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

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

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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

$MO_{2\ max}$: Maximum oxygen consumption

BL: Body length

FL: Fork length

GLM: Generalized linear model

AIC_c: Corrected Akaike information criterion

w_i: 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.

CHAPTER 2: Alterations to dam-spill discharge influence sex-specific activity, behaviour and passage success of migrating adult sockeye salmon. Burnett N.J., S.G. Hinch, M.R. Donaldson, N.B. Furey, D.A. Patterson, D.W. Roscoe, and S.J. Cooke.

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.*

CHAPTER 3: Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. Burnett N.J., S.G. Hinch, D.C. Braun, M.T. Casselman, C.T. Middleton, S.M. Wilson, and S.J. Cooke.

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_{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_{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 difficultly 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): $48.1 \pm 2.4 \times 10^{-2}$ m^3 s^{-1}) in which the FWRG (1.7 m^3 s^{-1}) and siphons #1 and #3 were open ($45.4 \pm 2.8 \times 10^{-3}$ 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 ($13.7 \pm 7.7 \times 10^{-3}$ m^3 s^{-1}) and siphon #1 were open ($20.0 \pm 1.5 \times 10^{-2}$

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

$$M\text{O}_2 = [2.81 + (0.89 \times \text{RMS acceleration}) + (0.05 \times \text{Water temperature (°C)}) - (0.03 \times \text{FL}) + 1.21 - (\text{RMS acceleration} \times 0.32)]^2 \tag{1}$$

White muscle fibers start to be recruited at ~ 80% of the critical swimming speed (U_{crit}) in migratory Pacific salmonids (Burgetz *et al*. 1998). Swimming speeds in the present study that were less than 80% U_{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_{crit} can be estimated using Equation 1. Swimming speeds from 80 to 100% U_{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_{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 $\geq U_{crit}$ was assumed to be the maximum oxygen consumption ($MO_{2\ max}$) 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 (AIC$_c$) 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 AIC$_c$ 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 α = 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 ± 1.40 m^3 s^{-1}) from the radial gate spillway compared with successful fish (0.64 ± 0.45 m^3 s^{-1}; Mann–Whitney U-test W = 241, p = 5.3 × 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 × 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 (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 ~ 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 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 ± 4.1 h; range: 0.5 – 114.8 h) than males (14.6 ± 3.2 h; range: 1.0 – 48.5 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 ± 0.3 times) and female (1.1 ± 0.1 times) Gates Creek sockeye salmon (Mann–Whitney U-test W = 479, p = 0.18), males exhibited a larger range (range: 0 – 5 times) in the number of tailrace crossings compared with females (range: 0 – 3 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 ($1.7 \pm 0.5\%$) and female sockeye salmon ($14.4 \pm 5.2\%$), 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-

26

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_{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^{-1}; ± SE) of successful and unsuccessful Gates Creek sockeye salmon (*O. nerka*) at the release site, radial gate spillway and fishway entrance area.

Fate	Location		
	Release site	Radial gate spillway	Fishway entrance area
Successful	1.4 ± 0.1 (6)^{ab}	1.1 ± 0.1 (11)^{a}	1.7 ± 0.1 (8)^{b}
Unsuccessful	1.1 ± 0.1 (3)^{ab}	1.1 ± 0.1 (4)^{a}	1.7 ± 0.5 (2)^{ab}

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*).

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

Models are ranked from lowest to highest ΔAIC_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_2 kg^{-1} min^{-1}; $\pm$ 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*).

