Evaluating the effects of dam-altered flow regimes on the swimming activity, behaviour and survival of adult sockeye salmon (*Oncorhynchus nerka*)

by

Nicholas J. Burnett

B.Sc., Queen’s University, 2011

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science in Biology

Carleton University
Ottawa, Ontario

© 2014, Nicholas J. Burnett
ABSTRACT

Anadromous adult Pacific salmon (*Oncorhynchus* spp.) encounter hydraulically challenging areas of difficult passage (high-gradient reaches, dams) during their reproductive migration. While the direct effects of dam operations on wild fishes are well documented (e.g., delayed movements, excessive energy-use), comparatively little is known as to the delayed, post dam passage effects of these barriers. Using acoustic accelerometer transmitters and model selection analyses, Chapter 2 assessed how managed flow releases from a dam influenced the swimming activity, behaviour and passage success of sockeye salmon (*O. nerka*). Building on this framework, Chapter 3 explored the potential for high-flow-induced burst swimming below the dam to predict the mortality of sockeye salmon. Findings from this research provide novel insight into the mechanisms that contribute to the delayed mortality of migratory fishes. Future studies investigating the indirect effects of dams will improve our ability to provide effective passage solutions to watersheds that are impacted by hydropower development.
ACKNOWLEDGEMENTS

I would like to thank my supervisors, S.J. Cooke and S.G. Hinch, for providing me with invaluable guidance and opportunities over the past two years, and allowing me to complete my degree from distance. Without your continued support, I would not be the scientist I am today.

Many thanks to members of the Hinch Lab for their field and analytical assistance, feedback, peer support, and general comradery; specifically, M.R. Donaldson, N.N. Bett, D.C. Braun, N.B. Furey, C.T. Middleton, M.T. Casselman, S.M. Wilson, E.J. Eliason and A.G. Lotto. Fieldwork would not have been possible without the help of Instream Fisheries Research Ltd. and the DFO Environmental Watch Program. Funding for this research was provided by BC Hydro, St’át’imc Eco-Resources Ltd., and Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants to S.J. Cooke and S.G. Hinch. I received financial support from NSERC CGS-M and Ontario Graduate Scholarship programs.

I am grateful to the Cayoosh Creek and N’Quatqua First Nations for teaching me the true cultural importance of Pacific salmon. I thank W. Payne, B. Dunn, T. Creasey, J. Hopkins, the O’Donahae’y’s and C. Fletcher for their support and generosity.

To my family – thank you for your understanding and encouragement through the years. And finally – thank you to Elyse for your love, emotional support and patience throughout this fishy business.
# TABLE OF CONTENTS

**ABSTRACT** ....................................................................................................................... ii

**ACKNOWLEDGEMENTS** ............................................................................................ iii

**TABLE OF CONTENTS** ........................................................................................... iv

**LIST OF TABLES** ........................................................................................................... vi

**LIST OF FIGURES** ........................................................................................................ vii

**GLOSSARY** ...................................................................................................................... ix

**CO-AUTHORSHIP STATEMENT** ................................................................................. x

**CHAPTER 1: General Introduction** ................................................................................. 1

  Background .................................................................................................................. 1

  Thesis overview and research objectives .................................................................. 8

**CHAPTER 2: Alterations to dam-spill discharge influence sex-specific activity, behaviour and passage success of migrating adult sockeye salmon** .... 10

  Abstract .................................................................................................................. 10

  Introduction ............................................................................................................ 11

  Methods .................................................................................................................. 14

    *Study site* ........................................................................................................ 14

    *Fish capture, tagging and tracking* ................................................................. 16

    *Data analysis and statistics* ........................................................................... 18

  Results .................................................................................................................... 21

    *Comparison among successful and unsuccessful fish* .................................... 22

    *Sex-specific differences* ................................................................................... 24

    *Effects of the operational regime* ................................................................. 26

  Discussion ................................................................................................................ 26
Management implications

CHAPTER 3: Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon

Abstract

Introduction

Methods

Study site

Fish capture, tagging and tracking

Swimming activity analyses

Model selection, multimodel averaging and inference

Results

Dam passage

Anaerobiosis in areas of high flow

Migration success to spawning grounds

Discussion

CHAPTER 4: General Discussion

Findings and implications

Future directions

LITERATURE CITED
LIST OF TABLES

Table 2.1. Mean swimming speeds (BL s\(^{-1}\); ± SE) of successful and unsuccessful Gates Creek sockeye salmon (\(O.\ nerka\)) at the release site, radial gate spillway and fishway entrance area. ..............................................................................................................................................................33

Table 2.2. Candidate generalized linear models (GLM) to predict passage success, attraction efficiency and tailrace delay of Gates Creek sockeye salmon (\(O.\ nerka\)). ........44

Table 2.3. Mean oxygen consumption (mg O\(_2\) kg\(^{-1}\) min\(^{-1}\); ± SE) of male and female Gates Creek sockeye salmon (\(O.\ nerka\)) at the release site, radial gate spillway, fishway entrance area and forebay. Numbers within parentheses represent sample sizes (\(n\)). ......35

Table 3.1. Model selection statistics summary for generalized linear models (GLM) predicting dam passage, anaerobic recruitment in areas of high flow below Seton Dam, tailrace crossings, and the ability of Gates Creek sockeye salmon (\(O.\ nerka\)) to reach natal spawning streams. ..........................................................................................................................................................................................61
LIST OF FIGURES

Figure 2.1. A map depicting the Seton-Anderson watershed in southwestern British Columbia, Canada, the terminal spawning grounds for Gates Creek sockeye salmon (*O. nerka*), as well as the location of the Seton Dam and fishway (inset). Minimum flows at the Seton facility are released through the fish water release gate (FWRG) to attract migrating sockeye salmon to the fishway entrance (FENT). Seven sentinel acoustic receivers (A) were placed within the tailrace area to capture activity data. A single fixed radio receiver (R) with a 5-element Yagi antenna was positioned at the dam to quantify tailrace delay before eventual pass through the fishway exit (FEXIT) or fallback out of the Seton system. Schematic of the Seton Dam and fishway adapted from Pon et al. (2009a) and used with permission. ....................................................................................36

Figure 2.2. Logistic regression fitted to the tailrace delay (log-transformed; A) and number of tailrace crossings (B) of successful and unsuccessful migrants. The line shows the predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing the Seton Dam.................................................................37

Figure 2.3. Box-and-whisker plot (median: solid line, mean: closed circle, extreme value: open circle, 25% and 75% quartiles) comparing the swimming speed (BL s\(^{-1}\)) of male (shaded grey) and female (white) Gates Creek sockeye salmon (*O. nerka*) at the release site, radial spillway, fishway entrance area and forebay. Optimal (~1.0 BL s\(^{-1}\)) and critical (\(U_{\text{crit}}\); 2.1 BL s\(^{-1}\)) swimming speeds of Gates Creek sockeye salmon are shown along the y-axis; the swimming speed at which anaerobic muscle fibers start to be recruited (~1.7 BL s\(^{-1}\)) is also shown. Sample sizes (n) are presented below each box-and-whisker, and lowercase letters represent significant differences (p < 0.05) from ANOVA and Tukey post hoc tests.....................................................................................38

Figure 3.1. Map of the Seton-Anderson watershed in southwestern British Columbia, Canada, the natal spawning streams of Gates Creek sockeye salmon (*O. nerka*), and the location of Seton Dam and vertical-slot fishway (inset). Dotted trace within the inset represents the high flows from the FWRG and siphon #1. A: acoustic receiver. P: pass-through passive integrated transponder (PIT) antenna. ★: release site for fishway non-naïve individuals. ...............................................................................................................62

Figure 3.2. Beanplot (mean: black horizontal line) comparing the swimming speed (BL s\(^{-1}\)) of male (black) and female (grey) Gates Creek sockeye salmon (*O. nerka*) in the radial gate spillway, surrounding the fishway entrance, within the fishway and dam forebay. Shaded curved polygons (beans) depict the estimated density of the distribution of individual swimming speed values (white horizontal lines). Optimal (\(U_{\text{opt}}\); 1.0 BL s\(^{-1}\)) and critical (\(U_{\text{crit}}\); 2.1 BL s\(^{-1}\)) swimming speeds are shown as dotted horizontal lines; the swimming speed at which anaerobic muscle fibers start to be recruited (80% \(U_{\text{crit}}\)) is also shown. Sample sizes (n) are presented below each bean, and lowercase letters represent significant differences (p < 0.05) from one-way analysis of variance (ANOVA) and Tukey post hoc tests............................................................................................................63
**Figure 3.3.** Predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing Seton Dam (A; *n* = 54) and reaching natal spawning streams (B; *n* = 44) visualized by fitting a logistic regression to the anaerobic recruitment of successful and unsuccessful migrants.

**Figure 3.4.** Predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing Seton Dam relative to the maximum Seton River temperature individual fish experienced while directly below the dam.

**Figure 3.5.** Model-averaged standardized coefficients for models describing (A) dam passage, (B) anaerobic recruitment in areas of high flow below Seton Dam, (C) tailrace crossings and (D) the ability of Gates Creek sockeye salmon (*O. nerka*) to reach natal spawning streams. Coefficients have been highlighted in grey if the error bars (represent 95% confidence intervals) do not cross zero. Capture location was included in all models as a fixed factor and has been included to show its relative effect on the response variables. Note the different secondary y-axes scales.
GLOSSARY

EMG: Electromyogram
TBF: Tail beat frequency
PIT: Passive integrated transponder
HDX: Half-duplex
RMS: Root mean square
$U_{opt}$: Optimal swimming speed
$U_{crit}$: Critical swimming speed
EPOC: Excess post-exercise oxygen consumption
$T_{opt}$: Optimal temperature for aerobic scope
GSE: Gross somatic energy
$MO_2$: Oxygen consumption
$MO_2\text{ max}$: Maximum oxygen consumption
BL: Body length
FL: Fork length
GLM: Generalized linear model
AIC$_c$: Corrected Akaike information criterion
$w_j$: AIC$_c$ weight
ANOVA: Analysis of variance
SE: Standard error
VIF: Variance inflation factor
FWRG: Fish water release gate
ADCP: Acoustic Doppler Current Profiler
CFD: Computational fluid dynamics
CO-AUTHORSHIP STATEMENT

N.J. Burnett was the primary contributor to the study design, data collection and analyses, and manuscript preparation. However, research presented herein was part of a collaborative effort and all co-authors contributed to its completion.


N.J. Burnett, S.G. Hinch and S.J. Cooke helped with study design. Fieldwork was completed by N.J. Burnett and M.R. Donaldson. N.B. Furey helped with data analyses. All writing was conducted by N.J. Burnett. All co-authors provided comments and feedback on the manuscript. A version of this chapter has been published in Ecohydrology.


N.J. Burnett, S.G. Hinch and S.J. Cooke conceived the study. Fieldwork was completed by N.J. Burnett, D.C. Braun, M.T. Casselman and C.T. Middleton. D.C. Braun and S.M. Wilson assisted with data analyses. All writing was conducted by N.J. Burnett. All co-authors provided comments and feedback on the manuscript. A version of this chapter has been submitted for publication in Physiological and Biochemical Zoology.
CHAPTER 1: General Introduction

Background

Migration

Migrations are classified as predictable and directed movements away from an animal’s home range for survival, feeding and/or breeding purposes (Dingle 1996). These movement behaviours are fuelled by a reallocation of energy reserves and have unique departing and arriving characteristics (Dingle 1996). Indeed this biological phenomenon is widespread across several taxonomic groups, encompassing a diversity of habitat types (air, land and water) and methods of locomotion (flying, drifting, walking and swimming). While much of the migration ecology research to date has focused on terrestrial and aerial migrations (e.g., wildebeest *Connochaetes* spp., monarch butterfly *Danaus plexippus*, Arctic Tern *Sterna paradisaea*), there has also been considerable interest in the migrations of adult salmon (Pacific *Oncorhynchus* and Atlantic *Salmo* spp.). Pacific salmon endure physiologically- and energetically-challenging reproductive migrations, making them an exemplary group of fish for exploring the consequences of energetic state and energy-use on migratory behaviour and fate.

Anadromous adult Pacific salmon undertake remarkable once-in-a-lifetime (i.e., semelparity) migrations from oceanic feeding grounds to natal freshwater spawning sites in an attempt to contribute genetic material to future generations. Somatic energy conservation plays a central role in this final life-history stage, as these animals cease feeding upon river entry and rely on fixed, ocean-accrued energy reserves to fuel their
movements and reproduction (Brett 1995, Crossin and Hinch 2005). Sockeye salmon (*O. nerka*) have been studied the most out of all the Pacific salmon species, likely owing to their cultural, ecological, economical and political importance to countries of the North Pacific rim. Within the Fraser River watershed in British Columbia (BC), Canada, there are over 100 genetically distinct populations of sockeye salmon (Beacham *et al.* 2005) that migrate varying distances (upwards of 1100 km) and elevation gains, and experience a suite of environmental conditions dependent on the timing of their migration (early July to late November). Sockeye salmon are known to perish along the way and on breeding grounds before spawning (*en route* and pre-spawn mortality, respectively), highlighting the challenging nature of this upstream migration (Cooke *et al.* 2004a, Keefer *et al.* 2008, Hinch *et al.* 2012).

Pacific salmonid migration success is largely governed by water temperature and river discharge (Alabaster 1970, Gilhousen 1990, Rand *et al.* 2006, Farrell *et al.* 2008). As ectotherms, minor changes in water temperature can modify key physiological functions (e.g., growth, swimming performance, metabolic rate) that can in turn influence the survival of Pacific salmon (Brett 1971, Lee *et al.* 2003a,b, Farrell *et al.* 2008). Fraser River sockeye salmon are locally adapted to the temperature conditions they encounter upon river entry (Eliason *et al.* 2011). As such, exposure to conditions above the optimal temperature for aerobic scope (*T_{opt}* can lead to reductions in whole-animal performance and mortality (Brett 1971, Lee *et al.* 2003a,b, Farrell *et al.* 2008, Eliason *et al.* 2013). A growing body of literature suggests that high river discharge is associated with energy depletion, physiological stress and migration failure in sockeye salmon (Rand *et al.* 2006, Nadeau *et al.* 2010). Of conservation concern, mortality is exacerbated in female sockeye
salmon that encounter supra-optimal water temperatures and high flows as they travel upstream (Nadeau et al. 2010, Martins et al. 2012). Taken together, these findings represent a significant management challenge given the anticipated changes in Fraser River hydroclimatology (Rand et al. 2006, Patterson et al. 2007, Hague et al. 2011).

**Physical barriers to migration**

Watersheds are modified through changes in land use associated with urbanization, agriculture and industrialization (Vörösmarty et al. 2010). On a global scale, river corridors have become physically transformed and increasingly regulated through impoundments and diversions (e.g., dams and weirs) to maximize human access to water and meet energy and transportation needs (Nilsson et al. 2005, Murchie et al. 2008). Dam facilities obstruct the upstream and downstream movements of migratory fishes, and can lead to changes in habitat quality, population sizes, community structure, and ecosystem function (Nehlsen et al. 1991, Slaney et al. 1996, Waples et al. 2007). With the continued and rapid proliferation of hydropower development throughout the world, the ecological impact of these physical barriers remains a major conservation concern to date (Sutherland et al. 2013).

