereby velocity is reduced (Fish, 2010), which may explain the presence of some hours of relatively low muscle activity during high discharges. Maintaining contact with a solid bottom surface has been observed in bull trout swimming in tunnels (e.g. Mesa *et al*., 2004) and in the wild by snorkelling observations (e.g. Swanberg, 1997). This study demonstrated that bull trout are capable of maintaining position without beating their tail under a range of average river velocities. Our crude proxy for river velocity (i.e. hourly average river discharge measured at REV) did not take into account the fine-scale microhabitat created by physical obstructions and substrate. However, the fact that bull trout have the capacity to maintain position in a river without swimming reminds us that the direct relationships between water flows and swimming speeds derived from the laboratory may be tenuous when applied to free-swimming fishes.

Facey and Grossman (1992) used the relationship between water velocity and metabolic rate of four species of fishes in the laboratory (Facey and Grossman, 1990) to estimate metabolic rate of fishes in the field, based on snout velocities measured by snorkellers (Facey and Grossman, 1992). Rainbow trout and rosyside dace were over-represented at lower velocities, as predicted by the energetic cost hypothesis (Facey and Grossman, 1992). Mottled sculpin and rosyside dace were able to hold position without swimming by clinging to the substrate or by using enlarged pectoral fins to generate downward pressure (i.e. negative lift), which is a behaviour also observed in Atlantic salmon parr (Arnold *et al*., 1991). Furthermore, Geist *et al*. (2005) found that light levels and temperature, but not discharge, were related to swimming speeds and oxygen consumption of juvenile white sturgeon (*Acipenser transmontanus*) in the Snake River, Idaho.

Some prolonged feeding attempts likely occurred at opportunistic times when discharges were not necessarily high, thus resulting in activity values that were greater than average for a given discharge. However, very few hourly average swimming speeds were observed in the upper range of speeds (>1.35 BL/s), a value that is well below critical swimming velocities of bull trout estimated by Mesa *et al*. (2004). Swimming speed estimates suggested that bull trout spend the majority of their time not actively swimming despite maintaining position in the river. EMG values below their minimum swim speed may simply reflect the muscle tension required to maintain positive rheotaxis without actually beating their tail.

Our second objective was to determine if bull trout swimming activity was elevated during within-hour fluctuations in river flow. No relationship between swimming activity and the degree of within-hour change in river discharge was evident. Similarly, Murchie and Smokorowski (2004) found that periods of changing discharge (up-ramping and down-ramping) had no greater effect on activity than relatively stable discharges in the Magpie River, Ontario. A number of other studies have found no effect of short-term changes in river discharge on fish movement when locating fish at weekly (Cocherell *et al*., 2011), daily (e.g. Broadhurst *et al*., 2011) and subdaily scales (e.g. Heggenes *et al*., 2007). From a management perspective, this suggested that 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. In contrast, microhabitat use by fishes, as influenced by changing flows, has been documented by snorkelling observations (Pert and Erman, 1994),

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electrofishing (Valentin *et al*., 1994) and conventional positional radio telemetry (Bunt *et al*., 1999). Furthermore, Cocherell *et al*. (2011) found that rainbow trout had significantly higher swimming activity during the initial peaking phase of flow releases in the American River, California.

The relationship between discharge and SEMG was also significantly different at each receiver but did not follow a downstream attenuation pattern. The discharge/SEMG relationship was strongest downstream of the tailrace and at 7.0 km and was weakest at 2.5 km from the dam. Channel morphology and habitat structure have been found to moderate the effect of river flow on fish swimming activity (e.g. Hinch and Rand, 1998). Although we did not measure habitat structure at each receiver site, more complex underwater habitat (i.e. presence of logs, rocks or gravel bars) at receiver site 2 may disrupt river flow, providing refuge and reducing the effect of discharge.