Location	Males	Females
Release site	10.9 ± 1.0 (2)	12.8 ± 0.5 (7)
Radial gate spillway	10.3 ± 0.5 (4)	11.8 ± 0.4 (11)
Fishway entrance area	13.5 ± 0.4 (3)	14.3 ± 0.2 (7)
Forebay	12.3 ± 0.9 (3)	12.6 ± 0.1 (6)
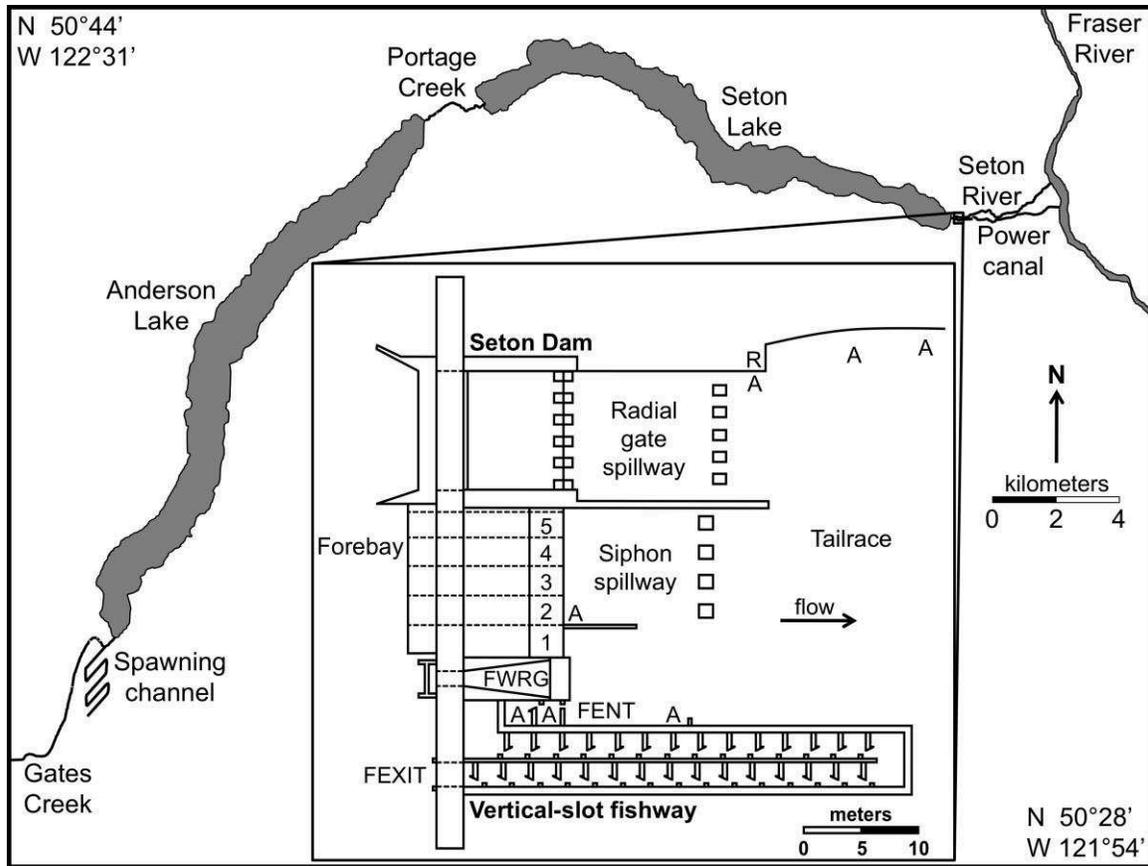
Figure 2.1. A map depicting the Seton-Anderson watershed in southwestern British Columbia, Canada, the terminal spawning grounds for Gates Creek sockeye salmon (*O. nerka*), as well as the location of the Seton Dam and fishway (inset). Minimum flows at the Seton facility are released through the fish 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.
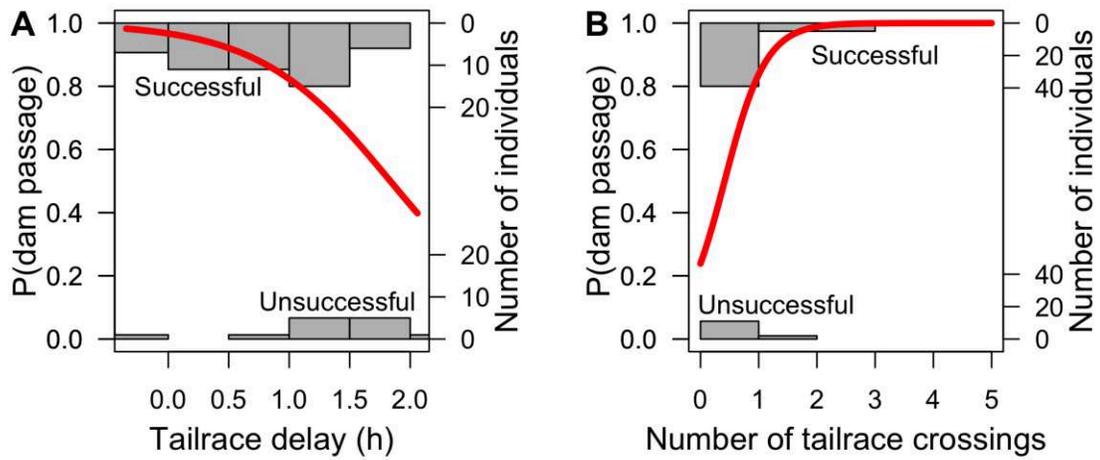
Figure 2.2. Logistic regression fitted to the tailrace delay (log-transformed; A) and number of tailrace crossings (B) of successful and unsuccessful migrants. The red line shows the predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing the Seton Dam.
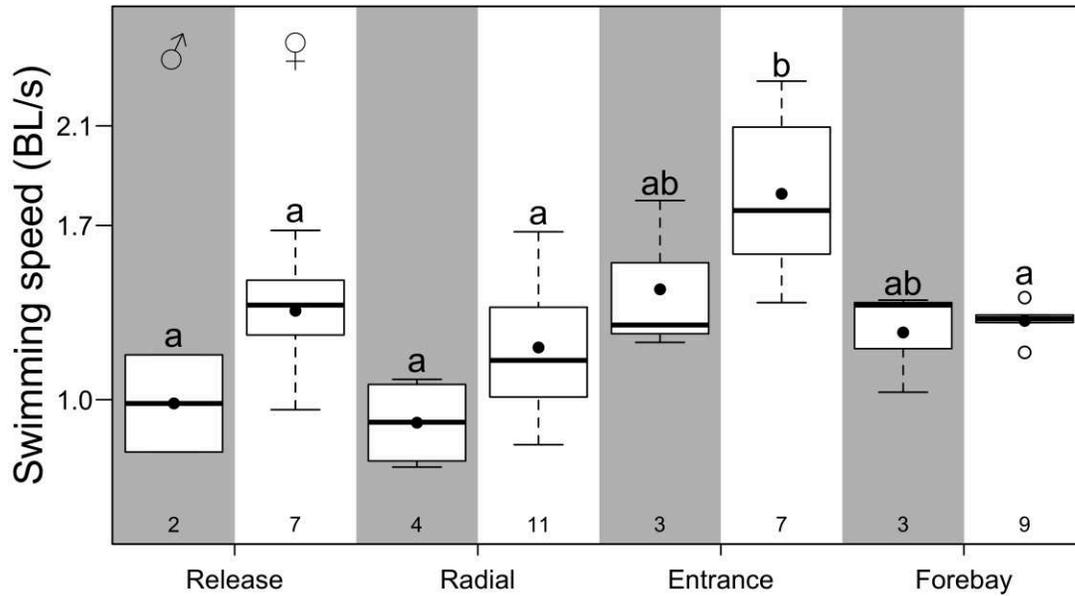
Figure 2.3. Box-and-whisker plot (median: solid line, mean: closed circle, extreme value: open circle, 25% and 75% quartiles) comparing the swimming speed (BL s^{-1}) of male (shaded grey) and female (white) Gates Creek sockeye salmon (*O. nerka*) at the release site, radial spillway, fishway entrance area and forebay. Optimal (~ 1.0 BL s^{-1}) and critical (U_{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.[2]

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_{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_{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:

$$M\text{O}_2 = [2.81 + (0.89 \times \text{RMS acceleration}) + (0.05 \times \text{Water temperature (°C)}) - (0.03 \times \text{FL}) + 1.21 - (\text{RMS acceleration} \times 0.32)]^2$$

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 m^2; 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 m^2). 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 ($m^3 s^{-1}$) 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 AIC_c (for small sample sizes) to determine the most parsimonious models. Models were further analyzed using AIC_c weights (w_i), 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.*

2003a). 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 $\geq U_{crit}$. 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.