Fish passage structures (e.g., fishways and fish locks; Clay 1995) are designed to restore connectivity to regulated or constrained watersheds and to enable the passage of migratory fishes without imposing detrimental effects on fitness (Castro-Santos et al. 2009, Bunt et al. 2011). However, dam tailraces act as bottlenecks to migration, preventing or slowing the movement (hereafter, delay) of fishes through complex, convoluted flow patterns (Bunt 2001, Keefer et al. 2004, Naughton et al. 2005, Caudill et
al. 2006, 2007). Delayed migrations are costly to the long-term fitness of anadromous fishes, as the energy reserves that are intended for gonad development are used to maintain position in the high-velocity flows downstream of a migration barrier (Dingle 1996, Geist et al. 2000, Brown et al. 2006). To understand the mechanisms underlying slowed migrations, several studies have investigated the potential for dam operations to inhibit the ability of migrants to traverse these areas of difficult passage (e.g., Keefer et al. 2004, Naughton et al. 2005, Caudill et al. 2007). Altering the total dam-spill discharge of a facility can increase delay and decrease passage success at individual dams and through multi-dam reaches (Caudill et al. 2006, 2007). Other studies using this broad-scale hydraulic approach, however, have shed little insight into the influence of managed flow releases on the migration behaviour and passage success of sockeye salmon (Pon et al. 2009a, Roscoe et al. 2011). To date, there have been no published attempts at linking detailed hydrodynamic data to individual-level responses in swimming activity, behaviour and survival.

Swimming performance in fish

Fish exhibit a diverse set of swimming strategies to facilitate movement over a range of speeds and acceleration rates (Webb 1995). Optimal strategies are selected to reduce the drag and transport costs associated with moving through water (Weihs 1974, Videler 1993). In the case of the Pacific salmonids, several swimming strategies have been described in the literature based on observations of fish exhibiting these behaviours in the laboratory and wild. ‘Steady-state swimming’ minimizes energy expenditure (per distance travelled) by moving large distances at metabolic optimal speeds (Webb 1995).
As they approach critical swimming speeds ($U_{\text{crit}}$), fish employ a ‘burst-and-coast’ swimming strategy in habitats with fast-flowing water to benefit from significant energy savings and reduced physiological stress (Weihs 1974, Videler and Weihs 1982, Webb 1995). At these speeds, aerobic and anaerobic metabolic pathways (slow-red and fast-white muscle fibers, respectively) contribute to the swimming effort (Burgetz et al. 1998). Anaerobic metabolic pathways exclusively power swimming at speeds > $U_{\text{crit}}$, where short bouts of burst (or ‘sprint’) swimming are fuelled by the breakdown of glycogen in white muscle fibers (Black et al. 1966). Adult sockeye salmon elicit burst swimming behaviours to negotiate and minimize exposure to areas with energetically demanding turbulent flows (Hinch and Bratty 2000, Standen et al. 2002, Brown et al. 2006). Lactate anions and metabolic protons accumulate in the swimming muscle of fish as a result of depleting glycogen reserves, resulting in a cascade of metabolic disturbances (Wood et al. 1983, Wood 1991). Following exhaustive exercise, sockeye salmon require additional oxygen uptake (known as excess post-exercise oxygen consumption, EPOC) and long recovery times to re-establish ion gradients, lactate processing, pH balance, and restore tissue and cellular oxygen levels (Lee et al. 2003b). Migrants that fail to re-establish metabolic homeostasis can perish hours or even days after prolonged periods of severe muscular exertion (Black 1958, Priede 1977, Wood et al. 1983).

Releasing water adjacent to fishways is part of the standard operational protocol for most dam facilities, as it is known to improve the attraction of fishes towards passage structures (Bunt 2001, Andrew and Geen 1958). However, these practices have the potential to create ‘velocity barriers’ that force fish to swim at non-optimal, supra-critical
speeds during their attempts at passage (Bunt et al. 1999, Castro-Santos 2004, 2005, Haro et al. 2004, Brown et al. 2006). In southwestern BC, Canada, Roscoe et al. (2011) found that migration through the Seton Dam tailrace had post-passage survival consequences for Gates Creek sockeye salmon, a Fraser River population that negotiates high-velocity flows near the entrance to a vertical-slot fishway. One might expect that dam-successful migrants would have relied on the recruitment of white muscle fibers in these turbulent areas, potentially impairing reproductive development and contributing to the high levels of en route mortality observed in this watershed (Roscoe et al. 2011). Nevertheless, there is little empirical evidence suggesting that burst swimming by migratory fishes downstream of velocity barriers has carryover effects on the remainder of their freshwater migration (Caudill et al. 2007, O’Connor et al. 2014).

*Estimating energy-use in wild fish*

Ecologists have long been interested in the movement behaviours and energy expenditure of fishes, however there are several challenges and limitations associated with estimating these parameters in the wild. Advancements in biotelemetry technology have provided researchers with tools to estimate the swimming speed of fishes by recording the activity of the muscles that generate the propulsive force (Cooke et al. 2004b). Electromyogram (EMG) radio transmitters record the electrical activities of the swimming muscles (Sullivan et al. 1963, Videler 1993); these measurements are strongly correlated with the tail beat frequency (TBF) and instantaneous swim speeds (in body lengths [BL] per second, BL s\(^{-1}\)) of Pacific salmon (Hinch and Rand 1998, Geist et al. 2003, Cooke et al. 2004b). EMG telemetry, however, involves an invasive surgical
tagging procedure where electrodes must be inserted into aerobic swimming muscle, increasing handling time and related stress (Cooke et al. 2004b). Imprecision of electrode placement and variability in the performance of tag components requires the calibration of each tag upon implantation to yield reliable data on fish activity (e.g., Hinch and Rand 1998, Brown et al. 2007). Yet, countless studies have successfully used EMG devices to assess the swimming activity and behaviour of migratory fishes in dam tailraces, within fish passage structures and in regulated rivers (Brown et al. 2006, Pon et al. 2009b, Hasler et al. 2012, respectively).

Tri-axial accelerometers represent a relatively new tool for investigating the swimming activity and behaviour of wild aquatic animals. Rather than trying to infer TBF from a proxy (as in EMG telemetry), accelerometers can enable the direct measurement of tail beats in fishes. Accelerometer biologgers record activity levels at high frequencies (upwards of 300 Hz), but have limited applications due to the inherent difficulty of retrieving the tags from organisms in the wild (Wilson et al. 2006, Gleiss et al. 2010, Brownscombe et al. 2013). Of late, accelerometer sensors have been incorporated into acoustic telemetry transmitters that can be gastrically implanted into anadromous fishes that have ceased feeding (Wilson et al. 2013). In the stomach, transmitters are positioned at the center of mass to avoid large errors generated by centripetal acceleration (Videler 1993). Accelerometer transmitters record activity at lower frequencies (10 Hz) compared to biologgers, and transmit the root mean square (RMS) acceleration to fixed receiver arrays every 13 – 17 seconds to minimize battery drain. RMS acceleration takes into account the contributions of acceleration from each of
the three axes \((X, Y, Z)\), and is strongly correlated with TBF, swimming speed and oxygen consumption \((MO_2)\) in adult sockeye salmon \((Wilson \ et \ al. \ 2013)\).

**Thesis overview and research objectives**

Research presented within this thesis examines the swimming activity and behaviour of adult Gates Creek sockeye salmon downstream of Seton Dam and its effects on the remaining 50 km of their freshwater spawning migration. Compared to previous research \((Caudill \ et \ al. \ 2006, \ 2007, \ Pon \ et \ al. \ 2009a, \ Roscoe \ et \ al. \ 2011)\), I have adopted and present a more detailed hydraulic approach to assessing the influence of dam operations on the spawning migrations of anadromous fishes. For the purposes of this thesis, I put forward three main objectives. I aimed to: (1) investigate how Seton Dam operations influence the swimming activity and behaviour of sockeye salmon, (2) determine whether or not these potential energetic and behavioural alterations contribute to a delayed (or failed) migration, and (3) identify dam operational strategies that provide optimal migration conditions for sockeye salmon by minimizing delay and excessive energy-use.

Chapter 2 assesses the effects of managed flow releases from Seton Dam on the swimming activity, behaviour and passage success of Gates Creek sockeye salmon. Although it has been recognized that sockeye salmon have greater difficulty locating and entering the vertical-slot fishway compared with passage through the structure \((Pon \ et \ al. \ 2009a,b, \ Roscoe \ et \ al. \ 2011)\), a proximate cause for this is unknown. Through the use of acoustic accelerometer transmitters and generalized linear models, I investigated whether
the unique hydraulic conditions migrants experienced in the dam tailrace could predict their ability to locate, enter and ascend the fishway.

Using similar approaches, Chapter 3 examines how the excessive recruitment of anaerobic metabolic pathways surrounding the fishway entrance affects the ability of sockeye salmon to complete their reproductive migration. Research by Pon et al. (2009b) showed that Gates Creek sockeye salmon do not elicit burst swimming behaviours within the fishway. However, the results from a more recent study suggest that passage through the dam tailrace has post-passage survival consequences, particularly for females (Roscoe et al. 2011). With our understanding that severe muscular activity can lead to delayed mortality in fishes (Black 1958, Priede 1977, Wood et al. 1983), I hypothesized that anaerobiosis would be required to negotiate the turbulent flows in the dam tailrace but contribute to the high levels of en route mortality observed in this watershed (Roscoe et al. 2011).

Chapter 4 synthesizes the findings from my research (Chapter 2 and 3), discusses the implications of the results from both fundamental and applied perspectives, and presents future avenues of research.
CHAPTER 2: Alterations to dam-spill discharge influence sex-specific activity, behaviour and passage success of migrating adult sockeye salmon.¹

Abstract

Delays in the freshwater spawning migrations of anadromous fishes at upstream barriers are well documented, but underlying mechanisms causing slowed migrations are seldom known. Using acoustic accelerometer transmitters and generalized linear models, I investigated how alterations in flow at a diversion dam in British Columbia, Canada, affected the activity, behaviour and passage success of a Fraser River sockeye salmon population (*Oncorhynchus nerka*). Spilling excess water through the radial gate of the dam decreased the attraction efficiency of a vertical-slot fishway by 90% and increased delay below the dam by 2 h, which had adverse effects on passage. Relative to males, female sockeye salmon had significantly lower passage success (73% vs. 94%), attraction efficiency (79% vs. 100%) and passage efficiency (89% vs. 94%) at a fishway, delayed longer in the dam tailrace (mean ± standard error (SE): 20.8 ± 4.1 h vs. 14.6 ± 3.2 h), and resorted to anaerobic swimming efforts for a greater percentage of time (0 – 61.3% vs. 0.7 – 2.7%). Given that the persistence of Pacific salmon populations relies on the spawning success of females, understanding how males and females vary in their response to modified flow regimes will improve the management of complex fish-passage problems.

Introduction

Adult Pacific salmon (*Oncorhynchus* spp.) migrate from oceanic feeding grounds to natal freshwater spawning sites on fixed, endogenous energy reserves. The upriver spawning migration is energetically expensive (Hinch *et al*. 1996), requiring fish to possess a set of behaviours, morphologies and swimming strategies that conserve energy so that they can reach spawning grounds with sufficient energy to spawn (Hinch and Rand 2000, Liao *et al*. 2003). Consequently, there is a strong selection for energy-conserving traits, wherein migrants from distal spawning areas are more streamlined, smaller, exhibit a more efficient swimming gait, increased aerobic capacity, and produce fewer and smaller eggs than short-distance migrants (Hinch and Rand 2000, Crossin *et al*. 2004, Eliason *et al*. 2011). During their migration, Pacific salmon encounter a myriad of natural (e.g., rapids and high-gradient reaches) and anthropogenic hydraulic challenges (e.g., dams and weirs) that impede or slow their movement (Keefer *et al*. 2004, Caudill *et al*. 2007) and require elevated swimming speeds to overcome (i.e., hyperactivity; Hinch and Bratty 2000). Compared to males, female sockeye salmon (*O. nerka*) have lower passage success through hydraulically challenging reaches (Hinch and Rand 1998, Crossin *et al*. 2008, Roscoe *et al*. 2011) and are more sensitive to natural and anthropogenic stressors, particularly when environmental conditions are difficult for migration (Gilhousen 1990). Despite a growing understanding of the roles that discharge can have on migration success (Alabaster 1970, Hinch and Rand 1998, Rand *et al*. 2006), sex-specific energetic and behavioural responses to altered flow conditions remain poorly studied.

It is typical for dams to be operated in a manner where minimum discharges are
maintained to provide orientation cues for fishes attempting to reach passage facilities (e.g., fishways and fish locks; Clay 1995, Bunt et al. 2011). Though fishways are designed to restore river connectivity in regulated, constrained systems (Clay 1995), hydraulically complex and challenging flow regimes downstream of dams often generate a number of confusing migration pathways, causing fish to delay in selecting their optimal path and impeding their ability to locate and ascend fishways (Barry and Kynard 1986, Naughton et al. 2005). Recent electromyogram (EMG) telemetry research has linked alterations in flow dynamics at dam facilities to the activity (i.e., swimming speed), migration behaviour and energy expenditure of free-swimming adult salmon (Brown et al. 2006, Pon et al. 2009b, Hasler et al. 2012). Research by Brown et al. (2006) has demonstrated that Chinook salmon (O. tshawytscha) swim above their critical swimming speed ($U_{crit}$) and exhibit burst swimming in the Bonneville Dam tailrace. Further EMG telemetry work on Chinook salmon in the Puntledge River in British Columbia (BC), Canada, has shown that more of the variability in the activity of fish is attributed to inter-individual variation in swimming strategies than alterations in flow (Hasler et al. 2012). EMG telemetry, however, involves an invasive surgical tagging procedure where electrodes must be inserted into aerobic swimming muscle. Imprecision of electrode placement and variability in the performance of tag components requires the calibration of each tag upon implantation to yield reliable information on fish activity (Brown et al. 2007). In recent years, tri-axial accelerometers have become common tools for studying animal movement given that they do not require the intrusive placement of electrodes (Wilson et al. 2006, Gleiss et al. 2010). Rather than trying to infer tail-beat activity from a proxy (e.g., EMG activity), accelerometers can enable the direct
measurement of tail beats. Accelerometer sensors have been incorporated into acoustic telemetry transmitters that can be gastrically implanted in wild fish to monitor fine-scale behaviours and energy expenditure (Wilson et al. 2013). Since the identification of probable mechanisms behind passage success or failure at upstream barriers remains a research challenge (Naughton et al. 2006, Caudill et al. 2007), acoustic accelerometers have the potential of linking habitat-specific activity and migration behaviour to the unique hydraulic conditions fish experience.

