The behaviour and physiology of bull trout (Salvelinus confluentus) and mountain whitefish (Prosopium williamsoni) relative to short-term changes in river flow

by

Mark K. Taylor

A thesis submitted to the Faculty of Graduate and Postdoctoral
Affairs in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy

in

Biology

Carleton University
Ottawa, Ontario

Dedication

This thesis is dedicated to the Taylor family, especially my parents, for providing their unconditional support throughout all my life’s endeavours.

Acknowledgements

I would like to thank BC Hydro (Karen Bray and Guy Martel) as this work was performed under contract from the BC Hydro Water Licence Requirements. I also acknowledge the support of Golder Associates, especially Bronwen Lewis, Dustin Ford and Dana Schmidt. My field work would not have been completed without the efforts of Caleb Hasler, Alex Nagrodski, Natalie Stafl and Kathy Mai. I extend a sincere thanks to my thesis committee, Scott Findlay and Lenore Fahrig, for their guidance and polite encouragement. Scott Findlay and Andy Field's contribution to my quantitative skills learning was invaluable. Finally, my greatest appreciation is towards Steven Cooke for providing an unlikely graduate student with the greatest adventure of my life.

Abstract

The purpose of this thesis was to evaluate the sub-lethal responses of bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*) relative to unsteady river flows. Within-hour changes in river flow did not elicit hyperactive responses in either fish which suggested that hydropeaking was no more energetically costly than a stable flow regime. Considering that bull trout were able to maintain position for periods of time without beating their tail and reach-scale movements were depressed at high discharge, they were not at risk of washing out of the study reach. The majority of the variance in mountain whitefish swimming muscle activity was not related to the discharge hydrograph and blood physiology provided no evidence of a stress response or anaerobic swimming. Taken together, these results suggested that the activity metabolism portion of the energy budgets of these fish are not modulated by hydropeaking; further studies should examine feeding and growth.

Co-authorship

Meta-analyses of the effects of river flow on fish movement and activity. MK Taylor and SJ Cooke.

This study was conceived by Taylor and Cooke. Taylor performed all the analyses. Taylor and Cooke provided the interpretation. All writing was conducted by Taylor. The manuscript has been published with the following citation:

Taylor MK and Cooke SJ. 2012. Meta-analyses of the effects of river flow on fish movement and activity. Environmental Reviews **20**:211-212.

Reach-scale movements of bull trout (*Salvelinus confluentus*) relative to hydropeaking operations in the Columbia River, Canada. MK Taylor, CT Hasler, SG Hinch, B Lewis, DC Schmidt and SJ Cooke

While this study was my own, the work was a collaborative effort requiring the valuable assistance of my co-authors. The project was conceived by Cooke, Hinch and Schmidt. Fish captures were coordinated by Lewis. Telemetry field work was conducted by Taylor and Hasler. Telemetry data processing/management was performed by Taylor and Hasler. All data analysis was conducted by Taylor. Data were interpreted by Taylor, Hasler, Hinch, Lewis and Schmidt. All writing was conducted by Taylor. All coauthors provided feedback and comments on the manuscript. The manuscript is in review with Ecohydrology

Hydrologic correlates of bull trout (*Salvelinus confluentus*) swimming activity in a hydropeaking river. MK Taylor, CT Hasler, CS Findlay, B Lewis, DC Schmidt, SG Hinch and SJ Cooke.

While this study was my own, the work was a collaborative effort requiring the valuable assistance of my co-authors. The project was conceived by Cooke, Hinch and Schmidt. Fish captures were coordinated by Lewis. Telemetry field work was conducted by Taylor, Hasler and Lewis. Telemetry data processing/management was performed by Taylor and Hasler. All data analysis was conducted by Taylor with help from Findlay. Data were interpreted by Taylor, Hasler, Hinch, Findlay and Schmidt. All writing was conducted by Taylor. All coauthors provided feedback and comments on the manuscript. The manuscript is in review with River Research and Applications.

Behaviour and physiology of mountain whitefish (*Prosopium williamsoni)* relative to short-term changes in river flow. MK Taylor, KV Cook, CT Hasler, DC Schmidt and SJ Cooke.

While this study was my own, the work was a collaborative effort requiring the valuable assistance of my co-authors. The project was conceived by Cooke, Hasler and Schmidt. Fish captures were coordinated by Lewis. Telemetry field work was conducted by Taylor, Hasler and Lewis. Telemetry data processing/management was performed by Taylor and Hasler. Physiology sample collection was done by Taylor and Cook. Blood cortisol laboratory analysis performed by Cook. All data analysis was conducted by Taylor. Data were interpreted by Taylor, Hasler, Cook and Schmidt. All writing was conducted by Taylor. All coauthors provided feedback and comments on the manuscript. The manuscript has been published with the following citation:

Taylor MK, Cook KV, Hasler CT, Schmidt DC and Cooke SJ. 2012. Behaviour and physiology of mountain whitefish (*Prosopium williamsoni)* relative to short-term changes in river flow. Ecology of Freshwater Fish **21**: 609-616.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

Altered flow regimes

The community structure of rivers depends largely on the quantity and timing of its water supply (Poff et al. 1997). Intra- and interannual patterns in river discharge define disturbance regimes that promote habitat heterogeneity (Tockner et al. 2000) and provide longitudinal and lateral access to spawning, recruitment, and foraging habitats (Junk et al. 1989). Extreme events such as floods and drought select for specific life histories (Lytle and Poff 2004; Mims and Olden 2012) and can have detrimental impacts on the fitness of aquatic organisms (e.g., Weyers et al. 2003; Xu et al. 2010; Young et al. 2010). The range of flow variation over recent historical time is referred to as the natural flow regime and can be described by five critical components: the magnitude, frequency, duration, timing and rate of change of hydrologic conditions (Poff et al. 1997). These components can be used to characterize the entire range of flow and the ecological consequences of particular human activities can be considered explicitly by defining flow regimes in these terms (Poff et al. 1997).

Hydropower regulation is one anthropogenic impact that artificially changes river flow. In particular, hydropeaking is an operational strategy used by hydro utilities in which river water is stored in a reservoir and released at different rates depending on the demand for electricity. The regulation of water release downstream of a dam can lead to diurnally and seasonally variable water pulses–often rapid and short term-in the river below the power station (Cushman 1985). Altered flows is used as an umbrella term that includes turbulence (i.e. chaotic vertical flows of multiple strengths and sizes superimposed on a mean velocity; Liao 2007) and unsteady flows (i.e. flows in which the velocity varies spatially or temporally relative to the earth frame of reference; Liao 2007). Quantitative reviews of ecological responses to altered flow regimes (i.e. Haxton and Findlay 2008; Poff and Zimmerman 2010) found that fishes consistently responded negatively to changes in flow magnitude (irrespective of the direction of flow change). In fact, there is growing recognition that river flow (extreme low and peak flows) can affect the growth (Weyers et al. 2003; Korman & Campana 2009), abundance (Liebig et al. 1999) and mortality (e.g., Weyers et al. 2003; Xu et al. 2010; Young et al. 2010) of fishes. Yet, there is less known about underlying mechanisms to explain these effects.

Sub-lethal responses of fishes

One of the challenges in understanding the impacts of altered flow regimes on downstream biota is that changes at the community and population level can take years of monitoring to assess (e.g., Penczak et al. 2004; Lamouroux et al. 2006). Furthermore, population change cannot be linked to any specific component of flow (magnitude, frequency, timing, rate of change and duration) as flow changes occur on a daily and hourly basis; a time scale much too short to measure population response. Therefore, there is a need to understand the immediate, sub-lethal responses of fish to altered flow regimes across a range of flow manipulations under non-forced, volitional conditions (Katopodis 2005).

Fish movement (physical displacement from one position to another) studies are useful to understand mechanisms explaining the effects of river flow on population abundance and structure, because properties of the physical environment (e.g., water velocity, temperature) modulate the distribution of fish, largely through their effect on swimming performance (Domenici and Kapour 2010). Movement is also among the most important of behaviours because it allows animals to respond to changing environmental conditions to maximize growth, survival and reproductive success (Kahler et al. 2001). For example, pulse flows may impact community structure and survival when fish are forced downstream away from preferred habitat. Indeed, abrupt changes in water discharge have been documented to cause “wash-out” in juvenile fishes (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000), presumably because of their reduced swimming performance relative to large-bodied fishes. For example, Heggenes and Traaen (1988) found that salmonid fry were eventually forced downstream when they were subjected to increasing velocities in a series of steps (velocity increments). Displacement from habitats with water velocities above maximum swimming speeds has resulted in mortality (e.g., Quinn and Peterson 1996). Out of concern for downstream forcing of adult fishes, researchers have attempted to document fish movements relative to river discharge 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) while others showed no effect (e.g., Heggenes et al. 2007).

A second relevant sub-lethal response is locomotor activity which is defined as any external body movement of an animal (e.g., swimming). In fish, swimming 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 that can explain significant variances in individual growth rates (Boisclair and Leggett, 1989; Marchand and Boisclair, 1998; Hölker and Breckling, 2002). Studies have examined the effects of various stressors on forced swimming performance using swim tunnels that produce water velocities at defined speeds which elicit station-holding responses in fish (see Beamish 1978). Impairments of swimming performance or stamina are measured in terms of maximum sustained swimming speed, critical velocity, or time to exhaustion (Katopodis and Gervais 2012). The majority of the stressor-induced studies looked for impairments in swimming performance caused by aquatic toxicants such as ammonia (Shingles et al. 2001) and copper (Waiwood and Beamish 1978) with fewer studies examining the effect of water flow parameters such as flow magnitude or turbulence (but see Enders et al. 2003 and Nikora et al. 2003).

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, because these studies use fish that are contained within a chamber (i.e. forced swimming), fish have limited opportunity to use behavioural strategies to reduce drag such as "flow refuging" - minimizing the energetic costs of swimming by taking advantage of low flow microhabitats such as pools, behind physical obstructions, or within the boundary flow against a solid surface (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. Furthermore, mottled sculpins (*Cottus bairdii)* and Atlantic salmon (*Salmo salar* L.) hold position in flow by clinging to substrate with enlarged pectoral fins that generate downward force as water passes over them (Facey and Grossman 1990; Arnold et al. 1991). The inability of fish to use these 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 in the wild. Yet, activity estimates of wild fishes are scarce in the literature; therefore, the relationship between water flow and swimming activity in free-swimming fishes is largely unknown.

A third method to evaluate the sub-lethal response of free-swimming fishes to altered river flows is by measuring blood-borne physiological variables (parameters that have some relevance to fitness) in relation to river flow. Over the last three decades, endocrinologists have developed minimally invasive sampling techniques to measure hormone levels in wild animals in response to various human-related stressors (e.g., Wasser et al. 1997; Millspaugh and Washburn 2004; Hasler et al. 2009a; Donaldson et al. 2010). This type of research usually focused on measuring glucocorticoid (GC) hormones as a marker for stress (we defined a stress response as the suite of physiological and behavioural mechanisms used to cope with a noxious stimulus; Romero (2004)).

Release of cortisol, the primary GC in fish, is delayed post-contact with the stressor. Therefore, if cortisol is sampled properly, obtained values are not influenced by capture stress and can provide baseline GC concentrations (Gamperl et al. 1994). If a stress response remains uncorrected for days or weeks, the result is chronic stress which is detrimental to health and fitness (Busch & Hayward 2009). The use of stress physiology to indentify hydropower-induced stressors has been accomplished sparingly, despite the excellent potential to do so (Hasler et al. 2009a). Flodmark et al. (2002) exposed juvenile brown trout (*Salmo trutta*) to fluctuations in water flow to simulate hydropeaking conditions. When subjected to daily cyclical fluctuations over 7 days, plasma cortisol levels were significantly elevated on the first day compared to undisturbed fish. However, on the fourth and seventh day, no elevation in plasma cortisol above control levels was observed, thus indicating a habituation response to unsteady flow. This suggested that prior experience with heightened flow magnitude is an important factor in flow-related stress physiology and hydropower regulators can benefit from knowing that predictable flow pulses may be less harmful to fish than unpredictable ones.

Objectives

The overall purpose of this thesis is to evaluate the sub-lethal responses of bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*) in relation to unsteady river flow at multiple scales (between- and among-hours). Prior to my own data collection, I conducted meta-analyses on the topics of river flow and fish movement and activity (Chapter 2). My objective was to quantify the overall population effects and identify central trends across a multitude of studies while avoiding the biases associated with narrative reviews. This allowed me to better place my movement results in the context of what is known/has been done. In Chapter 3, I examined reach scale movements (> 100 meters) of bull trout, determined by tracking radio-telemetered fish during hydropeaking events in the Columbia River. Specifically, I determined if river flow parameters (12-hour discharge magnitude and rate of change) had effects on bull trout movement while controlling for other factors such as temperature and light.

Radio-tracking my study species resulted in movement estimates at a relatively coarse scale (> 100m). Given this, I used electromyogram telemetry (details can be found in subsequent chapters of this thesis and in Cooke et al. 2004) to record fine-scale swimming activity of bull trout and mountain whitefish in response to hydrologic parameters associated with steady and unsteady river flows in the Columbia River. The objective was to determine if there was a statistical effect of peaking river flows on bull trout and mountain whitefish swimming activity (Chapters 4 and 5). Specifically, I regressed axial swimming muscle electromyograms against hourly river discharge magnitude while controlling for the individual variation in fish responses, as well as exogenous factors such as temperature and light. When discharge changes in a river, so does the spatial arrangement of energetically favourable positions and fish may shift from one position to another to compensate for the changing habitat quality (Kraft 1972). Given this, our second objective was to determine if within-hour fluctuations in river flow (i.e. hourly rate of change) had an effect on fish swimming activity.

Furthermore, I related relative swimming muscle activity of bull trout to swimming speeds using a spontaneous swimming chamber (i.e. the fish is not enclosed). Estimated swimming speeds from free-swimming bull trout were compared to bull trout critical swimming speeds from the literature. In chapter 5, I paired activity data with physiological blood parameters to determine if mountain whitefish were exhibiting a stress response during high (or low) river flows. I measured baseline plasma cortisol in mountain whitefish to determine if elevated (or reduced) river discharges were associated with GC release. I also measured lactate concentrations relative to river discharge from a different set of free-swimming mountain whitefish to test for evidence of exhaustive exercise (i.e. burst-type swimming).

Study area

The Revelstoke Dam (REV) is Canada's tallest hydropower dam and is located on the Columbia River in the town of Revelstoke, B.C. REV was brought into service in 1984 and was constructed primarily to control flooding in downstream areas (lower Columbia River, U.S.A). However, using the combined storage capacity of Revelstoke Reservoir and the upstream Kinbasket Reservoir (impounded by Mica Dam), REV also generates electricity. This hydropower facility provides 16 % of British Columbia's (BC) total hydroelectric capacity. The hydropower utility (i.e., BC Hydro) controls the release of water through turbines and thus 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, depending on the demand for electricity.

Species

REV is a barrier to bull trout migrations (McPhail and Baxter, 1996), consequently these fish are forced to carry out their life history within the confines of Revelstoke and Arrow Lakes (Hugh Keenleyside Dam dam is a downstream barrier to migration). These barriers have made large sections of the Columbia River unavailable to bull trout. In the Columbia River, bull trout often attain a large size and have a reputation as aggressive predators (McPhail and Baxter, 1996). Their large body size is a direct result of their piscivorous feeding behaviour, as they eat species such as kokanee (*Oncorhynchus nerka*) and mountain whitefish (McPhail and Murray, 1979).

Mountain whitefish are widespread in BC and western Alberta and although a lotic dwelling species, they also occupy lakes and reservoirs. Adult habitat is variable, consisting of shallow riffles, moderate runs and deep pools (Northcote and Ennis, 1994). Mountain whitefish feed on aquatic invertebrates. However, in this study reach, zooplankton are the majority of their diet (B. Lewis, Golder Associates, personal communication). These two fish species were chosen for this study as they are sufficiently abundant within the study reach and can be readily captured. Moreover, in BC bull trout are “blue listed”, a designation recognizing that populations are regionally at risk.

CHAPTER 2: META-ANALYSES OF THE EFFECTS OF RIVER FLOW ON FISH MOVEMENT AND ACTIVITY

Abstract

Estimating the timing and magnitude of fish movements relative to environmental factors can provide insight into why fishes behave as they do. In order to make broad-level inferences about fish movement in lotic environments, we conducted random-effects meta-analyses on the effects of river flow magnitude on (i) non-migratory movements, (ii) upstream migratory movements, (iii) downstream migratory movements and (iv) fine-scale activity. We found a significant positive effect of river discharge on non-migratory movements ($\bar{r}$ = 0.41 (mean) ± 0.07 (SE), Z = 6.06, $p < 0.01$, k (sample size) = 27); fishes made larger/more frequent movements during periods of elevated discharge. Furthermore, non-salmonids were more affected by river flow than salmonids. River discharge also had a significant positive effect on the rate/frequency/probability of upstream migratory movements ($\bar{r}$ = 0.23 ± 0.10, Z = 2.24, $p < 0.05$, k = 8). However, the effect of discharge on the rate of downstream migratory movements ($\bar{r}$ = -0.05 ± 0.15, Z = -0.35, $p > 0.05$, k = 5) and fine-scale activity ($\bar{r}$ = 0.01 ± 0.11, Z = 0.08, $p > 0.05$, k = 5) were not significant. Heterogeneity of effect sizes was evident in all meta-analyses as well as inclusion and/or publication bias. Collectively, our meta-analyses suggested that changes to a river's flow regime can modulate non-migratory fish behaviour, the consequences of which need to be explored in terms of habitat use and energy budgets. However, more studies are needed to examine potential effect modifiers and improve sample sizes overall.

Introduction

There is growing recognition that alterations to river flow regimes threaten the biodiversity and ecosystem functions of rivers on a global scale (Nilsson et al. 2005). Transportation, water supply, flood control, agriculture and power generation can profoundly alter natural flow regimes (Poff et al.1997). Furthermore, climate change during the 21st century is expected to affect the magnitude and timing of low- and peak-flow events, especially in snowmelt dominated basins, producing hydrographs that are more similar to those of regulated rivers (Adam et al. 2009; Mantua et al. 2010). Given this, there is a need to develop a general quantitative understanding of aquatic ecosystem responses to various degrees of flow alteration to help support scientifically defensible flow standards that could be applied to rivers in the face of global environmental change (Poff and Zimmerman 2010).

Artificial increases in discharge are usually caused by “pulse flows” or “hydropeaking” in which water is retained in a reservoir and released as temporally variable water pulses downstream of a power station. However, river floods are an analogous event that increases river discharge, often very quickly, beyond its mean value and can also have detrimental effects on fish survival (e.g., Xu et al. 2010; Young et al. 2010). While natural flow regimes are inherently variable (Poff et al. 1997), which has contributed to the evolution of organisms highly adapted to dynamic conditions (Giller and Malmqvist 1998), extreme flood events and anthropogenic flow alterations may be significant challenges for fish.

Despite literature documenting negative effects of unpredictable spates of water flow on river/stream fishes (e.g., Haxton and Findlay 2008), there is less research investigating mechanisms to explain these population/community scale changes. Movement studies are useful because properties of the physical environment (e.g., river velocity, temperature) modulate the distribution of fish, largely through their effect on fish swimming performance (Domenici and Kapour 2010). For example, pulse flows may impact community structure and survival when fish are forced downstream away from preferred habitat. Indeed, abrupt changes in stream discharge have been documented to cause "wash-out" in juvenile fishes (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000), presumably because of their reduced swimming performance relative to large-bodied fishes. Out of concern for downstream forcing of adult fish, researchers have attempted to document their movements relative to river discharge. While some studies have found a significant effect of river flow on fish movement (e.g., Simpson and Mapleston 2002; Young et al. 2010), others have not (e.g., Scruton et al. 2005; Enders et al. 2008). Movement also enables migration between habitats used by different life-history stages. A number of studies have examined the effect of river flow on fish migrations and have found the timing to be correlated with both increases and decreases in the discharge hydrograph (e.g., Almeida et al. 2002; Miller and Scarnecchia 2008).

The precision of telemetry locations used to estimate fish movements is best suited for quantifying movement at a relatively coarse scale, and do not account for localized movements (< 1 meter; Lucas and Baras 2000). Fish can expend energy swimming to hold station against a river current without actually displacing themselves (Gee 1983). Therefore, swimming activity - specifically referring to the fine scale movements associated with swimming – is also relevant to the fitness and survival of fishes (Boisclair and Leggett 1989). Researchers have tested the effects of river flow on fish activity (e.g., Cocherell et al. 2011) with interest in determining the mechanisms to explain reduced growth associated with altered flow regimes (e.g., Korman and Campana 2009).

Given the conflicting knowledge on the effect of river flow on fish movement, migration and activity, we conducted meta-analyses on these topics. Our objective was to quantify the overall population effects and identify central trends across a multitude of studies to avoid the biases associated with narrative reviews. Meta-analyses are a more objective method of review (Schmidt 1992) using statistical techniques to synthesize assimilated independent studies while generating a measure of uncertainty for the average effect size. Originally used in medicine and epidemiology, meta-analyses are becoming increasingly used in natural sciences as part of evidence-based conservation (Pullin and Stewart 2006).

Methods

Data collection

We assembled relevant studies cited in our personal collections and then searched Web of Science database for studies that modeled the effect of some metric of river flow (e.g., river discharge or velocity) on fish non-migratory movements, upstream migratory movements, downstream migratory movements and fine-scale activity. Specifically, our searches used "flow", "discharge" and "flood" to describe river hydrology and fish "movement", "migration" and "activity" to describe behaviour. The citations from the top ten relevant papers in each category were then reviewed for additional studies. The searches yielded 135 references on the appropriate topic. Many studies examined the environmental correlates of fish migration using fish captures at dams, ladders, weirs and traps to quantify migration timing or dam passage (38). These studies were not used as it was unclear how river flow interacted with the fish passage structures to affect attraction/passage efficiency. Five movement studies that used mark-recapture techniques were also excluded as sample sizes (i.e. number of fish recaptured; often in the hundreds) were not compatible with sample sizes from electronic tagging studies (telemetry, PIT). Including mark-recapture studies would have biased results of our weighted meta-analysis (sample sizes were used to estimate variance associated with each effect size; see below).

Ten studies specifically examined the downstream forcing of juveniles and fry by high water velocity (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000). These studies were all conducted using artificial stream channels with some sort of downstream trap for counting "washed-out" individuals. Since these studies were not using free-ranging fish and did not actually quantify movement, we excluded them from the meta-analyses. Three studies examined the effect of changing vs. stable discharge on movement and activity. While these analyses were of interest to us, there were simply too few studies in this category to be effectively meta-analyzed.

