

**THE ROLE OF FISH PHYSIOLOGY, BEHAVIOUR, AND WATER
DISCHARGE ON THE ATTRACTION AND PASSAGE OF ADULT SOCKEYE
SALMON (*ONCORHYNCHUS NERKA*) AT THE SETON RIVER DAM
FISHWAY, BRITISH COLUMBIA.**

by

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B.Sc., University of British Columbia, 2005

**A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF**

MASTER OF SCIENCE

in

**THE FACULTY OF GRADUATE STUDIES
(Forestry)**

**THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)
April 2008**

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ABSTRACT

In many rivers, dams have interrupted the connectivity of migration routes for fish. While fishways can provide access between downstream and upstream habitats, it is important that passage can occur with minimal delay, energy expenditure, and physiological stress. The research presented here is based on investigations into fishway attraction and passage for the Gates Creek sockeye salmon (*Oncorhynchus nerka*, Walbaum) stock at the Seton River dam in British Columbia. The first part of this thesis examined the effect of changes in water discharge from the dam on the relationship between the physiological condition of sockeye and their behaviour in approaching the fishway entrance. Fish were caught and non-lethally biopsied under three normal operating discharge conditions at Seton River dam, and subsets of sampled fish were implanted with radio transmitters and released downstream of the dam. Indices of physiological stress and exhaustive exercise (e.g. plasma cortisol, glucose, lactate, osmolality and hematocrit) did not differ among the water discharge levels that were examined. Fish delayed in the tailrace below the fishway entrance significantly longer under intermediate discharge (19.9 h @ 12.7 m³s⁻¹) than either the high discharge (9.3 h @ 15.8 m³s⁻¹), or the low discharge (7.0 h @ 11.0 m³s⁻¹;) conditions ($P = 0.022$, and $P = 0.015$, respectively). Delay time was similar under high and low discharge conditions ($P = 0.617$), and passage success was found to be independent of discharge ($P = 0.356$). The second part of this thesis investigated how prior physiological condition and subsequent swimming energetics and behaviours effected fishway passage success. Fish were captured and biopsied, before being implanted with electromyogram (EMG) transmitters and released near the downstream entrance of the fishway. Very few differences existed between successful and unsuccessful fish in body size, initial plasma physiology and energy state, and mean swim speed and energy use during passage. However,

plasma Na^+ concentration was significantly lower in unsuccessful fish ($P = 0.022$), which is suggestive of a depressed ionic state for unsuccessful fish. Generally, fish did not employ burst swimming during successful or failed attempts at passage, indicating that failure was probably not related to metabolic acidosis.

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ACKNOWLEDGEMENTS

I would like to thank Dr. Scott Hinch for his valuable support and guidance throughout all stages of this research. Dr. Steven Cooke provided expertise and training in biopsy, surgery, and telemetry techniques in the field, as well as thorough manuscript reviews. Committee members Dr. Anthony (Tony) Farrell and Dr. Sarah Gergel also provided thorough reviews of the manuscripts. I would also like to recognize all members of the Hinch lab for their assistance with various components of this thesis. As well, Jayme Hills, Jeanette Garries, Kim Dales, Vanessa Ives, D'Arcy McKay, and Mark Shrimpton, were instrumental in conducting multiple physiological assays for this research. Thanks are extended to several field assistants for their contributions to fish capture, tagging, and radio-tracking: Jessica Redan, Bonnie Adolf, and Miriam Belisle. Funding for this research was provided by a grant from the Bridge Coastal Restoration Program (BCRP) to Scott Hinch and Steven Cooke, as well as a National Sciences and Engineering Research Council (NSERC) Discovery grant to Scott Hinch, and a NSERC Strategic grant to Scott Hinch, Tony Farrell, Michael Healey, and Glen Van Der Kraak. Funding was also provided by an NSERC postgraduate scholarship to myself. Logistics and project support were provided by David Patterson and the Fraser River Environmental Watch program.

DEDICATION

For those who have supported and inspired me

CO-AUTHORSHIP STATEMENT

Lucas Pon held primary responsibility for the fieldwork, data analysis, and writing of the manuscripts that comprise the present thesis. Use of the first person plural in Chapters 2 and 3 acknowledges the following co-authors, who will be named in the manuscript versions of these chapters (currently in preparation for submission to peer-reviewed publications): Scott Hinch Steven Cooke, David Patterson, and Tony Farrell. Lucas Pon retained principal responsibility for all other aspects of the study

CHAPTER 1

INTRODUCTION

Background

The anadromous life-history of the Pacific salmon (*Oncorhynchus* spp.) involves migrations over thousands of kilometres and across multiple habitat types. Hatched in freshwater, juveniles move to oceanic feeding grounds and a small percentage return to their natal environments as adults to spawn then die. These spectacular migrations between freshwater and oceanic environments can cover vast distances and represent strong selective forces for both the juvenile and adult life stages. The return migration made by adult salmon is characterized by several physiological changes (Hinch et al. 2006). They cease feeding prior to freshwater entry, and then rely exclusively on stored energy reserves to power their upriver migration, to complete reproductive development, and to engage in spawning activities (Brett 1995). They must also change their osmoregulatory and ionoregulatory systems before they encounter the hyperosmotic freshwater environment (Hinch et al. 2006).

Leading them from the open ocean back to their natal streams and lakes on the return migration are the incredible homing capabilities of Pacific salmon (Quinn et al. 1999). Fidelity to natal streams and lakes serves to maintain separate populations or ‘stocks’, which are generally considered to be reproductively isolated (Varnavskaya et al. 1994; Wood 1995). Natal environments within a watershed may be separated by hundreds of kilometres of migration distance (Quinn 2005). Consequently, salmon stocks can have distinct adaptations for managing energy during their migrations which involve differences in body size, body shape, body energy density, egg number, egg size, and swimming performance (e.g. Quinn et al. 1995; Kinnison et al. 2001; Quinn et al. 2001; Lee et al. 2003; Crossin et al. 2004; Hendry and Berg 1999; Hinch et

al. 2006). If migratory environments dramatically change from historic norms, energy management tactics may prove to be inadequate to ensure successful migration and reproduction (Rand et al. 2006).

Pacific salmon represent an important part of both river and ocean ecosystems, and have important economic values as well as cultural significance to coastal communities (Lichatowich 1999). Historically, salmon were highly abundant along the North American coast with a geographic distribution that ranged from southern California to Alaska. The past century however, has seen the decline of many salmon stocks (Nehlsen et al. 1991; Slaney et al. 1996). Over-harvesting, habitat destruction, and habitat fragmentation, among other causes, have all played a role in the decline of salmon numbers (Nehlsen et al. 1991; Lichatowich 1999). While many factors contribute to the decline of salmon, perhaps one of the greatest threats is the damming of rivers along migration routes (Nehlsen et al. 1991; NRC 1996). Among other effects, dams can reduce connectivity between habitats upstream and downstream of the dam site, and may delay or entirely restrict adult salmon in their efforts to reach upstream spawning grounds.

Dam construction on salmon-bearing rivers became increasingly prevalent in the latter half of the 20th century (Dynesius and Nilsson 1994; Rosenberg et al. 2000; Nilsson et al. 2005). In recognition of this fact, and the potential negative effects of dams on migratory fish, many studies have been undertaken to assess the impact of dams on fish passage efficiency (e.g. Leman and Paulik 1966; Gowans et al. 2003; Keefer et al. 2004; Brown et al. 2006; Scrutton et al. 2007). Modern assessments of fish bypass systems are typically made through the use of radio telemetry and counts, and generally measure passage rates and ratios of success to failure. Very few of these studies however, were able to assess the degree of difficulty associated with fish

passage around a dam. To address this paucity of research, the present study integrates established telemetry techniques with measurements of several indicators of the individual's physiological condition to assess passage rates and to better understand links between physiology and swimming patterns exhibited by fish migrating past an in-stream obstacle.

Pacific salmon migrations and fishways

The continued legacy of anadromous Pacific salmon relies on connectivity between freshwater spawning habitats and oceanic feeding grounds. Where this connectivity is severed or impaired, both the number and size of salmon populations can be drastically reduced (Nehlsen et al. 1991). Barriers to migration may be anthropogenic or entirely natural, and both can impede or limit habitat access. In 1914, a rockslide caused by tunnelling activities prevented many salmon from passing Hell's Gate on the Fraser River. Similarly in 1951, hundreds of thousands of Pacific salmon were prevented from completing their spawning migration in the Skeena River system after a rockslide blocked access to upstream habitat (Godfrey et al. 1954). In the last century, restricted access to habitat has become increasingly common with the construction of hydropower facilities and other waterway harnessing projects (Odeh 1999). Dam construction associated with such projects has led to extirpation of hundreds of salmon populations in the United States (Nehlsen et al. 1991), and dozens in British Columbia (Slaney et al. 1996).

To mitigate the negative effects of such barriers on adult salmon migration, by-pass facilities (e.g. fishways and fish ladders) have been constructed to enable upstream passage around dams in some areas (Clay 1961; Odeh 1999). While the primary function of such facilities is to enable passage, it is particularly important for migrant adult salmon that this is allowed to happen in as short of a time period as possible, and without fish needing to consume large amounts of energy or experience high levels of physiological stress, either of which could

impair reproductive development or otherwise hinder migrational success (Hinch et al. 2006). In heavily regulated rivers such as the Columbia River, USA, a segment of migrant Pacific salmon face the daunting prospect of having to successfully navigate their way past as many as eight separate dam structures where delay may last for up to five days at a given dam (Keefer et al. 2004). Such cases emphasize the importance of understanding fishway passage from a biologically relevant perspective, and developing structures and operation plans that are conducive to efficient passage based on this understanding.

Barriers to migration are often found where high water velocities or dams represent substantial changes in river elevation, such that fish are unable to continue upstream. To accommodate passage, fishways must be designed to allow fish a surmountable route around the restricting gradient (Clay 1961). Early fishway designs were crude and generally did not account for fish behaviour, swimming capacity, or site-specific hydraulic conditions (Odeh 1999). Early efforts in the 1900's began to incorporate fish science into fishway design, and by the mid-20th century, many fishway design standards were based on rigorous research on fish passage (Odeh 1999). Indeed, the management and conservation implications of fishway performance have led to numerous studies assessing fish passage rates and swimming capabilities, and how these relate to fishway design. Studies of pre-existing passage structures have frequently used radio telemetry (e.g. Gowans et al. 1999; Naughton et al. 2007) and, more recently, electromyogram (EMG) radio telemetry (e.g. Gowans et al. 2003; Brown et al. 2006). These devices allow researchers to monitor and record specific movements of free-swimming fish within fishway structures, and make recommendations for fishway improvements based on these observations.

Fish passage systems can take many forms, but all types share the common goal of allowing fish to effectively move beyond an impediment to forward progress. This means that

the gradient and flow velocity within the fishway must be properly designed to accommodate the swimming capabilities of the migrant fish species. Where fishways cater to multiple species, gradient and flow velocities should be designed to permit passage of the species with the lowest maximum attainable speed (Peake et al. 1997). Laboratory-based critical swimming speeds (U_{crit}) of fish have been used as a metric to determine suitable water velocities within fishways, although this technique may in fact underestimate the free-swimming capability of fish (Booth et al. 1997; Peake 2004). In addition to swim speed, the duration of fishway ascent has also been emphasized as an important aspect of fishway design (Peake 2004; Castro-Santos 2006). Commonly used fishway designs often incorporate a series of steps or pools that alternate areas of high velocity with areas of low velocity (Clay 1961; Odeh 1999). This design concept provides potential resting areas for fish to use in between bouts of forward movement, and thereby seeks to accommodate temporal limitations to high-speed (anaerobic) swimming efforts. Collectively, research on the swimming capacity of fish, and observations of fish behaviour within fishways have led to some improvements in design and effectiveness of modern fish bypass systems (Odeh 1999). There are however, other aspects of fishway passage that have not been extensively studied, yet play an important role in determining the amount of time fish may be delayed.

Prior to ever passing through a fishway, migrating salmon must first be able to locate and enter the fishway. Difficulty associated with locating the fishway entrance may cause unnecessary delays for some migrants, while preventing others from migrating beyond the obstruction entirely (Odeh 1999; Bunt 2001). Within the context of dam passage, migrational delay suggests an additional hindrance resulting from the obstruction. Delay downstream of a fishway can be highly variable, and may last anywhere from hours to weeks. A large-scale study

of Pacific salmon migrating past multiple dams on the Columbia River system showed that some dams could be surmounted within as little as 12 h, while others could take up to five days for some fish to pass (Keefer et al. 2004). Similarly, Karppinen et al. (2002) observed high variability in delay, ranging from days to weeks at a single dam on the Tuloma River in Russia. This excessive time spent downstream of a dam may have several negative consequences for migrants, including increased exposure to both predation and harvest threats (Dauble and Mueller 2000; Gowans et al. 2003). Additionally, movements downstream of fishways may be energetically costly, as swimming efforts have been shown in some cases to exceed anaerobic thresholds (Hinch and Bratty 2000; Brown et al. 2006). For Pacific salmon, excessive energy spent during migrations may impair or preclude spawning opportunities; hence minimizing migrational delay at fishways is an important management and conservation task.

The role of water flow has been established as an important factor in encouraging upstream migration (Banks 1969; Alabaster 1970; Winstone et al. 1985). Migrating fish are often observed seeking out stronger flows as they approach dams and other obstructions (Leman and Paulik 1966; Bunt et al. 1999; Rivinoja et al. 2001). Where strong flows emanate from non-fishway sources (e.g. dam spillways), delay time may be increased by false attraction to specific areas that do not have upstream passage options (Bjornn et al. 1995). An effective fishway entrance design should attract fish in an efficient manner, and enable passage with minimal energy expenditure (Clay 1961; Bunt 2001). However, few studies have examined how alterations to fishway entrances or water flow velocity affect attraction efficiency. Bunt et al. (1999) were able to enhance fishway attraction by enlarging the fishway entrance, and altering the approach area immediately downstream of the fishway. Experimentally increased attraction flows have also been shown to improve fishway entrance attraction in some cases (Moser et al.

2000), though not in others (Naughton et al. 2007). This lack of information related to the improvement of existing designs coupled with the prevalence of dams and other waterway obstructions emphasizes the need to understand how to minimise delay and passage difficulty associated with fishway structures.

Physiological stress and salmon migration

Fraser River bound adult Pacific salmon must migrate hundreds of kilometres down the Canadian Pacific coast before entering freshwater and moving upstream to natal spawning grounds. Freshwater segments of this migration may cover distances in excess of 1000 km and ascend total elevations greater than 700 m (Crossin et al. 2004). This impressive course of migration can be arduous both in terms of physical extent, and obstacles encountered en route. Along the way, some stocks must pass through incredibly challenging reaches (e.g. Hell's Gate) that may tax the metabolic limit of fish to the point of preventing further passage for some individuals (Hinch and Bratty 2000). Additionally, salmon may encounter abnormal deviations in river temperature and flow, which may expedite the consumption of limited energy stores (Rand and Hinch 1998). Salmon must also avoid a variety of threats including infection and disease, predation, and fisheries. These obstacles to migration can have the potential to impart physiological stress on salmon, which has been shown in some cases to hinder migrational success (Macdonald 2000; Cooke et al. 2006; Young et al. 2006).

The stress response exhibited by fish can manifest in both altered physiological condition and behaviour, and may be evoked by a number of factors including unfavourable water quality or conditions, predation/capture threat, and excessive exercise (Schreck et al. 1997; Wendelaar Bonga 1997). The primary physiological response to stress involves the release of catecholamines (i.e. epinephrine and norepinephrine), and the hypothalamo-pituitary-interrenal

response of releasing cortisol and other hormones into the circulatory system (Randall and Perry 1992; Sumpter 1997). This may last only several minutes under an acute stress, but may persist for days under chronic stress (Randall and Perry 1992). These hormones are the basis for secondary responses, which may include elevated heart rate, an increase in energy mobilization, and fluctuations in the body's hydromineral balance (Wendelaar Bonga 1997). Secondary stress responses often used as indicators to measure the degree of stress include plasma metabolites such as lactic acid and glucose, ionic concentrations, and haematological variables (Barton and Iwama 1991; Barton 1997). The degree of change observed in these variables can give an indication of the intensity and type of stressor acting on the individual.

McDonald and Milligan (1997) identify and distinguish between 'simple' and 'compound' stress, with the former comprising a physiological disturbance associated solely with the effects of cortisol and catecholamine release. In comparison, a compound stress includes the effects of other factors such as poor water conditions or vigorous activity in addition to that of the simple stress (McDonald and Milligan 1997). While both types of stress involve the elevation of catecholamines and cortisol, secondary stress responses tend to vary depending on the type of stressor. Under the majority of stressful conditions, freshwater fish tend to experience a net loss of ions, which is primarily due to an elevated brachial efflux associated with the relevant increase in epinephrine (Mazeaud and Mazeaud 1981; McDonald and Milligan 1997). Measurements of plasma ion concentrations following a simple stress reflect this with values lower than baseline (e.g. Postlethwaite and McDonald 1995; Ackerman et al. 2000). Compound stress responses however, may result in elevated plasma ion concentrations (e.g. Wood et al. 1983; Farrell et al. 2000) due to transcellular osmotic imbalances associated with elevated levels of muscle lactate (Graham et al. 1982; Milligan and Wood 1986).

Following the release of catecholamines into the circulatory system is the mobilization of energy stores in anticipation of the behavioural response to stress (e.g. fight or flight) (Wendelaar Bonga 1997). Stressors that push fish towards physical exhaustion require copious amounts of energy and can lead to the presence of lactic acid in the bloodstream. Plasma lactate levels begin to increase following stress, and may continue to increase to a peak approximately two hours after the stressful event. Under routine conditions, plasma lactate concentrations are generally under 2 mmol L^{-1} (Milligan 1996; Wagner et al. 2006). In contrast, blood samples taken from commercially gill-netted coho salmon (*O. kisutch*) had plasma lactate levels exceeding 20 mmol L^{-1} , consistent with a severe stress and exhaustion (Farrell et al. 2000). Under particularly severe cases of stress, metabolic acidosis may lead to delayed mortality (Wood et al. 1983; Farrell et al. 2001). While death may be an extreme consequence, the effects of stress tend to vary depending on both the duration and the severity of the stressor (Barton 1997; Wendelaar Bonga 1997). Following an acute stress, a fish may be able to fully recover to baseline conditions within a day or two. In contrast, a chronic stress may result in the persistence of the stress-related physiological condition to the point where habituation occurs, and the stress response may no longer be adaptive (Barton et al. 1987).

Of particular relevance to migrating adult Pacific salmon are the effects of physiological stress on energy use, the scope for activity, reproductive development, and disease resistance. The course of freshwater migration is powered entirely by stored energy, and under stressful conditions, energy is allocated towards efforts associated with survival (Moberg 1985; Wendelaar Bonga 1997). To compensate for these energetic costs, finite energy resources may be diverted away from less immediate demands such as reproductive development (Barton 1997). A threshold of 4 MJ/kg has been identified as the minimum energy density threshold

required to sustain life in adult sockeye salmon (*O. nerka*) on their spawning grounds (Crossin et al. 2004). Energy use associated with stress responses may threaten to bring migrant salmon closer to, or even below, this threshold prior to the completion of spawning activities.

Some evidence suggests that stress in fish compromises their swimming capabilities (Beamish 1978; Barton and Schreck 1987; Maule et al. 1988; Strange and Cech 1992). High levels of stress can increase oxygen consumption levels associated with maintenance of homeostasis, which represents a loading that effectively reduces performance potential within the metabolic scope for activity (Barton 1997). The accumulation of high levels of lactate and other metabolites resulting from anaerobic metabolism in white muscle and the depletion of tissue energy stores (e.g., glycogen, ATP, phosphocreatine) may impair swimming capabilities or necessitate long recovery periods from exhaustion (Stevens and Black 1966; Wedemeyer et al. 1990; Kieffer 2000; Peake and Farrell 2004). In particular, stressed fish may be limited in their anaerobic capacity and the ability to recover from challenging bouts of swimming. Impaired swimming performance may limit the capability of salmon to migrate past hydraulic challenges.