In southwestern BC, Canada, the Seton–Anderson watershed is a highly regulated system that offers a unique opportunity to evaluate the effects of a diversion dam on the behaviour and survival of migrating adult Pacific salmonids. Pon et al. (2009a,b) used EMG telemetry in conjunction with physiological biopsy to link the total discharge of the Seton Dam to the swimming behaviour and passage success of Gates Creek sockeye salmon. Although energy-use within a vertical-slot fishway did not differ among successful and unsuccessful migrants, unsuccessful fish appeared to be physiologically stressed (i.e., depressed plasma Na\(^+\)), perhaps because of their time spent in the highly turbulent flows of the tailrace prior to capture (Pon et al. 2009b). Although it has been recognized that Gates Creek sockeye salmon have greater difficulty locating and entering the Seton Dam fishway (i.e., attraction efficiency) compared with passage through the fishway (i.e., passage efficiency; Pon et al. 2009a, Roscoe et al. 2011), a proximate cause for this is unknown. As recommended by Pon et al. (2009a), more detailed analyses on the relationship between unique water flows downstream of the Seton Dam and passage success are warranted given that attraction efficiency does not appear to be affected by alterations to the total dam-spill discharge. Additional research in the Seton–Anderson
watershed indicated that migration through the dam tailrace and fishway has post-passage consequences for Gates Creek sockeye salmon (Roscoe et al. 2011). Of importance, the authors found that female sockeye salmon demonstrated significantly lower survival (40%) to reach spawning grounds compared with males (71%). In general, it is unclear why there is poor female performance in this watershed and why 20–30% of the annual Gates Creek sockeye salmon run fails to pass the Seton Dam upon reaching the tailrace (Pon et al. 2009a, Roscoe et al. 2011).

The objective of this study was to investigate the effects of managed flow releases at the Seton Dam on the activity, energy-use and passage success of sockeye salmon. Building on telemetry data collected in 2007, a secondary study objective was to assess the predictors of passage success, migration delay and attraction efficiency of Gates Creek sockeye salmon at the Seton facility. I hypothesized that alterations in the hydrodynamics below the dam would affect passage success by influencing sockeye salmon activity and behaviour. I predicted that: (1) faster-swimming (i.e., hyperactive), delayed migrants would be more likely to fail in passing the Seton Dam, and (2) female sockeye salmon would exhibit prolonged holding behaviours in the tailrace, impeding their ability to successfully pass the facility. To our knowledge, this research provides some of the first data on the relationship between detailed flow releases from a diversion dam and the passage success of wild, migrating adult Pacific salmon.

Methods

Study site

Gates Creek sockeye salmon are an ‘early Summer-run’ stock of Fraser River
sockeye salmon that migrate ~ 350 km in July and August from the mouth of the Fraser River to the Seton–Anderson watershed in southwestern BC, Canada. Adult sockeye salmon migrate an additional 50 km through the Seton River, Seton Lake, Portage Creek and Anderson Lake to reach their terminal spawning grounds at Gates Creek and an artificial spawning channel at D’Arcy, BC (Figure 2.1); spawning takes place between mid-August and mid-September. Approximately 775 m downstream of Seton Lake, the Seton Dam (operated by BC Hydro; Figure 2.1 inset) spills water down Seton River to attract adult sockeye salmon, in addition to diverting upwards of 125 m$^3$s$^{-1}$ down a 3.8 km long power canal to a powerhouse station on the Fraser River. Gates Creek sockeye salmon must negotiate the Seton Dam tailrace and locate and ascend the vertical-slot fishway (32 pools, two turning basins, 107-m-long, 6.9% grade, discharge: 1.0 – 1.3 m$^3$s$^{-1}$) to reach natal spawning sites. At the Seton facility, flows from the fish water release gate (FWRG) are used to attract adult migrants to the fishway entrance and any excess water spills through the remaining five siphons and/or radial gate spillway. In 2012, there were three distinct periods in the operational regime: (1) a high-discharge period from 17 to 20 August (mean total dam-spill discharge ± standard error (SE): 48.1 ± 2.4 × 10$^{-2}$ m$^3$s$^{-1}$) in which the FWRG (1.7 m$^3$s$^{-1}$) and siphons #1 and #3 were open (45.4 ± 2.8 × 10$^{-3}$ m$^3$s$^{-1}$); (2) a ramp-down event (systematic decrease in total dam-spill discharge) on 21 August in which the FWRG (9.2 ± 1.2 m$^3$s$^{-1}$, range: 1.7 – 14.0 m$^3$s$^{-1}$) and siphon #1 (29.7 ± 2.5 m$^3$s$^{-1}$, range: 19.9 – 45.3 m$^3$s$^{-1}$) remained open, siphon #3 was closed and the radial gate spillway was open (7.3 ± 1.7 m$^3$s$^{-1}$, range: 0.8 – 16.1 m$^3$s$^{-1}$) from 10:00 – 17:00; and (3) a low-discharge period from 22 August to 2 September (32.3 ± 0.4 m$^3$s$^{-1}$) in which the FWRG (13.7 ± 7.7 × 10$^{-3}$ m$^3$s$^{-1}$) and siphon #1 were open (20.0 ± 1.5 × 10$^{-2}$ m$^3$s$^{-1}$).
m$^3$s$^{-1}$, range: 19.8 – 21.2 m$^3$s$^{-1}$). Daily water temperatures in the Seton River in 2012 (17.2 ± 0.4°C, range: 14.7 – 18.9°C; YSI model Pro 30 water quality meter, Yellow Springs, OH, USA) were within the thermal optima for Gates Creek sockeye salmon (i.e., 17.5 °C, Lee et al. 2003a).

Fish capture, tagging and tracking

Twenty-six Gates Creek sockeye salmon were captured by dipnet between 17 and 28 August 2012 from the top pool of the Seton Dam vertical-slot fishway and immediately transferred to a V-shaped, foam-padded trough containing fresh Seton River water for sampling and tagging. During sampling, a DNA clip was obtained from the adipose fin for stock identification, fork length (FL) was measured (56.9 ± 0.4 cm, range: 53.5 – 62.0 cm), sex was estimated on the basis of secondary sexual characteristics present at this stage in the freshwater migration (e.g., male hump and kype), and gross somatic energy (GSE; mean ± SE: 6.3 ± 0.2 MJ kg$^{-1}$) was obtained through the use of a microwave energy meter (FM 692 Fish Fatmeter, Distell, Scotland, UK; see Crossin and Hinch, 2005).

Three tagging configurations were established: (1) eight individuals (three male and five female sockeye salmon) received a gastrically inserted (Cooke et al. 2005) acoustic accelerometer (Model V13A-1x, 69 kHz, 16 × 52 mm; VEMCO, Halifax, NS, Canada) as well as a radio transmitter (Pisces 5, 15 × 50mm; Sigma Eight Inc., Newmarket, ON, Canada) externally attached posterior to the dorsal fin as a ‘backpack’ using stainless-steel wiring inserted through the dorsal musculature; (2) eight individuals (one male and seven female sockeye salmon) received only gastrically-inserted acoustic
accelerometers to test the effects of the external-backpack method; and (3) ten individuals (three male and seven female sockeye salmon) received a gastrically-inserted radio transmitter to provide supplementary behavioural data. Acoustic accelerometers measure acceleration in three axes (range: 0 – 4.901 m s\(^{-2}\)) for 10 s at a sampling frequency of 10 Hz; acceleration data is then averaged for that 10 s period (root mean square (RMS) acceleration = \((X^2 + Y^2 + Z^2)^{0.5}\)) and transmitted every 13 – 17 s to sentinel receivers.

RMS acceleration can further be converted to swimming speed and oxygen consumption as described in the succeeding text. The sampling and tagging procedure took less than 2 min to complete, and fish were not anaesthetized to minimize handling time and related stress (Cooke et al. 2005). After tagging and sampling, fish were transported in an oxygenated, insulated 1000-l transport tank and released individually or in groups (maximum of six individuals) 350 m downstream of the Seton Dam on the southern bank of the Seton River (50°40’N, 121°58’W).

To monitor the activity and movement of free-swimming sockeye salmon in real-time, I used a combination of fixed and mobile acoustic and radio telemetry methods. An acoustic array consisting of nine single-channel receivers (VR2W, 69 kHz; VEMCO) was installed in the Seton River to remotely record the activity of fish tagged with acoustic accelerometers. Prior to the study period, the detection ranges of acoustic receivers were tested (e.g., 10 m in the radial gate spillway and < 1 m along the fishway outer wall) to ensure that no single transmission was detected on multiple receivers (i.e., overlap). Seven receivers were placed in the Seton Dam tailrace (Figure 2.1 inset), a single acoustic receiver was positioned in the dam forebay to capture the time that fish exited the fishway, and a single receiver was located at the release site to monitor immediate
post-release activity and behaviour. Two fixed radio receivers (SRX_400; Lotek Wireless Inc., Newmarket, ON, Canada) with five-element Yagi antennas were used throughout the 2012 study period. One was positioned at the dam to monitor the total amount of time any given fish spent within the tailrace area before eventual pass or fallback (hereafter, tailrace delay) and one fixed station located in the dam forebay to confirm the passage success of radio-tagged fish. Additionally, two SRX_400 radio receivers with three-element Yagi antennas were used for manual tracking purposes along the northern bank of the Seton River to provide detailed movement data from the release site to the dam tailrace.

Data analysis and statistics

RMS acceleration data were converted to a representative swimming speed (BL s$^{-1}$) using the calibrations and relationships described in Wilson et al. (2013). Acceleration data were further converted to estimates of oxygen consumption ($MO_2$, mg O$_2$ kg$^{-1}$ min$^{-1}$) for Fraser River ‘early Summer-run’ sockeye salmon (S. Wilson, unpublished data), based on the equation

$$MO_2 = [2.81 + (0.89 \times \text{RMS acceleration}) + (0.05 \times \text{Water temperature (°C)}) - (0.03 \times \text{FL}) + 1.21 - (\text{RMS acceleration} \times 0.32)]^2 \tag{1}$$

White muscle fibers start to be recruited at ~ 80% of the critical swimming speed ($U_{\text{crit}}$) in migratory Pacific salmonids (Burgetz et al. 1998). Swimming speeds in the present study that were less than 80% $U_{\text{crit}}$ (Gates Creek $U_{\text{crit}} = 2.10 \pm 0.05$ BL s$^{-1}$; Lee et
al. 2003a) represent purely aerobic swimming efforts. Oxygen consumed as a result of swimming at speeds less than 80% $U_{\text{crit}}$ can be estimated using Equation 1. Swimming speeds from 80 to 100% $U_{\text{crit}}$ (1.66 – 2.10 BL s$^{-1}$) have both an aerobic (Equation 1) and anaerobic portion, typical of a burst-and-coast swimming gait commonly found in migrating adult sockeye salmon (Weihs 1974). I applied an anaerobic ‘tax’ of 50.5% to all swimming speeds greater than 80% $U_{\text{crit}}$ to account for the oxygen consumed post-exercise (i.e., excess post-exercise oxygen consumption, EPOC) in Gates Creek sockeye salmon (Lee et al. 2003b). Oxygen consumed as a result of swimming at speeds $\geq U_{\text{crit}}$ was assumed to be the maximum oxygen consumption ($MO_2_{\text{max}}$) for Gates Creek sockeye salmon (15.10 mg O$_2$ kg$^{-1}$ min$^{-1}$; Lee et al. 2003a) with the additional tax to account for EPOC. Given the amount of oxygen consumed during aerobic swimming efforts and the amount consumed during EPOC, I was able to quantify the percentage of detected swimming efforts that recruited anaerobic muscle fibers. Acceleration data collected from the three acoustic receivers on the northern bank of the Seton River adjacent to the radial gate spillway (Figure 2.1 inset) were pooled and represent the swimming speeds and oxygen consumption data from the ‘radial gate spillway’ habitat (~300 m$^2$; non-turbulent flows unless radial gate opened). Data from all four acoustic receivers in and around the fishway entrance (Figure 2.1 inset) represent the swimming speed and oxygen consumption of Gates Creek sockeye salmon in the ‘fishway entrance’ habitat (~400 m$^2$; consistently turbulent).

I incorporated telemetry data collected in 2007 from a previous study (Roscoe et al. 2011) on Gates Creek sockeye salmon at the Seton Dam to allow for more robust analyses. Information regarding the operational regime in 2007 is described in detail in
Roscoe et al. (2011); however, it must be noted that the radial gate spillway was open (16.0 ± 3.1 m$^3$/s$^{-1}$, range: 0.7 – 30.6 m$^3$/s$^{-1}$) during the tagging and tracking period on 20 August 2007 from 11:00 – 20:00. Fish were collected in an identical procedure in 2007 and 2012 and were all released downstream of the Seton Dam to monitor migration behaviour and passage success. I constructed three generalized linear models (GLM) to predict the passage success and attraction efficiency (family: binomial; link: logit) and tailrace delay (family: Gaussian; link: identity) of Gates Creek sockeye salmon. Nine explanatory variables were used: (1) sex; (2) tailrace delay (in h); (3) number of detected, unique efforts to cross the turbulent tailrace area from the radial gate spillway towards the fishway entrance (hereafter, tailrace crossings); (4) GSE; and (5) study year to account for potential inter-annual differences in passage success and behaviour. Mean discharges from the (6) fishway, (7) FWRG and (8) siphon spillway were calculated for each individual fish while present in the dam tailrace, as well as (9) whether or not (binary) an individual was in the tailrace at the time of the radial gate opening on 20 August 2007 or 21 August 2012. All nine explanatory variables were included in each of the three models unless that variable was in fact the response variable (i.e., tailrace delay). Attraction efficiency was not included as an explanatory variable because of high passage efficiencies in 2007 and 2012 (93% and 89%, respectively). Multicollinearity among explanatory variables was tested, and no variables possessed a variance inflation factor greater than four, indicating that the explanatory variables were not highly correlated (O’Brien 2007). A total of 63 adult Gates Creek sockeye salmon (2007: 47 total, 14 males, 33 females; 2012: 16 total, 4 males, 12 females) were included in the three models. Twelve individuals tagged and released downstream of the Seton Dam in 2007.
were removed from the analyses because of a failure to reach the tailrace post-release. Similarly, all ten individuals tagged with only radio transmitters in 2012 were omitted because of a lack of sufficient detection data in the tailrace. I generated the top five candidate models using the R (Version 2.15.0; R Core Team, 2012) package ‘glmulti’ (Calcagno 2012) and then compared them by using the bias-corrected, second-order information criterion (AICc) to determine the most parsimonious models (Sugiura 1978). After the most parsimonious models were identified, F-tests were used to calculate significance levels of all retained variables to assess the relative importance among explanatory variables. Models were further analyzed using AICc weights (\(w_i\)), which describe the relative weighting of each candidate model based on the amount of information lost (Wagenmakers and Farrell 2004). One-way analysis of variance (ANOVA) and Tukey post hoc tests were used to compare the activity, energy expenditure, migration behaviour and flow conditions experienced by successful and unsuccessful, male and female Gates Creek sockeye salmon. In some cases, data were log transformed to meet the normality and homoscedasticity assumptions of parametric tests. Non-parametric tests (Kruskal–Wallis and Mann–Whitney U) were used when the assumptions of normality were not met. Data are presented as mean ± SE, and all statistical analyses were performed at \(\alpha = 0.05\).