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

ΔAIC$_c$ represents the difference in AIC$_c$ values between model i and the top-ranked candidate model. Models are ranked from lowest to highest ΔAIC$_c$ (highest to lowest w_i); all top-ranked models had a ΔAIC$_c$ of zero. *D* represents the percentage of deviance explained by a GLM. Capture location was included in all models as a fixed factor.
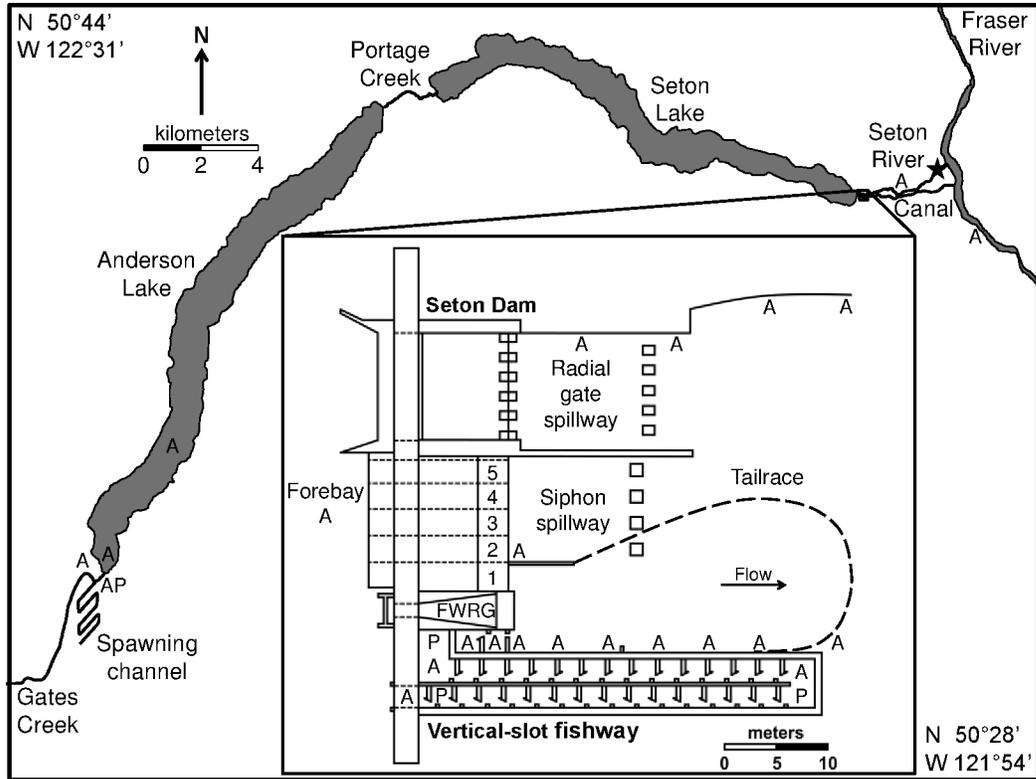
Figure 3.1. Map of the Seton-Anderson watershed in southwestern British Columbia, Canada, the natal spawning streams of Gates Creek sockeye salmon (*O. nerka*), and the location of Seton Dam and vertical-slot fishway (inset). Dotted trace within the inset represents the high flows from the FWRG and siphon #1. A: acoustic receiver. P: pass-through passive integrated transponder (PIT) antenna. ★: release site for fishway non-naïve individuals.
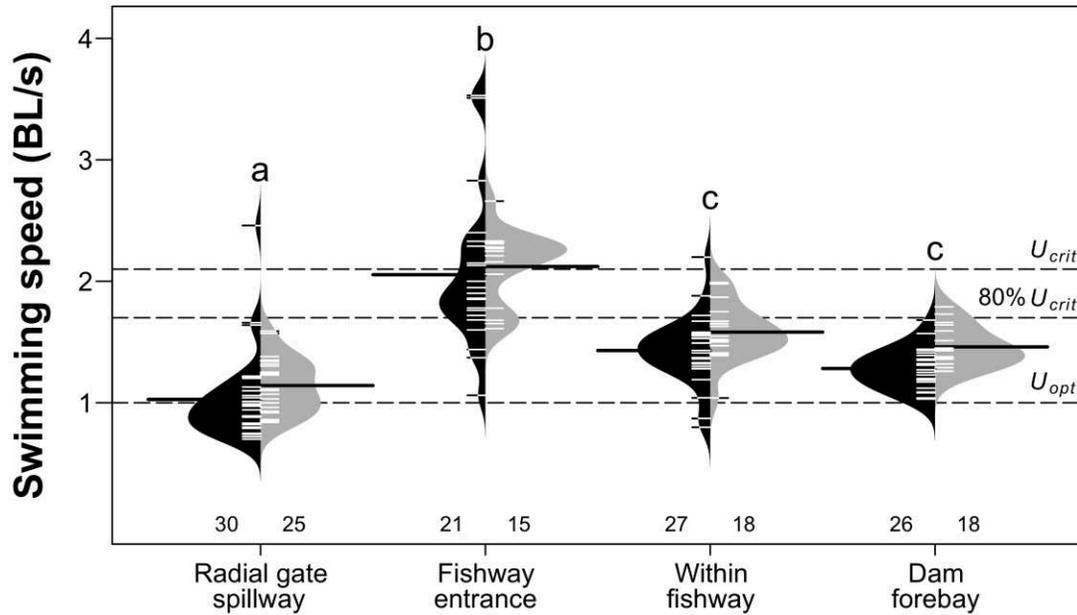
Figure 3.2. Beanplot (mean: black horizontal line) comparing the swimming speed (BL s^{-1}) of male (black) and female (grey) Gates Creek sockeye salmon (*O. nerka*) in the radial gate spillway, surrounding the fishway entrance, within the fishway and dam forebay. Shaded curved polygons (beans) depict 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.
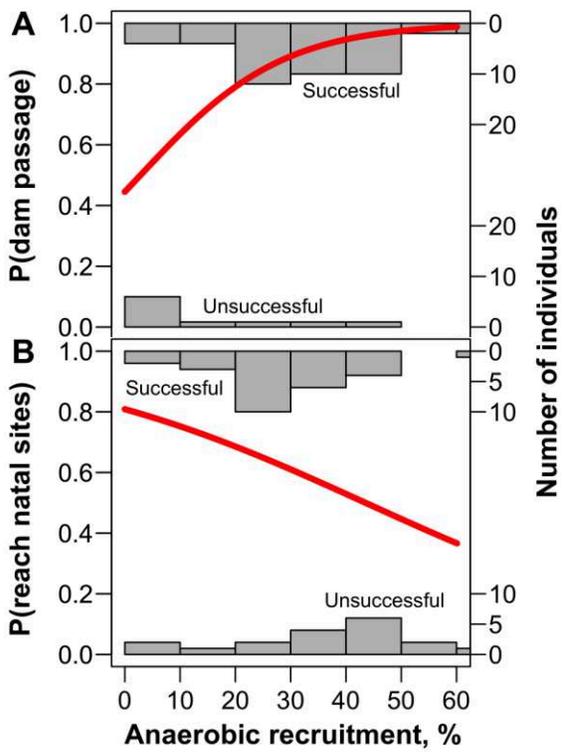
Figure 3.3. Predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing Seton Dam (A; $n = 54$) and reaching natal spawning streams (B; $n = 44$) visualized by fitting a logistic regression to the anaerobic recruitment of successful and unsuccessful migrants.
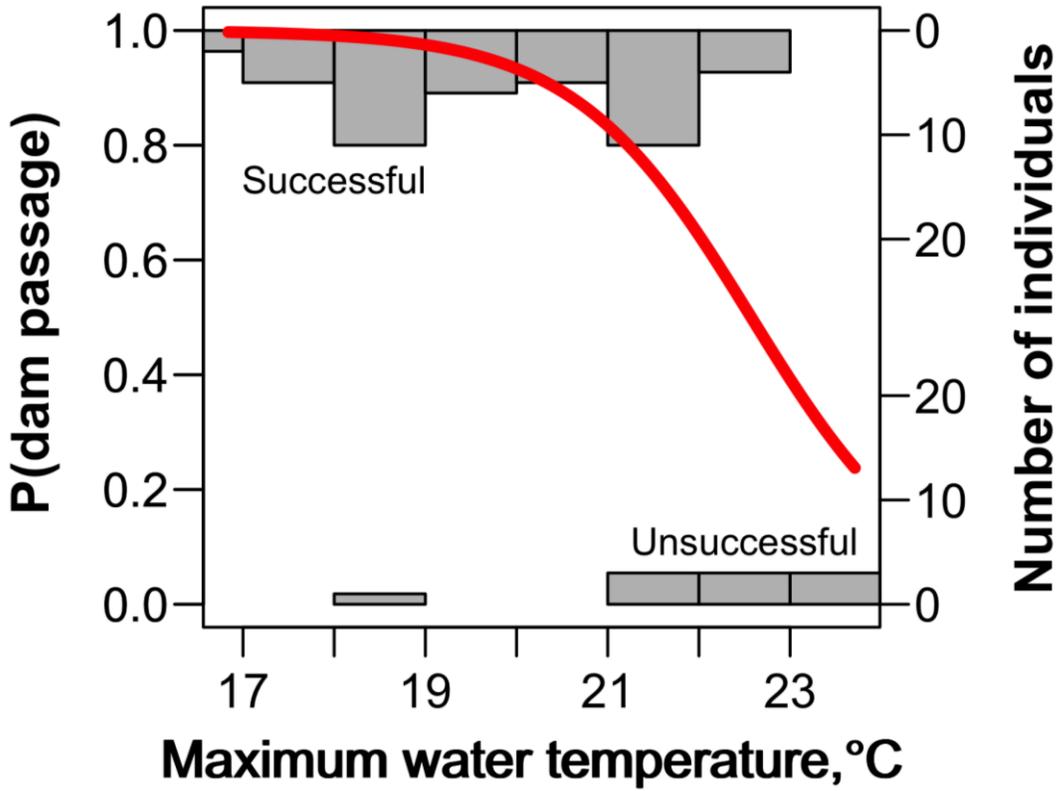
Figure 3.4. Predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing

Seton Dam visualized by fitting a logistic regression to the maximum Seton River

temperature successful and unsuccessful fish experienced while directly below the dam.
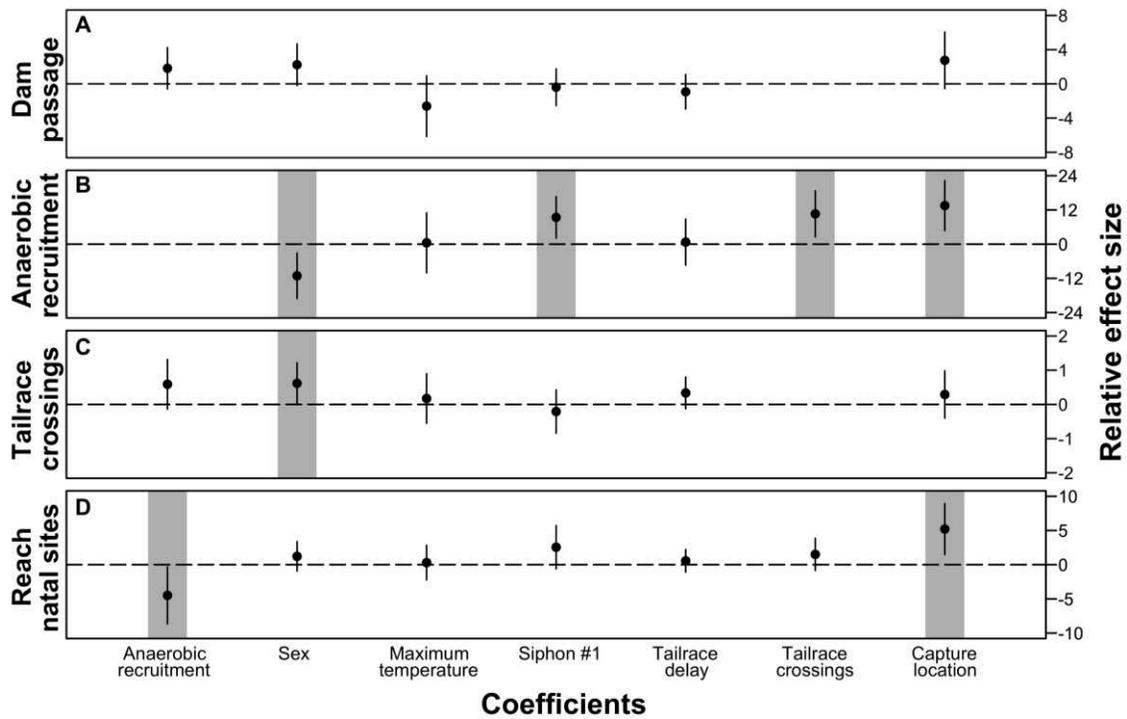
Figure 3.5. Model-averaged standardized coefficients for models describing (A) dam passage, (B) anaerobic recruitment in areas of high flow below Seton Dam, (C) tailrace crossings and (D) the ability of Gates Creek sockeye salmon (*O. nerka*) to reach natal spawning streams. Coefficients have been highlighted 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

Alabaster J.S. 1970. River flow and upstream movements and catch of migratory salmonids. Journal of Fish Biology 2:1–13.