It is not enough for a salmon to simply arrive at spawning grounds, as they must also become reproductively mature and still have adequate energy stores for courtship, nesting, and other spawning-related activities (Brett 1995; Healey et al. 2003). Stressors encountered en route to spawning locales may negatively affect reproductive development in several ways. As previously alluded to, extensive use of energy reserves to power migration may compromise those needed to fully develop gonads and secondary sexual characteristics. This may be particularly relevant for female sockeye salmon, which are thought to devote nearly 50% of their energy reserves to reproductive development (Crossin et al. 2003; Crossin et al. 2004). An experimental increase in migration rigor was associated with a decrease in ovarian mass

associated with smaller egg size in female Chinook salmon (*O. tshawytscha*) (Kinnison et al. 2001). As juvenile survival highly depends on maternal provisioning in egg investment, smaller egg size may have negative consequence for offspring survival (Kinnison et al. 2001).

Though research is limited and not always consistent, there is some evidence to suggest that elevated cortisol levels may be linked with the suppression of reproductive hormones in fish (Pankhurst and Van Der Kraak 1997; Wendelaar Bonga 1997). Hormone suppression may be associated with delay in the maturation process, which could result in a suboptimal spawning date. High cortisol levels may also make stressed fish more susceptible to disease and infection via immunosuppressive actions (Snieszko 1974; Maule et al. 1989). Pacific salmon that migrate up the Fraser River are exposed to the parasite *Parvicapsula minibicornis*, a kidney parasite endemic to the region (Jones et al. 2003). Severe infections with this parasite have been shown to compromise anaerobic capacity and recovery rates in sockeye salmon (Wagner et al. 2005). Severe infections could have a negative effect on the ability of migrant salmon to pass through areas with high water velocities. It is clear that physiological stress accrued by migrating salmon can have a diverse range of effects that collectively work against spawning migration success.

Study rationale and approach

Though many previous studies have assessed fishways for passage efficiency, few ever go beyond passage rates and ratios of successful to unsuccessful fish. This lack of study depth leaves questions related to why some fish pass while others fail unanswered. Migratory challenges within fishways and immediately downstream of fishways can influence the number of fish that successfully arrive on spawning grounds. To effectively manage or conserve salmon stocks it is important to understand the specific mechanisms behind these challenges and the extent to which salmon are able to cope with them.

Through the integrated use of telemetry and physiological sampling methods, both aspects of this study seek to gain a more intimate understanding of the response of migrant Pacific salmon to a compulsory migration obstacle. The spawning grounds of the sockeye salmon stock studied in this thesis are all located upstream of a dam and fishway site. Therefore, this migrational motivation presents an opportunity to elucidate potential behavioural or physiological factors that separate successful fish from unsuccessful fish without confounding issues associated with non-requisite passage (i.e. alternate spawning grounds located downstream of the dam site). Radio and EMG telemetry provide a means to observe the free-swimming patterns and behaviours of migrant salmon, while an understanding of the individual's physiological condition may help to better understand the underlying reasons behind these movements and behaviours.

The research presented in this thesis is divided into two complementary chapters, each addressing a specific aspect of fishway passage. Chapter 2, titled *A comparison of the physiological condition of migrant adult sockeye salmon and their attraction to the fishway at Seton River dam, British Columbia under three discharge rates*, focuses on the movements of migrant fish downstream of the fishway and specifically addresses issues associated with fishway entrance attraction. The study took advantage of two prescribed reductions in water spillage at the Seton River dam, to compare attraction rates and success among fish released under each of three discharge conditions (15.8, 12.7, and 11.0 m³·s⁻¹). Radio telemetry was used to monitor fish (total $n = 27$) as they moved within the tailrace of the dam. In this way, attempts to locate the fishway, success in locating and entering the fishway, total time spent in the area immediately downstream of the fishway, and fishway passage time were revealed. Collectively, these observations may give some indication of the degree of difficulty and delay associated with

fishway attraction under each of the three discharge conditions. Fish (total $n = 72$) were biopsied to allow comparisons among the physiological conditions of fish under each of the three different discharges. In Chapter 2, I tested the predictions that under higher flows, fish would be more physiologically stressed, and therefore would exhibit greater delay in locating the fishway entrance, and have reduced success at fishway passage.

Chapter 3 is titled *Physiological, energetic, and behavioural correlates of successful fishway passage in a population of adult sockeye salmon (*Oncorhynchus nerka*) in the Seton River, British Columbia*, focuses specifically on passage within the fishway structure. The discreet confines of the fishway permit a highly detailed investigation into specific movements of fish and the associated energy use via EMG telemetry. EMG tagged fish (total $n = 13$) were tracked as they attempted to move up the fishway. Observations of movements, resolved to within 1 m, were recorded and later associated with actual data gathered in real time on swim speed and energy use to compare swimming behaviours between successful and unsuccessful ascents of the fishway. The same fish were also biopsied in order to allow comparisons of the prior physiological condition of successful and unsuccessful fish. Through these methods, chapter 3 specifically addresses the predictions that sockeye salmon that fail to pass or display difficulty in attempting to pass are those that are characterized by a prior state of physiological stress, and energetically inefficient swimming behaviours when compared to those fish that were able to pass in an expedient manner.

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CHAPTER 2

A comparison of the physiological condition of migrant adult sockeye salmon (*Oncorhynchus nerka*) and their attraction to the fishway at Seton River dam, British Columbia under three discharge rates¹

INTRODUCTION

Large dam construction increased during the latter half of the 20th century (Dynesius and Nilsson 1994; Rosenberg et al. 2000; Nilsson et al. 2005). As a consequence, many formerly unconstrained large river systems were altered and in some cases, connectivity to upstream reaches became limited or completely severed. As a way to restore a means of connectivity for local fish populations, fish bypass systems (e.g. fishways, fish-lifts) were installed to facilitate passage around dams and other in-stream obstructions (Clay 1961; Odeh 1999). Though the earliest fish bypass structures were often poorly designed for local hydraulic conditions and fish species, designs began to accommodate biologically relevant factors by the early 1900's, and by the middle of the 20th century, design criteria became increasingly based on rigorous fish passage research (Odeh 1999). An important part of effective fishway design is the provision of a means for fish to be able to locate and enter the structure in a timely and energetically efficient manner (Andrew and Geen 1960; Clay 1961; Larinier 1998). Within the context of dam passage, migrational delay suggests an additional time-cost in moving upstream that would not have existed under pre-dam conditions. Indeed, many studies examining fish passage at dam sites have reported substantial periods of delay in dam tailraces as fish seek out and enter fishway entrances, though the exact cause of delay is generally unclear (e.g. Bjornn et al. 1995; Gowans et al. 2003; Keefer et al. 2004; Scrutton et al. 2007).

¹ A version of this chapter will be submitted for publication. Pon, L.B., S.G. Hinch, S.J. Cooke, D.A. Patterson, and A.P. Farrell. A comparison of the physiological condition of migrant adult sockeye salmon (*Oncorhynchus nerka*) and their attraction to the fishway at Seton River dam, British Columbia under three discharge rates.

Water flow velocity has long been recognized as an important aspect governing upstream movements of migrating fish (Banks 1969; Alabaster 1970), and the provision of suitable flow conditions downstream of a dam has been advocated as an effective method of reducing migration delay as fish seek out fishway entrances (Andrew and Geen 1960). For fish to be attracted towards a fishway, it is believed to be particularly important to have significant flows emanating from a point near the fishway entrance (Andrew and Geen 1960; Leman and Paulik 1966; Larinier 1998), presumably as an attractant of some kind. While most dam designs now provide a source of such ‘attraction flows’, few studies have empirically examined the relationship between flow and actual attraction at fishways, and those that have done so, report equivocal results. By changing the location from where attraction flows emanate, relative to locations of fishway entrances, researchers found that they could influence fishway selection for Pacific salmon (*Oncorhynchus* spp.) at the Rock Island Dam on the Columbia River, USA (Leman and Paulik 1966). Similarly, attraction of migrant American Shad (*Alosa sapidissima*) into a bypass lock on the Cape Fear River, North Carolina, USA was improved by increasing the velocity of water emanating from the entrance of the lock (Moser et al. 2000). Ide (*Leuciscus idus*) were also more likely to pass at a fishway in the River Vecht, the Netherlands as attraction flow increased relative to surrounding flows (Winter 2007). Similar improvements, however, were absent for Pacific salmon when flows were increased in fish-ladder weirs at the Lower Granite Dam on the Snake River, USA (Naughton et al. 2007), and on large rivers such as the Columbia River, attraction decreased at river discharges too strong for fish to navigate through (Leman and Paulik 1966).

Though changes to discharge can, in some cases, be a means of improving fishway attraction at dams, no previous study has examined how this relates to the physiological

condition of migrant fish. Under higher discharges fish may be exposed to less favourable environmental conditions, and therefore may become physiologically stressed. Hinch and Bratty (2000) noted that sockeye salmon (*O. nerka*) were commonly swimming above critical swim speeds (U_{crit}) in the swift currents downstream of the fishway situated at Hell's Gate on the Fraser River, British Columbia. They found that excessive burst swimming generally led to passage failure. Similarly, Chinook salmon (*O. tshawytscha*) were observed at times to be swimming at speeds approaching, and in some cases exceeding, anaerobic thresholds in the tailrace at Bonneville Dam on the Columbia River, USA (Brown et al. 2006). In fact, swim speeds observed in the tailrace area were higher than those observed within the fishway (Brown et al. 2006). Though both studies were conducted on large rivers, the observations suggest the possibility that fish become physically exhausted while attempting to locate a fishway entrance. Physical exhaustion in fish represents a stress, which can have several adverse effects on migrant salmon, including elevated energy expenditure (Barton and Schreck 1987), the suppression of reproductive hormones (Kubokawa et al. 2001), and even death (Black et al. 1962; Wood et al. 1983).

Freshwater spawning migrations of anadromous Pacific salmon, makes these species particularly susceptible to passage issues associated with dams and river discontinuity. Without dams, the spawning migrations of many populations of Pacific salmon are one of the most challenging stages of their lives, during which they must rely exclusively on stored energy reserves to complete their migration and become reproductively mature, all while maintaining adequate reserves for spawning activities (Brett 1995; Crossin et al. 2004). Nevertheless, in the Columbia River, USA, some populations of salmon must negotiate up to eight separate dams as they return to natal spawning grounds (Keefer et al. 2004). Excessive delay or exhausting

physical efforts associated with dam passage may compromise migration success by prematurely depleting energy supplies, and can therefore have negative consequences to lifetime fitness for these species (Geist et al. 2000; Keefer et al. 2004; Caudill et al. 2007).

In this study, we examined the relationship between delay downstream of a fishway, fishway passage success, and the physiological condition of salmon under several operational water discharges at a fishway-equipped dam. Migrating adult sockeye salmon from the Gates Creek population, a critically endangered salmon stock in British Columbia, Canada, were intercepted at the Seton River dam and non-lethally sampled in order to assess their physiological condition. A subset of these fish were implanted with radio transmitters and released downstream of the dam to examine delay associated with fishway entrance location and success of fishway passage. We compared the physiological condition of fish and the period of time fish were delayed downstream of the dam among three levels of water discharge released from the dam, with incremental decreases in flow of roughly 15-20% at each stage. We tested the prediction that under higher flows, fish would be more physiologically stressed, and therefore would exhibit greater delay in locating the fishway entrance, and have reduced success at fishway passage.

METHODS

Study site

The study was conducted on the Seton River, which is a tributary of the Fraser River (Figure 2.1). We focused on the Seton River dam and fishway that is operated by BC Hydro located approximately 5 km southeast of Lillooet, British Columbia, Canada (Figure 2.1).

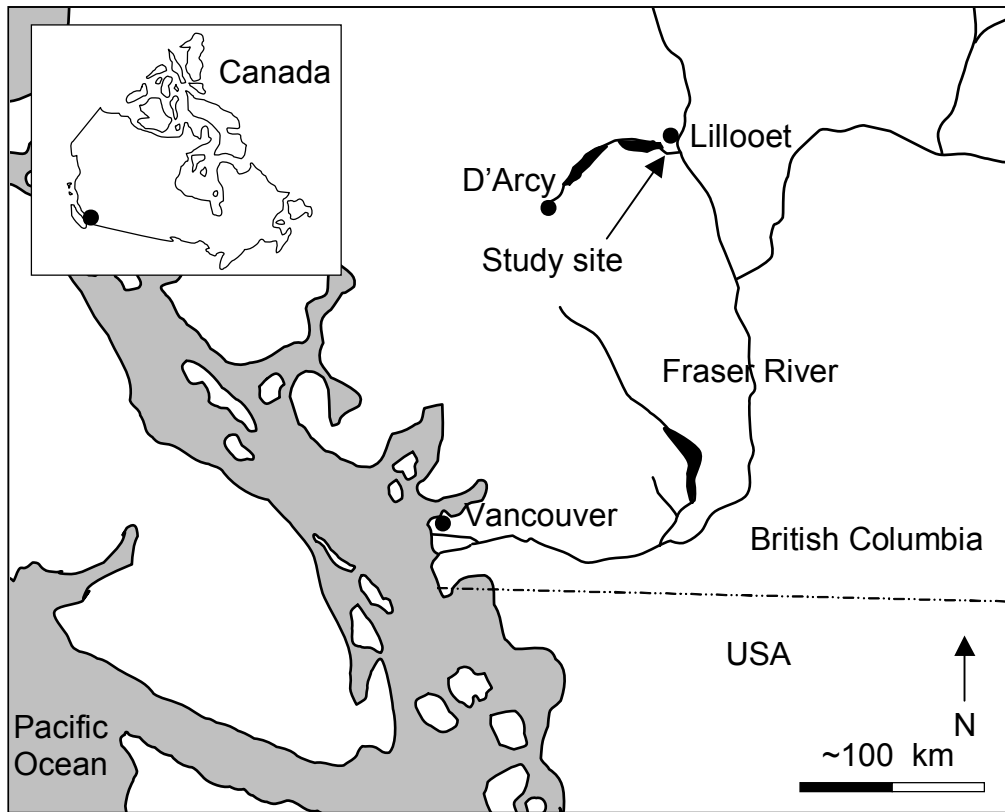


Figure 2.1. Map of south-western British Columbia, showing the location of the study site along the migration route of Gates Creek sockeye salmon, and inset map showing relative location in Canada. Fish were captured, tagged and tracked on the Seton River which is located near Lillooet, B.C. Terminal spawning grounds for this stock are located upstream of the Seton River dam near D'Arcy, B.C.

The Seton River dam is a diversion dam that directs a segment of total river discharge down a 4 km artificial channel to a hydroelectric generating station located adjacent to the Fraser River, <1 km downstream of the Seton River confluence. The balance of the total discharge is released into the Seton River and is regulated throughout the year, with mandated adjustments made during salmon migration times to meet minimum flow requirements (Andrew and Geen 1958). Between August 10 and 22 of 2005, $15.8 \text{ m}^3 \text{ s}^{-1}$ (hereafter 'high' discharge period) were spilled from the Seton River dam. This volume was decreased by approximately 20% to $12.7 \text{ m}^3 \text{ s}^{-1}$ (hereafter 'intermediate' discharge period) for the period of August 23 to September 5, 2005, and again by 13.4% to $11.0 \text{ m}^3 \text{ s}^{-1}$ (hereafter 'low' discharge period) from September 6, 2005 until

the end of the study period, September 23. The three discharge levels were set and pre-scheduled by BC Hydro and were not within our control. Instead, the present study uses these changes in an opportunistic fashion to examine fish attraction under a range of regular operational discharge conditions for the Seton River dam. In other years, passage at the Seton River dam appeared to be excluded at a discharge of $60 \text{ m}^3 \text{ s}^{-1}$, though fish were observed passing at a discharge of $30 \text{ m}^3 \text{ s}^{-1}$ (D. Roscoe, UBC, pers. comm.). Water temperatures were measured using ibutton temperature loggers (Maxim Integrated Products Inc., Sunnyvale, CA, USA). Mean daily water temperatures in the Seton River ranged from a high of 18.0° C to a low of 13.1° C (Figure 2.2). Mean daily Fraser River temperatures ranged from a high of 19.3° C to a low of 13.1° C , and followed a gradual decreasing trend (Figure 2.2).

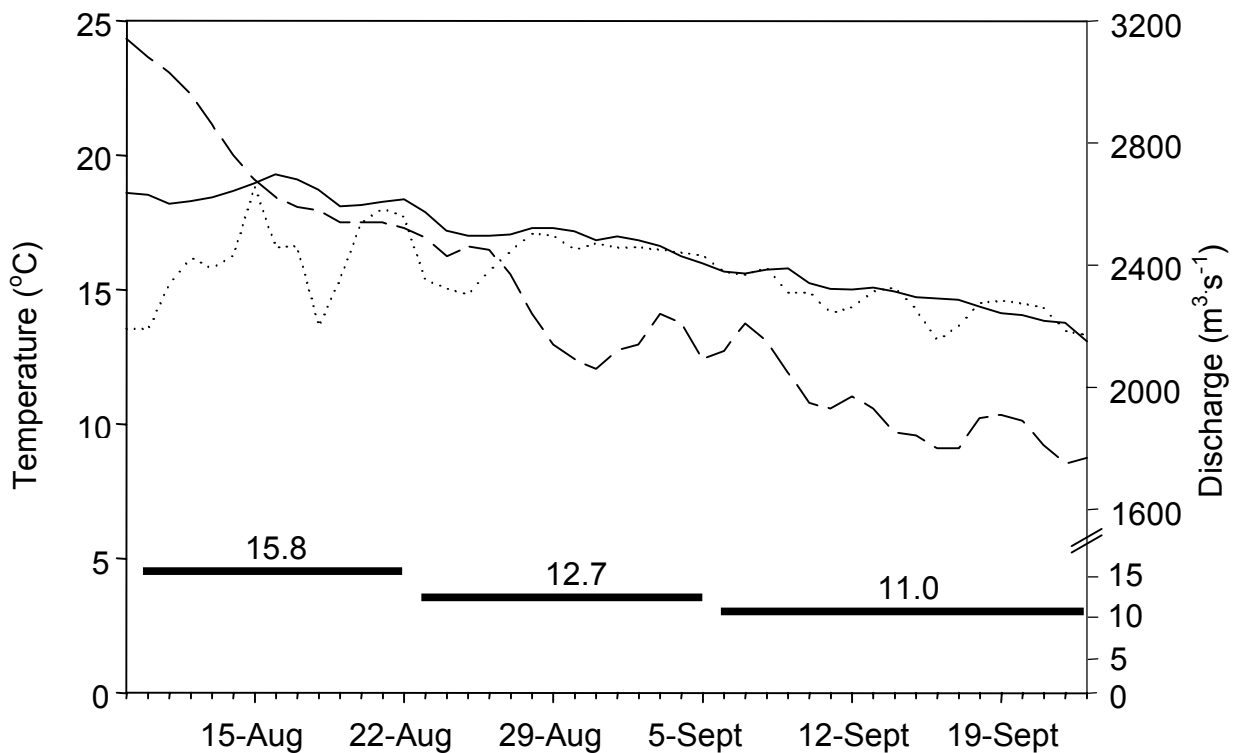


Figure 2.2. Mean daily water temperatures of the Seton River at the dam (dotted line), and the Fraser River near Hope, B.C. (solid line) from the beginning of August to the end of September, 2005. Mean daily discharge ($\text{m}^3 \text{ s}^{-1}$) for the Fraser River at Hope, B.C. (dashed line) is also presented. The three black bars represent the time periods when fish were tracked under each of the three discharges spilled at the Seton River dam.

The Seton River dam is comprised of two spillways separated by a concrete wall extending ~20 m downstream and perpendicular to the dam face (Figure 2.3). The radial spillway, located along the north bank, is ~12 m in width, and the siphon spillway, located along the south bank, is ~18 m in width. The fishway entrance is located against the south bank of the Seton River, and released a consistent discharge of $1.3 \text{ m}^3 \cdot \text{s}^{-1}$ throughout the study period. No means of passage is available from the radial spillway. A series of concrete baffles in each of the two spillways are designed to dissipate flow velocities. During the entire study period, discharge from the dam was controlled and released through the fish-water sluice in the siphon spillway, adjacent to the fishway entrance (Figure 2.3). Minor flows ($< 1 \text{ m}^3 \cdot \text{s}^{-1}$) caused by seepage emanated from the radial spillway throughout the study.