**Results**

Individuals were pooled from the three tagging configurations, as there were no significant differences among these groups in tailrace delay (ANOVA F = 0.11, df = 24, \(p = 0.75\)), fork length (ANOVA F = 0.49, df = 24, \(p = 0.49\)), GSE (Kruskal–Wallis H =
4.80, df = 2, p = 0.091), mean discharge experienced from the fishway (Kruskal–Wallis H = 5.11, df = 2, p = 0.08), FWRG (Kruskal–Wallis H = 3.45, df = 2, p = 0.18), siphon spillway (Kruskal–Wallis H = 0.87, df = 2, p = 0.65) and radial gate spillway (Kruskal–Wallis H = 1.18, df = 2, p = 0.55). I also found no difference in mean swimming speed at the release site (ANOVA F = 0.31, df = 7, p = 0.60) and within the tailrace (ANOVA F = 0.02, df = 13, p = 0.90) between fish that possessed an acoustic tag only and fish that were acoustically- and radio-tagged.

Of the 26 Gates Creek sockeye salmon tagged and tracked in 2012, 16 individuals [overall: 62%; males: 71% (5/7); females: 58% (11/19)] successfully re-ascended the fishway and passed the Seton Dam. A single female successfully passed the dam, only to descend the fishway at a later time; this individual was considered to have failed in passing the facility. All 26 sockeye salmon swam volitionally in schools up to the dam tailrace (1.1 ± 0.1 h, range: 0.4 – 3.2 h) along the southern shore of the Seton River immediately post-release and delayed there for 16.1 ± 4.9 h (range: 0.5 – 114.8 h) until eventual pass or fallback. Attraction efficiency (69%, 18/26) was considerably lower than passage efficiency (89%, 16/18) in 2012. We only captured 10.8 ± 2.7% (range: 1.2 – 39.2%) of the activity of the acoustically-tagged Gates Creek sockeye salmon within the tailrace (comparing total number of 10 s acoustic detections to tailrace delay for each fish). Overall, Gates Creek sockeye salmon used anaerobic swimming efforts 12.0 ± 4.4% (range: 0 – 61.3%) of their detected time within the tailrace.

Comparison among successful and unsuccessful fish

Successful (n = 50; 17 males, 33 females) and unsuccessful (n = 13; 1 male, 12
females) fish (2007 and 2012 pooled) did not differ with respect to their GSE (Mann–Whitney U-test $W = 338$, $p = 0.83$), the mean discharge experienced within the fishway (Mann–Whitney U-test $W = 419.5$, $p = 0.11$), FWRG (Mann–Whitney U-test $W = 437$, $p = 0.06$) nor siphon spillway (Mann–Whitney U-test $W = 330.5$, $p = 0.93$). However, unsuccessful fish experienced significantly higher mean discharges ($2.92 \pm 1.40 \text{ m}^3\text{s}^{-1}$) from the radial gate spillway compared with successful fish ($0.64 \pm 0.45 \text{ m}^3\text{s}^{-1}$; Mann–Whitney U-test $W = 241$, $p = 5.3 \times 10^{-3}$). Successful fish (1.4 ± 0.1 times, range: 0 – 5 times) crossed the tailrace towards the fishway entrance area significantly more times (Mann–Whitney U-test $W = 508.5$, $p = 2.03 \times 10^{-4}$) than unsuccessful fish (0.5 ± 0.2 times; range: 0 – 2 times).

One-way ANOVA and Tukey post hoc tests revealed that the mean swimming speeds of successful fish in the fishway entrance area in 2012 were significantly higher than the mean swimming speeds of successful and unsuccessful fish in the radial gate spillway (Table 2.1). While in the fishway entrance area in 2012, both successful (1.8 ± 0.1 BL s$^{-1}$, range: 1.30 – 2.28 BL s$^{-1}$) and unsuccessful (1.9 ± 0.3 BL s$^{-1}$, range: 1.57 – 2.13 BL s$^{-1}$) fish recruited anaerobic muscle fibers while exhibiting a burst-and-coast swimming strategy. Mean oxygen consumption ($\text{MO}_{2}$) did not differ between successful and unsuccessful fish in 2012 among locations (ANOVA $F = 1.51$, df = 27, $p = 0.22$). No significant differences were found among successful ($n = 12$) and unsuccessful ($n = 4$) fish in the relative proportion of the activity our acoustic array captured within the tailrace (ANOVA $F = 5.79$, df = 1, $p = 0.14$). As such, I was able to compare the anaerobic contribution to swimming efforts among successful (13.2 ± 5.4%, range: 0.2 – 61.3%) and unsuccessful fish (5.5 ± 3.1%, range: 0 – 14.2%)
and found no significant difference (ANOVA $F = 1.46$, $df = 1$, $p = 0.44$).

All five candidate models contained tailrace delay and tailrace crossings as significant predictors of passage success (Table 2.2). Each tailrace-crossing event increased the odds of passing the Seton Dam by $\sim 25\%$ ($e^{3.21}$; Table 2.2). The predicted probability of Gates Creek sockeye salmon passing the Seton Dam was visualized by fitting a logistic regression to the tailrace delay (Figure 2.2A) and tailrace crossings (Figure 2.2B) of successful and unsuccessful migrants using the R package ‘popbio’ (Stubben and Milligan, 2007). A migrant that possessed a GSE $1 \text{ MJ kg}^{-1}$ higher than other individuals delayed within the tailrace for $18\%$ less time ($e^{-0.20}$; Table 2.2).

**Sex-specific differences**

Male Gates Creek sockeye salmon in 2007 and 2012 had a higher passage success ($94\%$; 17/18) compared with females ($73\%$; 33/45). Attraction efficiency and passage efficiency in male sockeye salmon [$100\%$ (18/18) and $94\%$ (17/18), respectively] were higher than in females [$79\%$ (37/45) and $89\%$ (33/37), respectively]. Sex was retained within the attraction efficiency GLM and contributed significantly to all top-five candidate models. Female sockeye salmon delayed significantly longer ($20.8 \pm 4.1 \text{ h}$; range: $0.5 – 114.8 \text{ h}$) than males ($14.6 \pm 3.2 \text{ h}$; range: $1.0 – 48.5 \text{ h}$) in the tailrace (ANOVA $F = 4.87$, $df = 16$, $p = 0.04$). Although there was no significant difference in the number of tailrace crossings between male ($1.5 \pm 0.3 \text{ times}$) and female ($1.1 \pm 0.1 \text{ times}$) Gates Creek sockeye salmon (Mann–Whitney U-test $W = 479$, $p = 0.18$), males exhibited a larger range (range: $0 – 5 \text{ times}$) in the number of tailrace crossings compared with females (range: $0 – 3 \text{ times}$). Male and female sockeye salmon did not differ with
respect to their GSE (Mann–Whitney U-test $W = 385.5$, $p = 0.77$), the mean discharge experienced within the fishway (Mann–Whitney U-test $W = 450.5$, $p = 0.49$), FWRG (Mann–Whitney U-test $W = 457.5$, $p = 0.43$), siphon spillway (Mann–Whitney U-test $W = 452.5$, $p = 0.47$) and radial gate spillway (Mann–Whitney U-test $W = 381$, $p = 0.48$).

The mean swimming speeds of female sockeye salmon in the fishway entrance area were significantly greater (ANOVA $F = 6.5$, df = 35, $p = 6.28 \times 10^{-5}$) than the mean swimming speeds of females at all other locations (Tukey post hoc test; release site: $p = 0.030$; radial gate spillway: $p = 3.30 \times 10^{-5}$; forebay: $p = 0.018$) and males at the release site ($p = 4.40 \times 10^{-3}$) and in the radial gate spillway ($p = 3.60 \times 10^{-5}$) (Figure 2.3). An ANOVA ($F = 6.6$, df = 35, $p = 5.31 \times 10^{-5}$) and Tukey post hoc tests revealed that the mean oxygen consumption of female sockeye salmon was significantly higher in the fishway entrance area compared with male ($p = 3.43 \times 10^{-5}$) and female sockeye salmon ($p = 9.53 \times 10^{-4}$) in the radial gate spillway and males at the release site ($p = 0.012$). The mean oxygen consumption of male sockeye salmon in the radial gate spillway was significantly higher compared with males in the fishway entrance area ($p = 0.011$) and females at both the release site ($p = 0.018$) and in the forebay ($p = 0.045$).

Although it appears as if females exhibited higher mean oxygen consumption compared with males at all locations (Table 2.1), no differences were found in the mean oxygen consumption between male and female sockeye salmon at the same location. No significant differences were found among male and female sockeye salmon in 2012 in the relative proportion of the activity that our acoustic array captured within the tailrace (ANOVA $F = 0.32$, df = 2, $p = 0.63$). Though there was no significant difference (ANOVA $F = 0.023$, df = 2, $p = 0.89$) in the anaerobic contribution to swimming efforts.
between male (1.7 ± 0.5%) and female sockeye salmon (14.4 ± 5.2%), females exhibited a much larger range (0 – 61.3%) in detected anaerobic swimming efforts compared with males (0.7 – 2.7%).

**Effects of the operational regime**

All 26 Gates Creek sockeye salmon tagged in 2012 delayed (range: 0.5 – 114.8 h) in the radial gate spillway on the northern bank of Seton River. However, all individuals [9 total; \( n = 3 \) (2007), \( n = 6 \) (2012)] that experienced the opening of the radial gate failed to pass the Seton Dam. Opening the radial gate (hereafter, distraction flow) in 2007 and 2012 decreased attraction efficiency by 90% (\( e^{-2.35} \); Table 2.2) and increased tailrace delay by 2 h (\( e^{0.62} \); Table 2.2).

**Discussion**

Gates Creek sockeye salmon tagged with acoustic accelerometers in 2012 had habitat-specific and flow-dependent activity patterns in the Seton Dam tailrace. Contrary to our hypothesis and previous research on migrating Fraser River sockeye salmon (Hinch and Bratty 2000), the hyperactivity observed in these fish does not appear to contribute to failure in passing the dam. I found that all sockeye salmon that passed through the turbulent waters of the fishway entrance area recruited anaerobic muscle fibers while exhibiting a burst-and-coast swimming strategy, consistent with previous observations in the Seton Dam tailrace (Pon *et al.* 2009b) and hyperactivity reported in other tailraces (Brown *et al.* 2006, Enders *et al.* 2008). Burst swimming may not be required to ascend the Seton Dam fishway (Pon *et al.* 2009b); however, anaerobically-
fuelled locomotion (11.3 ± 4.1%, range: 0 – 61.3%) is typically needed to locate and enter the fishway entrance in a timely manner. Anaerobiosis is potentially costly, but whether or not it contributes to the observed failure of Gates Creek sockeye salmon to reach natal spawning sites (Roscoe et al. 2011) is unclear.

Female sockeye salmon delayed significantly longer within the Seton Dam tailrace than male sockeye salmon, and yet, male and female sockeye salmon did not differ with respect to GSE at the time of tagging and the flows encountered from the fishway, FWRG, siphon spillway, and radial gate spillway. Therefore, I infer that the reduced overall performance of female Gates Creek sockeye salmon at the dam may be the result of being sensitive to certain discharge conditions and associated flow patterns downstream of the facility. Crossin et al. (2008) hypothesized that greater energetic investment to gonad development in female sockeye salmon might render them more sensitive to environmental stressors such as warming temperatures and high flows in constricted passes or regulated systems. The results from the present study suggest that greater passage success in male sockeye salmon may be attributable to behavioural differences, as female sockeye salmon had a lower range in tailrace crossings and a lower attraction efficiency, which resulted in longer delays in the tailrace and a lower overall passage success. Moreover, female sockeye salmon appeared to have higher swimming speeds compared with males at all locations in the Seton River in 2012. Female sockeye salmon consistently swam above the optimal swimming speed and in some cases above the critical swimming speed \( (U_{\text{crit}}) \) of Gates Creek sockeye salmon (Lee et al. 2003a,b). Consequently, female sockeye salmon possessed a larger range of detected anaerobic swimming efforts compared with males and may support the notion that increased levels
of lactate accumulation and EPOC may contribute to the observed sex-specific
differences in dam passage and survival to spawning grounds (Roscoe et al.
2011). Certainly, it is possible that the significantly longer delays and higher mean
activity levels present in female sockeye salmon may contribute to energy depletion
within the tailrace and impede their ability to pass the facility.

Migration delay in the Seton Dam tailrace has a negative effect on passage.
Tailrace delay was a significant predictor of passage success, with an apparent threshold
tailrace delay of ~ 6 h in which the probability of passing the dam was 80%. Although
successful fish were able to pass after short and long bouts of delay, 12 of the 13
individuals that failed to pass the Seton Dam in 2007 and 2012 delayed for greater than 6
h. Passage probability diminished with tailrace delays greater than 6 h, lowering to 50%
with a delay of 60 h. This finding is of interest as Gates Creek sockeye salmon are known
to delay in the Seton Dam tailrace for up to 5 days and may be applicable to other
regulated watersheds in which migrants are known to spend several days downstream of
a barrier prior to eventual pass or fallback (Bjornn and Peery 1992, Geist et al. 2000,
Caudill et al. 2007). On the Columbia River, Caudill et al. (2007) found that unsuccessful
migrants delayed longer at nearly all encountered dams. Our finding that migrants with a
higher GSE delayed for significantly less time in the tailrace and had a higher passage
probability provides some insight into a biological mechanism for migrating adult salmon
passage success or failure at the Seton Dam. Previous work has shown that adult Pacific
salmon (sockeye salmon, Chinook salmon and steelhead *O. mykiss*) with lower GSE
travel slower through energetically demanding reaches and are less likely to successfully
complete their spawning migration (Young et al. 2006, Caudill et al. 2007).
I found that successful migrants crossed the turbulent flows of the tailrace towards the fishway entrance significantly more times than unsuccessful fish. This finding suggests that unsuccessful Gates Creek sockeye salmon may be unable to cross the tailrace enough times to locate the fishway entrance or decide to search for alternate migration routes after limited attempts at locating the fishway. Although the opposite behaviour was observed in actively migrating sockeye salmon attempting to locate the Hell’s Gate fishway in the Fraser River Canyon, BC (Hinch and Bratty 2000), research on Atlantic salmon (Salmo salar) found that successful adult migrants approached the fishway entrance upwards of ten times (Gowans et al. 1999). Some believe this behaviour allows fish to become accustomed with the entrances, flows and lowest pools of fishways (Laine 1995), whereas others have suggested it may be the result of confusion in selecting the desired migration path in areas with complex, convoluted flow patterns (Hinch et al. 2002). I am uncertain whether multiple, repeated attempts at crossing these energetically demanding areas contribute to the failure of migrants to reach natal spawning sites (Roscoe et al. 2011) given that Gates Creek sockeye salmon recruit anaerobic muscle fibers within these areas of the tailrace. Capturing Gates Creek sockeye salmon that have previous migration experience in the Seton Dam tailrace and fishway (Pon et al. 2009a, Roscoe et al. 2011, present study) could very well affect their ability to relocate the fishway entrance and pass the dam. To account for this, future passage studies at this facility should consider using dam- and fishway-naïve fish when generating efficiency estimates (Cooke and Hinch 2013).
Management implications

Opening the radial gate spillway at the Seton facility had adverse effects on Gates Creek sockeye salmon in both years that were examined. Spilling excess water from this portion of the dam decreased attraction efficiency by 90% and increased tailrace delay by 2 h. Interestingly, soon after the Seton Dam was constructed (i.e., 1956), Andrew and Geen (1958) observed that no serious migration delay occurred within the tailrace unless the radial gate was opened. Given that the radial gate spillway is located nearly 30 m from the fishway entrance on the opposite bank of the Seton River, I believe that flows emanating from the radial gate generate multiple pathways for sockeye salmon to choose, which likely distracts and confuses fish (Bunt 2001, Reischel and Bjornn 2003, Bunt et al. 2011). Further, Gates Creek sockeye salmon appeared to be equally affected when the ratio of the attraction to distraction flows released from the Seton Dam was 1:1 (2007) and even 2:1 (2012). By generating a number of confusing migration pathways, it is likely that the multidirectional currents downstream of the Seton Dam caused adult migrants to be less successful in selecting their optimal migration path as they were naturally attracted to the distraction flows released from the radial gate (Andrew and Geen 1958, Barry and Kynard 1986). Gates Creek sockeye salmon are known to delay within the closed radial gate spillway around the concrete baffles (Pon et al. 2009b), perhaps as an effort to use reverse flow fields to maintain their position in the tailrace while expending minimal energy (Bunt 2001, Liao et al. 2003). Releasing excess water through the radial gate not only attracts migrants to this part of the spillway but also does not allow holding to occur, reducing attraction efficiency and overall passage success (Pon et al. 2009a, Roscoe et al. 2011, present study). Yet, the radial gate is typically used
to spill excess water once during the annual Gates Creek sockeye salmon run in a single ramp-down event and thus, likely only affects fish immediately downstream of the Seton Dam at the time of the operational change. Research conducted elsewhere has shown that alterations to the operational regime during the migration period of anadromous fishes can adversely affect migration rates and passage success (Bjornn and Peery 1992).