Some researchers have found that the TBF/swim speed relationship remains the same across temperatures (e.g. Beddow and McKinley, 1999; Geist *et al*., 2000), whereas others have found that it changes (e.g. Taylor *et al*., 1996; Booth *et al*., 1997) possibly because of an increased mass of slow muscle and more effective tail beats (greater stride length at lower frequencies; Taylor *et al*., 1996). Our calibrations were completed at temperatures from 10°C to 12°C, whereas EMGs were logged in the field from 6°C to 12°C, so it is possible that we may have underestimated swimming speeds at temperatures lower than our calibration temperatures.

A diversity of swimming responses to discharge was seen among individual bull trout as demonstrated by the addition of the random intercept and slope coefficients in the SEMG model. Although the topic of individual variation in locomotor performance is of interest to fish physiologists (Kolok, 1999), it is unclear whether individual variation in the slopes and intercepts in our uncalibrated EMG model is due to the transmitters themselves or the actual performances of individuals (Brown *et al*., 2007). Therefore, we controlled for this individual variation using random coefficients while focusing on the main effect of hydrology. We used R^2 as our effect size, which is independent of intercepts and slopes, and therefore, these effect sizes should be interpretable as individual variation in the actual behavioural response of fish. We observed a range of discharge effect sizes ($R^2 = 0.01–0.50$) from individual fish. This may have been due to individual variation in microhabitats that are utilized by bull trout.

Receivers were positioned in areas where the majority of bull trout resided in the study area during year 1, and consequently, 59% of bull trout from year 1 were recorded at these receivers for at least 100 continuous (or noncontinuous) hours. However, only 40% and 19% of bull trout released in years 2 and 3 were logged for the minimum amount of time to be included in the model. These minimum thresholds were chosen somewhat arbitrarily, but our modelling suggested that the number of observations per individual fish did not moderate the effect of discharge. The number of bull trout logged at the receivers decreased after year 1. Although it was possible that some fish died because of the direct or indirect effects of tagging and calibration, no dead fish were found during the course of the study. Furthermore, 14 transmitters were returned by anglers from bull trout caught in the reservoir (downstream of the study area; Figure 1) over 3 years, and these fish were reported to be in good general condition with incisions completely healed. We assumed that a large number of bull trout experienced 'fallback' (Frank *et al*., 2009); the downstream movements of fishes post-tagging have been documented in many telemetry studies (e.g. Bernard and Hasbrouck, 1999; Mäkinen *et al*., 2000). Because the focus of the study was on the effects of discharge in a riverine environment, we did not attempt to locate these fish downstream of the 10.6-km riverine study area, nor would we have been very successful considering the attenuation of radio signals in deep reservoir water.

The common variable associated with a potential increase in bull trout fallback was the calibration procedure in years 2 and 3. Confinement and handling can cause physiological stress (e.g. Vijayan *et al*., 1997). Capture, tagging and calibration required being netted and moved from a number of different novel environments (boat live well, holding pool, surgery table, calibration swim flume, etc.). Of the bull trout from which we did log EMG signals, we also assumed that their swimming behaviour was normal. Studies have explicitly tested for and found no effect of EMG transmitters on swimming performance of rainbow trout and Atlantic salmon (Beddow and McKinley, 1999; Cocherell *et al*., 2011).

This study has shown that the effect of river discharge, as a proxy for river velocity, may be moderated by behavioural traits that are not accounted for in traditional lab studies using enclosed swim flumes. Although the study could not replicate the detail of observations possible in controlled laboratory experiments, this work did improve on existing studies using free-swimming fishes, which paves the way for further advances. Considering that ubiquitous flow alteration threatens river biodiversity at the global scale (Nilsson *et al*., 2005), much effort is needed to develop scientifically defensible guidelines for developing flow standards that can be applied to all rivers (i.e. environmental flows; Poff and Zimmerman, 2010). Although this paper did not directly support such efforts, it did contribute to the overall understanding of how these fish cope from a behavioural and energetic perspective with their seemingly challenging environment. Understanding the relationship of fishes with their physical environment is important to help explain population-level responses to hydrologic changes, which cannot be derived from traditional stock assessment models.

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