In the present study, sockeye salmon from the Gates Creek population were captured during the period of August 10 to September 21, 2005. Sockeye from this population are classified as a 'summer run' Fraser River stock, with upriver migrations taking place between late July and September of each year. Having already migrated approximately 350 km upstream from the mouth of the Fraser River, Gates Creek sockeye must pass Seton Dam before traveling the final 50 km through Seton and Anderson Lakes and arriving on spawning grounds at Gates Creek (Figure 2.1). Spawning grounds for this stock consist of both natural stream habitat as well as an artificial spawning channel in D'Arcy, B.C. The study site represents a location 88% through the freshwater stage of Gates Creek sockeye migration.

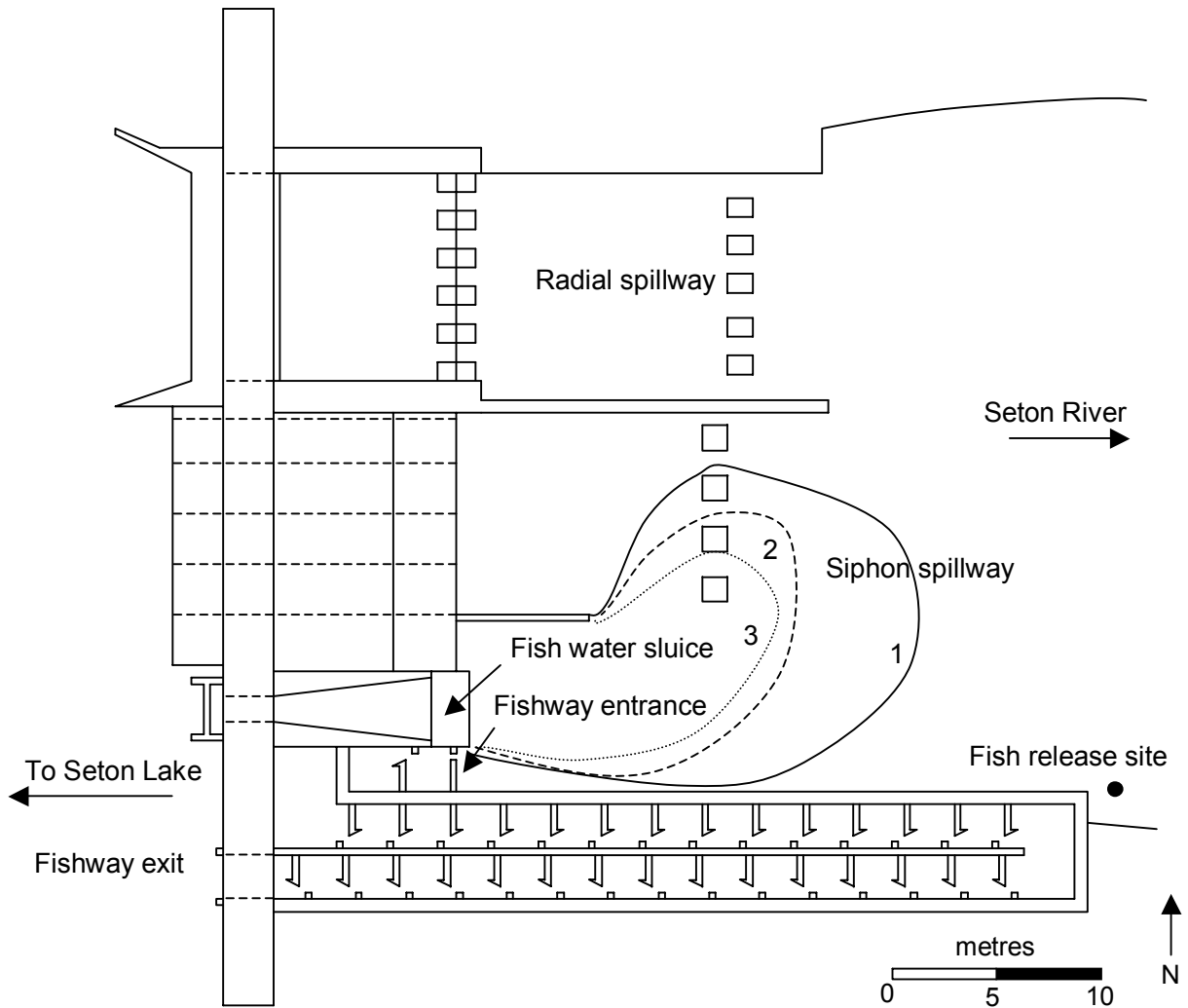


Figure 2.3. Detail of the structural layout of the Seton River dam and fishway. Throughout the study period, all discharge from the dam was released through the fish water sluice, with the exception of a consistent flow from the fishway entrance ($1.3 \text{ m}^3 \cdot \text{s}^{-1}$), and minor seepage from the radial spillway gate. Fish were captured at the fishway exit, tagged with radio transmitters, and released downstream of the fishway indicated by the black dot. The extent of visibly turbulent water (white-water) under each of the three discharges, (1- solid line) $15.8 \text{ m}^3 \cdot \text{s}^{-1}$, (2- dashed line) $12.7 \text{ m}^3 \cdot \text{s}^{-1}$, and (3- dotted line) $11.0 \text{ m}^3 \cdot \text{s}^{-1}$, are represented by the three curves adjacent to the fish water sluice.

Fish capture, biopsy, and tagging

Fish used in this study were individually captured by dip-net at the top pool of the fishway on Seton Dam. This location proved to be the only place where we could reliably capture fish on a regular basis, however, by catching fish here we selected a segment of the

population that had already been able to locate, enter and ascend the Seton Dam fishway. Fish for each discharge level were captured at least 24 h following a change to the water discharge rate. As fish ascended the fishway in ~1 h (Chapter 3), the physiological condition of individuals captured at the top of the fishway was expected to be representative of a recent migratory experience characteristic of the particular discharge periods they were caught under.

Following capture, fish were quickly transferred from the net to a foam-padded, v-shaped trough that was equipped with a constant supply of fresh Seton Creek water directed towards the mouth of the fish. The trough was deep enough that fish could be completely submerged and were only lifted out of water for each of the tagging and sampling procedures. Fish were initially placed ventral side up in the trough and were restrained by two sets of bare, wet hands. Blood (1.5 ml) was drawn from the caudal vein just posterior to the anal fin using a Vacutainer syringe (1.5” 21 gauge needle, 3 mL lithium heparin vacutainer, Becton Dickson, NJ). Blood samples were temporarily held on an ice-water slurry. Blood was typically drawn within the first 30 s of restraint, however if blood was not successfully drawn after 60 s, the fish was excluded from the study and released upstream of the dam. Fork length was measured and a uniquely coded cinch tag (Floy Manufacturing, Washington) was attached to the fish anterior of the dorsal fin for external recognition purposes. In order to obtain an indication of the energetic condition of fish, we assessed somatic lipid concentrations using a microwave energy meter (Distell fish fatmeter, model 692, Distell Inc., West Lothian, Scotland, UK; see Crossin and Hinch 2005). Readings were taken at two locations on the left side of the fish to be later converted to estimates of gross somatic energy density (GSE) using relationships developed by Crossin and Hinch (2005). Fish were not anaesthetised for the procedure in order to minimise handling time and related stress. The physiological biopsy procedure we used required less than two minutes, and has previously

been validated as having no ill effects on the migration success of adult sockeye salmon (Cooke et al. 2005).

We captured and biopsied 36, 16 and 20 fish during the high, medium and low, discharge periods, respectively, and a sub-sample were implanted with radio tags (13, 6, and 8; respectively) and were released downstream of the dam, and tracked as they attempted to locate and pass the fishway. A radio tag was gastrically inserted into the fish's stomach using a smooth plastic tube equipped with a plunger device. The antenna trailed posteriorly from the mouth and extended approximately 15-20 cm externally. We used two sizes of positional radio tags (Lotek Wireless, Newmarket, Ontario). Larger transmitters were 49 mm in length by 15 mm in diameter, weighed 12.5 g in air, and were inserted into larger sized fish (generally >15 cm range?). The smaller transmitters were 43 mm in length by 11 mm in diameter, weighed 7.9 g in air, and were inserted into smaller fish (generally <58 cm). In all cases, we followed the rule of less than 2% total fish weight rule with regard to the size of the transmitter (Winter 1996). Adverse influences of the transmitters on fish behaviour were not anticipated because recent studies which have compared migration times and success of adult salmon in regulated rivers have found no differences between fish carrying radio transmitters and those only carrying PIT tags (~0.1 g) which are very small relative to adult size (Matter and Sandford 2003; Rivinoja et al. 2006). After inserting the transmitter, the fish was placed in an 80 L container filled with Seton River water, and transferred to a point downstream of the fishway where it was released (see Figure 2.3). Total time from capture to release was typically 3-4 min. All procedures were approved by the UBC Animal Care Committee.

Tracking

Following release, fish movements were manually tracked using radio telemetry receivers (model SRX_400, Lotek Wireless, Newmarket Ontario) and three-element Yagi antennas. Study animals were extensively tracked throughout the study area, which extended from the top of the fishway at the dam to a point approximately 1 km downstream of the dam. Tracking occurred on a daily basis, generally beginning around 07:00 and concluding at 18:00. Tracking efforts rotated among the tagged fish (typically 3-4 at any given time), and followed individual fish movements for several minutes at a time. During this time period, we recorded the amount of time each fish spent swimming in the more turbulent water (white-water) spilled from the fish water sluice (see Figure 2.3), the time of successful fishway location (i.e. entrance), and of fishway passage.

For fish that never re-entered the fishway following release, we noted the time of last observation within the study area (within ~1 km downstream of the dam). Each evening, receivers were placed at the entrance and exit of the fishway and were set to scan through the frequencies of any tagged fish that had not previously been recorded passing through the fishway. This allowed us to confirm whether these fish were able to enter and pass the fishway, and to record the times of these events. Tracking of all individual fish continued until they either passed through the fishway or moved downstream of the lower bound of our study area, though periodic checks were made to confirm whether fish that moved downstream returned to the dam.

Physiological assays

In order to obtain an understanding of the physiological condition of fish, we used several metrics obtained from the blood samples that can be indicative of stress and exhaustive exercise. As spawning migrations are already stressful events (Hinch et al. 2006), we examined stress

indicators that generally would have been indicative of stress associated with recent physical activity. Specifically, Plasma lactate and glucose were measured, as elevated levels of these metabolites are indicative of anaerobic swimming and exhaustive exercise (Wood 1991; Barton 2002). Plasma ions (Na^+ , K^+ , Cl^-) and osmolality were measured to determine the osmoregulatory state of fish, a function which can be disturbed following prolonged or exhaustive swimming, as well as other stressors (Postlethwaite and McDonald 1995; McDonald and Milligan 1997). Similarly, hematocrit (Hct; the percent of packed red cell volume) can become elevated following vigorous aerobic exercise (Gallauger et al. 1992). We also examined cortisol because increased concentrations may occur following exposure to a stressor, or vigorous swimming activity (Wendelaar Bonga 1997), though it also increases naturally during spawning migrations of salmon (Carruth et al. 2000).

Following tagging and release of the fish, a small amount of the stored blood sample was transferred from the Vacutainer to a capillary tube to determine Hct using a Readacrit centrifuge (4.5 min at 5900 g; Clay Adams, USA). The balance of the blood sample was centrifuged using a Compact II centrifuge (6 min at 1163 g; Clay Adams, USA). Plasma was transferred into three separate 0.8 mL containers and locally stored on dry ice until they could be transferred to a -80°C freezer. Measurements of plasma concentrations of ions (Na^+ , K^+ , Cl^-), cortisol, lactate, and glucose, as well as osmolality were made following the methods outlined in Farrell et al. (2001). Plasma aliquots (5 μL) were diluted 1:200 with a $15\text{ mmol}\cdot\text{L}^{-1}$ lithium solution and measured for plasma $[\text{Na}^+]$ and $[\text{K}^+]$ using a model 510 Turner flame photometer. The photometer was calibrated prior to use, and subsequently checked against a standard after every five samples. Measurements were repeated if duplicate samples disagreed by $>2\%$. Plasma $[\text{Cl}^-]$ was measured in duplicate using a model 4425000 Haake Buchler digital chloridometer. Measurements were

repeated where duplicates disagreed by $< 2.5 \text{ mmolL}^{-1}$. Plasma osmolality was measured in duplicate on 10 μL samples using a model 5500 Wescor vapor pressure osmometer (Wescor Inc. Logan, Utah, USA). Repeat measurements were made where duplicates varied by $>3\%$. Plasma lactate and glucose levels were measured using a YSI 2300 lactate/glucose analyzer (Yellow Springs Instruments, Yellowspring, Ohio, USA). Cortisol concentrations were measured in duplicate using 96-well enzyme-linked immunosorbent assay (ELISA) kits (Neogen Corp., Lexington, Kentucky, USA). 17β -estradiol (E2) was measured using heat extraction methods described in Scott et al. (1982) and used to assign sex to individual fish. E2 measures were compared with those from non-study Gates Creek sockeye caught in 2005 for which sex was confirmed, with females generally having E2 values greater than 1.0 ng mL^{-1} (J. Hills, Fisheries and Oceans Canada, pers. comm.).

Data analysis

One-way ANOVA was used to compare mean daily water temperatures experienced by migrants during the three discharge periods. One-way ANOVAs were used to compare the physiologies of all of fish captured within the three discharge periods. Non-parametric Wilcoxon-Kruskal-Wallis tests were used where data could not be transformed to meet normality assumptions. Where significant differences were found, we used post-hoc Tukey tests to evaluate differences among the individual discharge periods. Exploratory analysis of data revealed a sex-specific difference in cortisol, a hormone which changes over the course of migration with sexual maturity (Carruth et al. 2000, 2002) and has previously be reported to be higher in mature female sockeye salmon (Kubokawa et al. 1999). Therefore, cortisol measures were compared separately by sex among each of the three discharges. Because we had sampled a disproportionately low number of females during the low discharge period ($n = 1$), cortisol was

only compared across the high and medium discharges for females. As no differences were observed for any of the other physiological measures, sexes were pooled for the remainder of analyses (Appendix 1). This is consistent with previous studies on migrating adult sockeye where sex-related differences have only been found in hormone levels and measurements of GSE taken at early stages in the migration (Cooke et al. 2006a, b; Young et al. 2006). Data for plasma lactate, glucose, and cortisol were log 10 transformed to meet normality assumptions. We compared physiological measures of our radio-tagged sub-groups of fish to non-radio tagged fish captured under the identical discharge, using one-way ANOVA.

To examine delay, we used a one-way ANOVA to compare the amount of time radio-tagged fish required to successfully pass the fishway following release. We also used a one-way ANOVA to examine the relative amount of time that fish spent in turbulent water released from the dam (see Figure 2.3) in order to get an indication of the extent to which fish were actively searching for a way upstream. To calculate this, we divided the amount of time we recorded fish swimming in turbulent water by the total amount of time fish were manually tracked within the study area. The proportions of fish that successfully re-located the fishway entrance under each of the three discharge periods were examined using a χ^2 test. We used a one-way ANOVA to compare the average fishway ascent time among the three discharge periods. All statistical analyses were conducted with SAS v. 9.1 (SAS Institute, USA). Results are reported as significant at $\alpha = 0.05$, with sequential Bonferroni corrections applied to groupings of statistical comparisons relevant to each prediction. Post-hoc power analyses were conducted to address the high number of non-significant results detected among physiological variables.

RESULTS

Mean daily water temperature at the Seton Dam significantly differed among discharge periods ($F = 11.798$, $P < 0.001$). Temperatures during the low discharge period (mean daily average (SE): 14.5 (0.2) °C) were cooler than the other periods (both $P < 0.001$), however temperatures did not differ between the high and intermediate discharge periods (mean daily average (SE): 16.1 (0.5) °C, 16.2 (0.2) °C, respectively; $P = 0.725$).

We caught and sampled 36 fish under high discharge, 16 fish under intermediate discharge, and 20 fish under low discharge. Overall, the three groups did not differ in the measured physiological variables, energy condition or size (Table 2.1). Specifically, we found no differences among groups for plasma lactate, glucose, Hct, ionic status (Na^+ , Cl^- , K^+ , osmolality), gross somatic energy or fork length (all $P > 0.05$). Among male fish, no differences were detected in cortisol levels among the three groups ($P = 0.439$). For female fish, we found no difference in cortisol among the high and the intermediate discharge groups ($P = 0.593$). The level of statistical power varied from as low as 0.07 for male cortisol levels, up to 0.55 for plasma K^+ , indicating that there was the possibility of a type 2 error in our data analysis for some of the physiological variables such as cortisol, Cl^- , and lactate among others (Table 2.1). We found no differences in the physiological measures among radio-tagged fish and the non-radio tagged fish under the high ($n = 13$, $n = 22$ respectively), intermediate ($n = 6$, $n = 10$), and low ($n = 8$, $n = 11$) discharges (all $P > 0.05$), and no differences were found among the three discharge periods in any of the physiological measures using only radio tagged fish (all $P > 0.05$). Therefore the larger sample sizes (i.e. combined radio tagged and non-radio tagged fish) were used for the analysis of associations with the delay and passage results. Means and standard

errors for both the combined and radio-tagged only groups of fish are presented for comparison (Table 2.1).

All fish that entered the fishway successfully passed the fishway. Of 13 fish tagged and released under the high discharge period, 10 (77%) fish successfully located and passed the fishway. Under the intermediate discharge period, 6 fish were tagged and released and all located and passed the fishway. Under the low discharge period, 8 fish were tagged and released, and 5 (63%) successfully located and passed the fishway. No statistical differences were detected among the proportions of successful attraction and passage under the three discharge periods ($\chi^2 = 3.841$, $P = 0.147$). Two fish were excluded from data analysis; both made a successful passage. One fish was released under high discharge and it was the only fish to move downstream out of our study area where we lost track of it for several days and could not account for its whereabouts. It re-entered our study area and ascended the fishway with a total delay time of 107 h (roughly 12-times the average delay period under the high discharge period for all other fish). The other fish was also released under high discharge and was detected swimming out of the upstream end of the fishway but was excluded because we were unable to obtain a fishway entrance time or assess time of fishway passage.

Table 2.1. Means, SE and sample sizes for physiological and condition variables measured on fish under three discharge levels are presented for all fish sampled and for the radio-tagged fish for comparison. F or χ^2 , P -values, and power statistics are presented for the contrasts within each variable for all sockeye. One-way ANOVAs were performed for most statistical comparisons with the exception of plasma Cl⁻ and osmolality, for which non-parametric Wilcoxon-Kruskal-Wallis tests were performed. Statistical significance was assessed at a Bonferroni corrected $\alpha = 0.05$ for groupings of variables: for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions, Hct), for fish condition $\alpha = 0.025$ (gross somatic energy and fork length). Measures with an asterisk were log₁₀ transformed prior to analysis but pre-transformed means and SE are presented.