Modifying the Seton Dam operational regime to improve attraction efficiency should be considered, particularly during the latter parts of the sockeye salmon migration period when energy levels are lower, and subsequent delays within the tailrace are longer. Alterations to the flow regimes at the Seton facility would not result in a loss of power generation, but at hydroelectric dams, the power generated could be affected by altering the specific location and magnitude of flow releases. Ultimately, the operating strategies that mitigate delays in upstream migration would need to be balanced with other water-use goals for environmental protection, flood control and irrigation.

Although it is widely recognized that the hydraulic conditions downstream of dam facilities are site specific (Bunt 2001, Pon et al. 2009a), I feel that the results from the current study demonstrate a clear need for more detailed hydraulic analyses when addressing complex fish-passage problems. Several studies evaluating the effects of dam operations on the upriver spawning migrations of Pacific salmonids have found that changes in the total dam-spill discharge at a facility can increase delay and decrease passage success at individual dams and through multi-dam reaches (e.g., Caudill et al. 2006, 2007). However, others using this approach have been unable to understand the influence of managed flow releases on the migration behaviour and passage success of migrants (Pon et al. 2009a,b, Roscoe et al. 2011). Linking the total discharge at an
upstream barrier to passage success or failure does not reflect the complex flow patterns fish negotiate downstream. I highlight the importance of transitioning from using the total dam-spill discharge in analyses to more detailed flow releases. Improving our understanding of the interactions between anadromous fishes and hydrodynamics at natural and manmade barriers will aid in the management of fish passage.
Table 2.1. Mean swimming speeds (BL s\textsuperscript{-1}; ± SE) of successful and unsuccessful Gates Creek sockeye salmon (*O. nerka*) at the release site, radial gate spillway and fishway entrance area.

<table>
<thead>
<tr>
<th>Fate</th>
<th>Location</th>
<th>Release site</th>
<th>Radial gate spillway</th>
<th>Fishway entrance area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Successful</td>
<td>1.4 ± 0.1 (6)\textsuperscript{ab}</td>
<td>1.1 ± 0.1 (11)\textsuperscript{a}</td>
<td>1.7 ± 0.1 (8)\textsuperscript{b}</td>
<td></td>
</tr>
<tr>
<td>Unsuccessful</td>
<td>1.1 ± 0.1 (3)\textsuperscript{ab}</td>
<td>1.1 ± 0.1 (4)\textsuperscript{a}</td>
<td>1.7 ± 0.5 (2)\textsuperscript{ab}</td>
<td></td>
</tr>
</tbody>
</table>

Numbers within parentheses represent sample sizes (*n*) and lowercase letters represent significant differences (*p* < 0.05) from ANOVA and Tukey post hoc tests.
Table 2.2. Candidate generalized linear models (GLM) to predict passage success, attraction efficiency and tailrace delay of Gates Creek sockeye salmon (*O. nerka*).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model</th>
<th>$k$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passage success</td>
<td>Tailrace delay* (-3.13), tailrace crossings* (3.21), sex* (1.81), year* (-2.40)</td>
<td>4</td>
<td>0.00</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Tailrace delay*, tailrace crossings*, sex*, siphon spillway, FWRG</td>
<td>5</td>
<td>0.29</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Tailrace delay*, tailrace crossings*, siphon spillway, FWRG</td>
<td>4</td>
<td>0.35</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Tailrace delay*, tailrace crossings*, year</td>
<td>3</td>
<td>0.47</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Tailrace delay*, tailrace crossings*, siphon spillway*, FWRG, fishway</td>
<td>5</td>
<td>0.64</td>
<td>0.17</td>
</tr>
<tr>
<td>Attraction</td>
<td>Sex* (17.97), radial gate spillway* (-2.35)</td>
<td>2</td>
<td>0.00</td>
<td>0.31</td>
</tr>
<tr>
<td>efficiency</td>
<td>Sex*, radial gate spillway, tailrace delay</td>
<td>3</td>
<td>0.92</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Sex*, siphon spillway*, radial gate spillway, FWRG, tailrace delay, year</td>
<td>6</td>
<td>1.12</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>Sex*, radial gate spillway, siphon spillway, FWRG, tailrace delay,</td>
<td>5</td>
<td>1.23</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>Sex*, radial gate spillway*, siphon spillway</td>
<td>3</td>
<td>1.41</td>
<td>0.15</td>
</tr>
<tr>
<td>Tailrace delay</td>
<td>Radial gate spillway* (0.62), GSE* (-0.20), FWRG (0.05)</td>
<td>3</td>
<td>0.00</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>Radial gate spillway*, GSE*, FWRG, tailrace crossings</td>
<td>4</td>
<td>0.07</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Radial gate spillway*, FWRG*, tailrace crossings</td>
<td>3</td>
<td>1.25</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>Radial gate spillway*, GSE*, FWRG, fishway</td>
<td>4</td>
<td>1.61</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>Radial gate spillway*, GSE*, FWRG*, tailrace crossings, fishway</td>
<td>5</td>
<td>1.93</td>
<td>0.11</td>
</tr>
</tbody>
</table>

Models are ranked from lowest to highest $\Delta AIC_c$ (highest to lowest $AIC_c$ weight, $w_i$). Explanatory variables that contribute significantly ($p < 0.05$; one-way analysis of variance, ANOVA) to a GLM are marked with an asterisk. Numbers within parentheses represent the slope coefficients of the explanatory variables from the top-ranked models. $k$ is the number of model parameters.
Table 2.3. Mean oxygen consumption (mg O\textsubscript{2} kg\textsuperscript{-1} min\textsuperscript{-1}; ± SE) of male and female Gates Creek sockeye salmon (\textit{O. nerka}) at the release site, radial gate spillway, fishway entrance area and forebay. Numbers within parentheses represent sample sizes (\textit{n}).

<table>
<thead>
<tr>
<th>Location</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Release site</td>
<td>10.9 ± 1.0 (2)</td>
<td>12.8 ± 0.5 (7)</td>
</tr>
<tr>
<td>Radial gate spillway</td>
<td>10.3 ± 0.5 (4)</td>
<td>11.8 ± 0.4 (11)</td>
</tr>
<tr>
<td>Fishway entrance area</td>
<td>13.5 ± 0.4 (3)</td>
<td>14.3 ± 0.2 (7)</td>
</tr>
<tr>
<td>Forebay</td>
<td>12.3 ± 0.9 (3)</td>
<td>12.6 ± 0.1 (6)</td>
</tr>
</tbody>
</table>
Figure 2.1. A map depicting the Seton-Anderson watershed in southwestern British Columbia, Canada, the terminal spawning grounds for Gates Creek sockeye salmon (*O. nerka*), as well as the location of the Seton Dam and fishway (inset). Minimum flows at the Seton facility are released through the fish water release gate (FWRG) to attract migrating sockeye salmon to the fishway entrance (FENT). Seven sentinel acoustic receivers (A) were placed within the tailrace area to capture activity data. A single fixed radio receiver (R) with a 5-element Yagi antenna was positioned at the dam to quantify tailrace delay before eventual pass through the fishway exit (FEXIT) or fallback out of the Seton system. Schematic of the Seton Dam and fishway adapted from Pon *et al.* (2009a) and used with permission.
**Figure 2.2.** Logistic regression fitted to the tailrace delay (log-transformed; A) and number of tailrace crossings (B) of successful and unsuccessful migrants. The red line shows the predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing the Seton Dam.
Figure 2.3. Box-and-whisker plot (median: solid line, mean: closed circle, extreme value: open circle, 25% and 75% quartiles) comparing the swimming speed (BL s\(^{-1}\)) of male (shaded grey) and female (white) Gates Creek sockeye salmon (\textit{O. nerka}) at the release site, radial spillway, fishway entrance area and forebay. Optimal (~ 1.0 BL s\(^{-1}\)) and critical (\(U_{\text{crit}}\); 2.1 BL s\(^{-1}\)) swimming speeds of Gates Creek sockeye salmon are shown along the y-axis; the swimming speed at which anaerobic muscle fibers start to be recruited (~ 1.7 BL s\(^{-1}\)) is also shown. Sample sizes (\(n\)) are presented below each box-and-whisker, and lowercase letters represent significant differences (\(p < 0.05\)) from ANOVA and Tukey post hoc tests.
CHAPTER 3: Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon.

Abstract

Wild riverine fishes are known to rely on burst swimming to traverse hydraulically challenging reaches, and yet there has been little investigation as to whether swimming anaerobically in areas of high flow can lead to delayed mortality. Using acoustic accelerometer transmitters, I estimated the anaerobic activity of anadromous adult sockeye salmon (*Oncorhynchus nerka*) in the tailrace of a diversion dam in British Columbia, Canada and its effects on the remaining 50 km of their freshwater spawning migration. Consistent with my hypothesis, migrants that elicited burst swimming behaviours in high flows were more likely to succumb to mortality following dam passage. Females swam with more anaerobic effort compared to males, providing a mechanism for the female-biased migration mortality observed in this watershed. Alterations to dam operations prevented the release of hypolimnetic water from an upstream lake, exposing some migrants to supra-optimal, near-lethal water temperatures (i.e., 24°C) that inhibited their ability to locate, enter and ascend a vertical-slot fishway. Findings from this study have shown delayed, post dam passage survival consequences of high-flow-induced burst swimming in sockeye salmon. I highlight the need for studies to investigate whether dams can impose other carryover effects on wild aquatic animals.

---

Introduction

Reproductive migrations are challenging life-history stages, particularly for semelparous species that are limited to a single opportunity to secure lifetime fitness (Dingle 1996). Animals that travel through freshwater to reach their breeding grounds are vulnerable to changes in environmental conditions that are known to dictate their migration success (e.g., river discharge: Rand et al. 2006, water temperature: Farrell et al. 2008 and Martins et al. 2012). On a global scale, river systems have become increasingly regulated through the construction of dams, generating highly variable flow and thermal regimes that are energetically demanding environments to traverse (Rosenberg et al. 2000, Preece and Jones 2002, Nilsson et al. 2005). Designed to mitigate these issues, fish passage structures (e.g., fishways and fish locks; Katopodis 1992, Clay 1995) aim to restore connectivity to regulated or constrained watersheds by facilitating the upstream passage of migratory fishes without imposing detrimental effects on fitness (Castro-Santos et al. 2009, Bunt et al. 2011). Much of the fish passage research to date has focused on enumerating passage success at a single dam (Cooke and Hinch 2013), with comparatively little mechanistic research evaluating whether exposure to these ‘velocity barriers’ can lead to delayed, post dam passage mortality (Caudill et al. 2007).

Anadromous adult Pacific salmon (*Oncorhynchus* spp) undertake physiologically- and energetically-challenging migrations from oceanic feeding grounds to natal freshwater spawning sites. Somatic energy conservation plays a central role in this final life-history stage, as these animals cease feeding upon river entry and rely on fixed, ocean-accrued energy reserves to fuel their movements and reproduction (Brett 1995, Crossin and Hinch 2005). Energy-conserving traits are strongly selected for; migrants
with spawning areas further inland are more streamlined, smaller, exhibit a more efficient swimming gait, have an increased aerobic capacity, and produce fewer and smaller eggs than short-distance migrants (Hinch and Rand 2000, Crossin et al. 2004, Eliason et al. 2011). Fraser River sockeye salmon (O. nerka) populations (British Columbia, Canada) are locally adapted to the historic temperature conditions encountered upon river entry (Eliason et al. 2011). Consequently, reductions in whole-animal performance and mortality can result when individuals are exposed to conditions above their optimal temperature for aerobic scope ($T_{\text{opt}}$) (Lee et al. 2003a, Farrell et al. 2008, Eliason et al. 2013). Indeed, it is concerning that Fraser River summer temperatures have increased by 2°C since the 1950s (Patterson et al. 2007) and that this warming trend is anticipated to continue in the future (Hague et al. 2011). Several studies have demonstrated that migrants exposed to high flows can exhibit energy depletion, physiological stress and migration failure in naturally constrained reaches and regulated watersheds (Rand et al. 2006, Nadeau et al. 2010, Roscoe et al. 2011). Sockeye salmon are both sensitive and vulnerable to river fragmentation, whereby human-made alterations to the migration corridors of this species can affect habitat quality, population sizes, community structure, and ecosystem function (Nehlsen et al. 1991, Slaney et al. 1996). As such, sockeye salmon are an exemplary species for investigating the effects of dam operations on swimming activity and behaviour, given that any marked increase in migration difficulty could lead to population-level consequences.

Sex-specific differences in sockeye salmon energy-use, behaviour and survival are more apparent in areas with challenging migration conditions (Hinch and Rand 1998, Standen et al. 2002, Roscoe et al. 2011). For example, mortality is exacerbated in
females that are exposed to high in-river temperatures and elevated water velocities (Martins et al. 2012 and Nadeau et al. 2010, respectively). In regulated watersheds, female sockeye salmon exhibit lower passage success at dams and suffer exceptionally high levels of en route and pre-spawn mortality following dam passage (Roscoe et al. 2011, Burnett et al. 2013a). Evidence suggests that high levels of anaerobic swimming by females in areas of high flow may contribute to the female-biased mortality trends often observed post dam passage (Burnett et al. 2013a). Crossin et al. (2008) hypothesized that female sockeye salmon may be more sensitive to environmental stressors due to their increased energetic investment into gonad development compared to males. Future research aimed at understanding the mechanisms underlying these data will better inform the conservation and management of Pacific salmon. Linking sockeye salmon swimming activity and behaviour to detailed flow releases from a dam may shed valuable insight into the individual-level, sex-specific responses to challenging migration conditions.