This manuscript exclusively relied on electronic tagging studies (telemetry and PIT technologies) of free-ranging fish (78). However, many of these studies did not use quantitative methods or did not report enough detail in their statistics (33). For example, some manuscripts simply reported "no significant correlations were found". Others reported F-values and degrees of freedom (from which an effect size can be calculated), but did not indicate the direction of their non-significant effect (e.g., Berland et al. 2004; Cocherall et al. 2010). Three studies reported statistics on individual fish or reported an effect size for a multi-parameter model rather than partial correlations. Two studies reported AICs, but not effect sizes. Other researchers could not separate the effect of discharge from other factors that covaried with discharge such as temperature and season (5 studies). Finally, one study was excluded because of poor study design and one other because we were unable to understand the results.

Relevant studies were organized into four categories. The first category was the effect of river flow on non-migratory movements. These were resident fish movements that were not related to migration. This meta-analysis could not separate the effect of river flow between up- and downstream movements since most studies did not test for movement direction. The second category was the effect of river flow on upstream migration. This analysis included both anadromous and potamodromous migrations, but only in the upstream direction. The third category was downstream migratory movements of iteroparous species post-spawning. Finally, we examined the effect of river flow on fine-scale movement (i.e. activity) which we defined as any external body movement associated with swimming. These activity studies were conducted using electromyogram (EMG) telemetry (see Cooke et al. 2004 for background on EMG telemetry) or fluctuations in radio signal strength (see Thiem et al. 2010 for background on signal strength fluctuations as a measure of activity).

The following data were extracted from each study: 1) author and year of publication 2) study species 3) the number of subjects 4) units of river flow metric (discharge was used exclusively by all studies, although we would have accepted water velocity) and range of discharges tested 5) predictors used in addition to river flow 6) analysis time scale (e.g., hourly, daily, monthly or yearly) 6) whether the river flow regime was regulated or not and 7) effect sizes. The distance moved between subsequent locations (during some specified time period) was used most often to calculate rates of movement (e.g., metres/day). However, some studies reported other movement metrics such as the number subjects moved, total distance of movements, probability of movement and frequency of movement. Sometimes movements were estimated at one time period (e.g., daily), but analyzed at some other time scale (e.g., weekly or monthly).

We selected Pearson's correlation coefficient (r) as an appropriate effect size (Hunter et al. 1982). Coefficients were obtained for each study, when possible, in the following ways: (i) direct reporting of r, R^2, or partial correlation (ii) other statistical values such as: means and standard deviations; F-values and degrees of freedom; or p-values and sample sizes. These values were then converted to r using an online effect size calculator (http://www.lyonsmorris.com/ma1/index.cfm). P-values were assumed to be 2-tailed when not reported otherwise. Most authors reported multiple results from the same study when correlating river flow and fish movement/activity. Using several effect sizes from a single study could potentially give rise to non-independence (Gates 2002). However, multiple effect sizes from the same manuscripts in these analyses were usually the result of multiple species or seasons. For those manuscripts, multiple effect sizes (e.g., different species; Brown et al. 2001) were assumed to be independent.

Meta-analyses

Because effect sizes vary randomly from study to study, we used a random-effects model to account for both within-study variation and variability arising from differences among studies (Hedges and Vevea 1998). This method emphasises the need to correct for sources of error such as sampling error and reliability of measured variables by using the average correlation coefficient ($\bar{r}$) in which untransformed correlations (r_i) are weighted by the sample size (n_i) on which they are based (equation 1). While the random-effects approach usually produces larger standard errors (and therefore, less-significant effects) than using fixed effects models, our objective was to make unconditional inferences that generalize beyond the studies in the meta-analyses (Field 2001). Standard error ($SE_{\bar{r}}$) was calculated as the standard deviation (SD_r) of the observed correlation coefficients (equation 2) divided by the square root of the number of studies (k) being compared (equation 3; Schmidt and Hunter 1999). The significance of the mean effect size was obtained by calculating a Z score by dividing the mean effect size by the standard error of the mean (equation 4; Field 2001).

$$\bar{r} = \frac{\sum_{i=1}^{k} n_i r_i}{\sum_{i=1}^{k} n_i}$$

$$SD_r = \sqrt{\frac{\sum_{i=1}^{k} n_i (r_i - \bar{r})^2}{\sum_{i=1}^{k} n_i}}$$

$$SE_{\bar{r}} = \frac{SD_r}{\sqrt{k}}$$

$$Z = \frac{\bar{r}}{SE_{\bar{r}}}$$

Assessment of bias and heterogeneity

Publication bias (i.e. “file drawer problem”) is a concern in meta-analyses: studies that show large effects may be more likely to be published than those that show no difference (Rosenthal 1979). Therefore, we calculated the number of studies averaging null results that must be filed away before the overall probability of a Type I error is brought to p = 0.05 (i.e. the "fail-safe number"; equation 3; Orwin (1983)). Bias was also assessed using funnel plots (Egger et al. 1997), a graphical method in which the effect size and its associated measure of precision (i.e. sample size) is plotted. Studies with low precision should show a large scatter of effect sizes around the true values whereas as larger studies should have an effect size closer to the true value (Gates 2002). Funnel symmetry was determined by regressing k and r_i and using the intercept as a measure of asymmetry (the greater the deviation from zero, the greater the asymmetry). Of course the statistical power of these tests depends on sample sizes (which are generally small in ecological meta-analyses, including this one). We therefore based evidence of asymmetry on $p < 0.10$ (Egger et al. 1997). Deviance from this funnel pattern (i.e. asymmetry) may indicate bias in the studies in the meta-analysis (Gates 2002). Heterogeneity of effect sizes was assessed using the chi-square statistic (χ^2), calculated based on the sum of squared errors of the mean effect size (equation 4; Hunter and Schmidt (1990)).

$$K_{fs} = (k/2.706[k(\bar{Z}_k)^2 - 2.706]$$

$$\chi^2 = \sum_{i=1}^{k} \frac{(n_i-1)(r_i-\bar{r})^2}{(1-\bar{r}^2)^2}$$

Results

Is there an effect of river flow on non-migratory movements?

Effect sizes from a total of 27 individual tests (or models) were reported across 11 manuscripts (see Table S1 in Supporting Material). Of these 27 effect sizes, 20 were derived from regulated systems whereby hydropower infrastructure controlled river discharge. On average, the highest discharge events from each study were 40 times (range = 2 - 332) the magnitude of corresponding low discharge events within each study. Almost all movements were estimated using distance between locations (average or sum) during some specified time period (i.e. rate of movement). One study used percentage of fish moving as their movement metric. Movements were analyzed at the monthly (4), weekly (8), daily (7), and sub-daily (8) scales (Table S1). There was a significant positive effect of river flow on fish movement (no regard to direction of movement; $\bar{r} = 0.41$ (mean) ± 0.07 (standard error), $Z = 6.06$, $p < 0.01$, $k = 27$; Table 2.1), although heterogeneity of effect sizes was evident ($\chi^2 = 113$, $p < 0.05$). Eighteen additional studies with null effect would have to be published to reverse the effect ($k_{fs} = 18$). Funnel plots suggested inclusion and/or publication bias as Egger's test for funnel asymmetry was significant (intercept = 19.29; 95% confidence intervals (CI): 13.85 - 24.72; $p < 0.001$; Figure 2.1).

Is there an effect of river flow on upstream migratory movements?

Effect sizes from a total of 8 individual tests (or models) were reported across 6 manuscripts (see Table S2). All studies, except one, were conducted in regulated systems whereby hydropower infrastructure controlled river discharge in at least part of the study area. On average, the highest discharge events from each study were 10 times (range = 3 - 31) the magnitude of corresponding low discharge events within each study. Six effect sizes were generated using distance between locations as their movement metric. One study used probability of being detected at a receiver and another study used the frequency of movements. Most effect sizes were generated from analyses at the daily (6) or weekly (1) temporal scale. Only one study examined sub-daily movements (see Table S2). There was a significant positive effect of river flow on upstream fish migration ($\bar{r} = 0.23 \pm 0.10$, $Z = 2.24$, $p < 0.05$, $k = 8$; Table

2.1) and heterogeneity of effect sizes was evident ($\chi^2 = 20$, $p < 0.05$). The fail-safe number suggested that the effect was not robust ($k_{fs} = 0$). Furthermore, funnel plots suggested inclusion and/or publication bias as Egger's test for funnel asymmetry was significant (intercept = 34.20; 95% CI: 4.59 - 57.81; $p = 0.03$; Figure 2.1).

Is there an effect of river flow on downstream migratory movements?

Effect sizes from a total of 5 individual tests (or models) were reported across 4 manuscripts (see Table S3). All studies were conducted in regulated systems whereby hydropower infrastructure controlled river discharge in at least part of the study area. On average, the highest discharge events from each study were 5 times (range = 4 - 8) the magnitude of corresponding low discharge events within each study. All five effect sizes were generated using distance between locations during a specified time period as their movement metric. Four studies generated effect sizes from analyses at the daily temporal scale. One manuscript reported downstream movements at the weekly scale. There was no significant effect of river flow on downstream fish migration ($\bar{r} = -0.05 \pm 0.15$, $Z = -0.35$, $p > 0.05$, $k = 5$; Table 2.1), possibly because of heterogeneous effect sizes ($\chi^2 = 32$, $p < 0.05$). Funnel plots also suggested inclusion and/or publication bias as Egger's test for funnel asymmetry was significant (intercept = 50.52; 95% CI: -2.47 -103.51; $p = 0.06$; Figure 2.1).

Is there an effect of river flow on fish activity?

Effect sizes from a total of 5 individual tests (or models) were reported across 4 manuscripts (see Table S4). All 5 effect sizes were derived from regulated systems whereby hydropower infrastructure controlled river discharge. On average, the highest discharge events from each study were 7 times (range = 2-17) the magnitude of corresponding low discharge events within each study. Three effects sizes were generated using fluctuations in radio signal strength as their activity metric and two studies used electromyograms (Table S4). Correlations between river discharge and fish activity were analyzed at the hourly scale, although two effect sizes estimated activity at the daily scale (Table S4). There was no significant effect of river flow on swimming activity ($\bar{r} = 0.01 \pm 0.11$, $Z = 0.08$, $p > 0.05$, $k = 5$; Table 2.1). The chi-square statistic suggested homogeneity of effect sizes ($\chi^2 = 5$, $p > 0.05$); however, three effects were negative (reduced activity at relatively higher flows) and two effects were positive (heightened activity at relatively higher flows). Funnel plots suggested inclusion and/or publication bias as Egger's test for funnel asymmetry was significant (intercept = 20.49; 95% CI: 12.61 - 28.37; $p < 0.001$; Figure 2.1).

Discussion

Is there an effect of river flow on non-migratory movements?

We found an overall medium positive effect ($r = 0.41$; effects > 0.30 are considered "medium" effects; Cohen 1992) of river flow on non-migratory movements. Although fish telemetry literature is often descriptive and without statistical models (e.g., Linnik et al. 1998; David and Closs 2002), the studies that did provide the appropriate statistical effects suggested that the overall population effect is positive; increased water flow may stimulate or promote fish movement. While our meta-analysis suggested that relatively high discharge is correlated with larger/more frequent movements, extreme low discharge could also induce movement if habitat is being de-watered and fish move to avoid stranding (e.g., Armstrong et al. 1998). Some researchers qualitatively stated that no downstream forcing was evident (e.g., Bolland et al. 2008). However, the "flushing" effect observed in juveniles during high flows (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000) could not be reported as movement direction was not usually tested quantitatively in the studies assessed by this meta-analysis. In the few studies that did examine directionality, direction was usually unpredictable (e.g., Simpson and Mapleston 2002). Some evidence suggests that lateral movements (i.e. to side channels and adjacent floodplains) are an effective behaviour to avoid elevated flows associated with main stream channels (e.g., Degrandchamp et al. 2008). Habitat heterogeneity and/or size of the river may be an important factor that interacts with discharge; fish may be more likely to remain stationary in high flows when they have more refuge in the form of hydraulic retention areas (Scruton et al. 2005; Simpson and Mapleston 2002). Temperature could explain significant variation in movements in three manuscripts (Enders et al. 2008; Popoff and Neumann 2005; Young et al. 2010), but not in four other manuscripts (Clapp et al. 1990; Bolland et al. 2008; Brown et al. 2001; Degrandchamp et al. 2008), and was not tested in another three manuscripts (Scruton et al. 2005; Simpson and Mapleston 2002; Young and Isely 2007). Some studies did not explicitly test for an effect of temperature, but found seasonal differences in movement that may have been the result of temperature (e.g., Scruton et al. 2003). In addition, some researchers documented no response to elevated flow at the population level, but reported individual behaviours relative to discharge. Even when the population effect of discharge was statistically significant, large individual variation in movements was the norm in all studies.

Is there an effect of river flow on upstream migratory movements?

We found an overall small positive effect ($r = 0.23$; effects > 0.10 are considered “small” effects; Cohen 1992) of river flow on the rate/probability/frequency of upstream migration. However, the mean effect was not robust ($k_{fs} = 0$) and heterogeneity of individual effect sizes was evident. Miller and Scarnecchia (2008) found that paddlefish (*Polyodon spathula*) ascended the Missouri River during elevated discharge. Elevated discharges may have provided greater habitat area and cover from predators thus providing incentive to move. Despite the overall positive effect of discharge on upriver migratory movements, high discharge in the form of regulated releases or natural floods may also delay fish migrations when discharge reaches a certain threshold (Svendsen et al. 2004). For example, when discharge exceeded 72 m^3/s in the River Mondego, Portugal, sea lamprey's (*Petromyzon marinus L.*) upstream groundspeed was compromised (Almeida et al. 2002). Large individual variation in the rate of upstream migratory movements was noted by almost all authors. Temperature was a significant predictor of migratory movement in three studies (Svendsen et al. 2004; Paragamian and Wakkinen 2008; Erkinaro et al. 1999), non-significant in one study (Miller and Scarnecchia 2008) and not tested in two studies (Almeida et al. 2002; Jeffries et al. 2006).

Is there an effect of river flow on downstream migratory movements?

No significant effect of river flow on the rate of downstream migration was found. Four of five effect sizes in this meta-analysis were medium-large effects. However, two effects were negative and two effects were positive in direction, thus resulting in no significant effect when combined. For example, Aarestrup et al. (2002) found that the downstream migration speed of sea trout (*Salmo trutta*, L.) was positively correlated with discharge. In contrast, bull trout (*Salvelinus confluentus*) and paddlefish made faster and larger movements under relatively lower flow conditions (Monnot et al. 2008; Miller and Scarnecchia 2009). Only one study found no effect of discharge on downstream migratory movements (Atlantic salmon (*Salmo salar* L.); Aarestrup et al. 2002). Again, large individual variation in the rate of downstream migratory movements was noted by almost all authors. Temperature was a significant predictor of downstream movements in one study (Aarestrup et al. 2002 (brown trout (*Salmo trutta L.*))), but not in three other studies (Aarestrup et al. 2002 (Atlantic salmon); Monnot et al. 2008; Miller and Scarnecchia 2009) and was not tested in one study (Dedual and Jowett 1999).

Is there an effect of river flow on fish activity?

No significant effect of river flow on fish swimming activity was found. Similar to downstream migration, some individual effect sizes were negative and some were positive in direction, resulting in no significant effect when combined. Fish may become less active under relatively higher flows if the costs of foraging become too great. In contrast, fish may need to increase swimming speed in order to hold station at higher flows, but increased foraging in response to invertebrate drift has also been suggested as a possible mechanism (Cocherell et al. 2011). The effects of river flow on fish activity are likely based on complex foraging decisions that reflect trade-offs between swimming cost, prey availability, prey accessibility and the fish's internal energetic status (Huntingford and Thorpe 1988; Metcalfe et al. 1999). Temperature could explain significance in activity in one manuscript (Robertson et al. 2004), was not significant in one other manuscript (Taylor et al. 2012a) and was not tested in two manuscripts (Cocherell et al. 2011; Stickler et al. 2007). Due to the low number of studies we could not explicitly test for a seasonal interaction with discharge. However, some researchers reported that the effect of discharge on activity varied among seasons (Robertson et al. 2004).

Assessment of bias and heterogeneity

Meta-analyses overcome some of the issues with narrative reviews, but they are not without problems. For example, bias in meta-analyses needs to be assessed (Gates et al. 2002).

Funnel plots and associated Egger tests suggested publication/inclusion bias in each of our four meta-analyses which may have biased our results. Furthermore, the homogeneity tests suggested that significant heterogeneity existed in each meta-analysis. There are many factors which may influence the effect size for any given study and it is important to identify these factors (Gates 2002). Therefore, we made post-hoc investigations into some possible sources of biological and methodological heterogeneity. For example, species-specific differences could potentially be a large source of heterogeneity as different guilds have different swimming capabilities, modes, and eco-morphological adaptations to deal with changes in flow (Videler 1993; Domenici 2003). For example, non-salmonids ($k = 9$ effect sizes) were more affected by river flow, in regards to non-migratory movement, compared to salmonids ($k = 18$) ($t(25) = 2.66$, $p = 0.01$). Effect sizes for non-migratory movements generated at the weekly or monthly scale ($k = 8$) were higher compared to those at the daily or sub-daily scale ($k = 18$; $t(24) = 2.20$, $p = 0.04$). A meta-regression (weighted by sample size) of the flow range (D_{max}/D_{min}, across each individual study period) and corresponding effect size within the non-migratory movement meta-analysis was used to examine additional potential effect modifiers. Flow ranges and effect sizes were log transformed to achieve normality. The effect of flow range was not significant ($R^2 = 0.18$, $\beta = 0.07$, 95% CI: -0.00 - 0.15, $p = 0.06$, $k = 20$). Therefore, the relationship between river discharge and non-migratory movements was not modulated by the range of discharges tested within each study. In summary, some heterogeneity in effect sizes could be explained by our crude classification of species (salmonids vs. non-salmonids) and the time-scale of analysis (weekly/monthly scale versus daily/sub-daily) in non-migratory movements, but not the intensity of the intervention (range of flow conditions). Given the low sample sizes for upstream migratory movements, downstream migratory movements and activity studies, we were not able to test for sources of heterogeneity.

Haxton and Findlay (2008) suggested that heterogeneity in the effects of water management on invertebrate and fish abundance should be investigated using a single integrated study designed specifically to explore sources of heterogeneity. To accomplish this for fish movement would require that multiple species with different swimming capabilities be tagged simultaneously and tracked with a range of precision, at a variety of temporal scales, over multiple seasons, and across a range of flow manipulations. Ultimately, this would require that hydropower operators provide flow releases that are orthogonal (uncorrelated) with other pertinent variables such as temperature and day period. Many studies could not distinguish between the effect of discharge and temperature (e.g., Swanberg 1997; Geist et al. 2005) and were subsequently excluded from our meta-analyses despite meeting all the other criteria. As temperature can co-vary with discharge (Olden and Naiman 2010), much more effort is needed to separate these effects. Ultimately, this problem should be addressed in the study design phase of the project. Some statistical techniques are available to deal with collinearity, providing that collinearity is not too strong. We assumed that if collinearity was not discussed in a study, then it was not an issue and the effect of discharge was assumed to be a true effect. However, all fish movements studies need to report the magnitude of correlations amongst all predictors and their approach taken to ensure modelled effects are indeed true effects. Other variables that tend to correlate with discharge also need to be considered (e.g., turbidity; Miller and Scarnecchia 2008).

The meta-analyses presented here used exclusively electric tagging studies (telemetry and PIT technologies) to estimate fish movement and activity. Unfortunately, this excluded some excellent studies examining the effect of discharge on fish movement using other techniques (e.g., mark recapture; Albanese et al. 2004). Recaptures via either electrofishing or weir/dam counts typically number in the hundreds and are therefore not directly comparable to sample sizes used in telemetry. Very few non-migratory movement papers actually examined directionality of movements and we encourage researchers to do so when possible. Activity studies were exclusively performed on salmonids which could bias the overall population effect considering that salmonids are considered to be quite strong swimmers (Beamish 1978).

While our meta-analyses have not defined an exclusive set of movement rules for all species, our objectives were to make broad-level inferences about fish movement from multiple independent studies. This provides fundamental insight into the constraints imposed on fish by their environment. In addition, from an applied perspective our findings should improve the ability to anticipate the immediate and cumulative effects of water management practices. Indeed, there is growing recognition that river flow (extreme low and peak flows) can affect growth (e.g., Korman & Campana 2009), abundance (e.g., Liebig et al. 1999) and mortality (e.g., Xu et al. 2010; Young et al. 2010) in fishes. Yet, there is less known about underlying mechanisms to explain these effects.

Our analyses show that changes in a river's flow regime do show the potential to modulate a fishes energy budget as some research has suggested that activity metabolism (the portion of the energy budget dedicated to fish movement and station-holding) represents one of the most important determinants of among-population variability in fish growth rates (Boisclair and Leggett 1989; Boisclair and Sirois, 1993; Aubin-Horth et al. 1999). For example, Korman and Campana (2009) found higher growth rates of rainbow trout (*Oncorhynchus mykiss*) on days when hydropeaking in the Colorado River was reduced, although no single study has linked flow regime to activity and growth rate. Understanding fish movement in response to changes in flow regime may help explain long term changes in the presence or absence of certain species from a river if the energetic costs of foraging outweigh the energetic gains from consumption. Furthermore, although we did not find direct evidence of downstream forcing of fishes in response to flow, this would also be a potential mechanism that reduces habitat availability and therefore explains population and community scale changes.

Table 2.1: Estimated effect size ($\bar{r}$), standard error (SE), Z score (Z), Chi-square test for heterogeneity (χ^2), number of effect sizes included in the meta-analysis (k), number of manuscripts (N), and fail safe Ns (k_{fs}) for each meta-analysis.