Andersson A.G., D.E. Lindberg, E.M. Lindmark, K. Leonardsson, P. Andreasson, H. Lundqvist, and T.S. Lundström. 2012. A study of the location of the entrance of a fishway in a regulated river with CFD and ADCP. Modelling and Simulation in Engineering 2012:327929.

Andrew F.J., and G.H. Geen. 1958. Sockeye salmon and pink salmon investigations at the Seton Creek hydroelectric installation. Int. Pac. Salmon Fish. Comm. Prog. Rept. 4. 74 pp.

Barry T., and B. Kynard. 1986. Attraction of adult American shad to fish lifts at Holyoke Dam, Connecticut River. North American Journal of Fisheries Management 6:233–241.

Barton K. 2012. MuMIn: Multi-model inference. R package version 1.7.11. Available at http://CRAN.R-project.org/package=MuMIn.

Beacham T.D., M. Lapointe, J.R. Candy, K.M. Miller, and R.E. Withler. 2004. DNA in action: rapid application of DNA variation to sockeye salmon fisheries management. Conservation Genetics 5:411–416.

Beacham T.D., J.R. Candy, B. McIntosh, C. MacConnachie, A. Tabata, K. Kaukinen, L.T. Deng, K.M. Miller, R.E. Withler, and N. Varnavskaya. 2005. Estimation of stock composition and individual identification of sockeye salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. Transactions of the American Fisheries Society 134:1124–1146.

Bjornn T.C., and C.A. Peery. 1992. A review of literature related to movements of adult

    salmon and steelhead past dams and through reservoirs in the lower Snake

    River. U.S. Fish and Wildlife Service and Idaho Cooperative Fish and Wildlife

    Research Unit for U.S. Army Corps of Engineers, Walla Walla, Washington.

Black E.C. 1958. Hyperactivity as a lethal factor in fish. Journal of the Fisheries Board of

    Canada 15:573–586.

Black E.C., N.J. Bosomworth, and G.E. Docherty. 1966. Combined effect of starvation

    and severe exercise on glycogen metabolism of rainbow trout, *Salmo gairdneri*.

    Journal of the Fisheries Research Board of Canada 23:1461–1463.

Brett J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal

    relations in the physiology and freshwater ecology of sockeye salmon

    (*Oncorhynchus nerka*). American Zoologist 11:99–113.

Brett J.R. 1995. Energetics. Pages 3-68 *in* C Groot, L Margolis, WC Clarke, editors.

    Physiological ecology of Pacific salmon. UBC Press, Vancouver.

Brown R.S., D.R. Geist, and M.G. Mesa. 2006. Use of electromyogram telemetry to

    assess swimming activity of adult Chinook salmon migrating past a Columbia

    River dam. Transactions of the American Fisheries Society 135:281–287.

Brown R.S., C.P. Tatara, J.R. Stephenson, and B.A. Berejikian. 2007. Evaluation of a

    new coded electromyogram transmitter for studying swimming behavior and

    energetics in fish. North American Journal of Fisheries Management 27:765–

    772.

Brown D.D., R. Kays, M. Wikelski, R. Wilson, and A.P. Klimley. 2013. Observing the

    unwatchable through acceleration logging of animal behavior. Animal

Biotelemetry 1:20. DOI 10.1186/2050-3385-1-20.

Brownscombe J.W., J.D. Thiem, C. Hatry, F. Cull, C.R. Haak, A.J. Danylchuk, and S.J.

Cooke. 2013. Recovery bags reduce post-release impairments in locomotory

activity and behaviour of bonefish (*Albula* spp.) following exposure to angling-

related stressors. Journal of Experimental Marine Biology and Ecology

440:207–215.

Bunt C.M. 2001. Fishway entrance modifications enhance fish attraction. Fisheries

Management and Ecology 8:95–105.

Bunt C.M., C. Katopodis, and R.S. McKinley. 1999. Attraction and passage efficiency of

white suckers and smallmouth bass by two Denil fishways. North American

Journal of Fisheries Management 19:793-803.

Bunt C.M., T. Castro-Santos, and A. Haro. 2011. Performance of fish passage structures

at upstream barriers to migration. River Research and Applications 28:457–478.

Burgetz I.J., A. Rojas-Vargas, S.G. Hinch, and D.J. Randall. 1998. Initial recruitment of

anaerobic metabolism during submaximal swimming in rainbow trout

(*Oncorhynchus mykiss*). Journal of Experimental Biology 201:2711–2721.

Burnett N.J., S.G. Hinch, M.R. Donaldson, N.B. Furey, D.A. Patterson, D.W. Roscoe,

and S.J. Cooke. 2013a. Alterations to dam-spill discharge influence sex-specific

activity, behaviour and passage success of migrating adult sockeye salmon.

Ecohydrology DOI: 10.1002/eco.1440.

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

transponders using manual tracking and fixed antenna arrays. North American Journal of Fisheries Management 33:7-13.

Burnham K.P., and D.R. Anderson. 2002. Pp. 1–515 in Model selection and multimodel inference. Springer, New York.

Calcagno V. 2012. glmulti: Model selection and multimodel inference made easy. R package version 1.0.6. http://CRAN.R-project.org/package=glmulti.

Castro-Santos T. 2004. Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences 61:1602–1615.

Castro-Santos T. 2005. Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. Journal of Experimental Biology 208:421–432.

Castro-Santos T., A. Cotel, and P.W. Webb. 2009. Fishway evaluations for better bioengineering: an integrative approach. *In* Challenges for Diadromous Fishes in a Dynamic Global Environment, A. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffit, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, T.S. Avery, editors. American Fisheries Society Symposium, Bethesda, Maryland.