Measure	Discharge	Mean ± S.E all sockeye	<i>n</i>	Mean ± S.E tagged sockeye	<i>n</i>	Statistical output (all sockeye)		
						F or χ^2	P	Power
*Plasma lactate (mmolL ⁻¹)	High	2.90±0.32	36	2.89±0.41	14	0.025	0.975	0.11
	Medium	2.33±0.31	15	2.03±0.18	6			
	Low	2.62±0.20	20	2.52±0.14	9			
*Plasma glucose (mmolL ⁻¹)	High	4.76±0.16	34	4.48±0.17	12	0.786	0.460	0.16
	Medium	4.49±0.27	16	4.37±0.24	6			
	Low	4.53±0.21	20	4.48±0.19	9			
*Plasma cortisol (ng mL ⁻¹) (Male)	High	237.64±43.38	21	224.99±60.51	8	0.842	0.439	0.07
	Medium	187.793±41.21	8					
	Low	171.93±43.37	18	181.82±62.54	7			
*Plasma cortisol (ng mL ⁻¹)(Female)	High	348.97±46.37	12	348.96±83.01	6	0.289	0.593	0.08
	Medium	317.39±62.78	11	352.73±113.73	4			
Plasma [Na ⁺] (mmolL ⁻¹)	High	148.51±1.43	36	147.43±2.37	14	2.304	0.108	0.53
	Medium	143.84±1.28	16	142.17±1.35	6			
	Low	147.65±1.39	20	143.22±0.92	9			
Plasma [Cl ⁻] (mmolL ⁻¹)	High	136.48±1.85	36	134.33±3.21	14	0.421	0.658	0.12
	Medium	134.23±2.26	16	137.93±1.27	6			
	Low	135.10±1.44	20	133.03±1.49	9			
Plasma [K ⁺] (mmolL ⁻¹)	High	2.57±0.14	36	2.75±0.18	14	2.387	0.099	0.55
	Medium	2.73±0.26	16	2.21±0.51	6			
	Low	3.11±0.18	20	3.07±0.18	9			
Osmolality (mosmolL ⁻¹)	High	304.68±2.10	36	303.04±3.80	14	1.627	0.443	0.17
	Medium	303.25±2.36	16	304.33±1.50	6			
	Low	307.13±2.08	20	304.56±1.71	9			
Hct (%)	High	39.94±0.60	36	37.64±0.91	14	0.801	0.453	0.18
	Medium	39.56±0.52	16	40.33±1.02	6			
	Low	38.70±0.94	20	38.78±1.54	9			
Gross somatic energy (MJ kg ⁻¹)	High	6.42±0.14	36	5.99±0.68	14	2.903	0.062	0.51
	Medium	5.88±0.27	16	5.38±0.57	6			
	Low	5.72±0.35	20	5.45±0.50	9			
Fork length (cm)	High	57.72±0.40	36	57.99±0.68	14	1.170	0.317	0.24
	Medium	56.50±0.69	16	56.00±0.86	6			
	Low	56.98±0.79	20	57.89±1.49	9			

Under the high discharge period, fish that successfully located and entered the fishway required an average (SE) of 9.3 (2.1) h, while under the intermediate discharge period, fish required an average (SE) of 19.9 (4.8) h to locate and enter the fishway, and under the low discharge period, fish required an average (SE) of 7.0 (1.7) h to locate and enter the fishway. ANOVA revealed a significant difference among the duration of delay for the three discharge regimes ($F = 4.616$, $P = 0.026$). Post-hoc Tukey tests revealed significant differences between the high and intermediate discharge periods ($P = 0.022$), and among the low and the intermediate discharge periods ($P = 0.015$) but not between the high and low discharge periods ($P = 0.617$). Under all discharge levels fish were generally observed alternating between holding in calm waters ~30-50 m downstream of the fishway entrance, and actively swimming near the source of attraction flow, presumably in an attempt to find a way to move upstream. Under high discharge, fish spent 27% of the time actively swimming in the turbulent water released from the fish water sluice (Figure 2.3) while under the intermediate discharge, fish spent 16%, and under the low discharge, fish spent 15%. These values however were not statistically different ($F = 1.100$, $P = 0.356$). Fishway passage times were recorded for five fish under the high discharge period (mean, (SE); 42 (6.6) min), five fish under the intermediate discharge period (49 (6.5) min), and four fish under the low discharge period (42 (3.8) min). No differences were detected among these times ($F = 0.531$, $P = 0.602$).

DISCUSSION

Anadromous salmonid migrations are physiologically stressful events. For example, cortisol levels are often elevated because of responses to transitional salinity environments experienced when moving from oceans to rivers (or vice versa), reproductive development, and

swimming challenges associated with high flow or temperatures (see Hinch et al. 2006). Thus, we need to put into perspective the relative stress levels caused by our treatments relative to what would be expected normally for the spawning migration life history stage. The prediction of higher levels of physiological stress in fish which experienced the highest attraction flows proved unfounded despite an approximately 30% difference in discharge between the high and low periods. Throughout the study period, fish were generally found to be in an ‘unstressed’ condition relative to a level of background stress expected in migrant adult sockeye. Plasma ion concentrations were consistent with those previously reported in migrating adult Fraser sockeye which had not encountered dams or fishways (Shrimpton et al. 2005; Crossin et al. 2008). Glucose and lactate levels were similar or lower than those reported for other stocks of wild migrating Fraser sockeye, caught by dipnet, and near spawning grounds which are similar approaches to those used in our study (e.g. $\sim 4.5 \text{ mmol l}^{-1}$ and $\sim 5 \text{ mmol l}^{-1}$ respectively, Young et al. 2006). In fact, lactate levels in the present study were closer to levels observed in captive adult sockeye at rest in a swim tunnel respirometer ($\sim 2 \text{ mmol l}^{-1}$) than those observed following exercise to U_{crit} (6 mmol l^{-1}) (Jain et al. 1998; Wagner et al. 2006). Plasma cortisol levels were elevated relative to what would be considered an unstressed condition, though this was to be expected as cortisol plays an important role in reproductive maturation and is naturally elevated during spawning migrations (Carruth et al. 2000, 2002). Nevertheless, plasma cortisol and Hct levels were both consistent with those reported in other sockeye populations nearing spawning grounds (Magnoni et al. 2006; Crossin et al. 2008). Collectively, our stress indicators suggested that fish were not becoming physiologically exhausted while approaching or passing the Seton River dam. Though not significantly different, there was some indication of lower energy status (GSE) in fish caught later in the study period than in those caught earlier. This is not surprising

as fish caught later in the season would have already invested more energy into reproductive development than those caught earlier (Crossin et al. 2004). Nevertheless, the trend in GSE did not appear to be related to delay as passage was slowest under the intermediate discharge period.

Despite cooler water temperatures in the Fraser River, later migrants did not appear any less stressed than earlier migrants. The lack of exercise-related stress in fish caught at Seton River dam may be due in part to relatively favourable environmental conditions in both the Fraser and Seton Rivers during the course of the Gates Creek sockeye run. In 2005, water temperature and discharge in the lower Fraser River were consistent with long term averages, and were not unusual for the time of year coinciding with our study period (Patterson et al. 2007). Average water temperatures in the Seton River were 16.3° C and 15.0° C during the months of August and September, respectively. These values are very close to the optimal temperature for aerobic scope in adult Gates Creek sockeye (16.5° C; Lee et al. 2003). Thus, the environmental conditions experienced by our fish in 2005 may have minimised migration related stress, particularly in the lead up to capture at Seton River dam. Indeed, the stress indices that we used would have primarily reflected recent environmental experiences as all typically respond to a stressor within an hour, though their expression may persist in plasma for several hours after initial response (Wendelaar Bonga 1997; Postlethwaite and McDonald 1995; McDonald and Milligan 1997).

It is possible that the range of discharges we examined was not sufficiently broad enough to include flows that would cause significant physiological stress or exhaustion to fish. However, in a companion study (Chapter 3) in which fish were implanted with electromyogram (EMG) radio transmitters and tracked in the fishway and downstream of the dam, we observed individuals swimming at speeds that occasionally approached and exceeded critical swim speeds

(U_{crit} ; i.e. anaerobic metabolism) while volitionally swimming in turbulent water (white-water) near the fish-water sluice (Appendix 2). While this phenomenon was observed under both the high and intermediate discharge periods, fish generally did not swim at these speeds for extended periods of time. Furthermore, EMG data revealed that several fish which successfully ascended the fishway were clearly employing swimming tactics in the fishway to minimize energy costs during their ascent (Chapter 3). Thus, high discharge does not necessarily impart an increased physiological demand, as fish may be able to use reverse flows or upwellings created by structures downstream of the dam to minimise swimming efforts. Such behaviours have previously been observed in upriver migrating sockeye (Hinch et al. 2002), and have been shown to allow fish to hold position in flowing water while expending little energy (Liao et al. 2003). Indeed, in the present study, fish were commonly observed swimming near concrete baffles designed to interrupt and dissipate flow emanating from the dam, suggesting that they may have been using reverse flow fields to aid in their migration (e.g. Hinch and Rand 2000).

Though we found no differences in the physiological condition among fish caught under the three discharge periods, we did find that fish were delayed over twice as long under the intermediate one, than either high or low discharge periods. Water temperature did not appear to be a significant factor affecting delay as we found no difference in temperature between the high and intermediate discharge periods, despite a clear difference in migration delay between them. Water temperatures were slightly cooler (an average decline of ~ 2 °C) during the lowest, and final, discharge period, yet migration delay was the same as that observed during the highest, and first, discharge period. If temperature were to be a major factor affecting delay, we would have expected that delay would have been longest during the lowest discharge period because

temperatures were closest to optimal for maximum aerobic scope in adult Gates Creek sockeye (Lee et al. 2003) during the high and intermediate discharge periods.

Fishway passage time did not differ among the three discharge periods, and was generally under an hour, suggesting that locating the fishway entrance was the primary mechanism in passage delay. Previous studies that have found differences in fishway attraction in relation to flow have typically compared only two flow periods (e.g. Moser et al. 2000; Laine et al. 2002), or describe a linear trend of increased delay with decreasing attraction flows (e.g. Winter 2007). In such cases, the rationale behind attraction improvement is that increases to attraction water helps to distinguish flow emanating from the fishway relative to other point sources along the dam (Larinier 1998). At many dams, attraction flow ‘competes’ with other flows, and as a result fish may ignore the entrance as they pursue stronger currents elsewhere (Schwalme et al. 1985; Gowans et al. 1999; Bunt 2001; Karppinen et al. 2002). At the Seton River dam, however, all water discharged during the present study was released adjacent to the fishway entrance as ‘attraction flow’ indicating that other factors were responsible for the discharge-related differences we observed in delay. Regardless, our results demonstrate that there need not be a straight forward relationship between increasing attraction flow levels and reductions in delay.

It is possible that currents created by the highest and lowest discharge periods offered better directional cues for locating the fishway entrance and more direct pathways towards the entrance. As migrant adult salmon are negatively rheotactic they tend to orient into currents, but complex flow patterns may disrupt directional cues and cause delay in migrant salmon (Hinch and Rand 1998; Hinch et al. 2006). When confronted with fast flows, migrating salmon seek out and exploit low flow paths and reverse-flow vortices, often near river banks, as they travel upstream (Hinch and Rand 2000; Hinch et al. 2006). The high discharge period at Seton River

dam may have discouraged fish from swimming in the centre of the channel where water velocities would have been greatest and the most turbulent. Turbulent waters can increase the energetic cost of swimming (Hinch and Rand 1998; Enders et al. 2003), and fish may avoid these areas (Smith et al. 2005; Cotel et al. 2006). Instead, fish may have been attracted to the more laminar flows associated with the ~ 40 m wall of the fishway structure, which forms the river's south bank, and consequently could have tracked relatively directly towards the fishway entrance. In contrast, under reduced discharge periods (intermediate and low flow) fish may have attempted to make forward progress in pathways away from the south bank, where water was more turbulent. Under the low discharge period, the water directly emanating from the fishway entrance (11% of total dam spillage) may have generated more distinctive directional cues than under intermediate discharge where fishway flows are more dilute (9% of total dam spillage). Thus, fish may have been able to locate the fishway entrance more readily under the low discharge period than under the intermediate discharge period. To fully address these issues, a thorough investigation of flow hydraulics and fish migration pathways is needed under different discharge levels at our study site.

Of the 27 tagged fish released over three operational discharge levels, six fish did not re-enter the fishway and hence failed to migrate past the dam. This represents an attraction efficiency of 78%. However, because we caught fish from within the fishway structure, we were unable to sample 'fishway-naïve' fish, and consequently, our estimates of attraction efficiency may have been conservative. Other studies of adult migrating salmon have reported both lower and higher rates of passage failure. However, comparisons of studies may be difficult to make due to variation in the migration stage of fish, fish-handling procedures, and unique river conditions. Nevertheless, Brown et al. (2006) reported that 18% of tagged Chinook salmon

failed to pass the Bonneville dam on the Columbia River, USA. Other estimates of passage failure at dams along the Columbia River have been much lower (e.g. 2-10%) (Bjornn et al. 1995; Keefer et al. 2007, 2008), though the cumulative effects of multiple dams may ultimately be the more important factor limiting passage on heavily regulated rivers (Naughton et al. 2005). At Hells Gate rapids on the Fraser River, 25% of migrant sockeye salmon were unsuccessful at passage despite the presence of fishways (Hinch and Bratty 2000). As in the present study however, these studies also examined fish that had previously demonstrated the ability to locate and enter the fishways at their respective study locations. In contrast, a study that examined passage using fish captured at a location downstream of the dam reported passage failure rates of up to 37% among Atlantic salmon (*Salmo salar*) moving through the River Conon system, northern Scotland (Gowans et al. 1999). Passage failure at the Seton River dam may have proved higher than 22% if we had been able to capture ‘fishway-naïve’ fish.

There is a distinct lack of studies that have truly estimated the impact a dam has on preventing a segment of a migrating population from passing upstream; this is perhaps due in part to a lack of established protocols. Ideally, a study should be able to identify where passage exclusion can be attributed specifically to the presence of a dam, as well as the magnitude of this effect. For telemetry based studies, efforts should be made to intercept migrant fish at a location downstream of the dam in order to sample fish that are naïve to the presence of existing passage routes. Tracking efforts of fish movements must have high detection efficiency in order to accurately compare the number of fish that approach the dam, with the number of fish that successfully pass the dam. It is also important to consider the motivation for a fish to pass. If viable spawning habitats exist both upstream and downstream of a dam it may be more difficult to determine the effect a dam has on migration, as fish may not need to pass upstream. Inclusion

of physiological measures may also help in assessing the impact of a dam on migrant fish as demonstrated in the present study. However, in light of the low statistical power observations, it is important to consider the expected effect size, and sample accordingly.

The results from the present study support the notion that manipulation of attraction water discharge can be a viable means of reducing the amount of time that migrant fish are delayed downstream of a dam. However, there are obvious limitations to this approach that must be taken into consideration prior to implementing operational changes. The uniqueness of each dam site means that effective attraction water flows at one location may not be effective at another (Bunt 2001; Sprankle 2005). Therefore, the discharge values presented here should not be considered as specific management recommendations for sockeye salmon. Instead, a range of appropriate flows should be examined using an adaptive management approach specific for a given site and operational conditions. Additionally, management decisions must take into consideration several limits to the range of potential attraction water discharges. As in the case of the Seton River dam, where all flow is spilled as attraction water, a minimum limit may be set by the minimum flow requirement for the protection of downstream habitat and access (Richter et al. 1997). In other cases, minimum discharges of attraction water may have to be considered within the context of other flows emanating from dam sites, as false attraction may occur where fish are distracted by stronger flows elsewhere (Bunt et al. 1999). Maximum discharge may be limited by the swimming capacity of target fish species, and should be designed to accommodate the weakest swimming species where multiple species use the fishway (Schwalme et al. 1985; Peake et al. 1997).

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CHAPTER 3

Physiological, energetic, and behavioural correlates of successful fishway passage in a population of adult sockeye salmon (*Oncorhynchus nerka*) in the Seton River, British Columbia²

INTRODUCTION

Reproductive migrations of anadromous adult Pacific salmon (*Oncorhynchus* spp.) from ocean feeding grounds to natal freshwater streams are physiologically challenging and energetically demanding, particularly for populations that must travel long distances or pass through hydraulically complex reaches en route to spawning locations (Bernatchez and Dodson 1987; Brett 1995; Hinch et al. 2006). Adult salmon bound for spawning grounds stop feeding prior to entering freshwater and rely exclusively on energy reserves to reach spawning grounds, complete sexual maturation, and engage in spawning events (Brett 1995). Because Pacific salmon are semelparous, (i.e. die following reproduction) the ability to successfully reach spawning grounds with adequate energy reserves to complete gonad development and engage in spawning activities is imperative to their life-time fitness (Burgner 1991).

Anthropogenic migration barriers have dramatically reduced the number and size of salmon populations, and have become increasingly commonplace in the last century with the construction of hydropower facilities and other waterway alterations (Odeh 1999). Dam construction has led to the extirpation of hundreds of Pacific salmon populations in the United States (Nehlsen et al. 1991), and dozens in British Columbia (Slaney et al. 1996), often because migration routes were made impassable and prevented salmon from reaching terminal spawning grounds (Odeh 1999; Keefer et al. 2004). In some cases, fishways or other passage structures have been constructed to facilitate migrations past dams (Clay 1961). Nevertheless, a segment of

² A version of this chapter will be submitted for publication. Pon, L.B., S.G. Hinch, S.J. Cooke, D.A. Patterson, and A.P. Farrell. Physiological, energetic, and behavioural correlates of successful fishway passage in a population of adult sockeye salmon (*Oncorhynchus nerka*) in the Seton River, British Columbia

migrant fish are often unable to pass despite the presence of a fishway [e.g. Bonneville Dam, Columbia River, USA, 18% of adult Chinook salmon (*O. tshawytscha*), (Brown et al. 2006); Hells Gate rapids, Fraser River, British Columbia, Canada, 25% of adult sockeye salmon (*O. nerka*), (Hinch and Bratty 2000); River Conon system, northern Scotland, up to 37% of adult Atlantic salmon (*Salmo salar*), (Gowans et al. 2003)]. Though in some cases fishways may present velocity barriers to passage (Haro et al. 2004; Castro-Santos 2005), few studies have documented the scope of this issue and such observations raise the question of why some adult migrants within a run can successfully ascend fishways while others are unsuccessful.

Hinch and Bratty (2000) observed differences between successful and unsuccessful adult sockeye salmon migrating through the Hells Gate rapids and fishway in the Fraser River using electromyogram (EMG) telemetry and behavioural observations. Unsuccessful fish were characterized by repeated attempts to enter the fishway, extended periods (i.e. several hours) of bursting to swimming speeds beyond critical swim speeds (U_{crit} ; i.e. anaerobic metabolism), and were frequently observed swimming in areas of relatively higher water velocity and turbulence in the approach to the fishway. In contrast, the successful fish entered the fishway upon first attempt, spent relatively little time swimming at fast speeds and swam in areas where water velocity was slower. Hinch and Bratty (2000) suggested that failure to pass into and through the Hells Gate fishway may have been related to elevated physiological stress and physical exhaustion in fish which chose to migrate in fast and turbulent flows. Interestingly, some species of fish are able to successfully migrate through fast flows using very slow swim speeds by utilizing reverse flow fields, boundary layers and other behavioural tactics (Hinch et al. 2002; Liao et al. 2003). However, there have been no studies to assess how physiological condition may affect the behavioural tactics used in and around fishways with fast or turbulent flows.

Recent biopsy-telemetry studies in the main stem of the Fraser River found that sockeye salmon that failed to reach spawning grounds had higher physiological stress levels as indicated by elevated plasma lactate, glucose and plasma ions compared with fish that successfully reached spawning grounds (Cooke et al. 2006a,b; Young et al. 2006). Thus, hydraulically challenging sections of rivers and fish passage structures may not only cause physiological exhaustion and stress, but also act as bottlenecks for migrating salmon, specifically selecting against fish that already have relatively higher levels of physiological stress. This is perhaps not an unexpected finding given a much larger data base for laboratory studies, which clearly show that fish swimming at speeds in excess of U_{crit} for extended periods of time will experience physiological stress, including ionic and osmotic disturbances, the depletion of tissue energy stores (e.g., glycogen, ATP, phosphocreatine), the accumulation of high levels of lactate, and metabolic acidosis that can result in death (Black et al. 1962; Wood et al. 1983; Wood 1991; Jain et al. 1998; Kieffer 2000). Minimally this type of exhaustive exercise impairs subsequent swimming capabilities and necessitates long recovery periods from exhaustion (Stevens and Black 1966; Wedemeyer et al. 1990; Kieffer 2000; Peake and Farrell 2004). Thus, the ability to migrate through hydraulically fast and complex riverine areas, such as those near and in fishways, may be compromised in individuals that become physiologically exhausted and stressed (Jain et al. 1998; Hinch et al. 2006).

The present study investigated the linkage between physiological condition, energetics, and swimming behaviour and the ability of migrating adult sockeye salmon to successfully pass through a vertical slot fishway en route to spawning grounds. EMG radio telemetry (Cooke et al. 2004) was used in combination with biopsy sampling to obtain tissue samples for physiological analysis (Cooke et al. 2005) to test two predictions: a) that sockeye salmon which successfully

ascend a fishway are characterized by lower levels of physiological stress relative to sockeye salmon that are unsuccessful in ascending, and b) that successful migrants display much lower swim speeds and consequently exhibit lower energy use than unsuccessful migrants.