Behaviour	**Effect size ($\bar{r}$)**	**SE**	**Z**	**$\chi 2$**	**k**	**N**	**k_{fs}**
1. Non-migratory movements	0.41	0.07	6.06	113	27	11	18
2. Upstream migratory movements	0.23	0.10	2.24	20	8	6	0
3. Downstream migratory movements	-0.05	0.15	-0.35	32	5	4	n/a
4. Activity	0.01	0.11	0.08	5	5	4	n/a

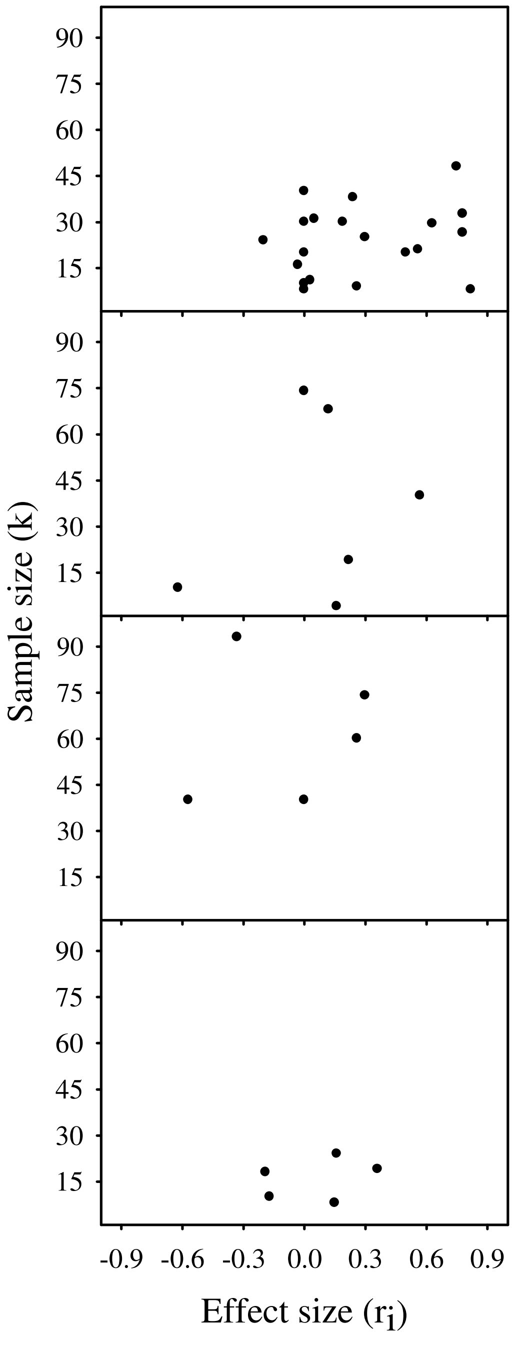

Figure 2.1: Funnel plots for the effects of river discharge on (a) non-migratory movements (b) upstream migratory movements (c) downstream migratory movements (d) fine-scale activity

1 Table S1. Summary of all effect sizes, grouped by manuscript, used in meta-analysis of the effect of river discharge on fish movement.

Study	Metric used	Sampling scale	Analysis scale	Species	Predictors	D_i range	n	r_i	How obtained effect size?	Comment
Bolland et al. 2008	mean distance between locations	daily	daily	chub	discharge, temperature	0-0.8 m^3/s	32	0.75	direct reporting of r from text	wild fish 2005
Bolland et al. 2008	mean distance between locations	daily	daily	chub	discharge, temperature	0-7 m^3/s	32	0.80	direct reporting of r from text	wild fish 2006
Bolland et al. 2008	mean distance between locations	daily	daily	chub	discharge, temperature	0-7 m^3/s	34	0.78	direct reporting of r from text	stocked fish 2006
Brown et al. 2001	total distances between locations	every 5 days	weekly	brown trout	discharge, temperature	6.2 - 87.0 m3/s	25	0.30	converted from R^2 reported in text	
Brown et al. 2001	total distances between locations	every 5 days	weekly	white sucker	discharge, temperature	6.2 - 87.0 m3/s	20	0.50	converted from R^2 reported in text	
Brown et al. 2001	total distances between locations	every 5 days	weekly	common carp	discharge, temperature	6.2 - 87.0 m3/s	21	0.56	converted from R^2 reported in text	
Clapp et al. 1990	mean distance between observations	every other day during summer, every two weeks in winter	monthly	brown trout	temperature and discharge	mean annual = 6.5 m3/s	8	0.82	converted from R^2 reported in text	
DeGrandshamp et al. 2008	mean distance between observations	monthly	weekly	silver carp	temperature, river stage	128-130 m	21	0.28	direct reporting of r from text	2004
DeGrandshamp et al. 2008	mean distance between observations	monthly	weekly	silver carp	temperature, river stage	128-128.5 m	32	0.75	direct reporting of r from text	2005
DeGrandshamp et al. 2008	mean distance between	monthly	weekly	bighead carp	temperature, river stage	128-130 m	25	0.63	direct reporting of r	2004

	observations								from text	
DeGrandshamp et al. 2008	mean distance between observations	monthly	weekly	bighead carp	temperature, river stage	128-128.5	35	0.62	direct reporting of r from text	2005
Popoff and Neumann 2011	total distance between locations	2-3/week summer, 1/week winter	daily	brown trout	discharge, temperature	158 - 1500 m3/s	30	0.44	converted from R^2 reported in text	1st year holdover
Popoff and Neumann 2011	total distance between locations	2-3/week summer, 1/week winter	daily	brown trout	discharge, temperature	158 - 1500 m3/s	30	0.00	inferred from graph	second year holdover
Popoff and Neumann 2011	total distance between locations	2-3/week summer, 1/week winter	daily	brown trout	discharge, temperature	158 - 1500 m3/s	30	0.14	converted from R^2 reported in text	stocked
Sruton et al. 2005	total distance during flow trial	12 hours	12 hours	Atlantic salmon	high stable, low stable, upramping and downsramping	0.62 – 2.95 m^3/s	11	0.36	converted from mean±SE presented in figures	summer 2002 (day)
Sruton et al. 2005	total distance during flow trial	12 hours	12 hours	Atlantic salmon	high stable, low stable, upramping and downsramping	0.62 – 2.95 m^3/s	11	-0.10	converted from mean±SE presented in figures	summer 2002 (night)
Sruton et al. 2005	total distance during flow trial	12 hours	12 hours	Atlantic salmon	high stable, low stable, upramping and downsramping	0.62 – 2.95 m^3/s	11	0.10	converted from mean±SE presented in figures	winter 2003 (day)
Sruton et al. 2005	total distance during flow trial	12 hours	12 hours	Atlantic salmon	high stable, low stable, upramping and downsramping	0.62 – 2.95 m^3/s	11	-0.23	converted from mean±SE presented in figures	winter 2003 (night)
Simpson 2002	cumulative distance between locations	approx every 10 days	monthly	Mary River cod	discharge	5 - 115 m^3/s	9	0.26	F-values and df from model results	

Young and Isely 2010	total distance during treatment	every two hours	daily	bass	treatments: no generation, generation and pumping	?	38	0.24	mean ±SD from different treatments reported in text	
Young et al. 2010	mean distance between observations	every 4 days	daily	brown trout	daily average flow, daily average temp	0.5 - 166 m^3/s	48	0.69	converted from R^2 reported in text	
Young et al. 2010	percentage of fish moving	every 4 days	daily	brown trout	daily average flow, daily average temp	0.5 - 166 m^3/s	48	0.81	converted from R^2 reported in text	
Enders et al. 2008	mean radial distance moved (RDM)	3 times/day	not available	rainbow trout	discharge and temperature	0.3-7.9 m^3/s	31	0.05	converted from mean±SE presented in low vs. high discharge figure	
Scruton et al. 2003	distance between locations	start and end of experimental period	2 hr	Atlantic salmon	high vs. low and upramping vs. downramping	1.2 - 4.6 m^3/s	24	-0.23	calculated form mean±SD from figures	summer
Scruton et al. 2003	distance between locations	start and end of experimental period	2 hr	Atlantic salmon	high vs. low and upramping vs. downramping	1.2 - 4.6 m^3/s	24	-0.16	calculated form mean±SD from figures	fall
Scruton et al. 2003	distance between locations	start and end of experimental period	2 hr	brook trout	high vs. low and upramping vs. downramping	1.2 - 4.6 m^3/s	24	0.00	calculated form mean±SD from figures	summer
Scruton et al. 2003	distance between locations	start and end of experimental period	2 hr	brook trout	high vs. low and upramping vs. downramping	1.2 - 4.6 m^3/s	24	-0.05	calculated form mean±SD from figures	fall

Table S2. Summary of effect sizes, grouped by manuscript, used in meta-analysis of the effect of river flow on upstream migration.

Study	Metric used	Sampling scale	Analysis Scale	Species	Predictors	D_i range	n	r_i	How obtained effect size?	Comment
Almeida et al. 2002	mean distance between locations	weekly	weekly	sea lamprey	discharge	4.8-150 m^3/s	10	-0.62	direct reporting of r from text	
Jeffries et al 2009	mean distance between locations	daily	daily	Sacramento sucker	discharge	12.5 - 56.7	4	0.53	converted from R^2 reported in text	
Miller and Scarnecchia 2009	mean distance between locations	fixed stations record continuously. Manual tracking was used, but no indication of how often tracked	not indicated, although discharge was measured at daily scale	paddlefish	daily average flow, temperature, suspended solids	167-1300 m^3/s	40	0.57	converted from p value and sample size.	
Paragamian et al. 2005	frequency of movements	1-5 times/week	daily	burbot	average daily discharge	200 - 650 m^3/s	68	0.30	converted from p value and sample size.	
Paragamian et al. 2005	mean distance between locations	1-5 times/week	daily	burbot	average daily discharge	200 - 650 m^3/s	68	-.07	converted from mean±SE in text	
Svendson et al. 2005	distances moved in first 3 days of migration	every 3rd day – 1/week	3 hours	sea trout	discharge, temperature	0.5 - 4.5 m^3/s	19	0.22	converted from R^2 change	
Svendson et al. 2005	probability of being detected at receiver	continuous monitoring	daily	sea trout	discharge, temperature	0.5 - 4.5 m^3/s	19	0.69	converted from p value and sample size	
Erkinaro et	distance	every three	daily	Atlantic	discharge,	15 – 3500 m^3/s	38	0.50	direct reporting	

al. 1999	between locations/time (swim speed)	days	salmon	temperature	of p value, sample size and direction of effect

Table S3. Summary of effect sizes, grouped by manuscript, used in meta-analysis of the effect of river flow on downstream migratory movements.

Study	Metric used	Sampling scale	Analysis Scale	Species	Predictors	D_i range	n	r_i	How obtained effect size?	Comment
Aarestrup et al. 2002	distance/day	daily for 1 week and then every 2nd day	daily	sea trout	mean temperature and discharge between locations; gill Na+, K+, -ATPase activity	2 - 9 m^3/s	60	0.26	direct reporting of R^2 – wild trout (2 years) and stocked trout were grouped	wild trout and hatchery trout grouped together
Aarestrup et al. 2002	distance/day	daily for 1 week and then every 2nd day	daily	Atlantic salmon	mean temperature and discharge between locations; gill Na+, K+, -ATPase activity	2 - 9 m^3/s	40	0.00	direct reporting of R^2	
Monnot et al. 2008	distance/day	weekly	weekly	bull trout	weekly average temperature and discharge, fish size	4 - 17 m^3/s	93	-0.33	converted from p value and sample size – direction inferred from text	
Dedual and Jowett 1999	distance between locations/time interval (i.e. rate)	3 times/week	daily	rainbow trout	discharge, variation in discharge, barometric pressure, change in barometric pressure, sex, length and reproductive status	25-150 m^3/s	74	0.30	direct reporting of R^2	
Miller and Scarnecchia	distance between locations	not available	not available	paddlefish	daily average flow, temperature and suspended solids	167-1300 m^3/s	40	-0.57	converted from p value and sample size – direction inferred from text	

Table S4. Summary of effect sizes, grouped by manuscript, used in meta-analysis of the effect of river flow on downstream migratory movements.

Study	Metric used	Sampling scale	Analysis Scale	Species	Predictors	D_i range	n	r_i	How obtained effect size?	Comment
Cocherell et al. 2010	EMG signals calibrated to swim speed	continuous when fish are present near antenna	hourly	rainbow trout	sex, length, weight, river kilometer, discharge, pulse stage, days in the river	5-85 m^3/s	18	-0.18	converted from p value and sample size. Direction based on scatterplot of discharge and swim speed	
Robertson et al. 2004	movements/hour based on fluctuations in signal strength	continuous when fish are present near antenna	hourly	Atlantic salmon	flow (high and low), diel period and season	low flow (1.3 m^3/s) and high flow (5.2 m^3/s)	11	-0.28	converted from p value and sample size. Direction assumed from bar graphs.	mid-winter
Robertson et al. 2004	movements/hour based on fluctuations in signal strength	continuous when fish are present near antenna	hourly	Atlantic salmon	flow (high and low), diel period and season	low flow (1.3 m^3/s) and high flow (5.2 m^3/s)	15	-0.23	converted from p value and sample size	late-winter
Stickler et al. 2008	fluctuations in signal strength	continuous when fish are present near antenna	hourly	Atlantic salmon	discharge, day period, temperature	high (21.1±1.7SD) vs. low (11.1 ±1.7 SD)	24	0.16	converted from mean±SE presented in text	
Taylor et al. 2012a	hourly average EMG	continuous when fish are present near antenna	hourly	mountain whitefish	hourly average discharge, temperature and diel period	566-1524 m^3/s	19	0.36	direct reporting of R^2 from text	

CHAPTER 3: REACH-SCALE MOVEMENTS OF BULL TROUT (*SALVELINUS CONFLUENTUS*) RELATIVE TO HYDROPEAKING OPERATIONS IN THE COLUMBIA RIVER, CANADA.

Abstract

Despite the widespread use of on-demand hydropeaking operations for generating electricity from rivers, there is relatively little known about how unsteady flows influence the behaviour of fishes. We studied the movements of bull trout using radio telemetry in a hydropeaking reach of the Columbia River, near Revelstoke, British Columbia, Canada. Fifty-seven bull trout were located every twelve hours to evaluate the effect of twelve-hour mean discharge magnitude and rate of change on: (1) the odds of bull trout movement (probability of movement/probability of no movement); (2) movement distances; and (3) movement direction. In general, bull trout resided in one of three core areas and displaced themselves at least 100 m once every three days. Twelve-hour mean discharge magnitude had a negative effect on the odds of movement: for every 100 m^3/s increase in river discharge, movement-odds decreased by a factor of 0.91. We controlled for other environmental parameters and found that a 1 ℃ 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 documented some displacements up to four kilometers between locations during the coldest water temperatures (7 ℃) in December and up to eight kilometers between locations during late October (11 ℃). Movement direction was completely unpredictable which is consistent with the salmonid 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.

Introduction

There is growing recognition that altered river 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, less 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. 2009a). 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 may occur in a daily or sub-daily cycle (Cushman 1985). Globally, hydropower operations are developing rapidly on rivers of various sizes (Frey and Linke 2002; Bratich et al. 2004), but on medium to large rivers there is particular interest in hydropeaking systems given that power production can occur on demand with little time needed to start or stop production (Yuksel 2007). 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 spill flows (Young et al. 2011). Given the persistence of these types of flow regimes around the globe, researchers have been developing an understanding of the biotic responses of free-swimming fishes to unsteady flows (i.e. fluid velocity varies with respect to time for a given point in space; Liao 2007). Response metrics have included blood physiology (e.g., Flodmark et al. 2002; Taylor et al. 2012a), swimming energetics (e.g., Geist et al. 2005; 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 an important behaviour because it allows animals to respond to changing physical conditions in their immediate environment to maximize growth, survival and reproductive success (Kahler et al. 2001). For example, some evidence suggested that brook trout (*Salvelinus fontinalis*) make large movements to monitor stream habitat conditions at broad spatial scales to gain access to optimal foraging locations (Gowan and Fausch 2002). In a dynamic environment such as a regulated pulsed-flow river, habitat conditions and foraging potential change rapidly. Given the temporally-dynamic conditions, one may expect fish to displace themselves often as they reassess the foraging potential of their changing environment. The downstream forcing of fishes during periods of high river discharge 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) while 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 fish 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 and 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 piscivorous fish are characterized by their diverse life histories which can involve long-distance movements between spawning and overwintering habitat. Despite the existing literature on migratory movements (e.g., Swanberg 1997; Bahr and Shrimpton 2004; Mulfield and Morotz 2005), an understanding of the timing of movements outside of their spawning migration has not developed. Furthermore, previous bull trout telemetry studies located their subjects at a mean of 3 locations per month (Dare 2006), yielding movement estimates at a time scale much too short to correlate with dynamic river conditions.

Given this, the purpose of this study was to determine if there was a significant relationship between bull trout movements and the operational release of water from a hydropeaking dam on the Columbia River, near Revelstoke, British Columbia. We determined if river flow parameters (discharge magnitude and rate of change) had a significant statistical effect on bull trout movement while controlling for other factors such as temperature and light. Specifically, we tested for an effect of discharge magnitude and rate of change, at a twelve-hour time scale, on: (1) the odds of bull trout movement, (2) the distance of movements, and (3) the direction of movement.

Methods

Study site and fish surgery

The study site was the lotic portion of the Columbia River between Revelstoke Dam (REV) and the downstream Arrow Lakes Reservoir (Figure 3.1) in British Columbia, Canada. REV was constructed primarily as 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 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 using electromyogram (EMG) radio transmitters (Years 1 and 2) as well as traditional radio transmitters (Year 3). EMGs 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 review*). A total of eighty-two bull trout were collected by boat pulsed DC electroshocker over three years (Year 1: September 24-October 8, 2008; Year 2: September 28-October 07, 2009; Year 3: November 13, 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 8-11 °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 bath of 30 ppm clove oil. 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 either an EMG transmitter (CEMG2-R16-25; dimensions: 16x62 mm, weight: 25 grams in air; Lotek Wireless, New Market, Ontario) or a traditional radio transmitter (MCFT2-3A; dimensions: 16x46 mm, weight: 6.7 g in air; Lotek Wireless, New Market, Ontario) was inserted (mean tag/body mass ratio = 1.4%, range = 0.4 – 2.6% for both transmitters). In both scenarios, a 16 ½ gauge hypodermic needle was pushed through the body cavity wall and the antenna wires were passed through to the outside. The incisions were closed using four independent sutures (PDS II absorbable monofilament, 3/0, FSL needle). The entire procedure took approximately five (EMG transmitters) and two (MCFT transmitters) minutes per fish. 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 and 3) or were held overnight in the tank to await muscle activity calibrations (Year 2; relevant to EMG study only; see 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 and recovery of researchers. Each session lasted approximately three hours to scan the entire study area, therefore 12-hours was a time scale that was as short as possible while still allowing for the daily rest of operators. Tracking was conducted on foot, from shore, by a two-person team equipped with a 3-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 the operator was as close to the fish as possible on the adjacent shore. Once directly adjacent to the fish (distance from the fish depends 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 a waypoint into a 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 represent 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 are longitudinal only and in 100 m increments. Each fish location corresponds to a river section number representing the fish's distance from REV (e.g., section 0 is REV, and section 26 is 2600 m downstream of REV).

Data Analysis

When measurements are generated on multiple occasions on the same individuals, the data are not independent (Heck et al. 2011) 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) and presumably allows for a finer-scale understanding of the environmental correlates of movement. A second potential 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, species). Such issues can 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. 2011). Therefore, we used mixed-modeling procedures to test for this individual variation using random regression coefficients (i.e., random intercepts).

Intercepts did vary significantly among subjects for the bull trout movement odds model (Wald $Z = 3.245$, $p = 0.001$); however, only 8% of the total variation in movements could be explained as between subjects. Intercepts did not vary among subjects for the movement distance model (Wald $Z = 1.959$, $p = 0.050$) or direction of movement model (Wald $Z = 0.000$, $p > 0.05$). Because movement estimates were collected over three years, we also tested for a random “year” effect. Individual variance in intercepts among years was not significant for the movement odds model (Wald $Z = 0.936$, $p = 0.348$), the distance of movement (Wald $Z = 0.812$, $p = 0.417$) or direction of movement (Wald $Z = 0.002$, $p = 0.798$). Given that that there was not any significant variation in intercepts (except for movement odds that had only 8% of variation explained by subjects), we modeled the movement parameters using Generalized Estimating Equations (GEE) rather than a mixed effects approach. GEEs offer the advantages of being able to model correlated data with continuous, dichotomous, polychotomous, ordinal and event-count response variables (Zorn 2001). GEEs allowed us to account for correlations within individuals, but are a "population-averaged" approach rather than the "subject-specific" approach of mixed models (see 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 eventually move to a new position and absolute movement distances were right-skewed owing to the infrequent large movements. However, we considered the timing of departure to be as informative as the movement distance. Therefore, a binary-logistic model was used to predict the odds that a bull trout moved during a 12-hour period (probability of movement/probability of no movement) and movement direction (upstream or downstream). We modeled all non-zero movements as the number of 100 m quadrants (i.e., counts) the fish traversed in a fixed time period (i.e., 12 hours), using a negative binomial model. The negative binomial distribution is similar to the Poisson distribution, but is used when the variance is larger than its 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 fixed effects (Table 3.1) as well as 2 categorical predictors (sex, diel period). We had *a priori* predictions that river flow and temperature were related to fish movement based on previous research (see Taylor et al. 2012b). Therefore, these variables were added to the models first. We also explored other variables that may have had an effect on movement (see Table 3.1). 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 repeated measures for each fish were not independent such that 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. Furthermore, the AR1 covariance structure provided the lowest QICs in all movement models. No Pearson residuals were greater than two in the logistic models. Residuals for the movement distance model were plotted across the range of predictors and predicted values to assess homoscedasticity; some degree of imbalance was evident due to the skewed distribution. This was also evident in plots of fitted versus observed movement distance values. Therefore, despite using a model intended for overdispersed data, fitted movement distances were underestimates of the true distance for long range movements (>500 m).

Results

Movement odds

Bull trout movement odds were negatively related to 12-hour mean discharge (GEE, Wald $\chi = 23.639$, $p < 0.001$; Figure 3.3) and positively related to water temperature (GEE, Wald $\chi = 13.564$, $p < 0.001$; Figure 3.4). Day period also had a significant effect (GEE, Wald $\chi = 18.130$, $p < 0.001$); the odds of movement were greater in the AM (midnight – noon) than PM (noon – midnight). These three variables comprised the final model (Table 3.2). Twelve-hour change in discharge had no significant effect on movement odds (GEE, Wald χ = 2.965, p = 0.085), nor did visibility (GEE, Wald χ = 0.340, p = 0.560), sex (GEE, Wald χ = 0.751, p = 0.386), or size (GEE, Wald χ = 0.244, p = 0.621). For every 100 m^3/s increase in river discharge, movement-odds decreased by a factor of 0.91. For every 1 ℃ increase in water temperature, movement odds increased by a factor of 1.27. Finally, bull trout were more likely to move during the AM than the PM by a factor of 1.36.