Caudill C.C., C.A. Peery, W.R. Daigle, M.A. Jepson, C.T. Boggs, T.C. Bjornn, and D. Joosten. 2006. Adult Chinook salmon and steelhead dam passage behaviour in response to manipulated discharge through spillways at Bonneville Dam. Report for US Army Corps of Engineers, Portland District, Portland, Oregon.

Caudill C.C., W.R. Daigle, M.L. Keefer, C.T. Boggs, M.A. Jepson, B.J. Burke, R.W. Zabel, T.C. Bjornn, and C.A. Peery. 2007. Slow dam passage in adult Columbia

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.

Clay C.H. 1995. Design of fishways and other fish facilities (2nd Edition). Lewis
Publishers: Boca Raton, Florida.

Cook C.B., M.C. Richmond, and J.A. Serkowski. 2007. Observations of velocity
conditions near a hydroelectric turbine draft tube exit using ADCP
measurements. Flow Measurement and Instrumentation 18:148–155.

Cooke S.J., S.G. Hinch, A.P. Farrell, M.F. Lapointe, S.R.M. Jones, J.S. Macdonald, D.A.
Patterson, M.C. Healey, and G. Van Der Kraak. 2004a. Abnormal migration
timing and high en route mortality of sockeye salmon in the Fraser River, British
Columbia. Fisheries 29:22–33.

Cooke S.J., E.B. Thorstad, and S.G. Hinch. 2004b. Activity and energetics of
free- swimming fish: insights from electromyogram telemetry. Fish and
Fisheries 5:21–52.

Cooke S.J., G.T. Crossin, D.A. Patterson, K.K. English, S.G. Hinch, J.L. Young, R.
Alexander, M.C. Healey, G. Van Der Kraak, and A.P. Farrell. 2005. Coupling
non-invasive physiological and energetic assessments with telemetry to
understand inter-individual variation in behaviour and survivorship of sockeye
salmon: development and validation of a technique. Journal of Fish Biology
67:1342–1358.

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

practice. Ecological Engineering 58:123–132.

Crossin G.T., S.G. Hinch, A.P. Farrell, D.A. Higgs, and M.C. Healey. 2004. Somatic energy of sockeye salmon at the onset of upriver migration: a comparison among ocean climate regimes. Fisheries Oceanography 29: 22–33.

Crossin G.T., and S.G. Hinch. 2005. A nonlethal method for assessing the somatic energy content of freely migrating adult Pacific salmon. Transactions of the American Fisheries Society 134:184–191.

Crossin G.T., S.G. Hinch, S.J. Cooke, D.W. Welch, D.A. Patterson, S.R.M. Jones, A.G. Lotto, R.A. Leggatt, M.T. Mathes, J.M. Shrimpton, G. Van der Kraak, and A.P. Farrell. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Canadian Journal of Zoology 86:127–140.

Dingle H. 1996. Migration: the biology of life on the move. New York: Oxford University Press.

Eliason E.J., T.D. Clark, M.J. Hague, L.M. Hanson, Z.S. Gallagher, K.M. Jeffries, M.K. Gale, D.A. Patterson, S.G. Hinch, and A.P. Farrell. 2011. Differences in thermal tolerance among sockeye salmon populations. Science 332:109–112.

Eliason E.J., T.D. Clark, S.G. Hinch, and A.P. Farrell. 2013. Cardiorespiratory collapse at high temperature in swimming adult sockeye salmon. Conservation Physiology 1:10.1093/conphys/cot008.

Enders E.C., C.J. Pennell, R.K. Booth, and D.A. Scruton. 2008 Energetics related to upstream migration of Atlantic salmon in vertical slot fishways. Canadian Technical Report of Fisheries and Aquatic Sciences 2800:v+22p.

Farrell A.P., S.G. Hinch, S.J. Cooke, D.A. Patterson, G.T. Crossin, M. Lapointe, and M.T. Mathes. 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiological and Biochemical Zoology 81:697–708.

Finer M., and C.N. Jenkins. 2012. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. PloS ONE 7:e35126.

Fretwell M.R. 1989. Homing behaviour of adult sockeye salmon in response to a hydroelectric diversion of homestream waters at Seton Creek. Bulletin No. XXV. International Pacific Salmon Fisheries Commission, Vancouver, BC, 38pp.

Geist D.R., C.S. Abernethy, S.L. Blanton, and V.I. Cullinan. 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall Chinook salmon. Transactions of the American Fisheries Society 129:126–135.

Geist D.R., R.S. Brown, V.I. Cullinan, M.G. Mesa, S.P. Vanderkooi, and C.A. McKinstry. 2003. Relationships between metabolic rate, muscle electromyograms and swim performance of adult Chinook salmon. Journal of Fish Biology 63:970–989.

Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gilhousen P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. Bulletin XXVI. International Pacific Salmon Fisheries Commission, Vancouver, BC, 62pp.

Gleiss A.C., J.J. Dale, K.N. Holland, and R.P. Wilson. 2010. Accelerating estimates of

activity-specific metabolic rate in fishes: testing the applicability of acceleration data-loggers. Journal of Experimental Marine Biology and Ecology 385:85–91.

Gowans A.R.D., J.D. Armstrong, and I.G. Priede. 1999. Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. Journal of Fish Biology 54:713–726.

Grueber C.E., S. Nakagawa, R.J. Laws, and I.G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Hague M.J., M.R. Ferrari, J.R. Miller, D.A. Patterson, G.L. Russells, A.P. Farrell, and S.G. Hinch. 2011. Modelling the future hydroclimatology of the lower Fraser River and its impacts on the spawning migration survival of sockeye salmon. Global Change Biology 17:87–98.

Haro A., T. Castro-Santos, J. Noreika, and M. Odeh. 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences 61:1590–1601.

Hasler C.T., B. Mossop, D.A. Patterson, S.G. Hinch, and S.J. Cooke. 2012. Swimming activity of migrating Chinook salmon in a regulated river. Aquatic Biology 17:47–56.

Hinch S.G., and P.S. Rand. 1998. Swimming speeds and energy-use of upriver migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. Canadian Journal of Fisheries and Aquatic Sciences 55:1821–1831.