METHODS

Study site

The study took place at and immediately downstream of the Seton Dam approximately 5 km southwest of Lillooet, British Columbia, Canada (Figure 3.1). The Seton Dam and fishway were constructed in 1956, and is only one of two fishway-equipped dam facilities operated by BC Hydro in British Columbia. The Seton Dam is a diversion dam that spans the Seton River. The dam maintains base flow through the Seton River while routing excess water down a 4 km long canal to the Seton powerhouse located at the Fraser River just downstream of the Seton-Fraser confluence. Fish access to habitats upstream of the Seton Dam is enabled by a vertical-slot fishway located adjacent to the primary spillway. The fishway consists of 32 pools separated by concrete baffles, and makes two 180° turns and thus has two primary corner resting pools (Figure 3.2). The fishway has a length of 107 m and an elevation of 7.4 m, creating an effective slope of 6.9%. Vertical-slot type fishways are characterized by a series of pools separated by baffles designed to dissipate flows and create areas of refuge within the fishway. Maximum water discharge can reach $1.3 \text{ m}^3 \text{ s}^{-1}$, and water velocities can range from negligible to 2.1 m s^{-1} . Water flow through the fishway is determined by the fore-bay head and is unregulated, but was at a consistent height throughout the study period.

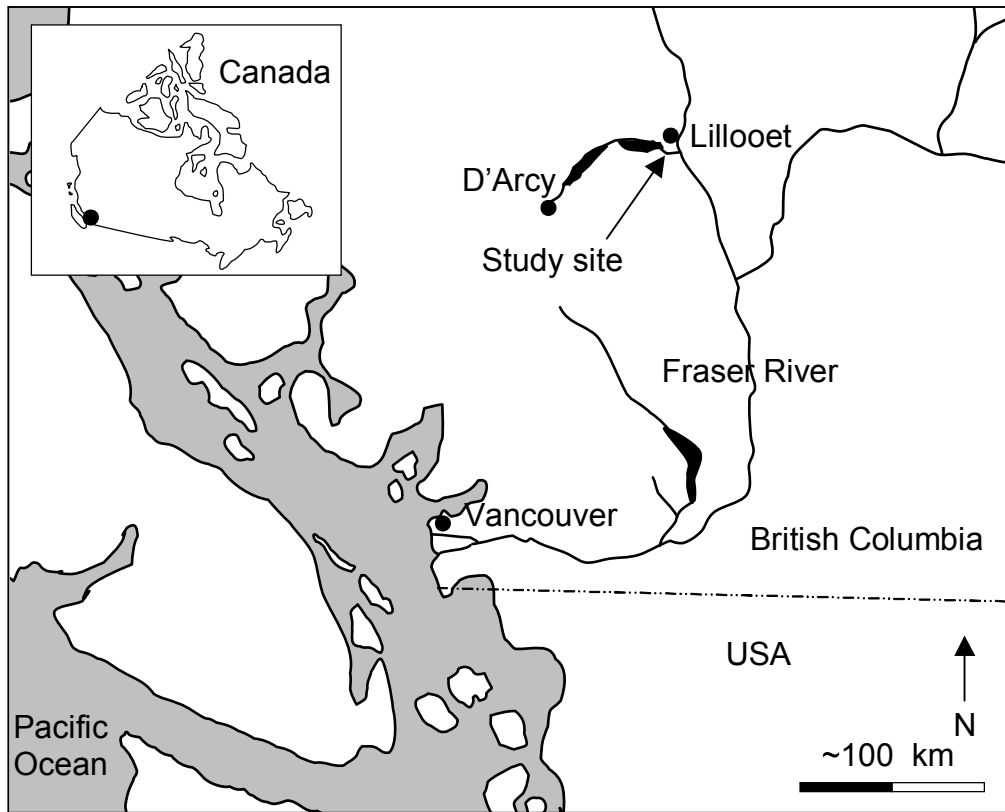


Figure 3.1. Map of south-western British Columbia, showing the location of the study site along the migration route of Gates Creek sockeye salmon, and inset map showing relative location in Canada. Fish were captured, tagged and tracked on site at the Seton River dam, approximately 5 km southwest of Lillooet, B.C. Terminal spawning grounds for this stock are located upstream of the Seton River dam site and near D’Arcy, B.C.

Our study focussed on sockeye salmon, bound for the Gates Creek spawning channel. The abundance of adult Gates Creek sockeye has declined precipitously over the past 12 years and has been categorized as ‘critically endangered’ by a recent IUCN assessment of global sockeye population status (Rand in review). Gates Creek sockeye are classified as a ‘summer-run’ Fraser River stock, with upriver migrations taking place between late July and early September. To reach the dam and fishway, sockeye salmon have already swum approximately 350 river km upstream from the mouth of the Fraser River (Figure 3.1). Upstream of the Seton Dam, Gates Creek sockeye must travel a further 50 km through Seton and Anderson Lakes in

order to reach spawning areas. Therefore, Gates Creek adult sockeye would have completed approximately 88% of the total distance of their upriver migration by the time they reach our study site.

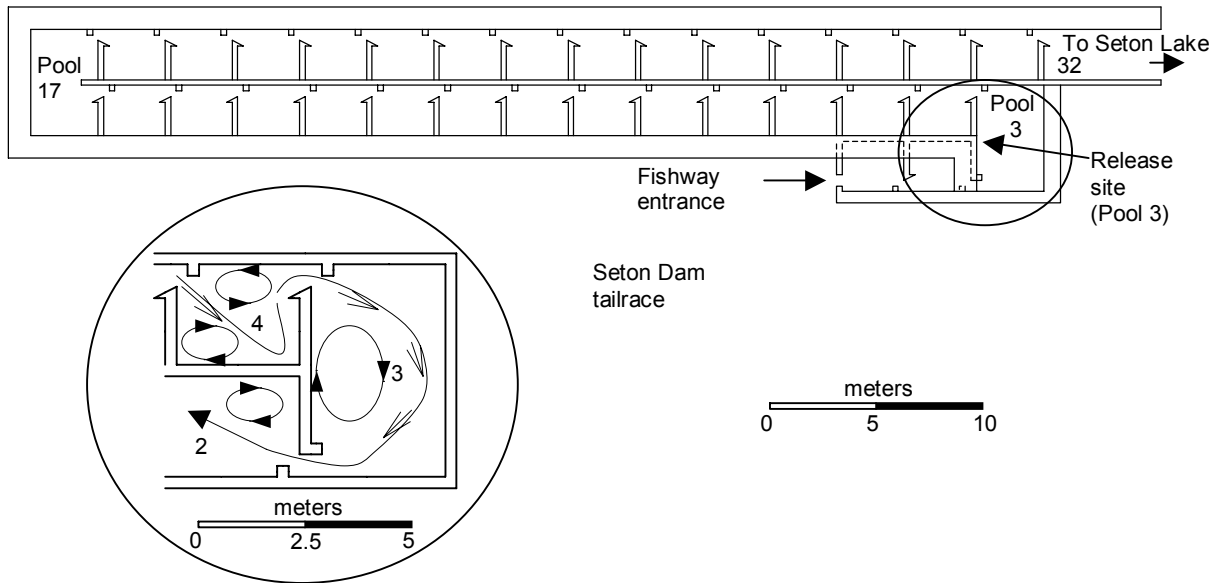


Figure 3.2. Overhead schematic of the Seton River fishway layout. Tagged fish were released in a low velocity area within pool number three as indicated by the arrow. Fish movements were tracked by hand from the catwalk running the length of the fishway. Note the inset detail showing a generalized pattern of the flow within each of the two representative pool types.

Fish capture, biopsy sampling, and tagging

Thirteen adult sockeye were captured by dip-net at the top pool of the fishway (Figure 3.2) as they migrated upstream during the period of August 11 to August 28, 2005 at the Seton Dam. This location was selected because fish could be captured quickly and consistently throughout the study period. This method of capture occurred quickly (<10 s), minimised the amount of time between capture and biopsy, and minimised handling-induced alterations to the

physiological variables that were being measured (although we recognize that capture created a response that was not measured). Fish were caught individually and immediately transferred (<10 seconds of net handling and air exposure) from the net to a foam-padded, v-shaped trough, which was continually supplied with fresh Seton River water directed through a tube aimed at the mouth of the fish. Once in the trough, fish were completely submerged in water and were only partially raised out for the biopsy procedures. Each fish was restrained in the trough by two people with bare, wet hands, while a third immediately sampled tissues. The biopsy sampling process included several procedures that have previously been validated as having no ill effects on survival or migration rates of adult sockeye salmon released back to the ocean (Cooke et al. 2005).

Blood (1.5 ml) was drawn from the caudal vein just posterior to the anal fin using a Vacutainer syringe (1.5” 21 gauge needle, 3 mL lithium heparin vacutainer, Becton Dickson, NJ) typically drawn within the first 30 s of restraint. However, fish were excluded from the study and released upstream of the dam if blood was not successfully drawn after 60 s. Blood was held in an ice-water slurry prior to centrifugation within 20 min and plasma storage on dry ice. Following blood sampling, light pressure was applied to the puncture wound to encourage blood clotting, while fork length was measured to the nearest 0.5 cm using a ruler built into one side of the holding trough. Following these procedures (generally lasting < 1 minute), the fish was gently transferred to an 80 L anaesthetic bath of MS-222 (tricaine methanesulfonate) ($65 \text{ mg}\cdot\text{L}^{-1}$) buffered with CaCO_3 ($65 \text{ mg}\cdot\text{L}^{-1}$) in preparation for surgical tag implantation. Somatic lipid concentration was assessed using a microwave energy meter (Distell fish fatmeter, model 692, Distell Inc., West Lothian, Scotland, UK; see Crossin and Hinch 2005) once the fish was sedated. Readings were taken at two locations on the left side of the fish to be later converted to

estimates of gross somatic energy density (GSE) using relationships developed by Crossin and Hinch (2005). A uniquely coded cinch tag (Floy Manufacturing, Washington) was attached to the anterior of the dorsal fin of the fully anaesthetised fish for external recognition purposes before the fish was transferred to the surgery trough where buffered anaesthetic (30 mg MS-222 L⁻¹) was pumped through tubes inserted into the oral cavity and out across the gills of the fish to maintain an anaesthetised state.

Non-coded EMG transmitters (cylindrically shaped, 53 mm length, 16 mm diameter and 18.5 g mass, and were equipped with 16 mm, 9 carat gold tips; Lotek Engineering, Newmarket, Ontario) were implanted followed techniques described in Hinch et al. (1996). Further descriptions of EMG transmitters can be found in Cooke et al. (2004). In brief, tags were inserted into the body cavity through a 2.5-3 cm ventral incision made just anterior of the pelvic girdle. Two electrode leads were placed into the red axial musculature just under the skin along the lateral line, and approximately 1 cm apart using a purpose-built pair of stainless steel plungers. The transmitter antenna was threaded through a small exit hole 1 cm posterior of the incision. The incision was then closed with 5-6 independent sutures (2-0 Ethicon braided silk, Markham, Ontario). Following surgery, the fish was transferred to a 100 L recovery tank equipped with a constant flow of fresh water. The entire surgical procedure took 5 to 6 minutes to complete.

Fish were held in recovery for approximately 2 h during which time, they were monitored for signs of recovery. This period of time was deemed adequate for recovery based on observations of regained equilibrium and increasing restlessness within the recovery tank. Following recovery, fish were released near the bottom of the fishway in pool number 3 (Figure 3.2). This particular release site represented one of two pools within the fishway that turned 180°

and was chosen because it had relatively large areas of low-flow velocities compared to the other pools near the downstream end of the fishway. To minimise the chance of disoriented fish being immediately flushed out of the fishway following release, fish were specifically released into a section of the pool where flow velocity was minimal (see inset Figure 3.2). By releasing fish within the fishway as opposed to the tailrace of the dam, we were able to provide a common challenge metric for all fish, and eliminate variability associated with fish attempting to locate the fishway entrance. Fish were lowered to the water using a knotless nylon-lined basket that was moistened prior to introducing the fish. Air exposure immediately prior to release was <10 s. A separate study examining the ability of Gates Creek sockeye to re-locate the fishway entrance is reported in Chapter 2. All procedures were approved by the UBC Animal Care Committee.

Immediately after release, fish were tracked by hand throughout the fishway using data-logging receivers (Lotek model SRX_400) equipped with hand-held three-element Yagi antennas. Because all fish were manually tracked, the detailed movements of fish were closely followed with a high degree of precision to accurately describe specific movements such as forays into adjacent pools within the fishway structure. The timing of specific fish movements within the fishway were recorded and later aligned with the time-stamped EMG pulse interval data. This allowed a recreation of the post-release history of each fish's swimming activity, describing both the timing and physical intensity of every significant movement within the fishway. Fish were classified as either 'successful' if they ascended and exited the upstream end of the fishway or 'unsuccessful' if they did not re-ascend the fishway and fell back out of the fishway entrance into the tailrace of the dam. All fish were continuously tracked while in the

fishway structure until they either reached the top pool of the fishway or moved downstream and into the dam tailrace.

Physiological assays

A small amount of the blood sample was transferred from the Vacutainer to a capillary tube to determine hematocrit (Hct; the percent of packed red cell volume) using a Readacrit centrifuge (4.5 min at 5900 g; Clay Adams, USA). The balance of the blood sample was centrifuged using a Compact II centrifuge (6 min at 1163 g; Clay Adams, USA). Plasma was transferred into three separate 0.8 ml containers and locally stored on dry ice until they could be transferred to a -80° C freezer.

Measurements of plasma concentrations of ions (Na^+ , K^+ , Cl^-), cortisol, lactate and glucose, as well as osmolality were made following the methods outlined in Farrell et al. (2001) to assess the physiological condition of the fish at capture, (i.e. following their first ascent of the fishway). Plasma aliquots (5 μL) were diluted 1:200 with a 15 mmol L^{-1} lithium solution and measured for plasma $[\text{Na}^+]$ and $[\text{K}^+]$ using a model 510 Turner flame photometer. The photometer was calibrated prior to use, and subsequently checked against a standard after every five samples. Measurements were repeated if duplicate samples disagreed by $>2\%$. Plasma $[\text{Cl}^-]$ was measured in duplicate using a model 4425000 Haake Buchler digital chloridometer. Measurements were repeated where duplicates disagreed by $< 2.5 \text{ mmol L}^{-1}$. Plasma osmolality was measured in duplicate on 10 μL samples using a model 5500 Wescor vapor pressure osmometer (Wescor Inc. Logan, Utah, USA). Repeat measurements were made where duplicates varied by $>3\%$. Plasma lactate and glucose levels were measured using a YSI 2300 lactate/glucose analyzer (Yellow Springs Instruments, Yellow Springs, Ohio, USA). Cortisol concentrations were measured in duplicate using 96-well enzyme-linked immunosorbent assay

(ELISA) kits (Neogen Corp., Lexington, Kentucky, USA). 17β -estradiol (E2) was measured using heat extraction methods described in Scott et al. (1982) and used to assign sex to individual fish. E2 measures were compared with those from non-study Gates Creek sockeye caught in 2005 for which sex was confirmed, with females generally having E2 values greater than 1.0 ng mL^{-1} (J. Hills, Fisheries and Oceans Canada, pers. comm.).

Data analysis and statistics

All recorded EMG pulse interval data were converted into instantaneous swim speeds (cm s^{-1}) following equations developed from the relationship between EMG pulse intervals and swim speeds, which are described in Hinch and Rand (1998). Using swim speed (cm s^{-1}), temperature ($^{\circ}\text{C}$), and fish mass (g) data, we estimated energy use ($\text{cal g}^{-1} \text{ h}^{-1}$) following the equation described in Healey et al. (2003). Because we did not measure individual mass of study animals, it was estimated using sex-specific regressions developed from fork length and mass data collected from other Gates Creek sockeye captured at Seton Dam in August, 2005 (D. Patterson, Fisheries and Oceans Canada, unpublished data). Length-mass regression equations were developed for males: $\text{mass} = 84.299 * \text{length} - 2871.3$, ($r^2 = 0.830$; $n = 18$), and for females: $\text{mass} = 117.47 * \text{length} - 4835.6$, ($r^2 = 0.874$, $n = 21$). Exploratory analysis of the data revealed no differences between sexes (all physiological variables, swim speed, and energy use) so sexes were pooled for subsequent analysis (Appendix 1). This observation is generally consistent with previous studies on migrating adult sockeye where sex-related differences have only been found in hormone levels and measurements of GSE taken at early stages in the migration (Cooke et al. 2006a, b; Young et al. 2006).

While observing fish swimming in the fishway, it became apparent that swim behaviours exhibited while moving within and between pools varied appreciably among individuals. To

quantify this observation, average swim speeds were calculated for each individual while they were: a) holding position within a pool of the fishways and not advancing or attempting to advance into an adjacent pool (termed ‘holding speeds’), and, b) actively moving or attempting to move into an adjacent pool (termed ‘progress speeds’). By plotting the ratio of mean holding speed to mean progress speed in pool 3 (the release site) for each individual, two different swimming strategies were identified ($n = 5$ fish per group; three fish could not be classified, one due to a faulty transmitter, and the other two did not demonstrate progress speeds before falling back; see Figure 3.3). One strategy was termed the ‘vigorous swimming strategy’ having a ratio >0.3 and the other termed the ‘conservative swimming strategy’ having a ratio < 0.15 . To confirm that these two strategies indeed reflected different energetic or behavioural classes of fish, we statistically contrasted the two groups in terms of mean individual: swim speed, holding speed, progress speed, and energy use using a series of ANOVAs. Lastly, we explored if there were any physiological differences between fish which adopted a conservative versus vigorous strategy by comparing plasma stress indicators, GSE, and Hct between fish in these two groups using a series of one-way ANOVAs.

To examine the prediction that passage success was related to initial physiological condition we compared plasma metabolites, ion concentrations, cortisol, GSE, and Hct using a series of one-way ANOVAs with fate (i.e. successful or unsuccessful) as the effect. To examine the predictions that energetics, swimming behaviour or swimming strategy affected fish fate, we compared average individual swim speeds, average individual holding speeds, average individual progress speeds, average individual energy use, and duration of residency in the release pool, between successful and unsuccessful fish, using a series of one-way ANOVAs. We also examined whether fish size (e.g. fork length) differed between successful and unsuccessful fish

using ANOVA. Because we had low sample sizes, power analyses were conducted for all comparisons. All statistical analyses were conducted using SAS v. 9.1 (SAS Institute, USA). Results are reported for significance at $\alpha = 0.05$, with sequential Bonferroni corrections applied to groupings of statistical comparisons relevant to each prediction. Bonferroni corrections can be highly conservative where many variables are compared, so we also present uncorrected P -values, and allow the reader to perform their own assessment of significance criteria (Moran 2003).

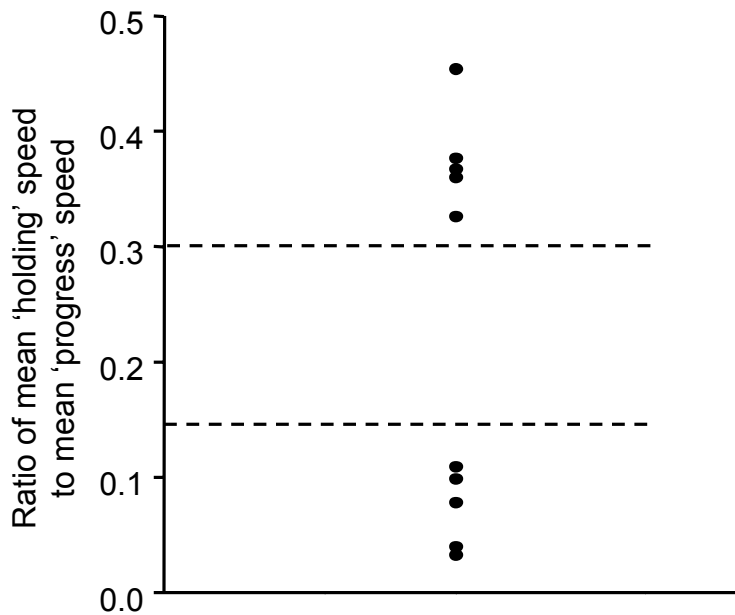


Figure 3.3. Detail of the classification basis for the two swim strategies. Vigorous strategy fish ($n = 5$) demonstrated mean holding speeds (i.e. no forward movement) greater than 0.30 of the observed mean progress speed (i.e. movements or attempts to move into the adjacent upstream pool). Conservative strategy fish ($n = 5$) demonstrated mean holding speeds less than 0.15 of the mean progress speed. Mean holding speed and mean progress speed are individual-specific values calculated from all swim speeds recorded in pool 3 (release site). Three fish could not be classified due to either a faulty transmitter, or an absence of recorded progress speeds.