Movement distance

The distance bull trout moved was not related to 12-hour mean water temperature (GEE, Wald χ = 1.629, p = 0.202) or visibility (GEE, Wald χ = 0.812, p = 0.368). Twelve-hour mean discharge magnitude had a significant effect on movement distance (GEE, Wald χ = 6.325, p = 0.012) as did twelve-hour change in discharge (GEE, Wald χ = 17.548, $p < 0.001$), but with very small effects sizes. For example, movement distances decreased by a factor of 0.995 and increased by a factor of 1.007 for every 100 m^3/s increase in discharge magnitude and within-hour change in discharge respectively. Diel period (GEE, Wald χ = 6.649, p = 0.010), sex (GEE, Wald χ = 14.987, $p < 0.000$) and size (GEE, Wald χ = 4.247, p = 0.039) remained in the final model (Table 3.2). Females made longer movements than males, by a factor of 1.05. Every 10 cm increase in fork length was related to an increase in bull trout movement distance by a factor of 1.02. Movement distances were longer during the AM than the PM by a factor of 1.02. On average, bull trout displaced themselves 400 ± 730 m (mean ± SD) every twelve hours (excluding zero movements). However, we documented some displacements up to 7.4 km in 12 hours.

Movement direction

We did not uncover any variables that were significant predictors of movement direction. Twelve-hour mean discharge magnitude did have a significant effect on the odds of moving downstream (GEE, Wald $\chi = 5.500$, $p = 0.019$), but only when controlling for every other candidate variable which themselves were not significant. Twelve-hour change in discharge (GEE, Wald $\chi = 0.088$, $p = 0.766$), water temperature (GEE, Wald $\chi = 1.896$, $p = 0.169$), visibility (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

Our first objective was to determine if river flow was correlated with the odds of bull trout movement. 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 change locations during relatively higher water flows if they perceive the cost of holding station to be greater than the benefit of staying. However, we found that bull trout movement odds were significantly depressed during periods of high discharge and found no evidence of downstream displacement during periods of high river discharge which suggested that the cost of maintaining position within a 100 m reach was within their physiological capacities. Furthermore, we found no evidence of bull trout stranding during periods of changing discharge, a phenomenon that has previously been observed in hydropeaking systems (Nagrodski et al. 2012). None of the other movement parameters (movement distance and direction) was well correlated with river discharge magnitude or rate of change within a given twelve-hour period.

The effect of changes in discharge magnitude 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, not temperature, in a hydrologically flashy tributary of the Mississippi River. Young and Isely (2007) found that daily striped bass (*Morone saxatilis*) movement (sampled every two hours) in a tail race increased during daily hypolimnetic release from a dam. Others have found that fish moved more during changing versus stable flows (e.g., Berland et al. 2004). However, a number of other studies have found no effect of short-term changes in river discharge 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 their 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 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 non-regulated river was less at low temperatures (0.0-0.9 ℃) in comparison to two higher temperatures (1.0 – 4.9 ℃). Zimmer et al. (2010) found that cumulative upstream movement of brown trout in a temperate, urbanized watershed was positively correlated with mean weekly temperature, but not river flow. Temperature can presumably have the opposite effect on fish movement if temperature 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 ℃). The current study did not examine bull trout movements near their upper lethal thermal range (20.9 ℃ based on acclimated chronic exposure method; Selong et al. 2001).

Female bull trout made larger movements than males. Sexual dimorphism in movement behaviour has been demonstrated in migrating paddlefish; males made numerous short range movements whereas females made less numerous but longer range movements (Miller and Scarnecchia 2011). Differences in energetic demands post-reproduction may explain dimorphism considering that this study was conducted in the post-spawning period. However, the management-related significance of this behaviour is not obvious unless one sex was preferentially excluded from the study reach due to high flows, but I found no evidence for an interaction between fish length and discharge.

Relatively larger bull trout made larger movements than smaller fish. This may have been the result of larger fish having relatively higher swimming performance (e.g., Brett 1965), have higher resource requirements (i.e., Maekawa and Nakano 2002) or predation risk (Railsback and Harvey 2002). Larger bull trout have also been shown to make faster downstream post-spawning movements from headwater streams, arriving at overwinter habitat sooner (Monnot et al. 2008). In most studies, the effects of body size and sex were not tested in relation to changes in river discharge (e.g., Brown et al. 2001; Heggenes et al. 2007), despite a large size differences between the smallest and largest fish (e.g., Young et al. 2010). In the few studies that did test for an effect of body size on movement in the context of hydropeaking, no effect was found (e.g., Cocherell et al. 2010).

We were surprised that visibility had no effect on movement considering that bull trout may be at less 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, temperature) seldom occur due to the logistical and financial costs. The relative contribution of each environmental driver of fish movement is difficult to assess because of collinearity amongst predictors (e.g., Swanberg 1997), 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. Typically, radio telemetry data is analyzed 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 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) found similar challenges when modeling spotted salamander (*Ambystoma maculatum*) movement rates using mixed-effects Poisson regression. However, the odds of movement model did fit well and this study also verified that bull trout were not being forced from the study area by high discharge events. Finally, this is one of few examples of telemetry studies whereby fish were located at a time scale that more-closely matches the scale of hydrologic change (see also Berland et al. 2004; Scruton et al. 2005; Heggenes et al. 2007). This research suggested that operational water release in a hydropeaking river does, at least partially, have an effect on movement behaviour and the consequences in regards to foraging success and growth/reproduction should be investigated.

Table 3.1: Summary of tracking statistics for bull trout in the Columbia River, Revelstoke, British Columbia, Canada. **#Locations** is the number of times an individual fish was located (i.e. one value per fish); **D_{MAG}** is the 12-hour mean discharge during the period of movement; **D_{CHANGE}** is the difference between the maximum and minimum instantaneous discharges during the period of movement; **T_{WATER}** is the 12-hour mean water temperature; **Visibility** is the number of kilometres with visibility from the Revelstoke airport (1-15 km); **Diel Period** is the period during which movement was estimated (AM or PM); **Length** is the fork length of the fish; **Sex** is the sex of the fish.

	2008		**2009**		**2010**	
Term	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
#Locations (count)	64	29-73	67	6-80	49	32-50
D_{MAG} (m^3/s)	639	68-1337	654	9-1534	1104	360-1494
D_{CHANGE} (m^3/s)	984	55-1650	828	178-1589	475	0-1375
T_{WATER} (℃)	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
Diel Period (AM/PM)	-	-	-	-	-	-
Length (mm)	669	544-830	562	455-714	635	467-830
Sex (Male/Female)	-	-	-	-	-	-

Table 3.2: Summary of GEE logistic and negative binomial movement models for bull trout in the Columbia River, Revelstoke, B.C. Parameter estimates for movement direction model was not included as no predictors were significant. “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.

Movement Odds					
Parameter	**Mean±SE**	**Wald χ**	**p**	**95% CI**	
				lower	**upper**
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					
Parameter	**Mean±SE**	**Wald χ**	**p**	**95% Wald CI**	
				lower	**upper**
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

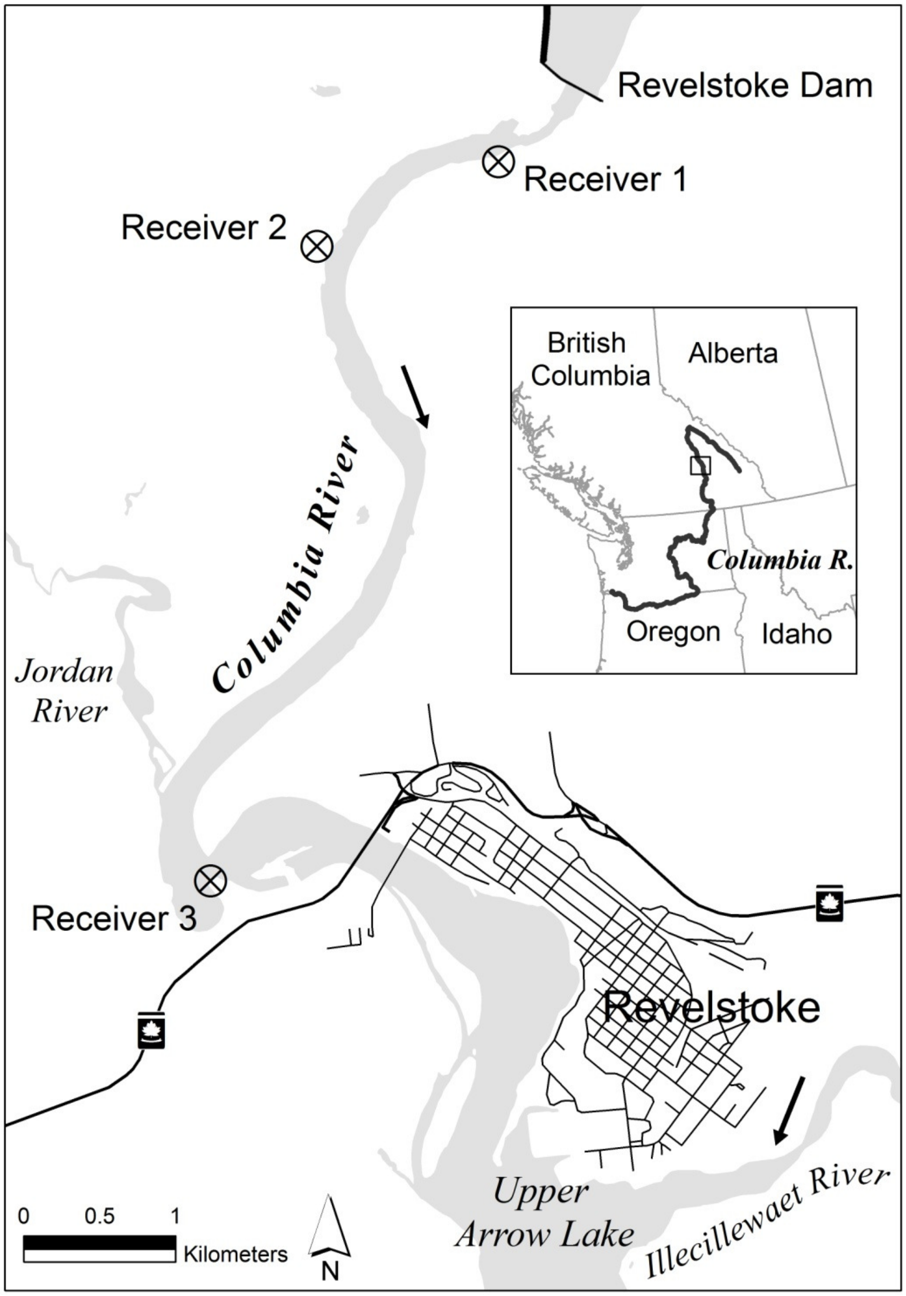

Figure 3.1: Map of the Columbia River downstream of the Revelstoke Dam (REV), Revelstoke, British Columbia, Canada. Study area was 10.6 km section from REV downstream to the Illecillewaet River. Circle with X represents the fixed receiver locations.

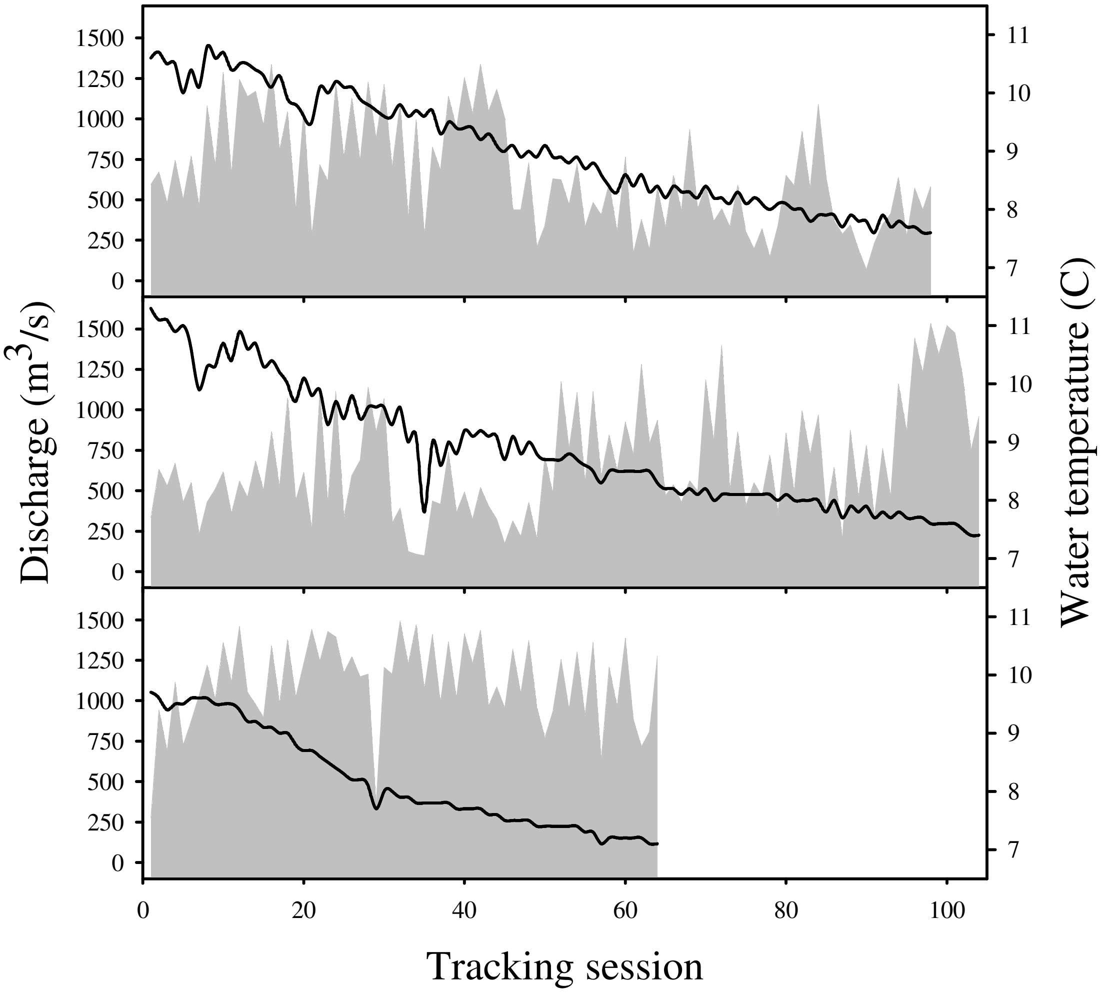

Figure 3.2: Twelve-hour mean discharge (m^3/s; shaded), twelve-hour mean water temperature (℃; black line) for the Columbia River downstream of REV. Discharge was measured from the dam. Some periods of zero discharge occur when REV does not release any water and the only water in the channel is residual flow, dam leakage and backfill from the downstream reservoir. These periods are not evident on the figure as discharge was averaged every twelve-hours. Water temperature was measured from gauging station 7 km downstream of REV. Tracking session is the numbered sequence of tracking sessions every 12 hours. Panel 1 is October 16 – December 3, 2008. Panel 2 is October 15 – December 5, 2009. Panel 3 is November 14 – December 14, 2010.

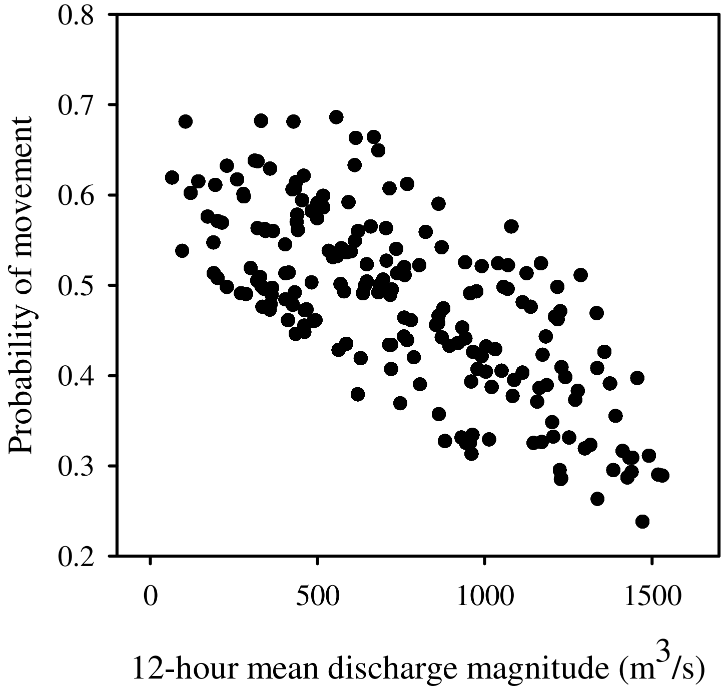

Figure 3.3: The predicted probability of bull trout movement (> 100 m) in relation to the 12-hour mean discharge magnitude (m^3/s) in the Columbia River, downstream of REV. The relationship between odds and probability: Odds = (probability of an event occurring/the probability of an event not occurring).

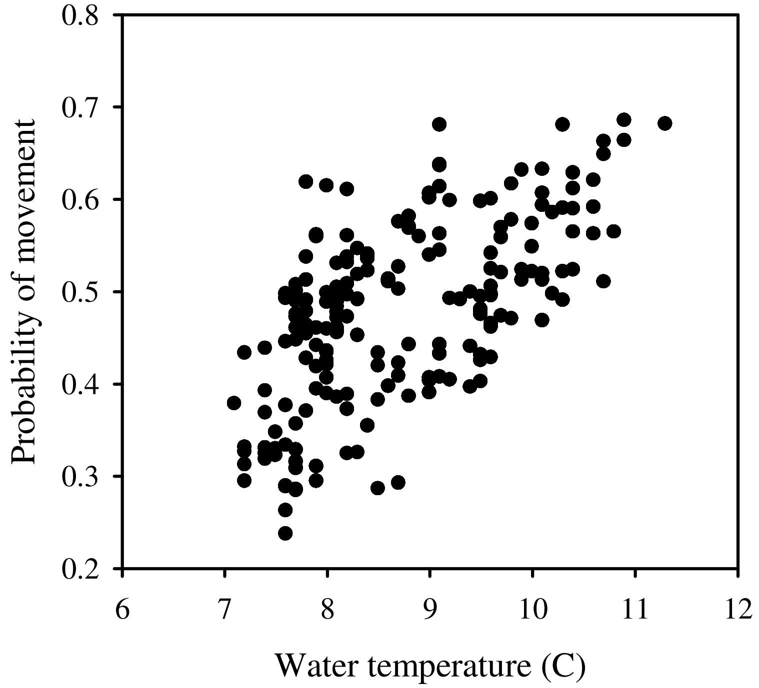

Figure 3.4: The predicted probabilities of bull trout movement (> 100 m) in relation to the seasonal decline in water temperature (℃) in the Columbia River, downstream of REV. The relationship between odds and probability: Odds = (probability of an event occurring/the probability of an event not occurring).

CHAPTER 4: HYDROLOGIC CORRELATES OF BULL TROUT (*SALVELINUS CONFLUENTUS*) SWIMMING ACTIVITY IN A HYDROPEAKING RIVER

Abstract

There is growing need to develop quantitative relationships between specific components of river flow and the behavioural response of fish. 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 0-1790 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 0-1045 m^3/s did not elicit a hyperactive response in bull trout. When a subset of EMG transmitters was calibrated to swimming speed, we found that most often these bull trout were not actively beating their tails. This may suggest that bull trout use behavioural strategies for energy economy such as "flow refuging" to reduce the drag forces of flowing water. Not including these periods of inactivity, bull trout swam at median hourly speeds of 0.53 BL/s.

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 response cannot be linked to any specific component of flow (magnitude, frequency, timing, rate of change and duration) as these components change at time scales much shorter than population responses. Therefore, there is a need to understand the immediate, sub-lethal responses of fish to altered flow regimes across a range of flow manipulations under non-forced, 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. For example, fish use low flow microhabitats to reduce drag (i.e., "flow refuging"; Webb 1998). To date, few studies have measured routine swimming activity relative to hydrologic variables in free-swimming fish (but see: Geist et al. 2005; Murchie and Smokowski 2004; Cocherel et al. 2011). Furthermore, the effect of unsteady flow (i.e. water flow varies with respect to time for a given point in space; Liao 2007) has not been well documented in free-swimming fish.

Given this, we used electromyogram (EMG) telemetry to determine if axial swimming muscle activity in free-swimming bull trout (*Salvelinus confluentus*) was correlated to hydrological parameters in a hydropeaking river. Electromyograms 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 estimates of 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). River discharge at our study site, the 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.

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 electromyograms while controlling for the individual variation in bull trout responses, as well as exogenous factors such as temperature and light. 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 habitat (Kraft 1972). Therefore, 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 electromyograms to kinematic variables (tail beats and swimming speed) with a subset of fish to estimate ecologically-relevant measures of behaviour that can be compared to 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 Revelstoke Dam (REV) and the downstream Arrow Lakes Reservoir (Figure 4.1). REV was constructed primarily as 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 Revelstoke and the downstream Arrow Lakes reservoir. Their relatively large body size is a direct result of the piscivorous feeding behaviour (McPhail and Baxter 1996).

Eighty-eight bull trout were collected from the entire 10.7 km study area by boat pulsed DC electroshocker during three years (Year 1: September 24-October 8, 2008; Year 2: September 28-October 07, 2009; Year 3: October 14-October 26, 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 8-11 °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 anesthesia (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. 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: 16x62 mm, weight: 25 grams in air; Lotek Wireless, New Market, Ontario; 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 rod and plungers. Electrode placement was standardized at 0.7 body length on the right side of the fish (Beddow and McKinley 1999). A 16 ½ 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 five minutes 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 (Year 2 and 3; details below).

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, 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 hours/day and recorded any fish within range of the station (estimated maximum distance of 400 m up- and downstream). Coded EMG signals were converted to hourly averages, a time scale that corresponded to a prolonged period of swimming (20 seconds – 200 minutes; Beamish, 1978). Only hourly averaged EMG values based on at least 100 EMG measurements were used to estimate the hourly average.

Studies have shown that EMG transmitters may behave differently in different fish (see Brown et al. 2007). Considering this, we tested for individual variation in intercepts and slopes when modeling the effect of discharge on uncalibrated EMGs. Because the intercepts varied across fish (Wald $Z = 3.907$, $p < 0.001$) and the intraclass correlation (ICC) 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, Illinois). We also used R^2 as the effect size which is independent of individual differences in slopes and intercepts. Preliminary analysis using OLS regression suggested autocorrelation in the model residuals due to the repeated electromyogram 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 modeling strategy is based on 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). 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 was 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 minute time delay for discharge at receiver 3. Since 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 (level 2 variable; i.e. one value for each fish) and hourly discharge magnitude (level 1 variable) 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 and discharge was also tested to see if fish that were observed more (or less) often had a stronger (or weaker) relationship with discharge. When interactions were significant, all main effect terms were also included even if they weren't significant (Heck et al. 2010). Following the addition of predictors, the model structure was evaluated in terms of random slopes and covariance structures using AICs (Heck et al. 2010; Field 2009). An unstructured covariance type for the random subject coefficients was found to be the best structure. Maximum Likelihood (ML) estimation was used.