Hinch S.G., and P.S. Rand. 2000. Optimal swimming speeds and forward assisted

    propulsion: energy conserving behaviours of upriver-migrating salmon.

    Canadian Journal of Fisheries and Aquatic Sciences 57:2470–2478.

Hinch S.G., and J. Bratty. 2000. Effects of swimming speed and activity pattern on

    success of adult sockeye salmon migration through an area of difficult passage.

    Transactions of the American Fisheries Society 129:598–606.

Hinch S.G., R.E. Diewart, T.J. Lissimore, A.M.J. Prince, M.C. Prince, and M.A.

    Henderson. 1996. Use of electromyogram telemetry to assess difficult passage

    areas for river-migrating adult sockeye salmon. Transactions of the American

    Fisheries Society 125:253–260.

Hinch S.G., E.M. Standen, M.C. Healey, and A.P. Farrell. 2002. Swimming patterns and

    behaviour of upriver migrating adult pink (*Oncorhynchus gorbuscha*) and

    sockeye salmon (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser

    River, British Columbia, Canada. Hydrobiologia 165:147–160.

Hinch S.G., S.J. Cooke, A.P. Farrell, K.M. Miller, M. Lapointe, and D.A. Patterson.

    2012. Dead fish swimming: a review of research on the early migration and high

    premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*.

    Journal of Fish Biology 81:576–599.

Katopodis C. 1992. Introduction to Fishway Design. Winnipeg, Freshwater Institute, 67p.

Keefer M.L., C.A. Peery, T.C. Bjornn, M.A. Jepson, and L.C. Stuehrenberg. 2004.

    Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and

    steelhead in the Columbia and Snake rivers. Transactions of the American

    Fisheries Society 133:1413–1439.

Keefer M.L., C.A. Peery, and M.J. Heinrich. 2008. Temperature- mediated en route

migration mortality and travel rates of endangered Snake River sockeye

salmon. Ecology of Freshwater Fish 17:136–145.

Kindt R., and R. Coe. 2005. Tree diversity analysis: a manual and software for common

statistical methods for ecological and biodiversity studies. World Agroforestry

Centre.

Laine A. 1995. Fish swimming behaviour in Finnish fishways. In Proceedings of the

International Symposium on Fishways '95 in Gifu, Japan (Komura, S., ed.), pp.

323–328. Gifu: Organising Committee for International Symposium on

Fishways '95 in Gifu.

Lee C.G., A.P. Farrell, A.G. Lotto, M.J. MacNutt, S.G. Hinch, and M.C. Healey. 2003a.

The effect of temperature on swimming performance and oxygen consumption

in adult sockeye salmon (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon

stocks. Journal of Experimental Biology 206:3239–3251.

Lee C.G., A.P. Farrell, A.G. Lotto, S.G. Hinch, and M.C. Healey. 2003b. Excess post-

exercise oxygen consumption in adult sockeye salmon (*Oncorhynchus nerka*)

and coho (*O. kisutch*) salmon following critical speed swimming. Journal of

Experimental Biology 206:3253–3260.

Liao J.C., D.N. Beal, G.V. Lauder, and M.S. Triantafyllou. 2003. Fish exploiting vortices

decrease muscle activity. Science 302:1566–1569.

Martins E.G., S.G. Hinch, D.A. Patterson, M.J. Hague, S.J. Cooke, K.M. Miller, D.

Robichaud, K.K. English, and A.P. Farrell. 2012. High river temperature reduces

survival of sockeye salmon approaching spawning grounds and exacerbates

female mortality. Canadian Journal of Fisheries and Aquatic Sciences 69:330–342.

Miller K.M., S. Li, K.H. Kaukinen, N. Ginther, E. Hammill, J.M.R. Curtis, D.A. Patterson, T. Sierocinski, L. Donnison, P. Pavlidis, S.G. Hinch, K.A. Hruska, S.J. Cooke, K.K. English, and A.P. Farrell. 2011. Genomic signatures predict migration and spawning failure in wild Canadian salmon. Science 331:214–217.

Miller K.M., A. Teffer, S. Tucker, S. Li, A.D. Schulze, M. Trudel, F. Juanes, A. Tabata, K.H. Kaukinen, N.G. Ginther, T.J. Ming, S.J. Cooke, M. Hipfner, D.A. Patterson, and S.G. Hinch. *In press*. Infectious disease, shifting climates and opportunistic predators: cumulative factors potentially impacting declining wild salmon populations. Evolutionary Applications.

Murchie K.J., K.P.E. Hair, C. Pullen, T.D. Redpath, H. Stephens, and S.J. Cooke. 2008. Fish response to fluctuating flow in regulated rivers: research methods, effects and opportunities. River Research and Management 24:197–217.

Nadeau P.S., S.G. Hinch, K.A. Hruska, L.B. Pon, and D.A. Patterson. 2010. The effects of experimental energy depletion on the physiological condition and survival of adult sockeye salmon (*Oncorhynchus nerka*) during spawning migration. Environmental Biology of Fish 88:241–251.

Naughton G.P., C.C. Caudill, M.L. Keefer, T.C. Bjornn, L.C. Stuehrenberg, and C.A. Peery. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 62:30–47.

Naughton G.P., C.C. Caudill, M.L. Keefer, T.C. Bjornn, and C.A. Peery. 2006. Fallback

by adult sockeye salmon at Columbia River dams. North American Journal of Fisheries Management 26:380–390.

Nehlsen W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16:4–21.

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

O'Brien R.M. 2007. A caution regarding rules of thumb for variance inflation factors. Quality and Quantity 41:673–690.

O'Connor C.M., D.R. Norris, G.T. Crossin, and S.J. Cooke. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere 5. DOI: 10.1890/ES13-00388.1.

Patterson D.A., J.S. Macdonald, K.M Skibo, D. Barnes, I. Guthrie, and J. Hills. 2007. Reconstructing the summer thermal history for the lower Fraser River, 1941 to 2006, and implications for adult sockeye salmon (*Oncorhynchus nerka*) spawning migration. Canadian Technical Reports of Fisheries and Aquatic Sciences 2724: 43 pp.