RESULTS

During August of 2005, Gates Creek sockeye experienced a mean daily water temperatures of $\sim 18^{\circ}\text{C}$ and a mean daily discharge level of $\sim 2800 \text{ m}^3 \text{ s}^{-1}$ in the lower Fraser

River. During our experiments in August in the Seton River mean daily water temperatures ranged from 14.8°C to 18.8°C and averaged 16.3 ° C, while water discharge was $\sim 15.8 \text{ m}^3 \cdot \text{s}^{-1}$. All but one fish maintained position within pool 3 for at least 10 min following release, and all fish were observed actively swimming in the vicinity of the entrance to pool 4, suggesting that fish were indeed attempting to move up the fishway. Of the 13 tagged fish, seven successfully re-ascended the fishway. Of those, EMG recordings of passage were made for all but one whose transmitter was faulty. Six fish were unsuccessful in re-ascending the fishway, and all eventually fell back out of the fishway and into the tailrace area immediately downstream of the fishway entrance. Unsuccessful fish were observed to remain in the tailrace of the dam for $36.6 \pm 14.4 \text{ h}$ ($\bar{x} \pm S.E.$), and during this time fish appeared to be attempting to find a means of upstream passage by swimming in turbulent water discharged from the dam (Appendix 2). No difference in fork length was found between successful and unsuccessful fish ($P = 0.678$). Sample sizes were too small to statistically assess for sex-related effects on passage success (successful fish - 4 females, 3 males; unsuccessful fish - 2 females, 4 males) and on swimming strategies (conservative strategy - 2 females, 3 males; vigorous strategy - 3 females, 2 males).

The average residency time spent at the release site (pool 3) prior to moving either upstream or falling back downstream was similar between successful and unsuccessful fish ($P = 0.611$) as was their mean swim speed ($P = 0.230$) and mean energy expenditure ($P = 0.237$) (Table 3.1). Equal numbers of successful fish and unsuccessful fish adopted the two strategies with three successful fish and two unsuccessful fish for each strategy. Mean swim speeds clearly distinguished the two swimming strategies, with the mean speed for the vigorous swimming strategy being nearly 8-times faster than the conservative swimming strategy ($\bar{x} \pm S.E.$; $38.65 \pm 12.57 \text{ cm} \cdot \text{s}^{-1}$, $4.93 \pm 1.03 \text{ cm} \cdot \text{s}^{-1}$, respectively; $P = 0.002$). This difference was reflected in a

nearly 5-times greater energy use for the vigorous swimming strategy compared to the conservative swimming strategy ($1.01 \pm 0.39 \text{ cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, $0.21 \pm 0.01 \text{ cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, respectively; $P = 0.020$; though not significant under Bonferroni correction) (Table 3.2). Mean holding speed for vigorous swimming strategy was over 7-times greater than those of conservative swimming strategy ($31.65 \pm 9.22 \text{ cm} \cdot \text{s}^{-1}$, $4.27 \pm 0.84 \text{ cm} \cdot \text{s}^{-1}$, respectively; $P < 0.001$). No difference was detected between the swim strategies for mean progress speed ($P = 0.591$) (Table 3.2).

Fish demonstrating the vigorous swimming strategy employed frequent bursts of swimming effort to maintain their position and avoid being washed down the fishway and did not appear to take advantage of low velocity areas within the fishway structure to the same extent that the conservative strategy fish did. Lacking forward progress, these bursts of activity often approached the speeds observed for pool-to-pool movements within the fishway (Figure 3.4). Even so, we rarely observed swimming efforts in excess of U_{crit} for extended periods of time during fishway ascent (Figure 3.4).

Among successful fish, the more conservative swim strategy was primarily characterized by fish alternating between short bursts of intensive forward movements between pools and followed by extended periods of lower intensity holding within the fishway (see fish numbers 3024, 3025, and 3042 in Figure 3.5). Low intensity swimming was often associated with observations of fish locating themselves within low-velocity areas of the fishway. In contrast, fish demonstrating the more vigorous swimming strategy had a less varied pattern of instantaneous swim speeds, lacking the distinctive holding periods in between bouts of forward progress (see fish numbers 3020, 3040, and 3079 in Figure 3.5). Further comparisons of the two swim strategies can be found in Appendix 3.

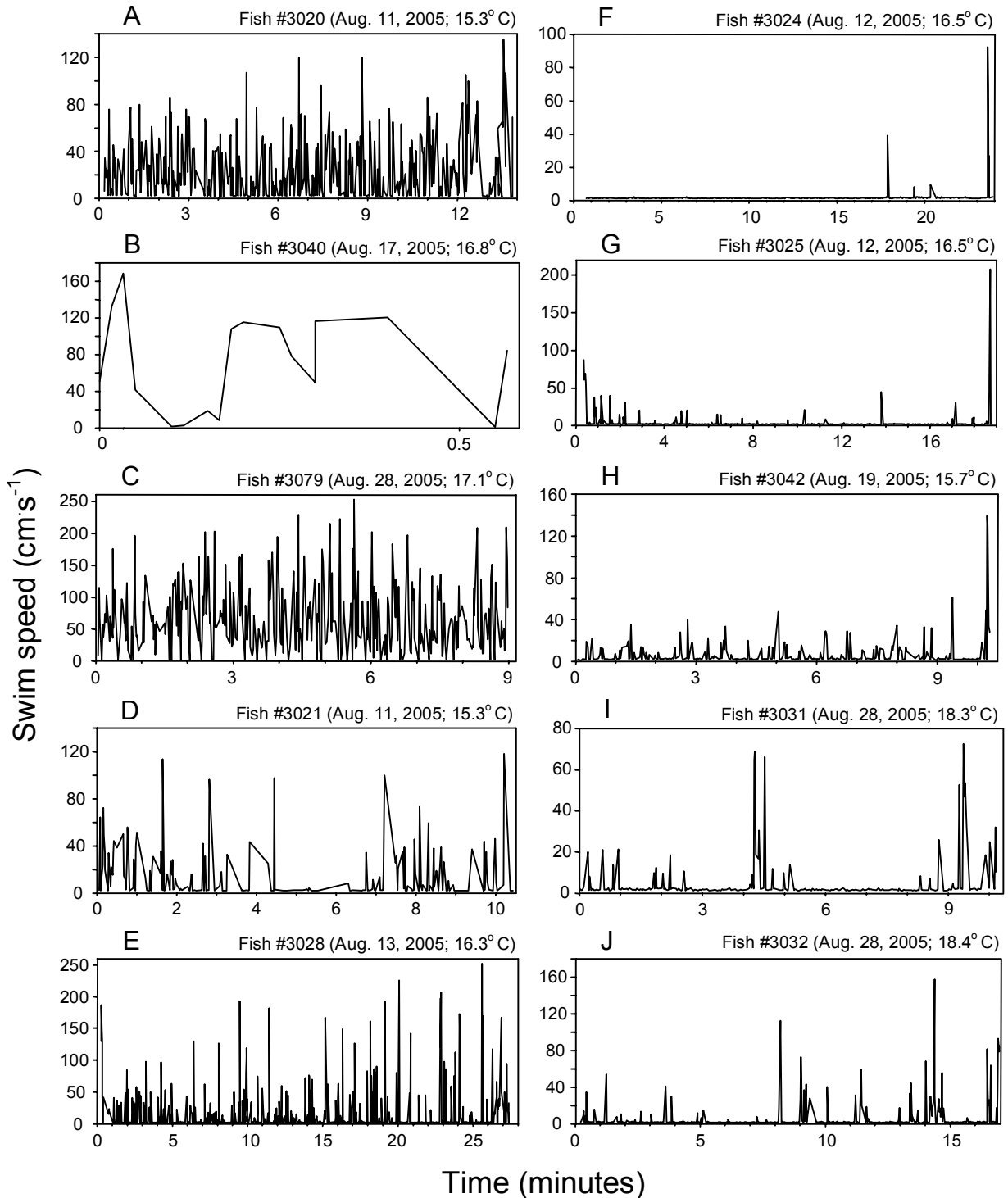


Figure 3.4. Plots of instantaneous swim speed estimates from EMG pulse interval data contrasting fish from the vigorous swim strategy (graphs A through E), and the conservative swim strategy (graphs F through J). Each graph represents the total time spent at the release site (i.e. pool 3) prior to upstream or downstream movement. From each strategy, three fish were successful (A,B,C,F,G, and H) and two were unsuccessful (D,E,I, and J). Note the variation in individual y-axis scales.

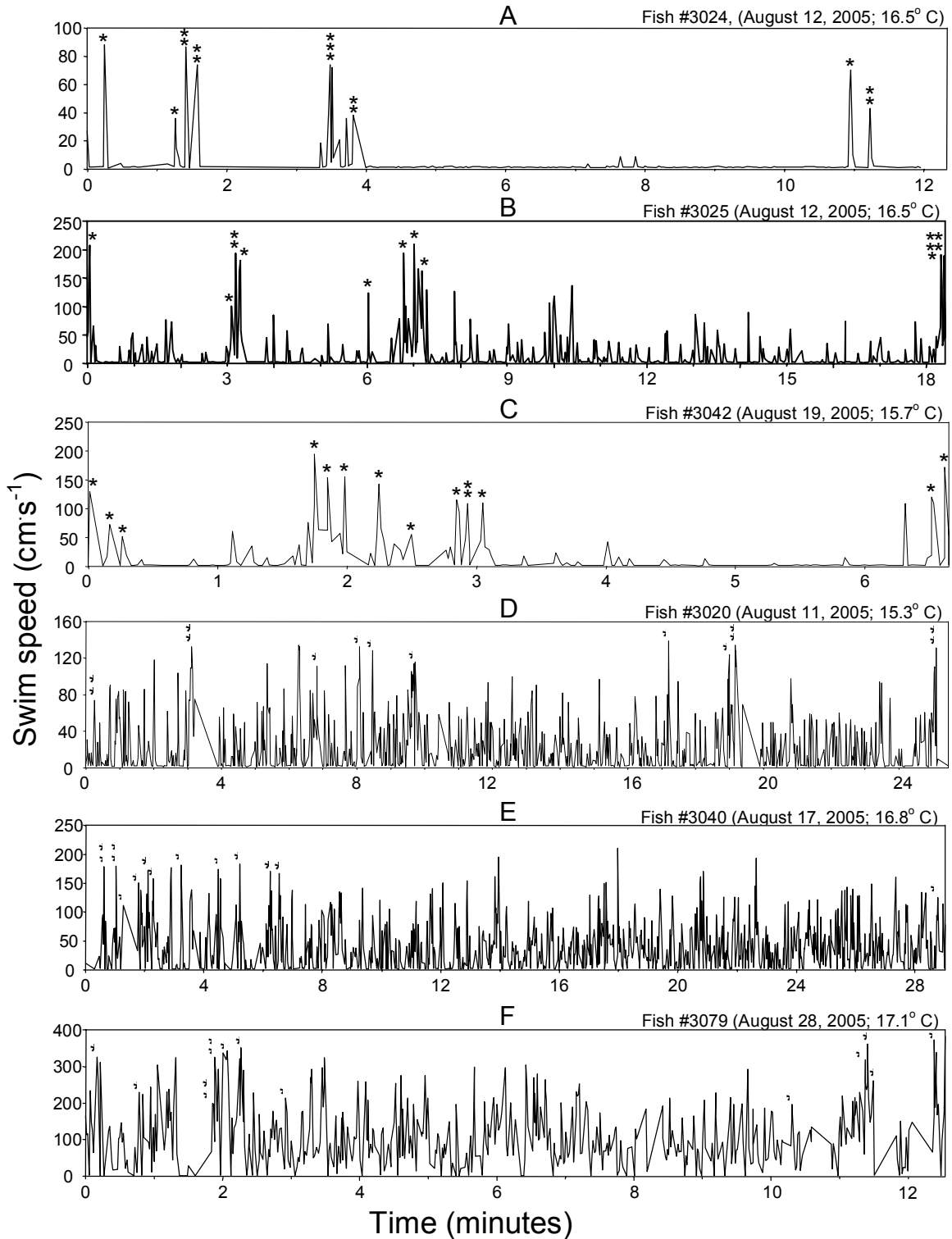


Figure 3.5. EMG trace graphs for six of the sockeye that successfully re-ascended the fishway. Graphs show fishway ascent from entry into pool 4 through entry into pool 17. Passage events between pools are represented by (*). Graphs A, B, and C show examples of the ‘conservative’ swim strategy. Graphs D, E, and F show examples of the ‘vigorous’ swim strategy. Note the differences among individual y-axis scales, detailing the variation in individual swim speeds.

Physiological measures revealed few statistical differences between successful and unsuccessful fish (Table 3.1), but statistical power was generally low for all comparisons ranging from 0.05 to 0.69. Even so, unsuccessful fish had lower plasma concentrations of Na⁺ ions than successful fish ($\bar{x} \pm S.E.$; 143.33±1.54 mmolL⁻¹, 149.64±1.74 mmolL⁻¹, respectively; $P = 0.022$; this was not significant under Bonferroni correction). No differences were detected between unsuccessful and successful fish for plasma osmolality and other plasma ions (K⁺, Cl⁻), lactate, glucose, and cortisol concentrations, gross somatic energy content, and Hct (all $P > 0.05$; Table 3.1). Similarly, no differences were found between the two swimming strategies for any of the physiological variables or for fish size (all $P > 0.05$; Table 3.2). Power analyses typically revealed low power levels among non-significant physiological variables (Tables 3.1 and 3.2).

Table 3.1. Summary of the one-way ANOVAs performed on physiological measures taken from successful (pass) and unsuccessful (fallback) fish, as well as swim speed, energy use, residency time in pool 3, and fork length. Data are shown as mean \pm standard error. Statistical significance was assessed with a Bonferroni corrected $\alpha = 0.05$; for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions, hematocrit), for fish condition $\alpha = 0.025$ (gross somatic energy and fork length), and for swim behaviour $\alpha = 0.02$ (Swim speed, energy use, time in release pool). Uncorrected significant P -values are denoted by (\dagger). Measures with an (*) were \log_{10} transformed prior to analysis but pre-transformed means and standard errors are presented.

Measure	Fate	Mean \pm S.E.	n	Statistical output		
				F	P	Power
Plasma lactate (mmol L ⁻¹)	Pass	1.83 \pm 0.32	7	1.232	0.291	0.161
	Fallback	2.75 \pm 0.81	6			
Plasma glucose (mmol L ⁻¹)	Pass	4.66 \pm 0.30	7	<0.001	0.981	0.050
	Fallback	4.68 \pm 0.53	6			
*Plasma cortisol (ng mL ⁻¹)	Pass	219.38 \pm 64.11	7	0.292	0.599	0.057
	Fallback	240.94 \pm 49.20	6			
Plasma [Na ⁺] (mmol L ⁻¹)	Pass	149.64 \pm 1.74	7	7.120	0.022 \dagger	0.693
	Fallback	143.33 \pm 1.54	6			
Plasma [Cl ⁻] (mmol L ⁻¹)	Pass	140.09 \pm 0.88	7	2.437	0.147	0.302
	Fallback	135.49 \pm 3.04	6			
Plasma [K ⁺] (mmol L ⁻¹)	Pass	2.91 \pm 0.22	7	1.224	0.292	0.182
	Fallback	3.31 \pm 0.29	6			
Osmolality (mosmol L ⁻¹)	Pass	306.21 \pm 1.92	7	2.113	0.174	0.284
	Fallback	300.00 \pm 4.06	6			
Hematocrit (%)	Pass	40.57 \pm 1.13	7	0.146	0.710	0.066
	Fallback	40.00 \pm 0.93	6			
Gross somatic energy (MJ kg ⁻¹)	Pass	6.49 \pm 0.27	7	0.461	0.511	0.091
	Fallback	6.79 \pm 0.37	6			
Fork length (cm)	Pass	58.14 \pm 1.00	7	0.181	0.678	0.070
	Fallback	58.67 \pm 0.61	6			
*Swim speed (cm s ⁻¹)	Pass	29.27 \pm 13.03	6	0.246	0.632	0.266
	Fallback	10.18 \pm 2.14	5			
*Energy use (cal g ⁻¹ h ⁻¹)	Pass	0.80 \pm 0.37	6	0.693	0.429	0.277
	Fallback	0.31 \pm 0.07	5			
Time in release pool (min)	Pass	11.41 \pm 2.88	6	0.240	0.637	0.069
	Fallback	13.66 \pm 3.71	5			

Table 3.2. Summary of the one-way ANOVAs performed on various measures comparing fish demonstrating the vigorous swim strategy with those demonstrating the conservative swim strategy. Data are shown as mean \pm standard error. Bold values indicate statistical significance for a Bonferroni corrected $\alpha = 0.05$; for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions, hematocrit), for fish condition $\alpha = 0.025$ (gross somatic energy and fork length), and for swim behaviour $\alpha = 0.013$ (Swim speeds and energy use). Uncorrected significant P-values are denoted by (\dagger). Measures with an (*) were \log_{10} transformed but pre-transformed means and standard errors are presented.

Measure	Swim strategy	Mean \pm S.E	<i>n</i>	Statistical output		
				<i>F</i>	<i>P</i>	Power
Plasma lactate (mmol L ⁻¹)	Vigorous	2.60 \pm 1.00	5	0.187	0.676	0.070
	Conservative	2.12 \pm 0.48	5			
Plasma glucose (mmol L ⁻¹)	Vigorous	4.32 \pm 0.36	5	0.828	0.389	0.130
	Conservative	4.76 \pm 0.32	5			
*Plasma cortisol (ng mL ⁻¹)	Vigorous	270.50 \pm 81.77	5	0.106	0.755	0.075
	Conservative	220.90 \pm 60.64	5			
Plasma [Na ⁺] (mmol L ⁻¹)	Vigorous	145.6 \pm 2.47	5	0.592	0.463	0.112
	Conservative	148.2 \pm 2.31	5			
Plasma [Cl ⁻] (mmol L ⁻¹)	Vigorous	135.44 \pm 3.55	5	1.317	0.284	0.233
	Conservative	139.76 \pm 1.26	5			
Plasma [K ⁺] (mmol L ⁻¹)	Vigorous	3.15 \pm 0.33	5	0.017	0.898	0.052
	Conservative	3.09 \pm 0.31	5			
Osmolality (mosmol L ⁻¹)	Vigorous	300.10 \pm 5.22	5	1.186	0.308	0.235
	Conservative	306.30 \pm 2.27	5			
Hematocrit (%)	Vigorous	41.60 \pm 1.17	5	0.204	0.663	0.070
	Conservative	41.00 \pm 0.63	5			
Gross somatic energy (MJ kg ⁻¹)	Vigorous	6.99 \pm 0.49	5	0.735	0.416	0.141
	Conservative	6.52 \pm 0.24	5			
Fork length (cm)	Vigorous	57.90 \pm 1.24	5	0.064	0.806	0.057
	Conservative	58.30 \pm 0.97	5			
*Swim speed (cm s ⁻¹)	Vigorous	38.65 \pm 12.57	5	20.136	0.002	0.649
	Conservative	4.93 \pm 1.03	5			
*Holding speed (cm s ⁻¹)	Vigorous	31.65 \pm 9.22	5	28.192	<0.001	0.478
	Conservative	4.27 \pm 0.84	5			
*Progress speed (cm s ⁻¹)	Vigorous	81.04 \pm 19.43	5	0.455	0.519	0.136
	Conservative	61.55 \pm 7.51	5			
*Energy use (cal g ⁻¹ h ⁻¹)	Vigorous	1.01 \pm 0.39	5	8.402	0.020 \dagger	0.358
	Conservative	0.21 \pm 0.01	5			

DISCUSSION

Spawning migrations for salmon are physiologically and energetically demanding, and become particularly stressful when thermal or discharge ‘extremes’ are encountered (Hinch et al. 2006). During our experiments in 2005 with Gates Creek sockeye, temperature and water discharge in the lower Fraser River were not unusual for that time of year (Patterson et al. 2007). In fact, the average daily water temperature in the Seton River and the tailrace of the dam (i.e. 16.3°C) was identical to the optimal temperature for aerobic scope in adult Gates Creek sockeye (i.e., 16.5°C, Lee et al. 2003). As such, environmental conditions in 2005 were probably as favourable as possible and our physiological stress measures indeed indicate that fish were not unduly stressed at the time of capture even though they had recently entered and ascended the fishway. Specifically, plasma glucose levels were similar and lactate levels lower than values reported from migrant adult Adams River sockeye, another Fraser sockeye stock, which were similarly intercepted and biopsied, and then successfully tracked to spawning areas in 2003; another year when environmental temperature or discharge were not unusual (Young et al. 2006). Our average lactate levels were closer to ‘routine levels’ ($\sim 2 \text{ mmol L}^{-1}$) derived from laboratory-held adult sockeye than measurements made after these same fish swam to U_{crit} ($\sim 6 \text{ mmol L}^{-1}$) (Wagner et al. 2006). Plasma cortisol levels were elevated relative to what would be considered an unstressed condition, though this was not surprising as cortisol plays an important role in reproductive maturation and is naturally elevated during spawning migrations (Carruth et al. 2000, 2002). Still, both cortisol and Hct results were within the range of values from previous biopsy results for other Fraser River sockeye stocks sampled near terminal spawning grounds (Crossin et al. 2008; Magnoni et al. 2006). Thus, the physiological state of adult Gates Creek sockeye in 2005 seemed to be consistent with that of other stocks of migrating Fraser River

sockeye in other years when environmental conditions were not ‘extreme’, and they are generally indicative of migrants with low levels of physiological stress related to exhaustive exercise.