Because multilevel models are an extension of regression, we tested all of the assumptions of ordinary least-squares (OLS) regression as well as some additional assumptions pertaining to the random coefficients. We visually inspected scatterplots 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 due to 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 time period. We fitted a model using a logit link with a binary distribution. The fitted GEE demonstrated that hourly discharge rate of change did not have an effect on the odds of detection (GEE, Wald $\chi^2(1) < 0.001$, $p = 0.99$). 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) 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 hours following surgery and then placed in the swim chamber. Bull trout usually faced the direction of the current and held station in one position in the flow 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 output 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. The time counter on the video camera was synchronized to the counter on the EMG receiver and fish were videotaped swimming while simultaneously recording EMG values. Fish were monitored in the chamber for ~20 minutes 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 Revelstoke dam).

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 of time when the fish exhibited approximately steady state swimming. The tail beat frequency (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 (consistent 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) swam adult sockeye salmon in an open flume and 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 tail beat frequency (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 modeled as an indicator of relative activity.

Results

Electromyogram data collection

Of eighty-eight fish tagged over three years, 24 males and 12 females (36 total; fork length = 628 ± 104 mm) yielded at least 100 hourly-averaged electromyogram values with each hourly-average comprised of 100 instantaneous EMGs. The remainder either 1) were never located in the 10 km study area; 2) were located in the study area, but were not located near the three fixed receivers; or 3) were located within range of the receivers, but for a relatively shorter time (i.e., < 100 hours). 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, seventeen bull trout were recorded at two receivers and nine were recorded at all three receivers.

Modeling axial swimming muscle activity

D_{MAG} had a significant positive effect on swimming muscle activity (MIXED, $F_{(1, 13560)} = 1706.88$, $p < 0.001$). D_{CHANGE} also a significant predictor (MIXED, $F_{(1, 11789)} = 16.45$, $p < 0.001$); however, due to the small effect (Table 4.1), 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, $F_{(2, 13441)} = 26.55$, $p < 0.001$) 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 ($\chi^2(1) = -220$, $p < 0.01$). In the final model (Table 4.2), D_{MAG} had a large effect at Receiver 1 ($R^2 = 0.31$), a medium effect at Receiver 2 ($R^2 = 0.13$) and a large effect at Receiver 3 ($R^2 = 0.25$). Pairwise comparisons, based on estimated marginal means of log (SEMG+1), suggest that muscle activity just downstream of the Revelstoke Dam (i.e., Receiver 1) is 1.08 and 1.2 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 two 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 for us to record at least ten tail beat/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, males and female bull trout where considered in separate models. For males, SEMGs could significantly predict TBF (MIXED, $F_{(1, 813)} = 1693.58$, $p < 0.001$). 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 significant variance in intercepts (Wald $Z = 2.632$, $p = 0.01$) and slopes (Wald $Z = 2.604$, $p = 0.01$) amongst fish, demonstrating that a group model to estimate TBF from all fish would not be appropriate.

For females, SEMGs could significantly predict TBF (MIXED, $F_{(1, 352)} = 116.22$, $p < 0.001$). 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, $F_{(1, 349)} = 0.35$, $p = 0.55$). While 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 4.2).

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]) tail beat frequency was 74 ± 18 beats/min. Correspondingly, estimated swim speeds were zero inflated (large peak at 0 BL/s) and showed a right-skewed distribution of swim speeds. 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. In fact, there was a significant positive relationship between river discharge magnitude and axial swimming muscle activity. This may be explained by the fact that for a fish to hold station, 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 a direct function of the fish's drag multiplied by the water's current velocity (Webb 1988). 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. There are a number of behaviours associated with energy economy in high flows. For example, "flow refuging" (Webb, 1998) allows fish to avoid the high costs of swimming by positioning themselves in low flow microhabitats. This behaviour may explain the presence of some hours of relatively low muscle activity during high discharge. Also, 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. For some species, river discharge does not appear to exert control over swimming activity. For example, 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.

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. This objective was of interest because changes in microhabitat use by fish, as influenced by changing flows, have been documented by snorkelling observations (Pert and Erman 1994), electrofishing (Valentin et al. 1994) and conventional positional radio telemetry (Bunt et al. 1999). Therefore, the fact that no significant effect of within-hour change in discharge (the variable we selected to represent hydropeaking operations) on swimming activity was of interest. Murchie and Smokorowski (2004) also found that rainbow trout and walleye relative activity mimicked discharge and that periods of changing discharge (up- and down-ramping) had no greater effect on activity than relatively stable discharges in the Magpie River, Ontario. In contrast, 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 from the dam (and therefore source of discharge), and was weakest at 2.5 km. Channel morphology and habitat structure has 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 flow providing low-flow refuge, thus reducing the effect of discharge.

Some researchers have found that the TBF/swim speed remains the same across temperatures (e.g., Geist et al. 2000; Beddow and McKinley 1999) where as others have found that it changes (e.g., Taylor et al. 1996; Booth et al. 1997) possibly due to 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 10-12 °C, while EMGs were logged in the field from 6 – 12 °C so it is possible that we may have underestimated swimming speeds at temperatures lower than our calibration temperatures.

Very few hourly average swim speeds were observed in the upper range of swimming 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. In addition to "flow refuging", bull trout may use other behaviours that promote energy economy such as station-holding against the substrate whereby velocity is reduced (Fish 2010). The behaviour of maintaining contact with a solid bottom surface has been observed in bull trout swimming in swim tunnels (e.g., Mesa et al. 2004) and in the wild by snorkeling observations (e.g., Swanberg et al. 1997). Facey and Grossman (1990) also showed that longnose dace (*Rhinichthys cataractae)* and mottled sculpin were able to hold station in a swim flume without swimming and therefore showed little change in energy use with changing current velocity.

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. While the topic of individual variation in locomotor performance is of interest to fish physiologists (see 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 performance of the individual (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 was likely due to individual variation in microhabitat that bull trout choose to maintained position amongst.

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 fifty continuous (or non-continuous) 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 modeling suggests 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. While it was possible that some fish died because of the direct or indirect effects of tagging and calibration, but no dead fish were found during the course of the study. Furthermore, fourteen transmitters were returned by anglers from bull trout caught in the reservoir (downstream of the study area; Figure. 1) over three 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 of the effects of discharge in a riverine environment, we did not attempt to locate these fish downstream of the 10 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. Swimming at both low and high velocities can cause physiological stress in fish (Young and Cech Jr. 1994). However, there is more evidence that confinement and handling 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. While the limitations of applying laboratory swimming performance data to the field has been acknowledged by physiologists (Plaut 2001), a combined approach using both laboratory and field studies is likely needed due to the relative constraints in both environments (e.g. Hasler et al. 2009c).

Table 4.1: Summary steps for fitting bull trout log (EMG+1) model. **D_{MAG}** is the hourly average discharge; **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, nightime 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 was 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.

Model	Fixed Effect	ΔR^2	p
	Level 1 Hydrologic predictors		
1	**D_{MAG}**	.17	.000
2	D_{MAG}, **D_{CHANGE}**	.00	.000
	Level 1 Environmental controls		
3	D_{MAG}, **T_{WATER}**	.01	.000
4	D_{MAG}, T_{WATER}, **Light**	.00	.000
	Level 2 Subjects		
5	D_{MAG}, T_{WATER}, **Size**	.00	.040
6	D_{MAG}, T_{WATER}, **Sex**	.00	.090
	Level 3 Organizational		
7	D_{MAG}, T_{WATER}, **Year**	.00	.381
8	D_{MAG}, T_{WATER}, **Rec**	.00	.000
	Cross-level Interactions		
10	D_{MAG}, T_{WATER}, Rec**, D_{MAG}*****Rec**	.01	.000
11	D_{MAG}, T_{WATER}, Rec, D_{MAG}*Rec, **D_{MAG}*****D_{MAG}_mean**	.00	.000
12	D_{MAG}, T_{WATER}, Rec, D_{MAG}*Rec, **D_{MAG}*****#observ**	.00	.256

Table 4.2: Parameter estimates for Linear Mixed Model predicting bull trout axial swimming muscle activity [log (SEMG+1)] based on $\mathbf{D_{MAG}}$, $\mathbf{T_{WATER}}$ and **Rec** in the Columbia River, British Columbia, Canada. All continuous predictors were log transformed.

Parameter	**Estimate (SE)**	**df**	**t**	**95% Confidence**		**p**
				Lower	**Upper**	
Intercept	0.655(0.067)	1585.446	9.695	0.523	0.788	0.00
$\mathbf{D_{MAG}}$	0.085(0.003)	13434.346	28.953	0.080	0.091	0.00
$\mathbf{T_{WATER}}$	-0.237(0.063)	1953.059	-3.762	-0.360	-0.113	0.00
Rec1	Reference	-	-	-	-	-
Rec2	0.030(0.012)	7821.699	2.439	0.006	0.054	0.06
Rec3	-0.093(0.018)	4079.416	-5.071	-0.130	-0.057	0.00
$\mathbf{D_{MAG}}$***Rec1**	Reference	-	-	-	-	-
$\mathbf{D_{MAG}}$***Rec2**	-0.024(0.004)	13561.600	-6.255	-0.032	-0.017	0.00
$\mathbf{D_{MAG}}$***Rec3**	0.004(0.005)	13298.147	0.829	-0.006	0.015	0.41

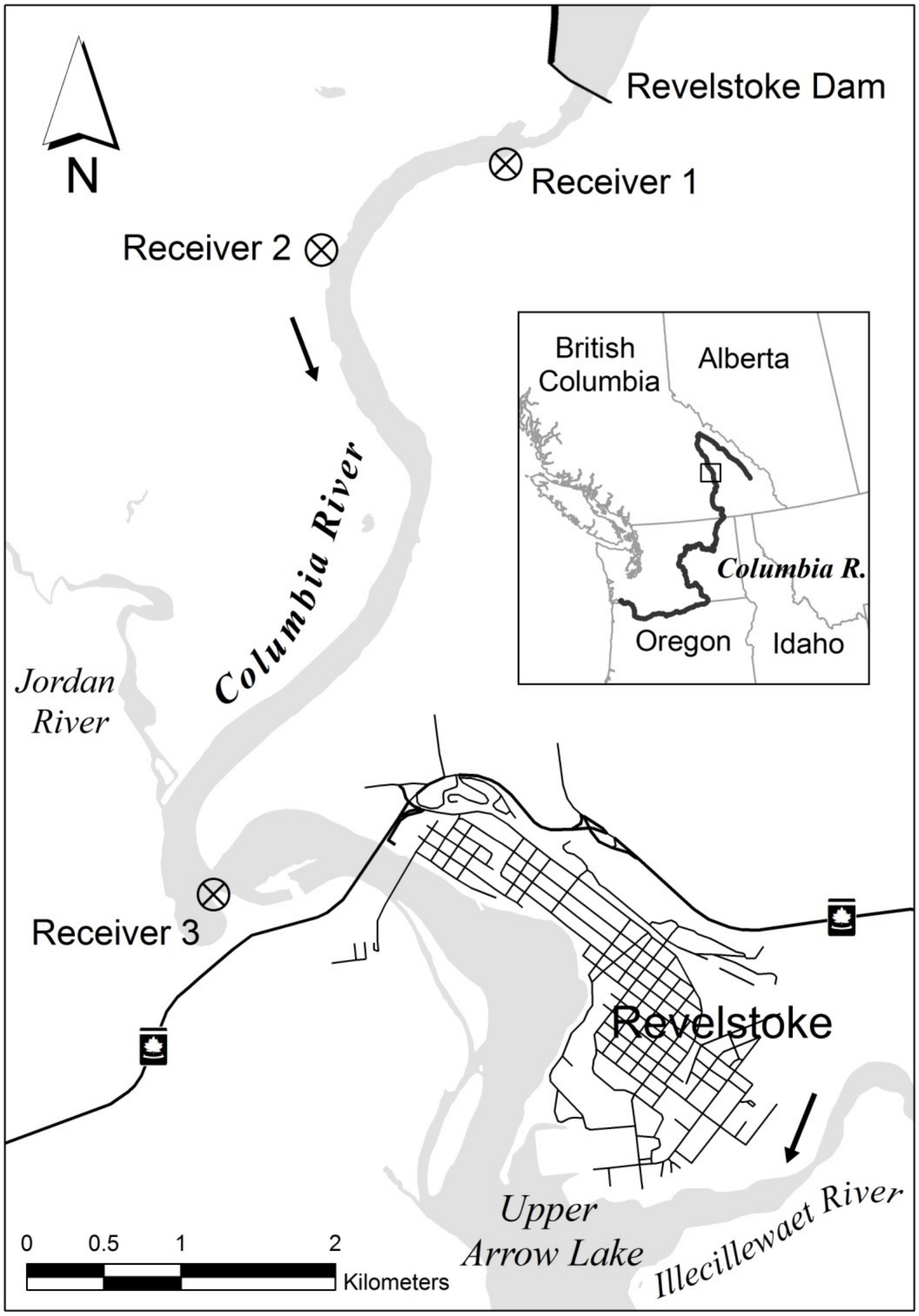

Figure 4.1: Map of the Columbia River downstream of Revelstoke Dam (REV), Revelstoke, British Columbia, Canada. Study area was 10.6 km section from REV downstream to the Illecillewaet River. Circle with X represents the fixed receiver locations.

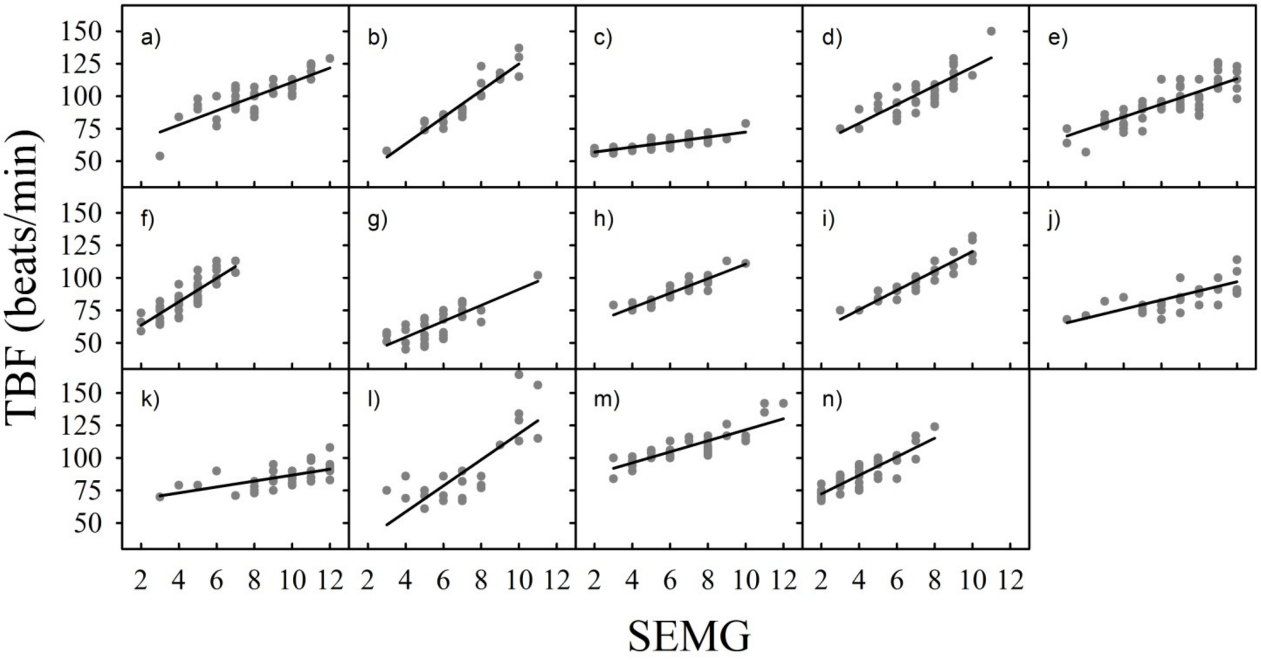

Figure 4.2: Scatterplot of the relationship between bull trout SEMG and tail beat frequency (TBF; beats/min). Fish a) TBF = 5.489(SEMG) + 55.94 (R^2=.66) b) TBF = 10.248(SEMG) + 22.45 (R^2=0.87) c) TBF = 1.92(SEMG) + 53.28 (R^2=0.60) d) TBF = 7.20(SEMG) + 50.36 (R^2=0.67) e) TBF = 4.84(SEMG) + 55.06 (R^2= .75) f) TBF = 9.04(SEMG) + 45.40 (R^2=0.73) g) TBF = 6.22(SEMG) + 29.03 (R^2=0.56) h) TBF = 5.58(SEMG) + 54.78 (R^2=0.84) i) TBF = 7.461(SEMG) + 45.64 (R^2=0.84) j) TBF = 4.72(SEMG) + 43.83 (R^2=0.65) k) TBF = 2.37(SEMG) + 62.64 (R^2=0.30) i) TBF = 10.02 + 18.48 (R^2=0.62) m) TBF = 4.24(SEMG) + 79.31 (R^2=0.68) n) TBF = 7.13(SEMG) + 50.917 (R^2=0.78).

CHAPTER 5: BEHAVIOUR AND PHYSIOLOGY OF MOUNTAIN WHITEFISH (*PROSOPIUM WILLIAMSONI)* RELATIVE TO SHORT-TERM CHANGES IN RIVER FLOW

Abstract

Despite the growing recognition that river flow can have an effect on the growth, distribution and survival of fishes, there is less known about the underlying mechanisms to explain these effects. Furthermore, there are few examples of integrated measures of behaviour and physiology to study the responses of fish to river hydrology. Here, axial swimming muscle electromyograms were logged as a sensitive indicator of activity from 19 mountain whitefish (*Prosopium williamsoni*) across a large range of hourly discharge magnitudes (mean = 621 m^3/s, range = 0-1770 m^3/s) in a hydropeaking reach of the Columbia River, Canada. Hourly mean discharge had a significant positive effect on swimming muscle activity. However, a large amount of the variance was unexplained, possibly due to social interactions, feeding and/or flow refuging behaviours. Fluctuating flows were no more energetically costly than stable flows. Discharge magnitude had a significant positive effect on blood cortisol concentrations. Yet, cortisol concentrations were low overall (mean ± SD = 1.60 ± 0.09 ng/ml) suggesting that the small observed response could be the result of routine physiological processes rather than a stress response *per se*. Based on low blood lactate concentrations, mountain whitefish were not swimming exhaustively (i.e. anaerobic burst-type swimming) at high flows.

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). The ecosystem response depends on how the components of flow (magnitude, rate of change, timing, frequency and duration) have changed relative to a river's natural flow regime (Poff et al. 1997). River flow (extreme low and peak flows) can affect the growth (Weyers et al. 2003; Korman & Campana 2009), abundance (Liebig et al. 1999) and mortality (e.g., Weyers et al. 2003; Xu et al. 2010; Young et al. 2010) of fishes. Yet, there is less known about underlying mechanisms to explain these effects.

Beyond some threshold swimming speed, fish may perceive their environment as noxious and exhibit a stress response (e.g., Young & Cech Jr. 1994). Stress can affect an individual on all levels of organization from rapid changes in blood physiology to whole animal performance over the longer term. The primary stress response includes endocrine changes such as increases in glucocorticoid (GC) stress hormones (Barton 2002). Release of cortisol, the primary GC in fish, is delayed post-contact with the stressor. Therefore, if cortisol is sampled properly, obtained values are not influenced by capture stress and can provide baseline GC concentrations (Gamperl et al. 1994). Secondary responses include changes in metabolism, hydromineral balance, cardiovascular, respiratory and immune functions. Finally, tertiary responses include whole-animal changes in performance, such as in growth and behaviour (Barton 2002). If a stress response remains uncorrected for days or weeks, the result is chronic stress which is detrimental to health and fitness (Busch & Hayward 2009).

Behavioural responses to stress could include changes in spontaneous swimming activity. Changes in activity (hypo- or hyperactivity) are among the first symptoms observed in the presence of a stressor (Scherer 1992). Frequently, these changes are reported non-quantitatively and secondary to other results (Scherer 1992), partly due to the lack of suitable recording techniques. Early work focused on contaminant induced changes in fish swimming behaviour (e.g., Bengtsson and Larsson 1981; Macfarlane and Livingston 1983). More recently, the use of biotelemetry has expanded the utility of activity studies to a variety of subtle stressors such as thermal pollution (e.g., Cooke and Schreer 2003) and fish stocking density (Cooke et al. 2000).

One technique to measure swimming activity is electromyogram (EMG) telemetry. Electromyograms are bioelectric voltage changes that are proportional to the degree and duration of muscle tension (Sullivan et al. 1963). Undulatory (or body/caudal) fin swimming in fish is powered by the segmented body musculature of the myotomes. The body and tail of a fish must push against the water to generate forward thrust when swimming. Thus, EMGs recorded from electrodes embedded into myotomes of the red oxidative muscles can be used as quantitative indicators of swimming activity (Cooke et al. 2004).

The purpose of this study was to determine if there was a relationship between the hydrological parameters of a hydropeaking river and mountain whitefish swimming energetics and stress physiological. Mountain whitefish are a lotic dwelling species, but also occupy lakes and reservoirs. River discharge at our study site, the 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.

Our first objective was to determine if there was a statistical effect of peaking river flows on mountain whitefish swimming activity. Specifically, we regressed axial swimming muscle electromyograms against hourly river discharge magnitude while controlling for the individual variation in mountain whitefish responses, as well as exogenous factors such as temperature and light. When discharge changes in a river, so does the spatial arrangement of energetically favourable positions and fish may shift from one position to another to compensate for the changing habitat quality (Kraft 1972). Given this, our second objective was to determine if within-hour fluctuations in river flow had an effect on mountain whitefish swimming activity. Our third objective was to determine if elevated (or reduced) river discharges were associated with GC release in mountain whitefish. And, although routine swimming would not be expected to increase lactic acid, exhaustive exercise would give rise to lactate production (Brown et al. 2008). Therefore, we also measured both baseline plasma cortisol and lactate concentrations relative to river discharge from a different set of free-swimming fish.

Methods

Study site and fish surgery

A total of 31 fish (mean ± SD fork length = 628 ± 104 mm) were collected by boat pulsed DC electroshocker during three years: 2008 (16 fish; September 24 – October 8), 2009 (12 fish; October 8 – 27) and 2010 (3 fish; October 26 – 27). Fish were captured at night using a large dip net, transferred into an aerated live-well and relocated to the surgery site. Water temperatures at the time of capture ranged from 8-11 °C among all years. 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-through water pumped from the river.