Pon L.B., S.G. Hinch, S.J. Cooke, D.A. Patterson, and A.P. Farrell. 2009a. A comparison of the physiological condition of migrant adult sockeye salmon and their attraction into the fishway at Seton River dam, British Columbia under three operational water discharge rates. North American Journal of Fisheries Management 29:1195–1205.

Pon L.B., S.G. Hinch, S.J. Cooke, D.A. Patterson, and A.P. Farrell. 2009b. Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia. Journal of Fish Biology 74:1323–1336.

Preece R.M., and H.A. Jones. 2002. The effect of Keepit Dam on the temperature regime of the Namoi River, Australia. River Research and Applications 18:397-414.

Priede I.G. 1977. Natural selection for energetic efficiency and the relationship between activity level and mortality. Nature 267:610–611.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rand P.S. 2011. *Oncorhynchus nerka*. *In*: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Available at http://www.iucnredlist.org.

Rand P.S., S.G. Hinch, J. Morrison, M.G.G. Foreman, M.J. MacNutt, J.S. Macdonald, M.C. Healey, A.P. Farrell, and D.A. Higgs. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. Transactions of the American Fisheries Society 135:655–667.

Reischel T.S., and T.C. Bjornn. 2003. Influence of fishway placement on fallback of adult salmon at the Bonneville Dam on the Columbia River. North American Journal of Fisheries Management 23:1215–1224.

Roscoe D.W., S.G. Hinch, S.J. Cooke, and D.A. Patterson. 2011. Fishway passage and
post passage mortality of up-river migrating sockeye salmon in the Seton River,
British Columbia. River Research and Applications 27:693–705.

Rosenberg D.M., P. McCully, and C.M. Pringle. 2000. Global-scale environmental
effects of hydrological alterations: introduction. BioScience 50:746-751.

Servizi J.A., and J.O. Jensen. 1977. Resistance of adult sockeye salmon to acute thermal
shock. International Pacific Salmon Fisheries Commission Progress Report 34.

Slaney T.L., K.D. Hyatt, T.G. Northcote, and R.J. Fielden. 1996. Status of anadromous
salmon and trout in British Columbia and Yukon. Fisheries 21:20–35.

Standen E.M., S.G. Hinch, M.C. Healey, and A.P. Farrell. 2002. Energetic costs of
migration through the Fraser River Canyon, British Columbia, in adult pink
(*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG
telemetry. Canadian Journal of Fisheries and Aquatic Sciences 59:1809–1818.

Stubben C.J., and B.G. Milligan. 2007. Estimating and analyzing demographic models
using the popbio package in R. Journal of Statistical Software 22:1–23.

Sugiura N. 1978. Further analysts of the data by Akaike's information criterion and the
finite corrections. Communications in Statistics - Theory and Methods 7:13–26.

Sullivan G.H., C. Hoefener, and V.W. Bolie. 1963. Electronic systems for biological
telemetry. Pages 83-106 *in* LE Slater, editors. *Bio-telemetry: the use of telemetry
in animal behaviour and physiology in relation to ecological problems.*
Pergamon Press, Oxford.

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,

K. Norris, L.S. Peck, S.V. Prior, J.P.W. Scharlemann, M.D. Spalding, and A.R. Watkinson. 2013 A horizon scan of global conservation issues for 2013. Trends in Ecology and Evolution 28:16–22.

Tierney K.B., and A.P. Farrell. 2004. The relationships between fish health, metabolic rate, swimming performance and recovery in return-run sockeye salmon, *Oncorhynchus nerka* (Walbaum). Journal of Fish Diseases 27:663-671.

Videler J.J., and D. Weihs. 1982. Energetic advantages of burst-and-coast swimming of fish at high speeds. Journal of Experimental Biology 97:169–178.

Videler J.J. 1993. *Fish swimming*. London: Chapman & Hall.

Vörösmarty C.J., P.B. McIntyre, M.O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S.E. Bunn, A. Sullivan, C.R. Liermann, and P.M. Davies. 2010. Global threats to human water security and river biodiversity. Nature 467:555–561.

Wagenmakers E.J., and S. Farrell. 2004. AIC model selection using Akiake weights. Psychonomic Bulletin and Review 11:192–196.

Waples R.S., R.W. Zabel, M.D. Scheuerell, and B.L. Sanderson. 2008. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. Molecular Ecology 17:84–96.

Webb P.W. 1995. Locomotion. Pages 69-99 *in* C Groot, L Margolis, WC Clarke, editors. *Physiological ecology of Pacific salmon*. UBC Press, Vancouver.

Weihs D. 1974. Energetic advantages of burst swimming of fish. Journal of Theoretical Biology 48:215–229.

Wilson R.P., C.R. White, F. Quintana, L.G. Halsey, N. Liebsch, G.R. Martin, and P.J.

Butler. 2006. Moving towards acceleration for estimates of activity-specific

metabolic rate in free-living animals: the case of the cormorant. Journal of

Animal Ecology 75:1081–1090.

Wilson S.M., S.G. Hinch, E.J. Eliason, A.P. Farrell, and S.J. Cooke. 2013. Calibrating

acoustic acceleration transmitters for estimating energy-use by wild adult Pacific

salmon. Comparative Biochemistry and Physiology A 164:491–498.

Wilson S.M., S.G. Hinch, S.M. Drenner, E.G. Martins, N.B. Furey, D.A. Patterson, D.W.

Welch, and S.J. Cooke. 2014. Coastal marine and in-river migration behaviour

of adult sockeye salmon en route to spawning grounds. Marine Ecology Progress

Series 496:71–84.

Wood C.M., J.D. Turner, and M.S. Graham. 1983. Why do fish die after severe

exercise? Journal of Fish Biology 22:189–201.

Wood C.M. 1991. Acid-base and ion balance, metabolism, and their interactions, after

exhaustive exercise in fish. Journal of Experimental Biology 160:285–308.

Young J.L., S.G. Hinch, S.J. Cooke, G.T. Crossin, D.A. Patterson, A.P. Farrell, G. Van

der Kraak, A.G. Lotto, A. Lister, M.C. Healey, and K.K. English. 2006.

Physiological and energetic correlates of en route mortality for abnormally early

migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River,

British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 63:1067–

1077.

Zuur A., E. Ieno, and C. Elphick. 2010. A protocol for data exploration to avoid common

statistical problems. Methods in Ecology and Evolution 1:3–14.