Fish exhibit a diverse set of swimming strategies to facilitate movement over a range of speeds and acceleration rates (Webb 1995). Optimal strategies are selected to reduce the drag and transport costs associated with moving through water (Weihs 1974, Videler 1993). Pacific salmon employ ‘burst-and-coast’ swimming in areas of fast-flowing water to benefit from significant energy savings and reduced physiological stress (Weihs 1974, Videler and Weihs 1982, Videler 1993). Both aerobic and anaerobic metabolic pathways (slow-red and fast-white muscle fibers, respectively) contribute to the burst-and-coast swimming effort (Burgetz et al. 1998). Anaerobic metabolic pathways exclusively power swimming at speeds exceeding their critical swimming speed \( U_{\text{crit}} \), where short bouts of burst (or ‘sprint’) swimming are fuelled by the
breakdown of glycogen in white muscle fibers (Black et al. 1966). Wild sockeye salmon elicit glycolytic-based, burst swimming behaviours to negotiate and minimize exposure to areas with energetically demanding high flows (Hinch and Bratty 2000, Standen et al. 2002, Brown et al. 2006). Lactate anions and metabolic protons accumulate in the swimming muscle of fish as a result of depleting glycogen reserves, resulting in a cascade of metabolic disturbances (Wood et al. 1983, Wood 1991). Following exhaustive exercise, sockeye salmon require additional oxygen uptake (known as excess post-exercise oxygen consumption, EPOC) and long recovery times to re-establish ion gradients, lactate processing, pH balance, and restore tissue and cellular oxygen levels (Lee et al. 2003b). Furthermore, if sockeye salmon experience temperatures above $T_{opt}$ while swimming at $U_{crit}$, cardiorespiratory collapse can occur due to an insufficient scope for heart rate (Eliason et al. 2013). Migrants that fail to re-establish metabolic homeostasis can perish hours or even days after prolonged periods of severe muscular exertion (Black 1958, Priede 1977, Wood et al. 1983), although field studies of that phenomenon are lacking. Despite our understanding of the physiological consequences associated with anaerobiosis, there is a growing need to investigate whether burst swimming by sockeye salmon in areas of difficult passage has carryover effects on migratory behaviour and survival (Caudill et al. 2007, O’Connor et al. 2014).

I studied sockeye salmon migration through a dam tailrace and vertical-slot fishway in southwestern British Columbia, Canada to determine the effects of anaerobiosis on dam passage success and post-passage survival. I hypothesized that dam operations would provide a significant hydraulic challenge for migrating sockeye salmon to overcome, requiring individuals to use burst swimming behaviours to negotiate high
flows surrounding the fishway entrance. I predicted that: (1) increased use of anaerobic metabolic pathways would reduce post dam passage survival, and (2) females would exhibit a higher degree of failure in dam passage and ability to reach natal sites compared to males. To my knowledge, this research is the first field-based study to reveal the delayed consequences of burst swimming on the spawning migrations of wild adult Pacific salmon.

Methods

Study site

I studied the swimming activity and behaviour of adult Gates Creek sockeye salmon below Seton Dam (operated by BC Hydro) in the Seton-Anderson watershed, British Columbia, Canada. Three hundred and fifty kilometers from the Pacific Ocean migrants encounter Seton Dam, a diversion dam that spills excess water down the Seton River as well as redirecting upwards of 125 m$^3$ s$^{-1}$ down a 3.8 km long power canal to a powerhouse station on the Fraser River (Figure 3.1). Adult sockeye salmon must locate and ascend a vertical-slot fishway (32 pools, 2 turning basins, 107 m long, 6.9% grade, discharge [mean ± standard error, SE]: 1.2 ± 2.0 × 10$^{-3}$ m$^3$ s$^{-1}$) to pass the dam and complete the remaining 55 km of their reproductive migration. Flows from the fish water release gate (FWRG) and siphon #1 are used to attract fish towards the fishway entrance, while excess water spills through the remaining four siphons and/or radial gate spillway (Figure 3.1 inset).
**Fish capture, tagging and tracking**

Sixty-three adult Gates Creek sockeye salmon were captured, tagged and released from 03 – 27 August 2013. Twenty-eight individuals (14 males, 14 females) were dip-netted from the top pool of the fishway (hereafter, fishway non-naïve), transported 50 m off of the dam in an oxygenated, insulated 1000-l transport tank, and held for upwards of 2 h in a 5000-l holding tank prior to sampling and tagging. Thirty-five individuals (18 males, 17 females) were captured by means of a full-spanning fence and trap (*ca.* 50 m long) located 200 m downstream of the dam in the Seton River (hereafter, fishway naïve) and were held temporarily in a flow-through holding pen prior to sampling and tagging. Fish were individually transferred to a V-shaped, foam-padded trough containing continuously flowing Seton River water directed towards the gills.

Tri-axial accelerometers have become common tools in ecology to monitor energy-use and behaviour in wild animals (Wilson *et al.* 2006, Gleiss *et al.* 2010, Brown *et al.* 2013). Of late, accelerometer sensors have been incorporated into acoustic telemetry transmitters that can be gastrically implanted into anadromous fishes that have ceased feeding (Wilson *et al.* 2013). In the stomach, transmitters are positioned at the center of mass to avoid large errors generated by centripetal acceleration (Videler 1993). Acoustic accelerometer transmitters (Model V13A-1x, 69 kHz, 16 × 52 mm; VEMCO, Halifax, NS, Canada) were inserted into the stomach cavity of all 63 sockeye salmon by means of a plastic plunger (Cooke *et al.* 2005). A DNA clip was obtained from the adipose fin for stock identification, fork length (FL) was measured to the nearest 5 mm (57.7 ± 0.4 cm, range: 49.0 – 62.5 cm), and sex was estimated on the basis of secondary sexual characteristics present at this stage in the freshwater migration (e.g., male hump
and kype). DNA analyses confirmed that all study subjects were of Gates Creek origin (Beacham et al. 2004). Fish were fitted with an external spaghetti tag (Floy Manufacturing, Seattle, WA, USA) attached posterior to the dorsal fin to aid in visual identification. A half-duplex (HDX) passive integrated transponder (PIT) tag (32 × 3.65 mm; Texas Instruments Inc., Dallas, Texas, USA) was inserted into the dorsal musculature of each fish using a sterile 6-gauge needle. Tagging and sampling took less than 2 min to complete and fish were not anaesthetized to minimize handling time and related stress (Cooke et al. 2005). Fishway non-naïve fish were transported and released 4 km downstream (N 50°40´, W 121°55´) of Seton Dam (★, Figure 3.1); fishway naïve fish were released directly above the fish fence.

A fixed acoustic array consisting of 18 single-channel receivers (VR2 and VR2W, 69 kHz; VEMCO) was installed in the Seton Dam tailrace to remotely record the swimming activity and behaviour of tagged fish (Figure 3.1 inset). Prior to the study period, the detection ranges of acoustic receivers were tested to ensure that no single acoustic transmission was detected on multiple receivers. Three pass-through PIT antennas (2.2 × 0.7-m) were positioned on the upstream-facing side of the vertical-slot baffles at the entrance, second turning basin and exit of the fishway (Figure 3.1 inset). PIT antennas were constructed out of 3.8-cm watertight polyvinyl chloride (PVC) pipe with 12-gauge stranded electrical wire; each antenna was connected to a remote tuner box (Oregon RFID, Portland, OR, USA) and all three antennas were connected to a multiplexor unit (Oregon RFID) via twin-axial cable (see Burnett et al. 2013b). PIT antennas within the fishway were manually tuned and tested prior to daily tagging to ensure optimal read range (~ 0.5 m) and tag-reading performance (see “Results”).
A three-antenna PIT array was also installed at the Gates Creek spawning channel to determine if migrants had reached spawning grounds. Two VR2W receivers were installed in Gates Creek and were positioned at the channel entrance to ensure optimal tag-reading performance. Detection efficiencies of acoustic- and PIT-telemetry arrays were calculated using the methods of Burnett et al. 2013b, and have been presented in the “Results”.

Fishway attraction efficiency (number of fish that located and entered the fishway divided by the total number of fish that reached the dam tailrace post-release) and passage efficiency (number of fish that passed the fishway divided by the number of fish that located and entered the structure) were determined using a combination of acoustic- and PIT-telemetry data. Following Burnett et al. (2013a), I quantified the total amount of time (in h) each fish spent within the dam tailrace before eventual pass or fallback (hereafter, tailrace delay), as well as the number of times each individual crossed the tailrace from the radial gate spillway towards the fishway entrance (hereafter, tailrace crossings). Hourly Seton River water temperatures were recorded from the top pool of the fishway using a TidbiT v2 Water Temperature Data Logger (Onset HOBO Data Loggers, Bourne, MA, USA).

Swimming activity analyses

Acoustic accelerometers measure acceleration in three axes (range: 0 – 4.901 m s\(^{-2}\)) for 10 s at a sampling frequency of 10 Hz; acceleration data is then averaged for that 10 s period [root mean square (RMS) acceleration = \((X^2 + Y^2 + Z^2)^{0.5}\)] and transmitted every 13 – 17 s to receivers. RMS acceleration data were converted to swimming speed in units
of body lengths per second (BL s\(^{-1}\)) following the calibrations and relationships of Wilson et al. (2013). Acceleration data were further converted to estimates of oxygen consumption (\(MO_2\), mg O\(_2\) kg\(^{-1}\) min\(^{-1}\)) for Fraser River ‘early Summer-run’ sockeye salmon using corresponding hourly Seton River temperatures. I strove to develop a model that incorporated a metric of the physiological differences of sockeye salmon populations, as well as acceleration, to predict \(MO_2\). Swimming speed data from Eliason et al. (2011) were used to estimate acceleration values based on a previously developed model (Wilson et al. 2013). Predicted acceleration values from Early Stuart, Chilko, Nechako, Quesnel, Lower Adams, Bowron, and Raft populations (Eliason et al. 2011) and actual acceleration values from acoustic-tagged Harrison River sockeye salmon (Wilson et al. 2013) were correlated with \(MO_2\) values from swim trials using a mixed effects model. RMS acceleration, temperature, FL, tunnel, acclimation rate, instrumentation, and one of run timing group, population, or migration difficulty index (see Wilson et al. 2014) were used as possible fixed effects to build candidate models. Subject ID was held as a random factor to account for non-independence of data, and a 95% confidence set was used (all models with cumulative summed AIC\(_c\) weights \((w_i) \geq 0.95\); Burnham and Anderson 2002). \(MO_2\) for Gates Creek sockeye salmon (intermediate difficulty category) was predicted using the simplified model:

\[
MO_2 = [2.81 + (0.89 \times \text{RMS acceleration}) + (0.05 \times \text{Water temperature (°C)}) – (0.03 \times FL) + 1.21 – (\text{RMS acceleration} \times 0.32)]^2
\]
For each study subject, I calculated the degree to which anaerobic glycolysis contributed to swimming in high flows surrounding the fishway entrance (hereafter, anaerobic recruitment). To do this, I divided the amount of oxygen consumed after anaerobic swimming efforts (i.e., EPOC; see Lee et al. 2003b) by the total amount of oxygen consumed as a result of aerobic and anaerobic contributions to swimming (see Burnett et al. 2013a for a detailed description). Anaerobic recruitment is expressed as a percentage, where higher values reflect the greater EPOC required to restore tissue and cellular oxygen levels and re-establish metabolic homeostasis following anaerobiosis. Acceleration data collected from four acoustic receivers on the northern bank of the Seton River adjacent to and in the radial gate spillway (Figure 3.1 inset) were pooled and represent the swimming speeds from the “radial gate spillway” habitat (ca. 300 m²; low flow area). Data from seven acoustic receivers along the outer fishway wall and the receiver in the first pool of the fishway were combined and represent the swimming speed of sockeye salmon in high flows surrounding the fishway entrance (ca. 400 m²). Within-fishway swimming speeds were pooled from four acoustic receivers positioned in the fishway (Figure 3.1 inset).

*Model selection, multimodel averaging and inference*

Generalized linear models (GLM) were used to predict dam passage (family: binomial, link: logit), anaerobic recruitment (family: Gaussian, link: identity), and tailrace crossings (family: Poisson, link: log) by Gates Creek sockeye salmon. A final GLM was used to predict the ability of migrants who successfully passed Seton Dam to reach spawning grounds in Gates Creek (family: binomial, link: logit). Seven explanatory
variables (biotic and abiotic) were included in each of the four model sets unless that variable was in fact the response variable. Biotic explanatory variables included: (1) sex (male [1], female [0]), (2) anaerobic recruitment (%), (3) tailrace delay (h), and (4) tailrace crossings. Abiotic explanatory variables included: (5) the maximum Seton River temperature (°C) and (6) mean flows (m³ s⁻¹) from siphon #1 each individual fish experienced while present in the dam tailrace. Cooke and Hinch (2013) reason that capture location (i.e., use of fishway naïve and non-naïve fish) affects the ability of migrants to locate, enter and ascend a fishway. Therefore, I included capture location (7; fence- [1] or fishway-caught [0]) as a fixed factor in all models to account for its effects when testing my main hypothesis. However, I do present the relative effect of capture location on all response variables to show the importance of considering capture location when conducting and interpreting the results of fish passage studies (Cooke and Hinch 2013). All variables were tested for multicollinearity using variance inflation factors (VIF); flows from the FWRG were collinear (VIF > 3) with the maximum Seton River water temperature fish experienced (Zuur et al. 2010). Consequently, FWRG was removed as an explanatory variable as the discharge from siphon #1 provided the vast majority of encountered flows below the dam during the study period. I did not model attraction efficiency because only one individual failed to pass the fishway after locating and entering the structure (i.e., 98% passage efficiency); therefore, results would be nearly identical to those of the dam passage model. Tailrace crossings was not included as an explanatory variable in the dam passage model as it was highly collinear with both attraction and passage efficiency. Nine individuals (2 males, 7 females) were omitted from the analyses due to a failure to reach the tailrace post-release; thus, a total of 54
adult Gates Creek sockeye salmon (fishway non-naïve: 19 total, 12 males, 7 females; fishway-naïve: 35 total, 18 males, 17 females) were included in the four models.

All candidate models were generated using the R (Version 3.0.2; R Core Team 2013) package ‘MuMIn’ (Barton 2012) and compared using AICc (for small sample sizes) to determine the most parsimonious models. Models were further analyzed using AICc weights (wi), which describe the relative weighting of each candidate model based on the amount of information lost (Wagenmakers and Farrell 2004). Average parameter estimates were calculated using the natural average method (Grueber et al. 2011) and a 95% confidence set (Burnham and Anderson 2002). I standardized all data by centering (subtracting the mean) and dividing by two standard deviations (Gelman 2008), allowing for the direct comparison of the relative effect sizes of explanatory variables. Model-averaged standardized coefficients for binary explanatory variables were exponentiated to provide an interpretable odds ratio. Model fits were evaluated using the percentage and significance of deviance explained by a GLM (Kindt and Coe 2005). A one-way analysis of variance (ANOVA) and Tukey post hoc tests were used to compare the swimming speeds of male and female Gates Creek sockeye salmon. Residuals were examined for homoscedasticity, normality and independence. Data are presented as mean ± SE throughout, and statistical analyses were considered significant at \( \alpha = 0.05 \).