The fact that our fish were not overly stressed at the time of capture made it difficult to test our prediction that fish with relatively high levels of physiological stress would be less likely to successfully re-ascend the fishway. Even so, 46% of our fish were unable to re-ascend after our handling, but few stress indicators were correlated with this failure. Fish that failed to re-ascend had lower plasma Na^+ concentrations (4.2%, $P = 0.022$) than those that succeeded. Similar trends in plasma Cl^- concentrations (3.3%, $P = 0.302$), osmolality (2.0%, $P = 0.284$) were observed, plus a tendency for elevated plasma lactate (33%, $P = 0.291$) and cortisol (9%, $P = 0.599$) were observed in unsuccessful fish, although none of these differences were statistically significant. A small sample size and low statistical power may have been contributing factors, but we would have needed to use from 40 to 100+ fish (depending on the variable) to have had statistical power of ~ 0.80 (Cohen 1988); a difficult feat given the logistics and cost associated with our study methods. Though previous studies have reported passage failure rates at fishways between up to 37% (e.g. Gowans et al. 2003), few studies have ever examined mechanisms behind unsuccessful passage.

Deviations from baseline ion values can be indicative of a previous ‘stressful’ event or bouts of significant exercise (McDonald and Milligan 1997). Following such events, plasma ion levels typically diverge from, and then return to baseline values over a period of 8-12 hours, though this period may persist under chronic exposure to unfavourable conditions (Postlethwaite and McDonald 1995; McDonald and Milligan 1997). Given the lack of strong differences between successful and unsuccessful fish in the non-ionic stress indicators, our ion results are likely indicative of recent migration experience leading up to capture (i.e. migration towards the

dam and initial passage through the fishway). In general, our plasma ion concentrations were similar to previously reported values for migrant adult sockeye (e.g. Crossin et al. 2008) although these values tend to naturally decrease over the course of freshwater migration, and therefore may be difficult to compare across stocks (Shrimpton et al. 2005; Hinch et al. 2006).

Stress and exercise are two important mechanisms that can cause plasma ion concentrations to fluctuate in migrant adult sockeye salmon (Hinch et al. 2006). In freshwater, salmon are hyperosmotic and must actively maintain ionic homeostasis by excreting dilute urine and taking up ions through the gills (Hoar 1988; Evans et al. 2005). Stress and exercise can cause a net loss of ions to the water primarily via an elevated brachial efflux associated with elevated circulating catecholamines (Wood and Randall 1973; Mazeaud and Mazeaud 1981; McDonald and Milligan 1997). However, plasma ion concentrations can change in either direction depending on the stressor mechanism (McDonald and Milligan 1997). Plasma ion concentrations tend to decrease following aerobic exercise, (Postlethwaite and McDonald 1995), though they may increase following anaerobic exercise (Graham et al. 1982; Milligan and Wood 1986; Wood 1991; McDonald and Milligan 1997). Our EMG data revealed little evidence of continuous anaerobic swimming activity associated with fishway ascent or during efforts made in the tailrace area by fish that failed to re-ascend (Appendix 2). If the salmon's first ascent of the fishway had involved similar swimming behaviours, the expectation would be that any stress- or exercise-related ion fluctuations associated with sockeye migrating past the Seton Dam would not have been excessive, not related to anaerobic exercise, and likely to decrease ion concentrations, which is consistent with our measurements.

There is the expectation that an ionic imbalance can contribute to the inability of fish to re-ascend the fishway as ion imbalances are generally thought to hinder swimming performance

by reducing the scope for activity (Barton and Schreck 1987; Strange and Cech 1992).

Swimming performance metrics such as U_{crit} have been shown to vary with plasma Na^+ concentrations, with optimal critical swim speeds occurring at 147 mEqL^{-1} in experiments with freshwater salmonids (Randall and Brauner 1991; Brauner et al. 1992). In the present study, plasma Na^+ concentrations were close to this optimum in successful fish. These fish reached a maximum swimming speed of 150 cm s^{-1} (2.48 bl s^{-1}) as they moved from pool 3 into pool 4, which corresponds to a U_{crit} speed for Gate's Creek sockeye of $\sim 2 \text{ bl s}^{-1}$ (Lee et al. 2003).

The reason for the high failure rate on the second ascent therefore cannot easily be explained by the metrics that we measured. This means that either unmeasured factors had predisposed the fish to poor swimming abilities, or the handling procedures were a contributing and variable factor. Though capture and handling undoubtedly had a stressful impact on fish, all fish were handled in a similar manner. Also, sockeye salmon have been shown to be a very resilient species, able to perform repeat critical swim speed tests to similar standards following exercise to exhaustion and only brief ($< 1 \text{ hr.}$) periods of recovery (Farrell et al. 1998; Jain et al. 1998). Anaesthesia during the majority of handling procedures, likely reduced the effects of handling stress (Strange and Schreck 1978; Wagner et al. 2003), but may have impacted swimming ability shortly afterwards. Previous studies using EMG telemetry to examine sockeye migration in the Fraser River have reported higher rates of migration success in tagged fish than we found, though some amount of drop-back was also observed (Hinch et al. 1996; Hinch and Rand 1998). In the present study, unsuccessful fish did not simply give up and drift back downstream. On the contrary, these fish remained in the tailrace of the dam for several hours to days during which time they were observed actively seeking passage upstream in visibly turbulent water spilled from the dam. Along with previous EMG-based studies, this observation

highlights the fact fish are still able to resume or attempt to resume upriver migration, despite the relatively invasive surgery associated with EMG transmitter implantation.

The present work was also able to eliminate swimming behaviour as a contributing factor to successful ascents at the Seton River fishway. We had predicted that lower swim speeds, and lower energy use would favour successful fishway ascent on the basis that exercise-related fatigue was less likely to occur among these fish. Many studies have examined fish moving past hydraulically challenging areas (e.g. Hinch and Rand 2000; Standen et al. 2002; Gowans et al. 2003; Brown et al. 2006), but only Hinch and Bratty (2000), who had sample sizes similar to the present study, have documented differences between successful and unsuccessful fish. Unlike their study however, we did not detect any difference in mean swim speed between successful and unsuccessful migrants. While we did find two swimming strategies similar to those described in Hinch and Bratty (2000), both were similarly successful and unsuccessful at re-ascent of the Seton River fishway. This discrepancy may reflect the substantially lower maximum water velocities of $\sim 2 \text{ m s}^{-1}$ in the Seton River fishway compared with the average surface velocities estimated for Hells Gate (6 m s^{-1}). The lower water velocities in the Seton River fishway may have necessitated less anaerobic swimming, which is generally needed at speeds exceeding 60-70% of the individuals' critical swim speed (U_{crit}) (Burgetz et al. 1998; Lee et al. 2003). For Gates Creek sockeye, anaerobic activity would be invoked at speeds $>93 \text{ cm s}^{-1}$ based on U_{crit} estimates of Lee et al. (2003), but we rarely observed fish continually swimming at speeds above this value while ascending the Seton River fishway, with perhaps the exception of fish 3079 (Figure 3.5).

The structure of a vertical slot fishway creates complex flow patterns such as reverse currents and upwellings as flow velocity is dissipated by a series of baffles (Clay 1961; Wu et al.

1999). In such an environment, fish can use reverse-flow fields to their advantage and make forward progress while expending relatively little energy (Hinch and Rand 1998; Hinch et al. 2002; Standen et al. 2004; Liao et al. 2003). Our swimming speed estimates suggest that some fish clearly used such hydraulic features (conservative swimming strategy) whereas others did not (vigorous swimming strategy). Active swimming tends to be the dominant component of energy consumption during migration (Brett 1995; Rand and Hinch 1998), but fish can reduce these costs by seeking out low or reverse flow areas, swimming at metabolically optimal speeds, and utilizing efficient behaviours such as burst and coast swimming (Weihs et al. 1974; Webb 1995; Hinch and Rand 2000). However, to reiterate, the two swimming strategies did not significantly influence successful ascents.

Given such marked differences between the two swimming strategies in terms of energy expenditure for successful ascent begs the question of whether these differences in energy expenditure are ecologically significant. As Pacific salmon must complete spawning migrations on a fixed energy budget, selection should favour fish that are able to minimise energetic costs associated with migration. Indeed, morphological, physiological, and behavioural adaptations conducive to energy conservation have all been noted in sockeye populations with difficult spawning migrations (Quinn et al. 1995; Hendry and Berg 1999; Kinnison et al. 2001; Lee et al. 2003; Crossin et al. 2004). We estimate, based on a 2 kg fish, that the conservative swimming strategy used approximately 517 calories during fishway ascent (based on a mean ascent time of 74 min; $n = 3$), while the vigorous swimming strategy used 4-times that amount (2180 calories based on mean ascent time of 65 min; $n = 3$). From previous estimates of energy use in Adams River sockeye, a stock with similar migratory distances and energy investments into gonads (Crossin et al. 2004), these rates of energy use would equate to approximately 0.6 km

(conservative swimming strategy) and 2.6 km (vigorous swimming strategy) of migration distance through typical reaches of the Fraser River, or distances nearly 6-times and 24-times the length of the Seton River fishway, respectively. Freshwater migrations typically consume up to 50% of the available energy reserves of sockeye salmon (Brett 1995), which is approximately $3 \text{ MJ}\cdot\text{kg}^{-1}$ in sockeye with migration distances similar to those of the Gates Creek stock (Crossin et al. 2004). Thus, the energy needed to ascend the fishway comprises only a small fraction of the total energy used by Gates Creek sockeye during migration for either of the two swimming strategies, and it is therefore unlikely that the less energetically efficient strategy would lead to energy exhaustion during the remainder of their migration to spawning grounds, a further distance of approximately 50 km. Indeed, representatives from each swimming strategy were later found to have successfully arrived on spawning grounds at Gates Creek, suggesting that the energetic consequences of fishway ascent were minor in the scheme of spawning migration as a whole.

Though little difference was found between successful and unsuccessful fish at the Seton River dam, higher stress may be present in years with unfavourable environmental conditions or at more difficult fishways than the one examined in the present study. The integrative use of physiological biopsy and EMG telemetry, as we used, has been recently advocated by Murchie et al. (2008), as an effective means of assessing mechanisms of fishway passage difficulty or mortality. As this was the first study to have applied these techniques in an examination of fishway passage, there were no existing protocols. As we showed however, these approaches may not be able to provide enough information on the physiological underpinnings of passage failure, and so care should be used in their application with respect to the expected effect size. Additional biochemical approaches such as gene array technology, which can simultaneously

examine the function and activity of thousands of genes is a promising approach and has been recently used in studies of migratory sockeye (Cooke et al. accepted with revisions), may enable a more detailed and powerful means of examining the physiological limitations of fishway passage.

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CHAPTER 4

Conclusions and future directions

This thesis investigated issues surrounding passage of migrant adult sockeye salmon at the Seton River dam. EMG and positional radio telemetry were used to examine how well fish locate and pass through a fishway in relation to their physiological condition as revealed by physiological biopsy before release. Chapter 2 specifically investigated potential linkages between water discharge at the dam and the physiological condition of fish, and how this impacted passage delay downstream of the dam. Chapter 3 evaluated the role of swim behaviour and physiological stress on passage through the fishway structure by comparing fish that successfully re-ascended the fishway with those that were unsuccessful. Collectively, the research presented in this thesis provides the first in-depth study of fishway passage at Seton River dam, and reveals insights into the physiology and behaviour of sockeye salmon migrating past an in-stream obstacle.

The first set of conclusions relate to management issues associated with dam passage. In chapter 3, fish biopsy at the top of the fishway after one ascent revealed low lactate levels, suggesting that the primarily aerobic swim speeds were used during passage. EMG telemetry of a second fishway ascent corroborated that it was possible to ascend the entire fishway with a minimum use of anaerobic burst swimming. Indeed, fish appeared relatively unstressed following fishway passage, suggesting that fishway ascent under the water discharge conditions examined was not a particularly stressful challenge. Though a 46% passage failure rate was observed among EMG tagged fish in chapter 3, this should not be interpreted as an accurate representation of the fishway efficiency. The invasive handling techniques associated with EMG surgery coupled with a rapid return of the fish to the fishway may have been a part of the reason why we observed a higher failure rate. Other studies that have examined migrant adult sockeye

in the Fraser River have not observed such high rates of drop back in EMG-tagged fish (e.g. Hinch et al. 1996; Hinch and Rand 1998) suggesting that there may have been other factors responsible for the higher rate of unsuccessful fish that we observed in chapter 3 than in chapter 2. One possibility may be related to the difference in release locations and the effects that flow cues may have had on fish attempting to resume their migration. Despite the high failure rate in EMG tagged fish, all radio-tagged fish that located the entrance to the fishway in the present study were successful in reaching the top of the fishway. Collectively, these results suggest that passage through the actual fishway structure is not a limitation at Seton River dam under the water discharge conditions examined.

Instead, locating the fishway entrance appears to be the primary issue confronting migrant salmon at the Seton River dam. In chapter 2, we found that fish were delayed on average between 7.7 to 20.7 hrs, depending on the rate of discharge spilled from the dam. Furthermore, 20% of the tagged fish that we released were never able to re-locate the fishway. This is likely a conservative estimate of passage failure as we were unable to catch ‘fishway-naïve’ fish during the study (i.e. all fish were collected from within the fishway structure). Previous dam-passage studies have reported similar or higher rates of passage failure (e.g. 37%, Gowans et al. 1999; 18%, Brown et al. 2006). Evidence suggested that delay could be reduced by changing the amount of water discharged from the Seton River dam, though the relationship between delay and discharge did not appear to be linear, suggesting that other factors may have influenced delay.

Expediting passage of salmon through areas of potential delay is likely to become an increasingly important part of the management and conservations of these species. Over the last 60 years, water temperatures in the Fraser River have increased by approximately 1.5° C

(Patterson et al. 2007), and further increases of several degrees more are predicted to occur over the next 50 to 100 years (Rand et al. 2006). Similar warming trends have also been predicted for the Columbia River, USA (Hamlet and Lettenmaier 1999; Mote et al. 2003). Warmer water temperatures have been associated with increased migrational delay (Keefer et al. 2004; Salinger and Anderson 2006), may impair passage at dams where temperatures approach 21° C (Quinn et al. 1997), and can lead to high rates of mortality in migrant salmon (Macdonald 2000; Rand et al. 2006, Crossin et al. 2008). In 2004, more than one million sockeye salmon were unaccounted for in the largely unregulated Fraser River system, and exceptionally high river temperatures (in some cases exceeding 21° C) were cited as a likely factor behind high mortality (SSFPSRC 2005).

In the heavily regulated Columbia River, USA, migrating adult salmon must pass through numerous dams en route to their spawning grounds. The limited energy reserves of migrant Pacific salmon mean that migration must be completed in a timely manner such that adequate energy remains to allow spawning to occur prior to death (Brett 1995; Crossin et al. 2004). Energetic modeling of Chinook salmon migration in the Columbia River revealed that in cases where delay amounts to five days or more per dam passage event, migration success may be compromised (Geist et al. 2000). Although such periods of delay are generally rare among Columbia River salmon, some fish have been observed to be delayed for periods in excess of five days at certain dams along the Columbia River (Keefer et al. 2004). Also, delay may occur more than once per dam if fish fallback downstream and have to re-pass a dam (Reischel and Bjornn 2003; Boggs et al. 2004; Naughton et al. 2006). Warmer river temperatures will reduce the allowable delay at dams for fish as their metabolic rates increase, and hence their rate of energy use. Though it has been suggested that the increase in river temperatures may be offset by lower

flows that allow rapid migration times (Rand et al. 2006), delay at dams ceases migratory progression and therefore can eliminate the offsetting benefits of reduced river flow.

Improvements to dams that help reduce migrational delay represent an important method for conserving salmon stocks in the future. As demonstrated in chapter 2, manipulation of attraction water flows may help reduce delay while not increasing physiological stress associated with dam passage. Due to the highly site-specific nature of dam layouts the findings presented in this thesis should be considered specific to the Seton River dam. However, the results presented here may be applicable to other dam sites within an adaptive-management context. Experimental manipulation of water discharge within allowable bounds may reveal an optimal level of discharge for attracting fish into fishways. At dams where a constant discharge is required, or where other factors prevent flow manipulation, the pattern of discharge may be manipulated by releasing water from multiple outlets across the dam face (e.g. multiple spillways or sluices).

Finding an optimal flow to minimise passage delay may be compatible with other river management goals. The restoration of natural flow regimes in altered rivers is an important part of conserving species and habitats downstream of dams (Stanford et al. 1996; Poff et al. 1997), and elevated flows are often released at times throughout the year to mimic natural flood conditions. At the Seton River dam, minimum flow requirements during salmon migration periods are higher than minimum flows mandated for other times of the year (Andrew and Geen 1958). Higher flows associated with salmon migration may help mimic natural flood cycles, without negatively impacting native resident fish species (Marchetti and Moyle 2001; Propst and Gido 2004). In determining suitable flows for fish attraction and passage at dams it may be possible to integrate periods of mimicked flood conditions to meet other management goals for regulated river systems.

The results presented in this thesis also offer insights into improvements in fishway design. Previous studies have shown that fishways designed for salmonids may not always be suitable for passage of non-salmonid species (Schwalme et al. 1985, Peake et al. 1997). No study however, has considered the effectiveness of fishway design in the context of intra-specific variability in swimming behaviour or ability. The two swim strategies identified in chapter 3 appeared equally capable of successfully ascending the Seton River fishway, but as shown, one group of fish (conservative swimming strategy) managed to do so while using roughly one-fifth of the energy the other group (vigorous swimming strategy) used. This finding suggests that improvements in fishway design should be tailored to accommodate less efficient swimmers.

One possible means of reducing the energetic cost of fishway ascent could be the incorporation of more low velocity pools into the fishway structure. Figure 3.5 shows that fish often moved through several fishway pools in rapid succession followed by extended periods of holding position. Placement of larger, less-steep pools in-line in the fishway may provide areas of refuge in between bouts of forward movement, though this would be dependant on the assumption that fish would take advantage of this feature. Similarly, improving flow cues associated with transitions between pools may help reduce passage time and therefore, the absolute energetic cost of ascent. The alternating pool and baffle design of vertical slot fishways provides an effective means of dissipating flow energy (Wu et al. 1999), but the resulting complex flows may make it difficult for fish to identify flow cues emanating from the adjacent upstream pool. Changes to baffle design may improve detection of cues, but must consider the effect on flow patterns, and recognise the fact that the current design may already suit energetically-efficient swimmers well.