Fish were individually anaesthetized to stage 3-4 anesthesia (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) and 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. 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. A coded EMG transmitter was inserted (CEMG2-R11-12; dimensions: 11x48 mm, weight: 8.8 grams in air). EMG electrodes were inserted ~ 10 mm apart, in the red axial musculature, using a rod and plunger. Electrode placement was standardized at 0.7 body length on the right side of the fish (Beddow & McKinley 1999). A 16 ½ 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 information regarding EMG surgeries can be found in Cooke et al. (2004). The entire procedure took approximately five minutes 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 at which time it was released back into the river.

Electromyogram data collection and analysis

Three fixed receiver stations (Lotek SRX600 telemetry receiver, Newmarket, ON) continuously logged EMG data from locations where fish were known to congregate (Figure 5.1). Two antennas pointing both upstream and downstream were fixed to nearby trees at each fixed receiver station. Each receiver scanned eight channels in succession, 24 hours/day and recorded any fish in the general vicinity of the station (estimated maximum distance of 400 m up- and downstream). Coded EMG signals were converted to hourly averages; therefore, we approximated a value that corresponded to a prolonged period of swimming (Beamish 1978). Only hourly averaged values that were comprised of at least 100 instantaneous (2 second) EMG values were used in the analysis.

Studies have shown that EMG transmitters may behave differently in different fish (see Brown et al. 2007). Considering this, we tested for individual variation in intercepts and slopes when modeling the effect of discharge on uncalibrated EMGs. Because the intercepts varied among fish (Wald $Z = 2.348$, $p = 0.019$), we controlled for this between-subject variation using random factors under the Linear Mixed Model framework (MIXED; SPSS Inc., Version 18, Chicago, Illinois). Secondly, R^2 was used as the effect size which is independent of individual differences in slopes and intercepts. Preliminary analysis using ordinary least-squares (OLS) regression suggested autocorrelation in the model residuals due to the repeated electromyogram measurements on the same fish (Durbin-Watson statistic $<<2$). Autocorrelation plots confirmed this; therefore, the mixed model analysis started with an autoregressive (AR1) covariance structure to account for this autocorrelation. Also, EMGs showed a different range for different fish, for example, a resting EMG for one fish may be “12” whereas for another fish a resting EMG may be “5”. Standardized EMGs (SEMG) were then calculated by subtracting a fish’s resting value from its EMGs.

We added predictors using a hierarchical technique of building successive models and accessing the behaviour of the model in response to each new predictor (Field 2009). Our two hydrologic predictors were added first: hourly mean discharge magnitude ($D_{MAG,}$ mean discharge across a given hour) and within-hour change in discharge (D_{CHANGE}, difference between instantaneous maximum and minimum discharges within a given hour). Control variables were then added (T_{WARER}, water temperature) and diel period (Diel, categorical value of nighttime or daytime). Not all fish were logged at all receivers. Because of an imbalance of data among receivers, data from all receivers were pooled. We also tested for a time-lag effect of water flow (measured at the dam) to reach receiver 1 (~1 km), receiver 2 (~2.5 km) and receiver 3 (~7 km) downstream of the dam. A 30 minute time delay for river flow to reach receiver 3 was accounted for. The interaction between D_{MAG} and Diel was tested. The interaction between the number of EMG observations for each fish (#Observ) and D_{MAG} was also tested to see if the number of observations modulated the effect of discharge. The model structure was evaluated in terms of random slopes and covariance structures using Akaike's Information Criterion (AICs; Field 2009; Heck et al. 2010). A Variance Components covariance type for the random subject coefficients was found to be the best structure. Maximum Likelihood estimation was used. Because multilevel models are an extension of regression, all of the assumptions of OLS regression were tested as well as some additional assumptions pertaining to the random coefficients.

Scatterplots of all combinations of predictors were inspected to find correlations (i.e. collinearity) that may affect the model's ability to address the main question. A significant positive correlation existed between D_{MAG} and D_{CHANGE} ($r = 0.30$). Furthermore, discharge was significantly greater during the day (mean = 879 m^3s^{-1}) than at night (mean = 450 m^3s^{-1}). These pairs of predictors were added both alone and together so as to look for suppressor/synergistic effects (Grafen and Hails 2002). We compared activity between day and night using estimated marginal means, thus controlling for the difference in discharges. Model residuals were positively skewed, therefore, SEMGs (+1) and predictors were log transformed. Residuals were plotted across the range of predicted values and met the assumption of homoscedasticity. Random intercepts were normal about their means.

Blood sampling and analysis

During each survey, eight to twelve mountain whitefish (mean ± SD fork length = 261 ± 34 mm) were captured and sampled one at a time. Surveys occurred every four hours over five 24-hour periods (November 4, 2008; November 12, 2009; June 3, 2010; and October 29, 2010) coinciding with daily stable low, stable high, rising and falling river flows. Fish were captured using boat shocking from multiple reaches of a 10.6 km segment downstream of REV. The same river segment was not re-sampled more than once in the same day. Once netted, a blood sample was taken via caudal puncture using a Vaccutainer (3ml with lithium heparin, 21g needle; Becton Dickson, NJ) within two minutes of capture. Laboratory studies have demonstrated that capture-related stress will not significantly influence cortisol concentrations if the sample is taken quickly (< 3 minutes; Sumpter et al. 1997).

Samples were held on ice slurry for no more than 100 minutes before blood was centrifuged for 6 min at 10,000 g. Plasma was then flash-frozen in liquid nitrogen and later stored frozen in a -80 freezer until analysis. Samples were analyzed using a commercial radioimmunoassay kit (immunoChem Cortsiol I25I RIA Kit, MP Biomedicals, Orangeburg, NY) routinely used to quantify cortisol concentrations in fish plasma (Gamperl et al. 1994) and a Cobra Auto-Gammer counter (Hewlett-Packard, Palo Alto, CA). Detailed methods can be found in Gamperl et al. (1994). All samples were assayed together and intra-assay variability was 3.4% as quantified from 16 samples run in duplicate. Lactate was measured on blood plasma by adding 10 ml of blood to a hand-held lactate meter (Lactate Pro LT-1710 portable lactate analyser; Arkray Inc., Kyoto, Japan). Appropriate standards and calibrations were used with meters prior to analysis as per manufacturer guidelines. The Lactate Pro has previously been validated as a reliable tool for field physiology including for fishes (Brown et al. 2008).

Because only one sample was taken from independent fish, a general linear model (GLM) was used to test for a relationship between river discharge on cortisol and lactate concentrations. An average discharge for each of 1-6 hours before blood was sampled was tested against cortisol concentrations to determine which time scale was the best at predicting cortisol; mean discharge from the preceding one hour before sampling produced the best model. We repeated this step with within-hour change in discharge. The mean temperature during the same one-hour sampling period was also controlled for. Temperatures never varied by more than 0.4 °C during any one sampling period; therefore, temperatures were most different among years. The diel effect of day and night was also controlled for. Dawn and dusk were considered to be one hour before and after sunrise and sunset. However, because of the relatively small amounts of data collected during the dawn/dusk period, these data were removed from the analysis. The reciprocal of cortisol was used to achieve normality of model residuals – more traditional transformations (e.g., log and square-root) were not effective. Residuals conformed to the assumption of homoscedasticity.

Results

Data collection

Of 31 mountain whitefish tagged over three years, 19 were recorded at fixed stations and yielded sufficient information for analysis of axial swimming muscle electromyograms. The remainder either 1) were never located in the 10.6 km study area 2) were located in the study area, but were not located near the three fixed receivers 3) or, were located within range of the receivers, but for a relatively short time. On average, 113 ± 116 (mean ± SD) hourly mean EMG values were logged for each whitefish during a mean hourly discharge of 621 m^3/s (range = 0-1770 m^3/s). Zero flow release from REV did occur, but residual river water, tributary inflow and back-up from the downstream Arrow Lakes prevents the river from completely dewatering. The mean difference between within-hour maximum and minimum discharge was 176 m^3/s (range = 0-920 m^3/s). The mean temperature was 10.2 °C (range = 7.5-12.2 °C).

Two hundred and one blood samples were collected over five 24-hour survey periods during an overall mean discharge of 900 m^3/s (range = 566-1524 m^3/s) and a mean temperature of 8.6 °C (range = 5.3–10.7 °C). All blood samples were analyzed for cortisol and a subset of ninety samples were analyzed for lactate.

Electromyogram data

D_{MAG} had a significant positive effect on swimming muscle activity (MIXED, $F_{(1, 2130)}$ = 126.80, $p < 0.001$). Upon adding D_{CHANGE}, T_{MEAN}, Diel and Year, only D_{MAG} (MIXED, $F_{(1, 2134)}$ = 108.71, $p < 0.001$) and Diel (MIXED, $F_{(1, 2128)}$ = 44.82, $p < 0.001$) were significant predictors and remained in the final model (Table 5.1). The #observ variable did not modulate the effect of discharge (MIXED, $F_{(1, 370)}$ = 0.94, $p = 0.33$). Finally, the addition of a D_{MAG} slope was not significant (Wald Z = 1.51, $p = 0.13$). In the final model, D_{MAG} and Diel explained 14% and 4%, respectively, of the variation in swimming muscle activity (Table 5.2). Pairwise comparisons, based on estimated marginal means of log(SEMG+1), suggested that muscle activity during the day was 1.11 times that of muscle activity during the night ($p < 0.001$) when controlling for discharge.

Blood physiology

All seasons combined, the mean cortisol concentration was 1.60 ± 0.09 ng/ml. There was a significant negative effect of hourly mean discharge on 1/cortisol (GLM, $F_{(1,196)} = 20.99$, $p < 0.001$, $R^2 = 0.10$). Within-hour change in discharge also had a significant negative effect on 1/cortisol (GLM, $F_{(1,196)} = 20.99$, $p < 0.001$, $R^2 = 0.05$). Water temperature had no effect on 1/cortisol (GLM, $F_{(1,196)} = 1.18$, $p = 0.28$). There was also no difference between 1/cortisol values from whitefish at night versus day (GLM, $F_{(1,196)} = 3.71$, $p = 0.08$).

All seasons combined, the mean plasma lactate concentration was 2.05 ± 2.11 mmol/L. There was no significant effect of discharge on log(lactate) (GLM, $F_{(1,83)} = 3.16$, $p = 0.08$). Mean daily water temperature did have a significant negative effect on log(lactate) (GLM, $F_{(1,83)} = 15.06$, $p < 0.001$, $R^2 = 0.15$). There was no difference between log(lactate) at night versus day (GLM, $F_{(1,83)} = 0.26$, $p = 0.61$).

Discussion

Our first objective was to determine if peaking river flows had an effect on mountain whitefish swimming activity. There was a significant positive correlation between hourly mean discharge magnitude and hourly mean swimming muscle activity. This may be explained by the fact that for a fish to hold station, it must maintain a constant position relative to the substrate, despite the flow of water exerting force to displace the fish downstream (Gee 1983). The energetic demand of swimming can be substantial and is a direct function of the fish's drag multiplied by the water's current velocity (Webb 1988). However, it was surprising that a large amount of variance in mountain whitefish muscle activity was unexplained by discharge. There are a number of behaviours associated with energy economy in high flows including “flow refuging” – avoiding the high costs of swimming by positioning themselves in low flow microhabitats – which may explain the presence of some hours of relatively low muscle activity during high discharge. Also, some prolonged feeding attempts or social interactions may have occurred at opportunistic times when discharges were not necessarily high, thus resulting in greater than average activity at a given discharge. This highlights one of the critical differences between studying fish swimming behaviour in a laboratory flume, whereby fish are forced to swim, versus wild free-swimming fish.

For some species, river discharge does not appear to exert control over swimming activity. For example, Geist et al. (2005) found that light levels and temperature, but not discharge were related to swim speeds and oxygen consumption of juvenile white sturgeon (*Acipenser transmontanus*) in the Snake River, Idaho. A diversity of responses to discharge was seen among individual fish as demonstrated by the random intercepts to the SEMG model. While individual variation in locomotor performance is a topic of interest to fish physiologists (see Kolok 1999), individual variation of intercepts in our uncalibrated-SEMG model is difficult to interpret because we are not sure whether it is due to the transmitters and/or the actual performance of the individual (Brown et al. 2007). Therefore, we controlled for this individual variation using random coefficients while focusing on the main effects of hydrology by using R^2 as our effect size which is independent of the intercepts.

Our second objective was to determine if within-hour fluctuations in river flow had an effect on mountain whitefish swimming activity. Large within-hour changes in discharge occurred (range = 0-920 m^3/s) which is unique to hydropeaking systems. However, no significant effect on swimming muscle activity was found. This was surprising considering changes in microhabitat use by fishes, as influenced by changing flows, have been documented by snorkelling observations (Pert & Erman 1994) and electrofishing (Valentin et al. 1994). Further, Cocherell et al. (2011) found that rainbow trout (*Oncorhynchus mykiss*) had significantly elevated swimming activity during the initial peaking phase of flow release in the American River, California.

The third objective of this study was to determine whether short term changes in river flow are perceived as a physiological stressor, as measured by circulating baseline cortisol concentrations. Cortisol did increase with hourly mean discharge and within-hour change in discharge when controlling for temperature and light. However, despite these correlations, overall mean (±SD) cortisol levels were only 1.60 ± 0.09 ng/mL - a values are in the range of "pre-stress" values reported for a number of salmonids (see Barton 2002). For example, baseline cortisol concentrations were 1.0 ± 0.3, 1.1 ± 0.3 and 1.7 ± 0.5 ng/mL for brown trout (*Salmo trutta*), arctic grayling (*Thymallus arcticus*) and rainbow trout, respectively. These fish had corresponding post-stress concentrations of 94 ± 11, 46 ± 4.4, and 43 ± 3.5 ng/mL, respectively, after a standard 30-second handling. Mountain whitefish plasma cortisol concentrations can be > 100 ng/mL following prolonged capture and holding (held in beach seine for > 20 min; Quinn et al. 2010). Flodmark et al. 2002 examined the effects of simulated hydropeaking on baseline cortisol concentrations of brown trout in an artificial stream channel and found that when fish were exposed to daily cyclical fluctuations of water flow, plasma cortisol levels were elevated on the first day compared to undisturbed fish. However, by the fourth day, cortisol remained at control levels leading to the conclusion that these fish showed rapid habituation to the stressor. This may be the scenario in the Columbia River whereby mountain whitefish are habituated to repeatedly fluctuating discharges. Krimmer et al. (2011) examined the stress response of brook trout to experimental water-withdrawal from a small mountain stream and found no differences between treatment and control reaches. However, blood samples were taken from anaesthetized fish at least 5 minutes post-capture and cortisol values were likely influenced by the sampling protocol. Erickson et al. (2005) also found no difference in baseline cortisol concentrations of brown trout between urban storm runoff and base flow events which included both significant changes in river flow and water quality parameters such as suspended solids and metals. Other than these three examples, we are not aware of any research examining the relationship between water flow and GC stress response.

Measuring blood lactate is a common method to assess the physiological consequences of swimming and fatigue (e.g., Gustaveson et al. 1991) as increased blood lactate reflects increased oxygen consumption during swimming. When oxygen availability for tissue function is impaired, glycolysis gives rise to increased lactate production. In this study, discharge showed no relationship with lactate, suggesting that study fish are not performing exhaustive anaerobic exercise during high flows. Prolonged recovery times of free-swimming fish to periods of peak discharge would leave fish vulnerable to predation as their capacity for anaerobic (i.e. “burst”) swimming would be impaired. Daily mean water temperature had a significant negative effect on lactate. Mean lactate concentrations from this study (2.05 ± 2.11 mmol/L) were less than those reported for rainbow trout following exhaustive catch and release scenarios (6.26 ± 0.4 mmol/L; Meka & McCormick 2005).

In summary, our results suggest that while axial swimming muscle activity increased at elevated discharges, the majority of the variation in activity was not explained by hydrology. Furthermore, physiology results reveal that discharge did not appear to be a stressor to mountain whitefish or cause exhaustive exercise. Our approach of integrating measures of both behaviour and physiology for the study of hydropower impacts on free-swimming fish is novel. We demonstrated that using mixed-modeling approaches, one can control for individual variation in biotelemetry data as well as account for the inherent violations of independence that occur when analysing data that were repeatedly measured from the same fish. We suggest that future research on fish responses to flow dynamics incorporate measures of both fish behaviour and physiology in an effort to further elucidate the complexity of animal-environment relationships, particularly in the context of water resource management.

Table 5.1: Summary of steps to fit Linear Mixed Model for mountain whitefish log(SEMG+1) in the Columbia River, Revelstoke, B.C. One fixed effect was added at a time and is bolded. **D_{MAG}** is the hourly average discharge; **D_{CHANGE}** is the difference between within-hour instantaneous maximum and minimum discharges; **T_{WATER}** is the hourly average temperature; **Diel** is a categorical value of daytime or nighttime; **Year** is the year in which data were collected (2008, 2009, or 2010). **#Observ** is the number of EMG values logged/fish. **ΔR^2** is the change in effect size from the previous model. Continuous predictors were log transformed.

Model	**Fixed Effect**	**ΔR^2**	**$p^{\text{(new term)}}$**
1	**D_{MAG}**	0.14	<0.001
2	D_{MAG}, **D_{CHANGE}**	0.00	0.234
3	D_{MAG}, **T_{WATER}**	0.00	0.075
4	D_{MAG}, **Diel**	0.04	<0.001
5	D_{MAG}, Diel, **Year**	0.00	0.447
6	D_{MAG}, Diel, **D_{MAG}*Diel**	0.00	0.141
7	D_{MAG}, Diel, **D_{MAG}*#Observ**	0.00	0.334

Table 5.2: Parameter estimates for Linear Mixed Model of mountain whitefish log(SEMG+1) in the Columbia River, Revelstoke, B.C. $\mathbf{D_{MAG}}$ is the hourly average discharge and **Diel** is a categorical value of Day or Night. "**Night**" was used as the reference category; therefore, the "Night" parameter estimate is redundant in the presence of the intercept parameter. Continuous predictors were log transformed.

Parameter	**Estimate**	**SE**	**df**	**t**	**95% Confidence int.**		**p**
					Lower	Upper	
Intercept	0.346	0.028	26	12.314	0.288	0.404	<0.001
Log($\mathbf{D_{MAG}}$)	0.050	0.005	2133	10.437	0.041	0.594	<0.001
Day	0.052	0.008	2128	6.695	0.036	0.067	<0.001
Night	Ref	-	-	-	-	-	-

CONCLUSION

The overall purpose of this thesis was to evaluate the sub-lethal responses of bull trout (*Salvelinus confluentus*) and mountain whitefish (*Prosopium williamsoni*) to unsteady river flow at multiple scales (between- and among-hours). To accomplish this, I developed relationships between behavioural and physiological parameters measured from free-swimming fish and the operational release of water from a hydropeaking river (Columbia River). Movement distances were only weakly associated with river flow parameters. However, by coarsening the scale of movement (i.e. from a continuous to a binary response), I demonstrated that reach-scale (>100 m) movements of bull trout in the Columbia River were significantly depressed during periods of high river discharge which suggested that the energetic costs of maintaining position within a 100 m reach were within their physiological capacities. The binary response indicates the timing of when a fish decided to move (regardless of when it stopped). Assuming that fishes move in response to changing river conditions to maximize fitness (Kahler et al. 2001), correlating the timing of movement with river conditions may provide insight into the physical conditions that fish perceive to be unsuitable. In contrast, movement distances may be more indicative of where the fish finds relatively more suitable habitat. The fact that the majority of movements were relatively small (i.e. 100 m) may suggest that suitable habitat was found relatively close by.

Knowing that bull trout were not forced out of the study reach was a positive result for hydropeaking managers; although it is no assurance that further increases in discharge magnitude could not force bull trout from preferred habitat. The fact that my results differed from the average result from the literature (i.e., Chapter 2; meta-analysis) was unexpected and may be explained by difference in the intensity of the interventions (i.e. range of flow conditions). Low or moderate increases in discharge fish may promote fish movement due to increased habitat area, but larger increases in discharge may provide a challenge for fish to move against high velocity water. Although river flow conditions did not have a significant modulating effect on the individual effects sizes from the meta-analysis, the effect was nearly significant (i.e. $R^2 = 0.18$; $p = 0.06$) and a larger sample size may have shown a stronger effect.

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. Indeed, bull trout axial swimming muscle activity was heightened during periods of high discharge which is consistent with the energy loss theory. However, when muscle activity was related to swimming speeds, I found that these fish were most often not beating their tail. This suggested that they were able to maintain position in the river with relatively smaller energetic costs compared to undulatory motion of their swimming muscles to maintain position. While we did not make direct observations on the fish (i.e. fish were not within view during tracking events), there are a number of behaviours that could allow a fish to maintain position in flowing water without beating their tail (discussed in Chapter 4). Furthermore, within-hour rates of discharge change were not significantly related to swimming activity. From a management perspective, this result suggested that hydropeaking managers 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.

The fact that bull trout have the capacity to maintain position in a river without swimming is a phenomenon that is not accounted for when applying critical velocity values to rivers or fish passage structures. In other words, the current perception that there is a linear relationship between water flow and swimming speed may be tenuous when applied to free-swimming fishes in the wild. This phenomenon may also have implications for current theoretical developments in regards to the energetic cost optimization hypothesis – the hypothesis that fishes traverse upstream pathways that minimize their energetic expenditure and that this cost is solely based on the physical environment (i.e. river flow; McElroy et al. 2012). My work suggested that the energetic cost for bull trout to maintain position in a river was only partially related to water flow as there was substantial variance in swimming activity that was unexplained by my current understanding of the physical environment. Although swimming cost functions for some fish may scale with the fish's relative velocity, bull trout appear to be capable of maintaining position without beating their tail under a range of average river velocities. My 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, according to the current energetic cost optimization hypothesis, the non-swimming behaviour of bull trout would only be possible in zero-velocity water which surely did not exist in the Columbia River, even with substantial flow refuging habitat. Therefore, the energetic cost hypothesis may need to be refined on species-specific bases, given that some species have been shown to be capable of resisting the drag force of flowing water (e.g., mottled sculpin and longnose dace; Facey and Grossman 1990)

Future research should attempt to elucidate the mechanisms by which bull trout are able to maintain position without swimming. Field studies would be most advantageous, albeit more difficult than laboratory studies. Snorkel observations have been used to document flow-refuging behaviour in free-swimming fish during regular seasonal variations in river flow. 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 snorkelers. Rainbow trout and rosyside dace were over-represented at relatively lower velocities, as predicted by the energetic cost hypothesis (Facey and Grossman 1992). Interestingly, benthic species (mottled sculpin and longnose dace) were able to hold position over a wide range of velocities (up to 8 body lengths per second) without a significant change in oxygen consumption (Facey and Grossman 1992). Mottled sculpin 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 (Arnold et al. 1991). Bull trout may also use these behaviours as a means of holding station without swimming. Mesa et al. (2004) attempted to perform critical swimming speed tests on bull trout in a confined flume and found that these fish were able to hold station at a range of velocities without beating their tail. The exact function of how they maintain station without beating their tail was not investigated, although bull trout were observed flaring their pectoral fins on the bottom of the flume. Morphological and kinematic studies of the pectoral fins (e.g., Wilga and Lauder 2001) could help elucidate the functional morphology that has allowed them to adapt to fast water environments. This would contribute to the overall knowledge of why bull trout our found in some environments that exclude other salmonids species.