Results

Seton River temperatures during the study period (19.3 ± 0.1°C, range: 16.0 – 23.7°C) were consistently above the thermal optima for Gates Creek sockeye salmon (i.e., 17.5°C; Lee et al. 2003a). Acoustic receivers in the radial gate spillway (100% [\( n = \)))
54), fishway entrance area (80% [n = 45]), within the fishway (100% [n = 45]), and in the dam forebay (100% [n = 44]) were all effective at detecting acoustic-tagged sockeye salmon. PIT arrays within the Seton Dam fishway and at the Gates Creek spawning channel had high detection efficiencies (91.7 ± 6.1% [n = 44] and 89.6 ± 1.6% [n = 25], respectively).

**Dam passage**

Anaerobiosis was required to reach the fishway entrance (Figure 3.2) and pass the dam (Figure 3.3A; Table 3.1). Fish exposed to warmer water temperatures while in the dam tailrace were less likely to locate, enter and ascend the fishway (Figure 3.4; Table 3.1). Compared to females, male Gates Creek sockeye salmon were 17% (e^{2.85}) more likely to locate and enter the fishway, and 9% (e^{2.24}; Figure 3.5A) more likely to pass the dam. Males made significantly more crossing events (1.37 ± 0.16 times, range: 0 – 4 times) towards the fishway entrance compared to females (0.88 ± 0.13 times, range: 0 – 2 times; Figure 3.5C). Anaerobic recruitment, maximum Seton River temperature and sex formed the top-ranked dam passage model, explaining 50% of the variation in the data after accounting for capture location (Table 3.1). Capture location, anaerobic recruitment, sex, and maximum temperature had similar effect sizes (Figure 3.5A). Fishway naïve individuals were 15% (e^{2.68}) more likely to locate and enter the fishway entrance, and 16% (e^{2.74}; Figure 3.5A) more likely to pass Seton Dam.
Anaerobiosis in areas of high flow

Fish that experienced higher flows from siphon #1 showed higher anaerobic recruitment near the fishway entrance (Figure 3.5B). Individuals that traversed the high flows multiple times used more anaerobic effort compared to fish that made fewer crossings of the tailrace (Figure 3.5B). Females swam with more anaerobic effort in areas of high flow compared to males (Figure 3.5B; Table 3.1). Fishway naïve individuals relied more on anaerobic glycolysis near the fishway entrance compared to fishway non-naïve individuals (Figure 3.5B). Flows from siphon #1, sex and tailrace crossings formed the top-ranked anaerobic recruitment model, explaining 46% of the variation in the data after accounting for capture location (Table 3.1). Swimming at their $U_{crit}$ (2.1 BL s$^{-1}$), fish swam significantly faster in the fishway entrance area compared to all other areas of the dam (one-way ANOVA $F = 70.94$, df = 3, $p < 2 \times 10^{-16}$; Figure 3.2). Fish swam faster within the fishway and in the dam forebay compared to when delaying in the radial gate spillway (one-way ANOVA; Figure 3.2). Four females swam at 80% $U_{crit}$ while in the fishway entrance area, while 11 other females swam consistently above $U_{crit}$ (Figure 3.2).

Migration success to spawning grounds

Individuals that used more anaerobic effort near the fishway entrance were less likely to reach natal spawning streams compared to fish that swam more conservatively (Figure 3.3B). Anaerobic recruitment had an equal, but opposite effect on fish reaching breeding grounds as capture location (Figure 3.5D). Anaerobic recruitment affected the ability of dam-successful migrants to reach natal sites, explaining 30% of the variation in the data after accounting for capture location (Table 3.1). Fishway naïve individuals were
154% (e^{5.04}; Figure 3.5D) more likely to complete their freshwater migration after passing Seton Dam compared to fishway non-naïve individuals. Forty-four percent (8/18) of the fish that failed to reach natal spawning streams after passing the dam died in Seton Lake; all other individuals (56%; 10/18) migrated to within 4 km of Gates Creek but perished in Anderson Lake prior to spawning.

**Discussion**

Anaerobiosis significantly decreased the probability of migrants to reach natal sites, explaining in part why Gates Creek sockeye salmon suffer exceptionally high mortality rates after passing Seton Dam (Roscoe *et al.* 2011). In a lab setting, Wood *et al.* (1983) found that forty-percent of rainbow trout (*O. mykiss*) perished within 12 hrs after 6 min of intensive exercise. Similarly, nearly half of the delayed mortality observed in the present study occurred in Seton Lake within 1 – 3 days of dam passage, likely owing to the greater EPOC and long recovery times associated with prolonged periods of swimming at critical speeds (Lee *et al.* 2003a,b). Using a swim tunnel respirometer at Seton Dam, Lee *et al.* (2003a,b) showed that Gates Creek sockeye salmon exhibit significantly higher anaerobic contribution to swimming and are less efficient swimmers compared to other Fraser River sockeye salmon populations. Consistent with an electromyogram telemetry study on Gates Creek sockeye salmon (Pon *et al.* 2009), I found that burst swimming is required to negotiate the Seton Dam tailrace but is not needed to ascend the fishway. Gates Creek sockeye salmon are known to cross the dam tailrace multiple times towards the fishway entrance (Burnett *et al.* 2013a), perhaps as an attempt to become accustomed to the entrance area (Laine 1995) or due to confusion in
selecting the desired migration path (Hinch et al. 2002). At Seton Dam, individuals may have simply been forced away from the fishway entrance due to the supercritical flows from siphon #1. Nevertheless, I found that this behaviour lead to significant increases in anaerobic recruitment. A trade-off exists, whereby multiple crossing events are associated with successful dam passage but contribute to the failure of migrants to reach breeding grounds (Burnett et al. 2013a). Releasing excess water from siphon #1 is part of the standard operational protocol at this facility, as it is believed to improve the attraction of fishes to the vertical-slot fishway (Andrew and Geen 1958). Fishways and their attraction flows should be designed to facilitate the upstream passage of aquatic species and minimize undue physiological stress (Clay 1995, Bunt 2001). Yet, my results indicate that small fluctuations (< 1 m$^3$ s$^{-1}$) in fishway attraction flows can compromise the survival of sockeye salmon. Indeed, there is likely a trade-off between attraction efficiency and the high flows designed to attract fish to a passage structure. Future research is needed to investigate whether there are management strategies that would reduce attraction efficiency and the supercritical flows around a fishway in a way that might lead to optimal net survival to natal spawning streams.

Female Gates Creek sockeye salmon are less successful at passing Seton Dam and demonstrate significantly lower survival to reach natal sites compared to males (40% vs. 71% in Roscoe et al. 2011; 44% vs. 69% Figure 3.5). A higher proportion of tagged females (2 males vs. 7 females) failed to reach the tailrace post-release, further emphasizing the susceptibility of female sockeye salmon to stress. Nadeau et al. (2010) demonstrated this in a holding study, whereby female sockeye salmon suffered higher mortality and exhibited elevated levels of physiological stress when exposed to high
water velocities. Despite making fewer crossings, females swam with more anaerobic effort in areas of high flow, indicating that females swam faster and less efficiently in the Seton Dam tailrace compared to males (Burnett et al. 2013a, Figure 3.2). Overall, female sockeye salmon that relied heavily on glycolytic-fuelled locomotion were more likely to succumb to mortality out of all individuals that passed the dam, providing a probable mechanism for the observed sex-specific differences in survival to spawning grounds in this watershed (Roscoe et al. 2011, Figure 3.5). A bimodal distribution in the swimming speeds of females near the fishway entrance (Figure 3.2) suggests individual variability in swimming strategies (Standen et al. 2002, Hasler et al. 2012). I highlight the need for future investigation into the swimming behaviours of anadromous fishes in areas of difficult passage, as it appears that some females (and most males) are capable of negotiating high flows with little to no anaerobic contribution to swimming effort.

Several telemetry studies on Fraser River sockeye salmon have revealed that females often demonstrate higher temperature-induced mortality compared to males (e.g., Crossin et al. 2008, Martins et al. 2012). Certainly, the greater energetic investment into gonad development in females could limit their ability to negotiate hydraulically challenging reaches and cope with high water temperatures (Crossin et al. 2008). Taken together, my results suggest that female sockeye salmon are at greater risk of en route mortality following exhaustive exercise and metabolic stress, particularly when exposed to challenging migration conditions.

I found that the maximum temperature fish experienced below Seton Dam had a significant effect on passage. During the study period, Seton River water temperatures were often above the thermal optima for the study population (i.e., > 17.5°C; Lee et al.
Corroborating my findings, telemetry research on sockeye salmon elsewhere has found similar high-temperature-related mortality trends (Naughton et al. 2005, Keefer et al. 2008, Martins et al. 2012). Exposure to supra-optimal water temperatures while swimming at critical speeds can decrease aerobic and cardiac scopes, increase EPOC and prolong recovery times in Fraser River sockeye salmon (Lee et al. 2003a,b, Farrell et al. 2008, Eliason et al. 2013). In the current study, Gates Creek sockeye salmon were exposed to near-lethal temperatures while performing exhaustive exercise, which could have resulted in cardiorespiratory collapse in the dam tailrace due to an insufficient scope for heart rate (Eliason et al. 2013). Indeed, 90% of the fish that failed to pass the dam experienced water temperatures near the species’ lethal limit (24°C; Servizi and Jensen 1977). Closures to the power canal during the study period prevented the release of hypolimnetic water from Seton Lake, resulting in 4°C increases in Seton River water temperatures. Managers should recognize the potential ecological consequences of such an operational change, especially considering female sockeye salmon are particularly sensitive to elevated water temperatures during their reproductive migration (Crossin et al. 2008, Martins et al. 2012).

Fish capture location had an effect on anaerobic recruitment in areas of high flow and the ability of migrants to reach natal sites. More specifically, fish that had previously passed Seton Dam (i.e., fishway non-naïve individuals) were much less likely to pass a second time and reach spawning grounds. Past telemetry studies on Gates Creek sockeye salmon were logistically constrained to capture study subjects from the top pool of the fishway, selecting for individuals that had previously demonstrated the ability to locate, enter and ascend the passage structure (Roscoe et al. 2011, Burnett et al. 2013a). Fishway
efficiency estimates from these previous studies were consistent among years, whereby sockeye salmon appeared to have greater difficulty locating and entering the vertical-slot fishway compared to passing it (i.e., attraction efficiency < passage efficiency).

Telemetry data from the present study suggests that fishway non-naïve individuals were more inclined to delay in the low flows of the radial gate and siphon spillways. I attribute the apparent lack of motivation in fishway non-naïve fish to traverse the high flows from siphon #1 to the EPOC required after their successful negotiation of the tailrace prior to capture. Indeed, the delayed mortality of fishway non-naïve Gates Creek sockeye salmon in the lakes upstream of Seton Dam is likely due to the higher EPOC and long recovery times required following two successful dam passages (Roscoe et al. 2011, Figure 3.5D).

Given the applicability and ecological significance of fishway efficiency estimates, I emphasize that researchers must consider a variety of biotic (e.g., study species motivation to migrate, timing of study) and abiotic factors (e.g., capture and tagging method, capture and release location) in their study design and analyses (Cooke and Hinch 2013). By tagging and releasing fishway naïve and non-naïve sockeye salmon under the same environmental conditions, my results highlight the importance of considering capture location when conducting fish passage research to avoid costly management decisions and biological consequences.

I do not rule out a probable infectious disease component to the inability of sockeye salmon to traverse the Seton Dam tailrace and complete their freshwater migration. Pacific salmon exposed to high water temperatures can become immunocompromised and more susceptible to parasites that exhibit accelerated rates of development in warm conditions (Miller et al. In press). Further, ill health has been
shown to impair the swimming performance of sockeye salmon (Tierney and Farrell 2004) and lead to eventual mortality (Crossin et al. 2008). I monitored the health of dead and moribund Gates Creek sockeye salmon (e.g., internal and external macroscopic injuries, presence of internal parasites) that failed to pass the dam and subsequently collected on the upstream side of the fish fence. Abundant parasitic nematodes (Anisakis spp) were present in the coelomic cavity of 60% (34/57) of the fish sampled, including a single acoustic-tagged female that was found moribund < 24 hrs post-release. I am unaware of any study to date that has investigated whether infectious disease plays a role in fish passage. My anecdotal findings emphasize the need for future research to advance our understanding of the contributing factors influencing migration success in anadromous fishes.

Models used to predict swimming speed and $MO_2$ from RMS acceleration were not as effective at high water velocities. Further, the sampling frequency of the acoustic accelerometer transmitter (10 Hz) may not have been high enough to capture the rapid successive tailbeats often exhibited in burst-and-coast swimming (Wilson et al. 2013). To account for this, I used the model to predict $MO_2$ for swimming speeds < $U_{crit}$ and assumed that maximum oxygen consumption (i.e., $MO_2$ max) occurred at swimming speeds ≥ $U_{crit}$. Thus, the swimming speeds, $MO_2$ and EPOC values presented herein may be underestimated. Regardless, my study clearly shows that dam passage success and post-passage survival are correlated with anaerobic muscle recruitment.