In chapters 2 and 3, we investigated potential physiological associations with passage failure but were unable to detect strong physiological differences among successful and unsuccessful fish. We did find evidence of a slight ionic disturbance among EMG transmitter fish that failed to re-ascend the fishway, however the other stress indicators (i.e. lactate, glucose, cortisol, Hct) did not support a stress-related mechanism. Admittedly, our statistical analyses frequently showed low power. While the integration of telemetry and physiological biopsy have been demonstrated to good effect in the past (e.g. Cooke et al. 2006 a, b; Young et al. 2006; Crossin et al. 2008), these techniques can be costly and studies may be limited in the number of fish that can be sampled and tagged. Natural changes and variability in plasma ions and cortisol (Carruth et al. 2000; Shrimpton et al. 2005) can make it difficult to detect and contextualize potential differences in these variables among migrant salmon. Other developing methods, such as gene array techniques, though even more costly than our plasma biopsy approach, may prove to be a more effective means of making physiological comparisons among migrant salmon (Cooke et al. accepted with revisions).

Though no behavioural differences were detected among successful and unsuccessful fish, the observation of two relatively distinct swimming strategies (the ‘conservative’ swimming strategy, and the ‘vigorous’ swimming strategy) in chapter 3 is an interesting finding that may be worth future investigation. There was no indication that individual fish alternated between strategies, and a given strategy did not appear to correlate with sex, size, or physiological condition, suggesting that it is either an individual trait or related to some unknown factor. While neither strategy favoured successful fishway ascent at Seton River dam, the characteristics of the two strategies were similar to those described by Hinch and Bratty (2000), where successful passage at Hells Gate favoured the more energetically efficient swimmers. If

migration obstacles are indeed selecting against less efficient swimmers, then we would expect to find fewer of these fish at later stages of the spawning migration. It is somewhat curious then, that we observed roughly equal numbers of the two strategies in our EMG tagged fish, as these fish had already completed the majority of their freshwater migration (88.5%), and had already passed through difficult river reaches such as Hells Gate. Nonetheless, this finding provides further evidence of inter-individual variability in swimming behaviour, which may have to be considered in future fishway designs.

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APPENDICES

Appendix 1 – Physiological comparisons among sexes for chapters 2 and 3.

Table A1.1. A comparison of the physiological measures made between male and female sockeye salmon used in chapter 2. Fish were captured from August 10 to September 23, 2005. Data are shown as mean \pm standard error. F or χ^2 , p-values, and power statistics are presented for the contrasts within each variable. One-way ANOVAs were performed for most statistical comparisons with the exception of plasma Cl⁻ and osmolality, for which non-parametric Wilcoxon-Kruskal-Wallis tests were performed. Bold values indicate statistical significance for a Bonferroni corrected $\alpha = 0.05$; for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions, hematocrit), for fish condition $\alpha = 0.025$ (gross somatic energy and fork length). Measures with an (*) were \log_{10} transformed but pre-transformed means and standard errors are presented.

Measure	Sex	Mean \pm S.E	n	Statistical output		
				F or χ^2	P	Power
*Plasma lactate (mmolL ⁻¹)	Male	3.22 \pm 0.40	46	1.123	0.2193	0.313
	Female	2.40 \pm 0.20	23			
*Plasma glucose (mmolL ⁻¹)	Male	4.71 \pm 0.15	45	1.486	0.227	0.278
	Female	4.39 \pm 0.17	23			
*Plasma cortisol (ngmL ⁻¹)	Male	213.17 \pm 25.34	46	12.297	<0.001	0.785
	Female	349.40 \pm 38.07	23			
Plasma [Na ⁺] (mmolL ⁻¹)	Male	147.34 \pm 1.22	47	0.299	0.634	0.079
	Female	146.43 \pm 1.05	23			
Plasma [Cl ⁻] (mmolL ⁻¹)	Male	134.14 \pm 1.47	47	2.308	0.129	0.560
	Female	138.50 \pm 0.56	23			
Plasma [K ⁺] (mmolL ⁻¹)	Male	2.70 \pm 0.14	47	0.574	0.451	0.122
	Female	2.87 \pm 0.16	23			
Osmolality (mosmolL ⁻¹)	Male	304.00 \pm 1.89	47	0.021	0.886	0.164
	Female	305.57 \pm 1.22	23			
Hematocrit (%)	Male	39.79 \pm 0.54	47	1.238	0.270	0.218
	Female	38.78 \pm 0.65	23			
Gross somatic energy (MJkg ⁻¹)	Male	6.06 \pm 0.19	47	0.111	0.739	0.065
	Female	6.16 \pm 0.13	23			
Fork length (cm)	Male	57.47 \pm 0.41	47	0.390	0.534	0.114
	Female	57.02 \pm 0.56	23			

Table A1.2. A comparison of the physiological measures made between male and female sockeye salmon used in chapter 3. Fish were captured from August 11 through August 28, 2005. Data are shown as mean \pm standard error. F or χ^2 , p -values, and power statistics are presented for the contrasts within each variable. One-way ANOVAs were performed for most statistical comparisons with the exception of plasma Cl⁻ and osmolality, for which non-parametric Wilcoxon-Kruskal-Wallis tests were performed. Bold values indicate statistical significance for a Bonferroni corrected $\alpha = 0.05$; for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions, hematocrit), for fish condition $\alpha = 0.025$ (gross somatic energy and fork length). Measures with an (*) were \log_{10} transformed but pre-transformed means and standard errors are presented.

Measure	Sex	Mean \pm S.E	n	Statistical output		
				F or χ^2	P	Power
*Plasma lactate (mmolL ⁻¹)	Male	2.68 \pm 0.74	7	0.445	0.518	0.159
	Female	1.77 \pm 0.19	6			
Plasma glucose (mmolL ⁻¹)	Male	4.71 \pm 0.51	7	0.019	0.892	0.052
	Female	4.63 \pm 0.22	6			
Plasma cortisol (ngmL ⁻¹)	Male	187.72 \pm 47.92	7	1.310	0.277	0.167
	Female	277.89 \pm 64.31	6			
Plasma [Na ⁺] (mmolL ⁻¹)	Male	147.29 \pm 2.56	7	0.159	0.698	0.065
	Female	146.08 \pm 1.25	6			
Plasma [Cl ⁻] (mmolL ⁻¹)	Male	136.85 \pm 2.89	7	0.082	0.775	0.103
	Female	139.28 \pm 0.53	6			
Plasma [K ⁺] (mmolL ⁻¹)	Male	3.21 \pm 0.26	7	0.426	0.527	0.091
	Female	2.97 \pm 0.25	6			
Osmolality (mosmolL ⁻¹)	Male	302.00 \pm 3.75	7	0.405	0.538	0.91
	Female	304.92 \pm 2.27	6			
Hematocrit (%)	Male	40.57 \pm 1.31	7	0.146	0.710	0.065
	Female	40.00 \pm 0.52	6			
Gross somatic energy (MJkg ⁻¹)	Male	6.94 \pm 0.34	7	2.752	0.125	0.218
	Female	6.26 \pm 0.18	6			
Fork length (cm)	Male	58.00 \pm 0.99	7	0.472	0.507	0.092
	Female	58.83 \pm 0.60	6			

Appendix 2 – Swim speeds of an EMG tagged fish swimming downstream of the dam.

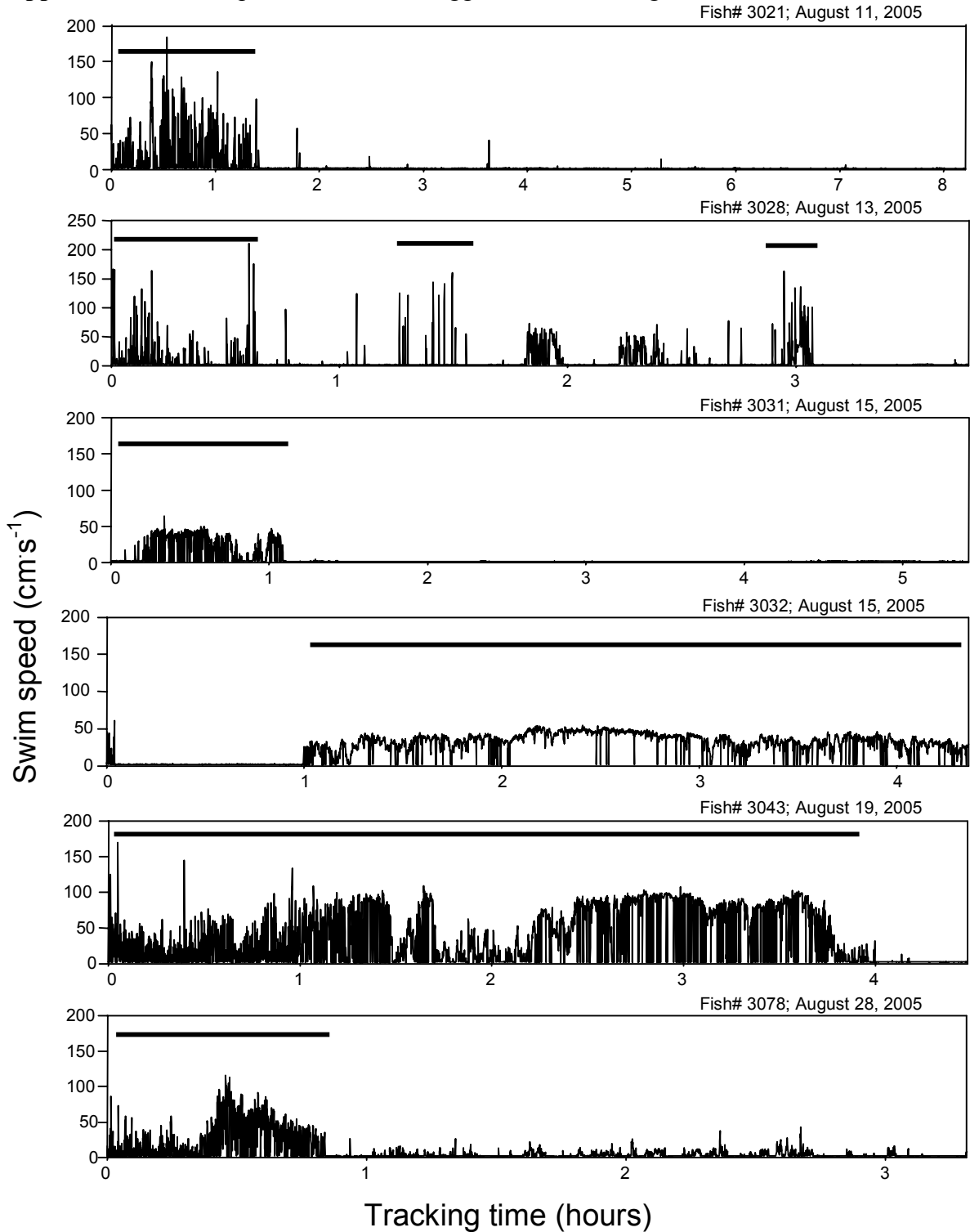


Figure A2.1. Swim speed traces of EMG-tagged fish swimming in the tailrace of the Seton River dam. Horizontal black bars correspond to periods of time in which fish were swimming in turbulent water near the fishway entrance. Swim speed traces without black bars represent periods of time where fish were holding in calmer water roughly 50 m downstream of the dam.

Appendix 3 – Further comparison of the two swimming strategies among fish that successfully re-ascended the fishway. Due to low sample sizes, statistical comparisons were not conducted.

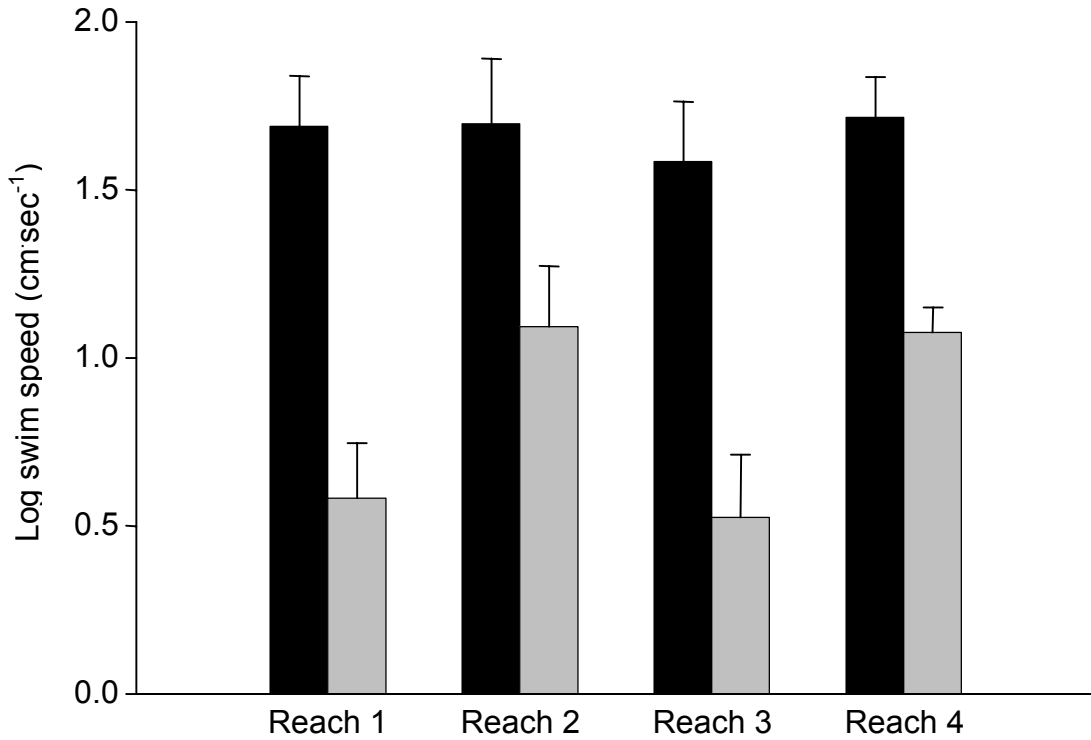


Figure A3.1. Comparison between swimming strategies for mean swim speed for each of four reaches defined within the fishway. Reach 1 consists of pool 3, reach 2 consists of pools 4 through 16, reach 3 consists of pool 17, reach 4 consists of pools 18 through 32 (see Figure 3.2). Black bars represent the vigorous swimming strategy ($n = 3$), and grey bars represent the conservative swimming strategy ($n = 3$). Means are presented with standard error bars.

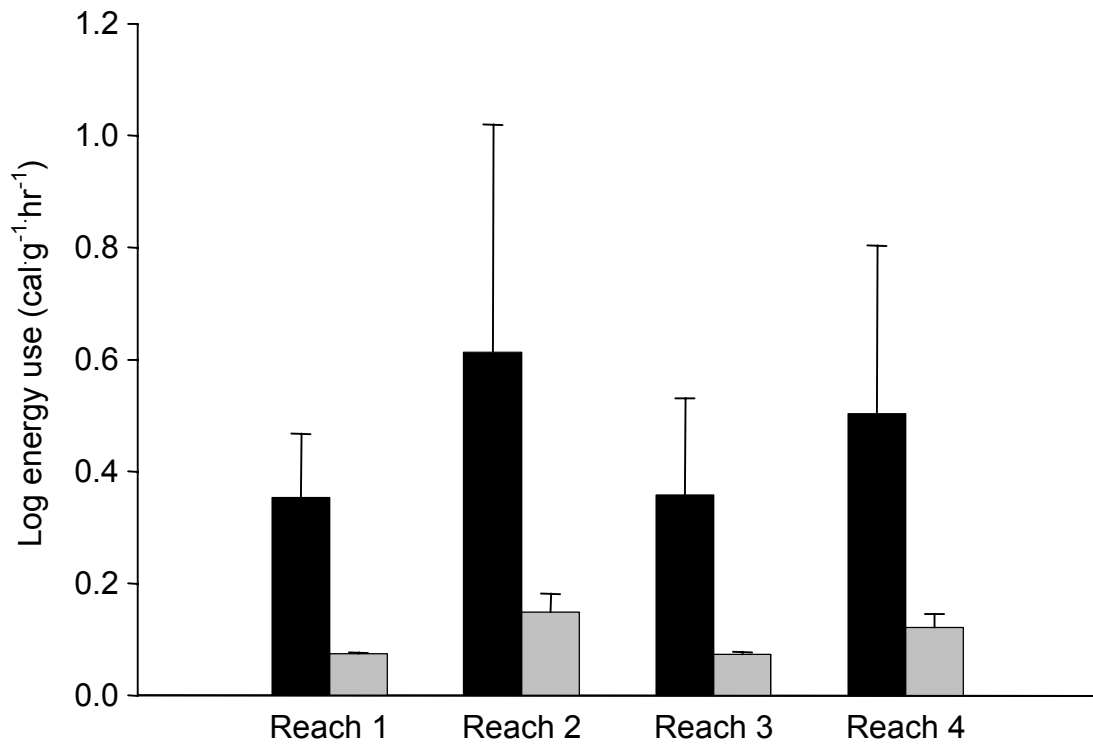


Figure A3.2. Comparison between swimming strategies for mean energy use for each of the four reaches defined within the fishway. See Figure A3.1 for a description of the reaches. Black bars represent the vigorous swimming strategy ($n = 3$), and grey bars represent the conservative swimming strategy ($n = 3$). Means are presented with standard error bars.

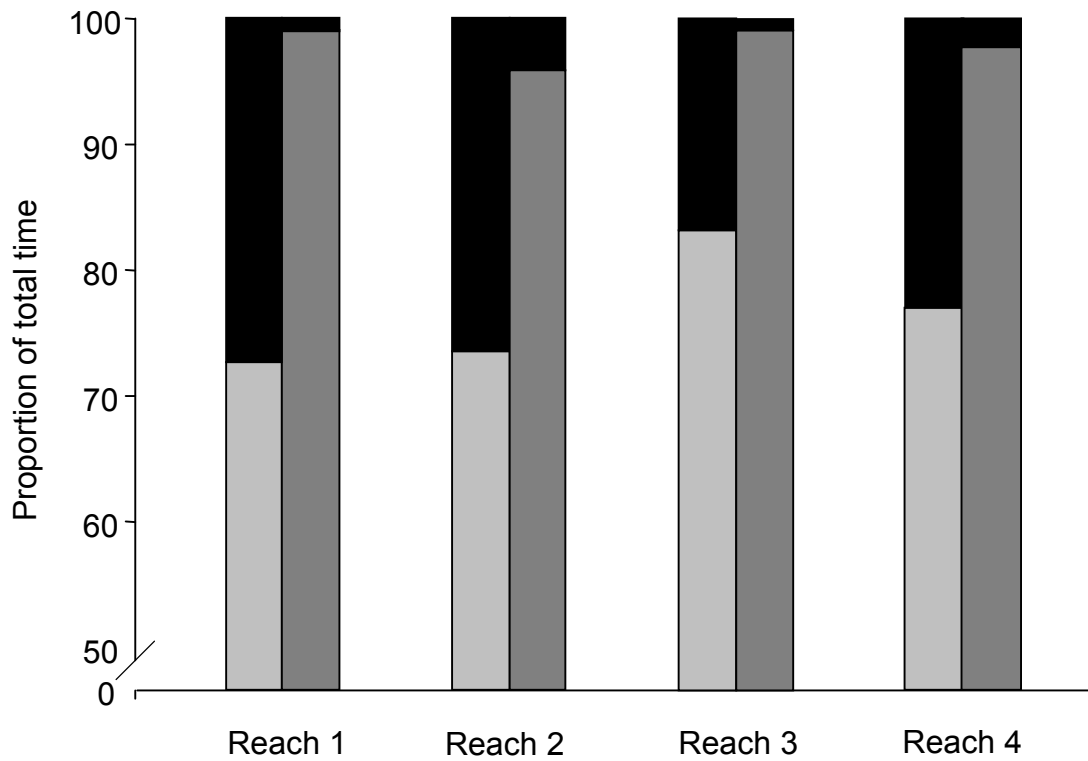


Figure A3.3. Proportion of total time swimming in each reach at aerobic speeds (light grey = vigorous swimming strategy ($n = 3$); dark grey = conservative swimming strategy ($n = 3$)), and non-aerobic speeds (black bars for each respective group). Non-aerobic speeds are defined as those greater than 70% of U_{crit} . See Figure A3.1 for a description of the reaches.