Similar to bull trout, hourly mean discharge measured from the Revelstoke Dam also showed a significant positive effect on mountain whitefish muscle activity. We expected a larger effect size for mountain whitefish (which was not the case) based on the fact whitefish maintain position in the mid-channel current (McPhail and Troffe 2001). However, mountain whitefish can exhibit schooling behaviour (Joyce and Hubert 2003; Northcote and Ennis 1994) which has been suggested to provide energetic advantages to fishes (Fish 2010). Also, I found no evidence of physiological stress, as measured from baseline blood cortisol and lactate, as the result of relatively high (or low) hourly-averaged discharge or within-hour discharge fluctuations.

The only other study that examined the effects of unsteady flow on the stress response of fish found that brown trout showed rapid acclimation to this stressor in a laboratory environment (i.e. Flodmark et al. 2002). Therefore, previous experience with flow conditions can modulate the physiological response. The effects of acclimation on sustained exercise performance have been studied (i.e., “exercise training”). For example, previous experience of fish at sustained swimming speeds can reduce the metabolic response and increase their time to fatigue during subsequent swimming challenges owing to the improved respiratory capacity, increased energy store and/or aerobic metabolic capacity of muscle tissue (Gallaugher et al. 2001; Fu et al. 2011). Furthermore, some evidence has suggested that resting exercised fish may have lower stress responses to forced swimming than resting non-exercised fish (e.g., Woodward and Smith 1985).

“Exercise training” has studied from a basic biological perspective; however, the topic is relevant to hydropower science when river flows are periodic or non-periodic, and fishes may or may not have prior experience with a given flow regime. A fish’s behavioural or physiological response may be attenuated when experiencing flows that occur weekly or monthly versus extreme events which may only happen on the scale of multiple years. Researchers may be able to use reciprocal transplants – moving fish from non-hydropower impacted systems to systems with high degrees of unsteady flow and turbulence. Future physiological studies of fish in response to altered river flows will also employ a variety of techniques to provide a greater mechanistic understanding of potential lethal environments. For example, Dr. James Liao at the University of Florida is using sensory neurophysiology to understand the behavioural response of free-swimming fish to turbulence by examining the organization and function of neurons at the lateral line while characterizing turbulence using particle image velocimetry.

Although this research examined the behavioural/physiological responses of fishes to two of the components of flow at different temporal scales, turbulence is another hydrologic parameter that was not investigated. Very little research has examined the effects of turbulence on fish behaviour in natural environments - these studies require the precise positioning of fish and corresponding measures of turbulence (Lacey et al. 2012). One study examined the effects of turbulence on habitat choice of free-swimming brown trout (Cotel et al. 2006). Cotel et al. (2006) made snorkeling observations relative to current speeds and measure turbulence intensity (TI) at fish focal point locations. Turbulence intensity was inversely related to current speed. Brown trout were usually found in the lower 5 cm of the stream, where shear forces result in high turbulence. Given that locations occupied by brown trout had lower TI than similar locations without brown trout, understanding the effects of turbulence on fish behaviour can also help explain species distributions and predict the loss of certain species following hydrologic change.

These early studies were relatively successful at documenting micro-habitat use of stream fishes in small streams. However, microhabitat use has not been documented in the similar detail in a relatively larger river. Nor has it been accomplished in the context of hydropeaking whereby the range of velocities far exceeds the relatively stable flows of unregulated streams - a formidable task given the constraints for safety and visibility. This was essentially the goal of my thesis whereby I would have liked to re-create the study of Facey and Grossman (1992) under the context of large unsteady flows associated with hydropeaking. Some challenges ensued. Firstly, we could not develop the velocity-metabolic rate relationship for bull trout given the technical challenges with swimming bull trout in an enclosed swim flume as discussed in Mesa et al. (2004) and in Chapter 4 of this thesis. Secondly, we could not record fine-scale velocities (i.e., snout-velocities) and our best proxy was river discharge as recorded from the Revelstoke Dam. Using discharge as a proxy for velocity seemed reasonable considering that positive relationships between discharge and average river velocity had been reported in the literature (e.g., Dare et al. 2002; Brown et al. 2001). An ideal study would quantify snout-velocity of free-swimming fish in order to gain the detail that has been accomplished using laboratory flumes.

Fine-scale velocity measurements can be made using technology such as acoustic Doppler current profilers (ADCP) and velocimeters (ADV) which has become the preferred approach for measuring river hydraulics (e.g., Yorke and Oberg 2002). These instruments transmit a known frequency acoustic pulse into the water, then analyse the frequency of sound scattered back to the instrument which is shifted in frequency by the Doppler effect (Pinkel 1980). These instruments can be used to measure velocities in shallow water (as shallow as 1.0 m) with a high degree of spatial resolution (0.10 m; Yorke and Oberg 2002). However, these techniques do have limitations. For example, water velocities cannot be measured near the substrate (Yorke and Oberg 2002), a location whereby bull trout may inhabit as refuge from high flows. It is also difficult to measure complex shedding from instream structures such as boulders (Lacey et al. 2012). Secondly, a measurement of mean velocity and relative turbulence intensity for large rivers is difficult due to the challenges with deploying equipment into deep and fast water (Lacey et al. 2012). Therefore, while the use of Doppler metres have been successful for hydrologist quantifying river flow, no studies have linked the behaviour of free-swimming fish with the complex, fine-scale distribution of velocities typically found in a large river.

Regardless of the challenges stated above, we could not position a fish at a fine-enough scale to be coupled with fine-scale velocity measurements given the depth and complexity of the Columbia River. However, 3D-telemetry systems are a relatively new technology whereby acoustic signals transmitted to an array of receivers can be used to position the fish a very fine scale (within ~25cm). 3D-telemetry has been used to monitor fish response to a variety of environmental variables including temperature (Hasler et al. 2009b), oxygen (Hasler et al. 2009c) and lunar cycles (Hanson et al. 2008). However, given that this technology is acoustic-based, it is considerably more difficult to use in a lotic environment where turbulence in flowing water interferes with the transmission of acoustic signals. Current research (funded by BC Hydro) is examining fine-scale behaviour of bull trout surrounding the hydraulically-complex flow intake at the Mica Dam, but the coupling of two datasets in time and space are difficult.

Future research in the field of hydro-ecology will include mathematical approaches to simulate and forecast 3-D behaviour of individual fish responding to abiotic stimuli *a priori* to field data collection (e.g., the Eulerian-Lagrangian-Agent Method (ELAM); Goodwin et al. 2006). An ELAM model is an individual-based model (IBM) coupling different frameworks to govern the hydrodynamics of water and the sensory perception/decisions and movement trajectories of individual fish (Goodwin et al. 2006). Spatially explicit IBMs use movement rules to determine when an animal departs its current location and to determine its movement trajectory (Railsback et al. 1999). Movement rules regard how an individual's expected fitness varies among locations, under the assumption that fish make the decision to move when they perceive that a new location will increase their fitness (Railsback et al. 1999). IBMs can be used for instream flow assessment models to compare the population benefits of alternative stream flow regimes. For example, InSTREAM models an individual fish at a daily time step, with population responses emerging from how individuals are affected by their habitat and each other (Railsback 2009).

The morphological and hydrodynamic complexity of natural rivers provide challenges for fish including seasonal changes in the hydrodynamic character of river flow as well as turbulence generated by flow past bluff bodies (Lacey et al. 2012). Exacerbating this is the effect of hydropower infrastructure (e.g., fish passage devices at dams) and the time-varying effects of operational flow releases from dams. Although a few laboratory studies have been undertaken to understand the effects of altered flows on fish abundance (e.g., Smith et al. 2005), physiological cost (e.g., Enders et al. 2003; Liao 2004), behaviour (e.g., Liao et al. 2003; Smith et al. 2005) and stability (e.g., Tritico and Cotel 2010), laboratory studies often represent simplified flow environments in comparison with flows occurring in natural rivers. The results from this thesis contribute to the growing evidence that the generalisation of forced-swimming laboratory studies to natural environments may be tenuous.

While the studies presented in this thesis could not replicate the detail, in regards to the spatial scale of responses (i.e., detailed behaviour) or intervention (i.e., description of flow conditions) found in laboratory studies, they did improve on existing studies using free-swimming fish 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). While this thesis did not directly support such efforts, it did contribute to the overall understanding of how these fish cope, from a behavioural and physiological perspective, with their seemingly challenging environment. Understanding the relationship of fishes with their physical environment is important to help explain population level responses to changes which cannot be derived from traditional “stock assessment” models.

REFERENCES

Aarestrup K, Nielsen C, Koed A. 2002. Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. *Hydrobiologia* **483**: 95-102.

Aebischer N, Robertson P, and Kenward R. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**: 1313-1325.

Adam JC, Hamlet AF and Lettenmaier DP. 2009. Implications of global climate change for snowmelt hydrology in the twenty-first century. *Hydrology Processes* **23**: 962-972.

Albanese B, Angermeier P, Dorai-Raj S. 2004. Ecological correlates of fish movement in a network of Virginia streams. *Canadian Journal of Fisheries and Aquatic Science* **61**: 857-869.

Almeida P, Quintella B, Dias N. 2002. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). *Hydrobiologia* **483**: 1-8.

Anderson WG, McKinley RS, Colavecchia M. 1997. The use of clove oil as an anesthetic for rainbow trout and its effects on swimming performance. *North American Journal of Fisheries Management* **17**: 301-307.

Armstrong JD, Braithwaite VA, Fox M. 1998. The response of wild Atlantic salmon parr to acute reductions in water flow. *Journal of Animal Ecology* **67**: 292-297.

Arnold GP, Webb PW, Holford BH. 1991. The role of the pectoral fins in station-holding of atlantic salmon parr (*Salmo salar L.*). *Journal of Experimental Biology* **156**: 625-629.

Aubin-Horth N, Gingras J, Boisclair D. 1999. Comparison of activity rates of 1+yellow perch (*Perca flavescens*) from populations of contrasting growth rates using underwater video observations. *Canadian Journal of Fisheries Aquatic Science* **56**: 1122-1132.

Bahr M, Shrimpton J. 2004. Spatial and quantitative patterns of movement in large bull trout (*salvelinus confluentus*) from a watershed in north-western British Columbia, Canada, are due to habitat selection and not differences in life history. *Ecology of Freshwater Fish* **13**: 294-304.

Barton BA. 2002. Stress in fishes: A diversity of responses with particular reference to changes in circulating corticosteroids. *Integrative and Comparative Biology* **42**: 517-525.

Beamish FWH. 1978. Swimming capacity. In *Fish Physiology – locomotion*, Hoar WS, Randall JR (eds.). Academic Press: New York; 101-187.

Beddow TA, McKinley RS. 1999. Importance of electrode positioning in biotelemetry studies estimating muscle activity in fish. *Journal of Fish Biology* **54**: 819-831.

Bengtsson BE, Larsson A. 1981. Hyperactivity and changed diurnal activity in flounders, *Platichthys flesus*, Exposed to DDT. *Marine Pollution Bulletin* **12**: 100-102.

Bennett A. 1990. Thermal-dependence of locomotor capacity. *American Journal of Physiology* **259**: 253-258.

Berland G, Nickelsen T, Heggenes J, Økland F, Thorstad EB and Hallebraker J. 2004. Movements of wild Atlantic salmon parr in relation to peaking flows below a hydropower station. *River Research and Applications* **20**: 957-966.

Bernard DR, Hasbrouck JJ. 1999. Handling-induced delay and downstream movement of adult chinook salmon in rivers. *Fisheries Research* **44**: 37-46.

Boisclair D, Leggett WC. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1859-1867.

Boisclair D, Sirois P. 1993. Testing assumptions of fish bioenergetics models by direct estimation of growth, consumption, and activity rates. *Transactions of the American Fisheries Society* **122**: 784-796.

Bolland JD, Cowx IG, Lucas MC. 2008. Movements and habitat use of wild and stocked juvenile chub, *Leuciscus cephalus* (L.), in a small lowland river. *Fisheries Management and Ecology* **15**: 401-407.

Booth RK, McKinley RS, Økland F, Sisak MM. 1997. In situ measurement of swimming performance of wild Atlantic salmon (*Salmo salar*) using radio transmitted electromyogram signals. *Aquatic Living Resources* **10**: 213-219.

Bratrich C, Truffer B, Jorde K, Markard J, Meier W, Peter A, Schneider M, Wehrli B. 2004. Green hydropower: a new assessment procedure for river management. *River Research and Applications* **20**: 865–882.

Brett JR. 1965. The relationship of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* **22**: 1491-1501.

Brett J. 1971. Energetic responses of salmon to temperature - study of some thermal relations in physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist* **11**: 99-113.

Brett JR. 1995. Energetics. In *Physiological ecology of Pacific salmon*, Groot C, Margolis L, Clarke WC. (eds.). University of British Columbia Press, Vancouver, B.C; 3-36.

Brown R, Power G, Beltaos S. 2001. Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. *Journal of Fish Biology* **59**: 1126-1141.

Brown RS, Tatara CP, Stephenson JR, Berejikian BA. 2007. Evaluation of a new coded electromyogram transmitter for studying swimming behavior and energetics in fish. *North American Journal of Fisheries Management* **27**: 765-772.

Brown JA, Watson J, Bourhill A, Wall T. 2008. Evaluation and use of the Lactate Pro, a portable lactate meter, in monitoring the physiological well-being of farmed Atlantic cod (*Gadus morhua*). *Aquaculture* **285**: 135-140.

Bunt CM, Cooke SJ, Katopodis C, Mckinley RS. 1999. Movement and summer habitat of brown trout (*Salmo trutta*) below a pulsed discharge hydroelectric generating station. *Regulated Rivers Research and Management* **15**: 395-403.

Busch DS, Hayward LS. 2009. Stress in a conservation context: A discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biological Conservation* **142**: 2844-2853.

Clapp D, Clark R, Diana J. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. *Transactions of the American Fisheries Society* **119**: 1022-1034.

Cocherell SA, Jones GJ, Miranda JB, Cocherell DE, Cech JJ Jr., Thompson LC, Klimley AP. 2010. Distribution and movement of domestic rainbow trout, *Oncorhynchus mykiss*, during pulsed flows in the South Fork American River, California. *Environmental Biology of Fishes* **89**: 105-116.

Cocherell SA, Cocherell DE, Jones GJ, Miranda JB, Thompson LC, Cech JJ, Klimley AP. 2011. Rainbow trout *Oncorhynchus mykiss* energetic responses to pulsed flows in the American River, California, assessed by electromyogram telemetry. *Environmental Biology of Fishes* **90**: 29-41.

Cohen J. 1992. A power primer. *Psychological Bulletin* **112**: 155-159.

Cooke SJ, Chandroo KP, Beddow TA, Moccia RD, McKinley RS. 2000. Swimming activity and energetic expenditure of captive rainbow trout *Oncorhynchus mykiss* (Walbaum) estimated by electromyogram telemetry. *Aquaculture Research* **31**: 495-505.

Cooke SJ, Schreer JF. 2003. Environmental monitoring using physiological telemetry - A case study examining common carp responses to thermal pollution in a coal-fired generating station effluent. *Water Air and Soil Pollution* **142**: 113-136.

Cooke SJ, Thorstad EB, Hinch SG. 2004. Activity and energetics of free-swimming fish: Insights from electromyogram telemetry. *Fish and Fisheries* **5**: 21-52.

Cotel AJ, Webb PW, Tritico H. 2006. Do brown trout choose locations with reduced turbulence? *Transactions of the American Fisheries Society* **135**: 610-619.

Cushman RM. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *North American Journal of Fisheries Management* **5**: 330-339.

Dare MR. 2006. Integration and application of radio telemetry data collected on a mobile fish species: a synthesis of bull trout movement research. Project Completion Report, Contract 143303G098. 67pp.

Dare MR, Hubert WA, Gerow KG. 2002. Changes in habitat availability and habitat use and movements by two trout species in response to declining discharge in a regulated river during winter. *North American Journal of Fisheries Management* **22**: 917-928.

David B, Closs G. 2002. Behavior of a stream-dwelling fish before, during, and after high-discharge events. *Transactions of the American Fisheries Society* **131**: 762-771.

Dedual M, Jowett IG. 1999. Movement of rainbow trout (*Oncorhynchus mykiss*) during the spawning migration in the Tongariri River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **33**: 107-117.

Degrandchamp KL, Garvey JE, Colombo RE. 2008. Movement and habitat selection by invasive Asian carps in a large river. *Transactions of the American Fisheries Society* **137**: 45-56.

Domenici P. 2003. Habitat, body design, and the swimming performance of fish. In *Vertebrate Biomechanics and Evolution*. Bells VL, Gasc JP, Casinos A (eds.). BIOS Scientific Publishers Ltd.: Oxford, UK; 137-160.

Domenici P, Kapour BG. 2010. Fish Locomotion, Science Publishers, Enfield, New Hampshire.

Donaldson MR, Clark TD, Hinch SG, Cooke SJ, Patterson MK, Gale MK, Frappell PB, Farrell AP. 2010. Physiological responses of free-swimming adult coho salmon to simulated predator and fisheries encounters. *Physiological and Biochemical Zoology* **83**: 973-983.

Egger M, Smith G, Schneider M, Minder C. 1997. Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal* **315**: 629-634.

Enders EC, Boisclair D, Roy AG. 2003. The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 1149-1160.

Enders EC, Boisclair D, Roy AG. 2005. A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 1079-1089.

Enders EC, Stickler M, Pennell CJ, Cote D, Alfredson K, Scruton DA. 2008. Variations in distribution and mobility of Atlantic salmon parr during winter in a small, steep river. *Hydrobiologia* **609**: 37-44.

Erickson JW, Kenner SJ, Barton BA. 2005. Physiological stress response of brown trout to stormwater runoff events in Rapid Creek, Rapid City, South Dakota. In: Effects of urbanization on stream ecosystems, American Fisheries Society (AFS) Symposium, Brown LR, Gray RH, Hughes RM, Meador MR (eds.). AFS, Maryland, USA; 117-132.

Facey DE, Grossman GD. 1990. The metabolic cost of maintaining position for four North American stream fishes: Effects of season and velocity. *Physiological Zoology* **63**: 757-776.

Facey DE, Grossman GD. 1992. The relationship between water velocity, energetic costs, and microhabitat use in four North American stream fishes. *Hydrobiologia* **239**: 1-6.

Fausch KD, White RJ 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1220-1227.

Field AP. 2001. Meta-analysis of correlation coefficients: A Monte Carlo comparison of fixed- and random-effects methods. *Psychological Methods* **6**: 161-180.

Field A. 2009. Discovering Statistics using SPSS. 3rd edition, Sage Publications: London.

Fish FE. Swimming strategies for energy economy. 2010. In *Fish Locomotion*. Domenici P, Kapour BG (eds.). Science Publishers: Enfield, New Hampshire; 90-122.

Flodmark LEW, Urke HA, Halleraker JH, Arnekleiv JV, Vollestad LA, Poléo ABS. 2002. Cortisol and glucose responses in juvenile brown trout subjected to a fluctuating flow regime in an artificial stream. *Journal of Fish Biology* **60**: 238-248.

Frank HJ, Mather ME, Smith JM, Muth RM, Finn JT, McCormick SD. 2009. What is “fallback”?: Metrics needed to assess telemetry tag effects on anadromous fish behaviour. *Hydrobiologia* **635**: 237-249.

Frey GW, Linke, DM. 2002. Hydropower as a renewable and sustainable energy resource meeting global energy challenges in a reasonable way. *Energy Policy* **30**: 1261–1265.

Fry FEJ. 1971. The effect of environmental factors on the physiology of fish. In *Physiology of Fishes*, vol. 1, Hoar WS, Randall DJ (eds.). Academic Press, London and New York; 1-98.

Fu S, Brauner CJ, Cao Z, Richards JG, Peng J, Dhillon R, Wang Y. 2011. The effects of acclimation to hypoxia and sustained exercise on subsequent hypoxia tolerance and swimming performance in goldfish (*Carassium auratus*). *Journal of Experimental Biology* **214**: 2080-2088.

Gallaugher PE, Thorarensen H, Kiessling A, Farrell AP. 2001. Effects of high intensity excercise training on cardiovascular function, oxygen uptake, internal oxygen transport and osmotic balance in Chinook salmon (*Oncorhynchus tshawytscha*) during critical speed swimming. *Journal of Experimental Biology* **204**: 2861-2872.

Gamperl AK, Vijayan MM, Boutilier RG. 1994. Experimental control of stress hormone levels in fishes: techniques and applications. *Reviews in Fish Biology and Fisheries* **4**: 215-255.

Gates S. 2002. Review of methodology of quantitative reviews using meta-analysis in ecology. *Journal of Animal Ecology* **71**: 547-557.

Gee JH. 1983. Ecological implications of buoyancy control in fish. In *Fish Biomechanics*, Webb PW. Weihs D. (ed.). Praeger: New York; 140-176.

Geist DR, Abernethy CS, Blanton SL, Cullinan VI. 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall chinook salmon. *Transactions of the American Fisheries Society* **129**: 126-135.

Geist DR, Brown RS, Cullinan V, Brink SR, Lepla K, Bates P, Chandler JA. 2005. Movement, swimming speed, and oxygen consumption of juvenile white sturgeon in response to changing flow, water temperature, and light level in the Snake River, Idaho. *Transactions of the American Fisheries Society* **134**: 803-816.

Giller PS, Malmqvist B. 1998. The biology of streams and rivers, Oxford University Press, Oxford and New York.

Goodwin RA, Nestler JM, Anderson JJ, Weber LJ, Loucks DP. 2006. Forecasting 3-D fish movement behaviour using a Eulerian-Lagrangian-agent method (ELAM). *Ecological Modelling* **192**: 197-223.