Pacific salmon must recruit white muscle fibers to successfully navigate areas of difficult passage (Hinch and Bratty 2000, Brown et al. 2006, Burnett et al. 2013a). Until now, there has been limited research examining the potential consequences of exhaustive
exercise on the spawning migrations of wild adult Pacific salmon. Human-made alterations to the Seton River’s flow and thermal regime had a direct impact on the ability of sockeye salmon to pass a diversion dam and complete their reproductive migration. Consistent with my predictions, I found that anaerobic swimming in high flows contributed to the inability of Gates Creek sockeye salmon to reach spawning grounds. This finding provides insight to the potential carryover effects of velocity barriers on other fish species. Moreover, it points for opportunities to refine the design and operation of fishway attraction flows. Future studies should focus on elucidating the specific physiological mechanisms by which anaerobiosis can lead to mortality, as well as the compounding effects of disease on survival. My findings also show the need for research that investigates whether dams can impose other carryover effects on wild aquatic animals (Caudill et al. 2007, O’Connor et al. 2014). I present the first field-based evidence that burst swimming by anadromous adult salmonids can result in delayed mortality, providing a foundation for future studies investigating the costs of swimming in wild aquatic animals.
Table 3.1. Model selection statistics for generalized linear models predicting (A) dam passage, (B) anaerobic recruitment in areas of high flow below Seton Dam, (C) tailrace crossings, and (D) the ability of Gates Creek sockeye salmon (*O. nerka*) to reach natal spawning streams.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model</th>
<th>log Lik</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Dam passage</td>
<td>Sex + maximum temperature + anaerobic recruitment</td>
<td>-12.97</td>
<td>37.20</td>
<td>0.00</td>
<td>0.12</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>Sex + maximum temperature</td>
<td>-14.29</td>
<td>37.40</td>
<td>0.21</td>
<td>0.10</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>Sex + anaerobic recruitment</td>
<td>-14.30</td>
<td>37.40</td>
<td>0.23</td>
<td>0.10</td>
<td>45</td>
</tr>
<tr>
<td>(B) Anaerobic recruitment</td>
<td>Sex + siphon #1 + tailrace crossings</td>
<td>-212.02</td>
<td>437.80</td>
<td>0.00</td>
<td>0.48</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>Sex + siphon #1 + tailrace crossings + maximum temperature</td>
<td>-212.01</td>
<td>440.50</td>
<td>2.63</td>
<td>0.13</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>Sex + siphon #1 + tailrace crossings + tailrace delay</td>
<td>-212.02</td>
<td>440.50</td>
<td>2.64</td>
<td>0.13</td>
<td>46</td>
</tr>
<tr>
<td>(C) Tailrace crossings</td>
<td>Sex + anaerobic recruitment</td>
<td>-62.51</td>
<td>133.80</td>
<td>0.00</td>
<td>0.14</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Sex + anaerobic recruitment + tailrace delay</td>
<td>-61.67</td>
<td>134.60</td>
<td>0.77</td>
<td>0.10</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Sex + tailrace delay</td>
<td>-62.95</td>
<td>134.70</td>
<td>0.89</td>
<td>0.09</td>
<td>22</td>
</tr>
<tr>
<td>(D) Reach natal sites</td>
<td>Anaerobic recruitment + siphon #1</td>
<td>-18.73</td>
<td>46.50</td>
<td>0.00</td>
<td>0.14</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Anaerobic recruitment + siphon #1 + tailrace crossings</td>
<td>-17.65</td>
<td>46.90</td>
<td>0.38</td>
<td>0.11</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Anaerobic recruitment + siphon #1 + sex</td>
<td>-18.07</td>
<td>47.70</td>
<td>1.23</td>
<td>0.07</td>
<td>39</td>
</tr>
</tbody>
</table>

ΔAIC<sub>c</sub> represents the difference in AIC<sub>c</sub> values between model i and the top-ranked candidate model. Models are ranked from lowest to highest ΔAIC<sub>c</sub> (highest to lowest w<sub>i</sub>); all top-ranked models had a ΔAIC<sub>c</sub> of zero. D represents the percentage of deviance explained by a GLM. Capture location was included in all models as a fixed factor.
Figure 3.1. Map of the Seton-Anderson watershed in southwestern British Columbia, Canada, the natal spawning streams of Gates Creek sockeye salmon (*O. nerka*), and the location of Seton Dam and vertical-slot fishway (inset). Dotted trace within the inset represents the high flows from the FWRG and siphon #1. A: acoustic receiver. P: pass-through passive integrated transponder (PIT) antenna. ★: release site for fishway non-naïve individuals.
Figure 3.2. Beanplot (mean: black horizontal line) comparing the swimming speed (BL s$^{-1}$) of male (black) and female (grey) Gates Creek sockeye salmon (O. nerka) in the radial gate spillway, surrounding the fishway entrance, within the fishway and dam forebay.

Shaded curved polygons (beans) depict the estimated density of the distribution of individual swimming speed values (white horizontal lines). Optimal ($U_{opt}$; 1.0 BL s$^{-1}$) and critical ($U_{crit}$; 2.1 BL s$^{-1}$) swimming speeds are shown as dotted horizontal lines; the swimming speed at which anaerobic muscle fibers start to be recruited (80% $U_{crit}$) is also shown. Sample sizes ($n$) are presented below each bean, and lowercase letters represent significant differences ($p < 0.05$) from one-way analysis of variance (ANOVA) and Tukey post hoc tests.
Figure 3.3. Predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing Seton Dam (A; \(n = 54\)) and reaching natal spawning streams (B; \(n = 44\)) visualized by fitting a logistic regression to the anaerobic recruitment of successful and unsuccessful migrants.
Figure 3.4. Predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing Seton Dam visualized by fitting a logistic regression to the maximum Seton River temperature successful and unsuccessful fish experienced while directly below the dam.
Figure 3.5. Model-averaged standardized coefficients for models describing (A) dam passage, (B) anaerobic recruitment in areas of high flow below Seton Dam, (C) tailrace crossings and (D) the ability of Gates Creek sockeye salmon (*O. nerka*) to reach natal spawning streams. Coefficients have been highlighted in grey if the error bars (represent 95% confidence intervals) do not cross zero. Capture location was included in all models as a fixed factor and has been included to show its relative effect on the response variables. Note the different secondary y-axes scales.
CHAPTER 4: General Discussion

This thesis aimed to improve our understanding of the mechanisms that contribute to a delayed (or failed) reproductive migration in Pacific salmon. Sockeye salmon were used as a model to investigate the immediate and delayed effects of a diversion dam on swimming activity, behaviour and survival. In Chapter 2, adult sockeye salmon were gastrically tagged with acoustic accelerometer transmitters to monitor individual-level energetic and behavioural responses to dam-altered flow regimes. Model selection analyses were used to investigate whether the hydraulic experience of migrants in the dam tailrace could predict their ability to locate, enter and ascend a vertical-slot fishway. Building on this framework, Chapter 3 explored the potential for high-flow-induced burst swimming behaviours to predict the post dam passage, en route mortality of sockeye salmon. I discuss how these findings advance our understanding of the migration ecology of anadromous fishes, and inform future conservation and management action. Research presented herein is the first to apply novel accelerometer tagging technologies to fish-passage research in the hopes of understanding the linkages between management strategies (i.e., dam operations) and biological responses.

Findings and implications

Hydropower development affects nearly 60% of the world’s largest river systems (Nilsson et al. 2005). In the Pacific Northwest, Pacific salmon-bearing watersheds have become increasingly regulated through the construction of dams, with little known as to the ecological impact of these physical barriers (Waples et al. 2007). Several studies have shown that alterations to the total dam-spill discharge of a facility can increase delay and
decrease passage success at individual dams and through multi-dam reaches (Caudill et al. 2006, 2007). Using this broad-scale hydraulic approach at the Seton Dam, Pon et al. (2009a) and Roscoe et al. (2011) were unable to propose operational strategies that optimize migratory conditions for sockeye salmon. While this may indicate that there are other factors to consider at Seton Dam, I suspect that the lack of conclusive evidence is an artifact of low statistical power. Regardless, Pon et al. (2009a) suggested that future studies at this facility should implement more thorough hydraulic analyses in the hopes of providing managers with accurate and meaningful recommendations.

In Chapter 2, I found that Gates Creek sockeye salmon exhibited habitat-specific and flow-dependent swimming activity patterns in the Seton Dam tailrace. Anaerobically-fuelled locomotion was needed to negotiate the turbulent flows surrounding the fishway entrance; females appeared to rely on burst swimming behaviours to a greater extent compared to males. Releasing excess water from the radial gate spillway of the dam lead to two notable and adverse biological responses: attraction efficiency of a vertical-slot fishway decreased by 90% and delay in the tailrace increased by 2 h. Certainly, there may not be other approaches that release excess water in a manner that does not conflict with other water-use goals for environmental protection, flood control and irrigation. Nonetheless, this finding confirms those of Andrew and Geen (1958) and should provide managers with the information needed to explore alternative methods for spilling excess water. Until now, little has been known about what constitutes a ‘biologically significant delay’ below the Seton Dam in which there are individual-level fitness and/or survival consequences (Fretwell 1989). Delays longer than 6 h resulted in significant reductions in the probability of migrants to pass the facility, perhaps because of prolonged exposure to
challenging migration conditions (e.g., flow and temperature) in the dam tailrace. Of course, this finding may be applicable to other regulated watersheds where migrants are known to spend several days downstream of a barrier prior to eventual pass or fallback (Bjornn and Peery 1992, Geist et al. 2000, Caudill et al. 2007). Here I emphasize that fish-passage problems are inherently complex, requiring the use of more detailed flow data in individual-based, model selection analyses. Certainly, this is a particularly useful approach for studies with low statistical power due to relatively small sample sizes.

Caudill et al. (2007) make a call for research focusing on the indirect effects of dam facilities, including delayed or carryover effects as a result of being exposed to these areas of difficult passage. I set out to address two fundamental questions in Chapter 3 that arose as knowledge gaps (in Chapter 2), both of which are related to the commentary by Caudill et al. (2007): (1) Are there delayed, post dam passage consequences for migrants that elicit burst swimming behaviours in turbulent flows surrounding the fishway entrance?, and (2) Why do female sockeye salmon suffer exceptionally high en route mortality in the lakes upstream of Seton Dam? Using the approaches developed in Chapter 2, I intended to address these questions to provide a more holistic understanding of the influence of altered flow regimes on the swimming activity, behaviour and survival of sockeye salmon.

Consistent with findings in Chapter 2, I found that anaerobic metabolic pathways were required to negotiate high flows surrounding the fishway entrance, but contributed to the failure of sockeye salmon to reach spawning grounds as a result of high levels of EPOC. Siphon #1 is routinely open throughout the sockeye salmon migration, as it is believed to improve the attraction of individuals towards the fishway entrance (Andrew
and Geen 1958). My results indicate that the high-velocity flows from siphon #1 can impose carryover effects on the physiology and survival of migrants, a finding that has implications for the conservation of endangered Gates Creek sockeye salmon (Rand 2011). I attribute the exceptionally high post dam passage, *en route* mortality of female sockeye salmon to elevated levels of glycolytic-fuelled locomotion in the dam tailrace (Roscoe *et al.* 2011). It is widely recognized that the operations and hydrodynamics downstream of dams are site-specific, often limiting managers to apply the results from a fish-passage study to the facility in question. However, the findings within Chapter 3 have more general implications for the design and operation of fishway attraction flows worldwide. One would expect similar results in other fish species that encounter velocity barriers (e.g., rapids, high-gradient reaches, dams, weirs). Establishing an operational strategy that reduces the supercritical flows around a fishway without compromising attraction efficiency will prove to be a challenge for managers. Preventing the release of hypolimnetic water from Seton Lake exposed migrants to supra-optimal, near-lethal water temperatures that inevitably compromised their migratory ability. Managers need to acknowledge that dam activity affects the thermal regime of downstream habitat and can result in sublethal and lethal physiological consequences for ectothermic species (Preece and Jones 2002). Indeed, this is relevant for regulated watersheds that support Pacific salmon, as females are particularly sensitive to high water temperatures during their reproductive migration (Crossin *et al.* 2008, Martins *et al.* 2012). Taken together, these results are the first to reveal the delayed consequences of burst swimming on the survival of migrating adult sockeye salmon.
Future directions

Understanding individual-level energetic and behavioural responses to altered flow and thermal regimes is critical to responsible fisheries management. Of course, this is particularly true for watersheds that will continue to undergo changes in hydroclimatology (e.g., Fraser River: Rand et al. 2006, Hague et al. 2011) and connectivity in the future (e.g., Andean Amazon: Finer and Jenkins 2012, Sutherland et al. 2013). In addition to the widespread need to maximize human access to water, it is equally important to understand the true ecological impact of dams before additional fragmentation occurs. Though this thesis has contributed valuable insight into the effects of physical barriers on the reproductive migration of sockeye salmon, it has also presented several worthwhile avenues of future research.

Acoustic accelerometer transmitters proved to be a valuable tool for assessing the energy-use and behaviour of sockeye salmon in dam tailraces and within fish passage structures. In regulated watersheds, managers can use the data from these devices to develop management strategies that optimize migratory conditions for aquatic species. Information relating to how wild aquatic animals cope with challenging migration conditions can also help develop superior forecast models. I emphasize that accelerometer transmitters can address a diversity of research questions on a variety of taxonomic groups, particularly for species with known ranges and in field environments that are not conducive to retrieving biologgers. Accelerometer transmitters currently possess low sampling frequencies to prolong battery life, highlighting the need for technological advancements in the power source of these tags. With higher sampling
frequencies, these devices will yield more accurate estimates of energy-use and cost of transport in wild animals.

Cooke and Hinch (2013) reason that a variety of biotic and abiotic factors must be considered in the design and analyses of a fish-passage study. Indeed, applying erroneous fishway efficiency estimates to the operation of a facility can lead to costly management decisions, and socio-economic and ecological consequences. While I show the importance of considering fish capture location, I believe there is merit in explicitly testing the relative importance of the other factors outlined by Cooke and Hinch (2013). For example, the findings presented in Chapter 3 have revealed the need to explore the role of infectious disease in fish passage. Using novel genomics approaches (Miller et al. 2011), future research should investigate the potential for disease to impair the migratory ability of fishes that encounter velocity barriers (Tierney and Farrell 2004). Research that takes into account these various factors will provide regulators with the information required to make responsible conservation and management decisions.

I acknowledge that there is likely a trade-off between attraction efficiency and the high flows designed to attract fish to a passage structure. However, the findings within this thesis demonstrate the need to develop an operational strategy that decreases attraction efficiency and the supercritical flows around a fishway in a way that optimizes net survival to spawning grounds. To do this, future research will likely have to adopt an experimental or adaptive management approach, releasing water from different conveyance structures and monitoring the subsequent biological response(s). Certainly our current understanding of the impact of flow releases at Seton Dam (i.e., siphon #1,
radial gate spillway) will help guide the planning of future flow manipulations at this facility and in regulated watersheds elsewhere.

Related to this thesis, Cook et al. (2007) and Andersson et al. (2012) show the validity of using an Acoustic Doppler Current Profiler (ADCP) to characterize the three-dimensional flow patterns in dam tailraces. Cook et al. (2007) discovered a gyre in the tailrace of the John Day Dam (Columbia River, USA), a structure that delays the upstream and downstream movements of migratory fishes. More recently, Andersson et al. (2012) used ADCP field measurements to validate computational fluid dynamic (CFD) simulations of attraction flows adjacent to a fishway in the Ume River, Sweden. Through an integrative use of CFD and ADCP, the authors were able to recommend a superior attraction flow strategy that took into account the intensity of turbulence near the fishway entrance. Aside from these two examples, I am unaware of other fish-passage studies that have adopted these numerical approaches. Future research that can successfully link accelerometry data to ADCP velocity measurements will provide a more holistic understanding of the subsurface flow features that energetically and behaviourally challenge wild fishes. Applying these methods to the field of ecohydrology will start to bridge the gap between biology and engineering, and will vastly improve our ability to provide effective passage solutions to watersheds that are impacted by hydropower development.
LITERATURE CITED


Burnett N.J., K.M. Stamplecoskie, J.D. Thiem, and S.J. Cooke. 2013b. Comparison of detection efficiency among three sizes of half duplex passive integrated


River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality. Canadian Journal of Fisheries and Aquatic Sciences 64:979–995.


Cooke S.J., and S.G. Hinch. 2013. Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and


Sutherland W.J., S. Bardsley, M. Clout, M.H. Depledge, L.V. Dicks, L. Fellman, E. Fleishman, D.W. Gibbons, B. Keim, F. Lickorish, C. Margerison, K.A. Monk,