Gowan C, Fausch K. 2002. Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes* **64**: 139-153.

Grafen A, Hails R. 2002. Modern Statistics for the Life Sciences, Routledge, Oxford University Press: Oxford, UK.

Gustaveson AW, Wydoski RS, Wedemeyer GA. 1991. Physiological response of largemouth bass to angling stress. *Transactions of the American Fisheries Society* **120**: 629-636.

Hasler CT, Pon LB, Roscoe DW, Mossop B, Patterson DA, Hinch SG, and Cooke SJ. 2009a. Expanding the "toolbox" for studying the biological responses of individual fish to hydropower infrastructure and operating strategies. *Environmental Reviews* **17**: 179-197.

Hasler CT, Suski CD, Hanson KC, Cooke SJ, Philipp DP, Tufts BL. 2009b. Effects of water temperature on laboratory swimming performance and natural activity levels of adult largemouth bass. *Canadian Journal of Zoology* **87**: 589-596.

Hasler CT, Suski CD, Hanson KC, Cooke SJ, Tufts BL. 2009c. The influence of dissolved oxygen on winter habitat selection by largemouth bass: an integration of field biotelemetry studies and laboratory experiments. *Physiology and Biochemical Zoology* **82**: 143-152.

Hanson KC, Arrosa S, Hasler CT, Suski CD, Philipp DP, Niezgoda G, Cooke SJ. 2008. Effects of lunar cycles on the activity patterns and depth utilization of a temperate sport fish, the largemouth bass (*Micropterus salmoides*). *Fisheries Management and Ecology* **15**: 357-364.

Haxton TJ, and Findlay CS. 2008. Meta-analysis of the impacts of water management on aquatic communities. *Canadian Journal of Fisheries and Aquatic Sciences* **65**: 437-447.

Heck RH, Thomas SL, Tabata LN. 2010. Multilevel and longitudinal modeling with IBM SPSS, Routledge, Taylor & Francis Group: New York, NY.

Hedges L, Vevea J. 1998. Fixed- and random-effects models in meta-analysis *Psychological Methods* **3**: 486-504.

Heggenes J, Traaen T. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology* **32**: 717-727.

Heggenes J, Omholt PK, Kristiansen JR, Sageie J, Økland F, Dokk JG, Beere MC. 2007. Movements by wild brown trout in a boreal river: response to habitat and flow contrasts. *Fisheries Management and Ecology* **14**: 333-342.

Hinch SG, Diewert RE, Lissimore TJ, Prince AMJ, Healey MC, Henderson MA. 1996. Use of electromyogram telemetry to assess difficult passage areas for river-migrating adult sockeye salmon. *Transactions of the American Fisheries Society* **125**: 253-260.

Hinch SG, Rand PS. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): Role of local environment and fish characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1821-1831.

Hodder KH, Masters JEG, Beaumont WRC, Gozlan RE, Pinder AC, Knight CM, Kenward RE. 2007. Techniques for evaluating the spatial behaviour of river fish. *Hydrobiologia* **582**: 257-269.

Hölker F, Breckling B. 2002. Influence of activity in a heterogeneous environment on the dynamics of fish growth: An individual-based model of roach. *Journal of Fish Biology* **60**: 1170-1189.

Hox JJ. 2002. Multilevel analysis: Techniques and applications. Lawrence Erlbaum Associates, Inc.: New Jersey.

Hunter JE, Schmidt FL, Jackson GB. 1982. Meta-analysis: Cumulating Research Findings across Studies. Sage, Beverley Hills, CA.

Huntingford MN, Thorpe J. 1988. Choice of Feeding Station in Atlantic Salmon, *Salmo salar*, parr: effects of predation risk, season and life-history strategy. *Journal of Fish Biology* **33**: 917-924.

IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 07 June 2012.

Jeffres C, Klimley A, Merz J, Cech J. 2006. Movement of Sacramento sucker, *Catostomus occidentalis*, and hitch, *Lavinia exilicauda*, during a spring release of water from Camanche Dam in the Mokelumne River, California. *Environmental Biology of Fishes* **75**: 365-373.

Joyce MP, Hubert WA. Snorkeling as an alternative to depletion electrofishing for assessing cutthroat trout and brown trout in stream pools. *Journal of Freshwater Ecology* **18**: 215-222.

Junk WJ, Bayley PB, Sparks RE. 1989. The Flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**: 110-127.

Kahler T, Roni P, Quinn T. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1947-1956.

Katopodis C. 2005. Developing a toolkit for fish passage, ecological flow management and fish habitat works. *Journal of Hydraulic Research* **43**: 451-467.

Katopodis C, Gervais R. 2012. Ecohydraulic analysis of fish fatigue data. *River Research and Applications* **28**: 444-456.

Kolok AS. 1999. Interindividual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 700-710.

Korman J, Campana SE. 2009. Effects of hydropeaking on nearshore habitat use and growth of age-0 rainbow trout in a large regulated river. *Transactions of the American Fisheries Society* **138**: 76-87.

Kraft ME. 1972. Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada* **29**: 1405-1411.

Krimmer AN, Paul AJ, Hontela A, Rasmussen JB. 2011. Behavioural and physiological responses of brook trout *Salvelinus fontinalis* to midwinter flow reduction in a small ice-free mountain stream. *Journal of Fish Biology* **79**: 707-725.

Lacey RWJ, Neary V, Liao JC, Enders EC, Tricito HM. 2012. The IPOS framework: Linking fish swimming performance in altered flows from laboratory experiments to rivers. *River Research and Applications* **28**: 429-443.

Lamouroux N, Olivier JM, Capra H, Zylberblat M, Chandesris A, Roger P. 2006. Fish community changes after minimum flow increase: testing quantitative predictions in the Rhone River at Pierre-Benite, France. *Freshwater Biology* **51**: 1730-1743.

Liao JC Beal DN, Lauder GV, Triantafyllou MS. 2003. Fish exploiting vortices use less muscle. *Science* **203**: 1566-1569.

Liao JC. 2004. Neuromuscular control of fish swimming in a vortex street: implications for energy economy. *The Journal of Experimental Biology* **207**: 3495-3506.

Liao JC. 2007. A review of fish swimming mechanics and behavior in altered flows. *Philosophical Transactions of the Royal Society B* **362**: 1973-1993.

Liebig H, Cereghino R, Lim P, Belaud A, Lek S. 1999. Impact of hydropeaking on the abundance of juvenile brown trout in a Pyrenean stream. *Archiv für Hydrobiologie* **144**: 439-454.

Linnik V, Malinin L, Wozniewski M, Sych R, Dembowski P. 1998. Movements of adult sea trout *Salmo trutta* L. in the tailrace of a low-head dam at Wloclawek hydroelectric station on the Vistula River, Poland. *Hydrobiologia* **372**: 335-337.

Lucas MC, Baras E. 2008. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries* **1**: 283-316.

Lyle DA, Poff NL. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**: 94-100.

Macfarlane RB, Livingston RJ. 1983. Effects of acidified water on the locomotor behavior of the Gulf Killifish, *Fundulus grandis*: A time-series approach. *Archives of Environmental Contamination and Toxicology* **12**: 163-168.

Maekawa K, Nakano S. 2002. Latitudinal trends in adult body size of Dolly Varden, with special reference to the food availability hypothesis. *Population Ecology* **44**: 17-22.

Mäkinen TS, Niemelä E, Moen K, and Lindström R. 2000. Behaviour of gill-net and rod-captured Atlantic salmon (*Salmo salar* L.) during upstream migration and following radio tagging. *Fisheries Research* **45**: 117-127.

Mantua N, Tohver I, Hamlet A. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change* **102**: 187-223.

Marchand F, Boisclair D. 1998. Influence of fish density on the energy allocation pattern of juvenile brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 796-805.

McElroy B, Delonay A, Jacobson R. 2012. Optimum swimming pathways of fish spawning migrations in rivers. *Ecology* **93**: 29-34.

McPhail JD, Murray CB. 1979. The early life history and ecology of Dolly Varden *(Salvelinus malma)* in the upper Arrow Lakes. Report to BCHydro and Ministry of Environment, Fisheries Branch, Nelson, British Columbia: 113 p.

McPhail JD, Baxter JS. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. *Fisheries Management Report No. 104*, B.C. Ministry of Environment, Lands and Parks: Victoria, B.C.

McPhail JD, Troffe PM. 2001. The mountain whitefish (*Prosopium williamsoni*): A brief review of the distribution, biology and life history of a neglected recreational species. In *Bull trout II Conference Proceedings*; 17-21.

Meka JM, McCormick SD. 2005. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fisheries Research* **72**: 311-322.

Mesa MG, Wellend LK, Zydlewski GB. 2004. Critical swimming speeds of wild bull trout. *Northwest Science* **78**: 59-65.

Metcalfe N, Fraser N, Burns M. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology* **68**: 371-381.

Miller SE, Scarnecchia DL. 2008. Adult paddlefish migrations in relation to spring river conditions of the Yellowstone and Missouri rivers, Montana and North Dakota, USA. *Journal of Applied Ichthyology* **24**: 221-228.

Miller SE and Scarnecchia DL. 2011. Sex-specific differences in migratory movement of adult paddlefish above Fort Peck Reservoir, Montana, USA. *Folia Zoologica* **60**: 181-188.

Millspaugh JJ, Washburn BE. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for applications and interpretation. *General and Comparative Endocrinology* **138**: 189-199.

Mimms MC, Olden JD. 2012. Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology* **93**: 35-45.

Monnot L, Dunham JB, Hoem T, Koetsier P. 2008. Influence of body size and environmental factors on autumn downstream migration of bull trout in the Boise River, Idaho. *North American Journal of Fisheries Management* **28**: 231-240.

Muhlfeld C, Marotz B. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. *North American Journal of Fisheries Management* **25**: 797-810.

Murchie KJ, Smokorowski KE. 2004. Relative activity of brook trout and walleye in response to flow in a regulated river. *North American Journal of Fisheries Management* **24**: 1050-1057.

Nagrodski A, Raby GD, Hasler CT, Taylor MK, Cooke SJ. Fish stranding in freshwater systems: sources, consequences, and mitigation. *Journal of Environmental Management* **103**: 133-141.

Nikora VI, Aberle J, Biggs BJF, Jowett IG, Sykes JRE. 2003. Effects of fish size, time-to-fatigues and turbulence on swimming performance: a case study of *Galaxias maculates*. *Journal of Fish Biology* **63**: 1365-1382.

Nilsson C, Reidy CA, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's river systems. *Science* **308**: 405-408.

Northcote T, Ennis G. 1994. Mountain whitefish biology and habitat use in relation to compensation and improvement possibilities. *Reviews in Fisheries Science* **2**: 347-371.

Olden JD, Naiman RJ. 2010. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology* **55**: 86-107.

Orwin RG. 1983. A fail-safe N for effect size in meta-analysis. *Journal of Educational and Behavioral Statistics* **8**: 157-159.

Paragamian VL, Wakkinen VD. 2008. Seasonal movement of burbot in relation to temperature and discharge in the Kootenai River, Idaho, USA and British Columbia, Canada. In *Burbot: Ecology, Management and Culture*, Paragamian VL, Bennett DH (eds.). The American Fisheries Society, Maryland; 55-77.

Peake S. 2004. An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. *Transactions of the American Fisheries Society* **133**: 1472-1479.

Peake SJ, Farrell AP. 2004. Locomotor behaviour and post-exercise physiology in relation to swimming speed, gait transition and metabolism in free-swimming smallmouth bass (*Micropterus dolomieu*). *Journal of Experimental Biology* **207**: 1563-1575.

Penczak T, Galicka W, Glowacki L, Koszalinski H, Kruk A, Zieba G, Kostrzewa T, Marszal L. 2004. Fish assemblage changes relative to environmental factors and time in the Warta River, Poland, and its oxbow lakes. *Journal of Fish Biology* **64**: 483-501.

Pert EJ, Erman DC. 1994. Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. *Transactions of the American Fisheries Society* **123**: 913-923.

Pinkle R. 1980. Acoustic Doppler techniques. In *Air-Sea Interaction Instruments and Methods*, Dobson F, Hasse L, Davis R (eds.). Plenum Press, New York; 171-199.

Plaut I. 2001. Critical swimming speed: Its ecological relevance. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology* **131**: 41-50.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The Natural Flow Regime. *Bioscience* **47**: 769-784.

Poff NL, Zimmerman JKH. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* **55**: 194-205.

Popoff N, Neumann R. 2005. Range and movement of resident holdover and hatchery brown trout tagged with radio transmitters in the Farmington River, Connecticut. *North American Journal of Fisheries Management* **25**: 413-422.

Pullin AS, Stewart GB. 2006. Guidelines for systematic review in conservation and environmental management. *Conservation Biology* **20**: 1647-1656.

Quinn T, Peterson N. 1996. The influence of habitat complexity and fish sire on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 1555-1564.

Quinn AL, Rasmussen JB, Hontela A. 2010. Physiological stress response of mountain whitefish (*Prosopium williamsoni*) and white sucker (*Catostomus commersoni*) sampled along a gradient of temperature and agrichemicals in the Oldman River, Alberta. *Environmental Biology of Fishes* **88**: 119-131.

Railsback SF, Lamberson RH, Harvey BC, Duffy WE. 1999. Movement rules for individual-based models of stream fish. *Ecological Modelling* **123**: 73-89.

Railsback SF, Harvey BC. 2002. Analysis of habitat selection rules using an individual-based model. *Ecology* **83**: 1817-1830.

Robertson M, Pennell C, Scruton D, Robertson G, Brown J. 2004. Effect of increased flow on the behaviour of Atlantic salmon parr in winter. *Journal of Fish Biology* **65**: 1070-1079.

Rosenthal R. 1979. The file drawer problem and tolerance for null results. *Psychological Bulletin* **86**: 638-641.

Scherer E. 1992. Behavioral-responses as indicators of environmental alterations: approaches, results, developments. *Journal of Applied Ichthyology* **8**: 122-131.

Schmidt F. 1992. What do data really mean? - research findings, meta-analysis, and cumulative knowledge in psychology. *American Psychology* **47**: 1173-1181.

Schmidt FL, Hunter JE. 1999. Comparison of three meta-analysis methods revisited: An analysis of Johnson, Mullen, and Salas (1995). *Journal of Applied Psychology* **84**: 144-148.

Scruton DA, Ollerhead LMN, Clarke KD, Pennell C, Alfreadsen K, Harby A, Kelley D. 2003. The behavioural response of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) to experimental hydropeaking on a Newfoundland (Canada) River. *River Research and Applications* **19**: 577-587.

Scruton D, Pennell C, Robertson M, Ollerhead L, Clarke K, Alfredsen K, Harby A, McKinley, R. 2005. Seasonal response of juvenile Atlantic salmon to experimental hydropeaking power generation in Newfoundland, Canada. *North American Journal of Fisheries Management* **25**: 964-974.

Selong J, McMahon T, Zale A, Barrows F. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society* **130**: 1026-1037.

Shingles A, McKenzie DJ, Taylor EW, Moretti A, Butler PJ, Ceradini S. 2001. Effects of sublethal ammonia exposure on swimming performance in rainbow trout (*Oncorhynchus mykiss*). *Journal of Experimental Biology* **204**: 2691-2698.

Singer JD, Willett JB. 2003. Applied longitudinal data analysis: Modeling change and event occurrence. Oxford University Press: New York.

Simpson R, Mapleston A. 2002. Movements and habitat use by the endangered Australian freshwater Mary River cod, *Maccullochella peelii mariensis*. *Environmental Biology of Fishes* **65**: 401-410.

Smith DL, Brannon EL, Odeh M. 2005. Response of juvenile rainbow trout to turbulence produced by prismatoidal shapes. *Transactions of the American Fisheries Society* **134**: 741-753.

Spencer WP. 1939. Diurnal activity rhythms in fresh-water fishes. *Ohio Journal of Science* **39**: 119-132.

Standen EM, Hinch SG, Healey MC, Farrell AP. 2002. Energetic costs of migration through the Fraser River Canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 1809-1818.

Stickler M, Alfredsen K, Scruton DA, Pennell C, Harby A, Okland F. 2007. Mid-winter activity and movement of Atlantic salmon parr during ice formation events in a Norwegian regulated river. *Hydrobiologia* **582**: 81-89.

Sullivan GH, Hoefener C, Bolie VW. 1963. Electronic systems for biological telemetry. In *Bio-Telemetry: The use of Telemetry in Animal Behaviour and Physiology in Relation to Ecological Problems*. Slater LE (ed.). Pergamon Press: Oxford; 83–106.

Summerfelt RC, Smith LS. 1990. Anesthesia, surgery and related techniques. In *Methods for Fish Biology*, Schreck CB, Moyle PB (eds). American Fisheries Society: Bethesda, MD; 213–272.

Sumpter JP. 1997. The endocrinology of stress. In *Fish Stress and Health in Aquaculture.* Iwama GK, Pickering AD, Sumpter JP, Schreck CB (eds). Cambridge University Press, Cambridge, UK; 95–118.

Svendsen J, Koed A, Aarestrup K. 2004. Factors influencing the spawning migration of female anadromous brown trout. *Journal of Fish Biology* **64**: 528-540.

Swanberg TR. 1997. Movement and habitat use by fluvial bull trout in the Blackfoot River, Montana. *Transactions of the American Fisheries Society* **126**: 735-746.

Swihart R, Slade N. 1985. Testing for independence of observations in animal movements. *Ecology* **66**: 1176-1184.

Taylor SE, Eggington S, Taylor EW. 1996. Seasonal temperature acclimatisation of rainbow trout: cardiovascular and morphometric influences on maximal sustained exercise level. *Journal of Experimental Biology* **199**: 835-845.

Taylor MK, Cook KV, Hasler CT, Schmidt DC, Cooke SJ. 2012a. Behaviour and physiology of mountain whitefish (*Prosopium williamsoni*) relative to short-term changes in river flow. *Ecology of Freshwater Fish* **21**: 609-616.

Taylor MK, Cooke SJ. 2012b. Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews* **20**: 211-219.

Taylor MK, Hasler CT, Findlay CS, Lewis B, Schmidt DC, Hinch SG, Cooke SJ. *In Review*. Hydrologic correlates of bull trout (*Salvelinus confluentus*) swimming activity in a hydropeaking river.

Thiem JD, Ebner BC, Clear RC. 2010. Validating variation in radio-signal strength as an index of aquatic fauna activity. *New Zealand Journal of Marine and Freshwater Research* **58**: 50-55.

Thorstad EB, Økland F, Koed A, McKinley RS. 2000. Radio-transmitted electromyogram signals as indicators of swimming speed in lake trout and brown trout. *Journal of Fish Biology* **57**: 547-561.

Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. *Hydrological Processes* **14**: 2861–2883.

Tritico HM, Cotel AJ. 2010. The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). *Journal of Experimental Biology* **213**: 2284-2293.

Valentin S, Sempeski P, Souchon Y, Gaudin P. 1994. Short-term habitat use by young grayling, *Thymallus thymallus* L., under variable flow conditions in an experimental stream. *Fisheries Management and Ecology* **1**: 57-65.

Vehanen T, Bjerke PL, Heggenes J, Huusko A, Maki-Petäyes A. 2000. Effect of fluctuating flow and temperature on cover type selection and behaviour by juvenile brown trout in artificial flumes. *Journal of Fish Biology* **56**: 923-937.

Veysey JS, Babbitt KJ, Cooper A. 2009. An experimental assessment of buffer width: Implications for salamander migratory behavior. *Biological Conservation* **142**: 2227-2239.

Videler JJ. 1993. Fish Swimming. Springer, New York, NY.

Vijayan MM, Pereira C, Grau EG, Iwama GK. 1997. Metabolic responses associated with confinement stress in tilapia: The role of cortisol. *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology* **116**: 89-95.

Waiwood KG, Beamish FWH. 1978. Effects of copper, pH and hardness on the critical swimming performance of rainbow trout (*Salmo gairdneri* Richardson). *Water Research* **12**: 611-619.

Wasser SK, Bevis K, King G, Hanson E. Noninvasive physiological measures of disturbance in northern spotted owl. *Conservation Biology* **11**: 1019-1022.

Webb PW. 1988. Simple physical principles and vertebrate aquatic locomotion. *American Zoologist* **28**: 709-725.

Webb PW. 1998. Entrainment by river chub *Nocomis micropogon* and smallmouth bass *micropterus dolomieu* on cylinders. *Journal of Experimental Biology* **201**: 2403-2412.

Weyers RS, Jennings CA, Freeman MC. 2003. Effects of pulsed, high-velocity water flow on larval robust redhorse and V-lip redhorse. *Transactions of the American Fisheries Society* **132**: 84-91.

Wilga CW, Lauder GV. 2001. Functional morphology of the pectoral fins in bamboo sharks, Chiloscyllium plagiosum: Benthic vs. Pelagic station-holding. *Journal of Morphology* **249**: 195-209.

Woodward JJ, Smith LS. 1985. Exercise training and the stress response in rainbow trout, *salmo gairdneri* Richardson. *Journal of Fish Biology* **26**: 435-447.

Xu CL, Letcher BH, Nislow KH. 2010. Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. *Journal of Fish Biology* **76**: 2342-2369.

Yorke TH, Oberg KA. 2002. Measuring river velocity and discharge with acoustic Doppler profilers. *Flow Measurement and Instrumentation* **13**: 191–195.

Young PS, Cech Jr, JJ. 1994. Effects of different exercise conditioning velocities on the energy reserves and swimming stress responses in young-of-the-year striped bass (*Morone saxatilis*). *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 1528-1534.

Young SP, Isely J. 2007. Diel behaviour of adult striped bass using tailwater habitat as summer refuge. *Transactions of the American Fisheries Society* **136**: 1104-1112.

Young RG, Wilkinson J, Hay J, Hayes JW. 2010. Movement and mortality of adult brown trout in the Motupiko River, New Zealand: Effects of water temperature, flow, and flooding. *Transactions of the American Fisheries Society* **139**: 137-146.

Young PS, Cech Jr. JJ, Thompson LC. 2011. Hydropower-related pulsed-flow impacts on stream fishes: A brief review, conceptual model, knowledge gaps, and research needs. *Reviews in Fish Biology and Fisheries* **21**: 713-731.

Yuksel I. 2007. Development of hydropower: a case study in developing countries. *Energy Sources* **2**: 113-121.

Zimmer M, Schreer JF, Power M. 2010. Seasonal movement patterns of credit river brown trout (*salmo trutta*). *Ecology of Freshwater Fish* **19**: 290-299.

Zorn C. 2001. Generalized estimating equation models for correlated data: A review with applications. *American Journal of Political Science* **45**: 470-490.