

**The Physiology, Behaviour, and Fate of Up-river Migrating Sockeye Salmon
(*Oncorhynchus nerka*) in Relation to Environmental Conditions in the Fraser
River, British Columbia**

By

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DEDICATION:

To my parents, who have always encouraged my pursuit of higher learning by supporting my academic endeavours since day one. To Shawn, who is truly my inspiration for furthering my education and who continues to guide me through every major life decision I make. To Lisa, who inspires me, who is willing to provide encouragement through thick and thin, and who simply never tires of talking about fish. Many thanks to my friends and colleagues in the Cooke lab, especially Steve, whom I look forward to collaborating with during my Ph.D. and beyond.

ABSTRACT:

One of the most challenging phases of the sockeye salmon (*Oncorhynchus nerka*) spawning migration is the transit through the freshwater environment. I utilized biotelemetry and thermal loggers to identify strong evidence for limited thermoregulatory behaviour of migrants through the Fraser River mainstem, British Columbia. I integrated biotelemetry and biosampling methods to identify the physiological, energetic, behavioural, and environmental factors that characterize individual migration fall back (i.e., anomalous movement down-river following release) and fate (i.e., survival to reach spawning grounds versus en-route mortality), in the freshwater environment. Fall back individuals had elevated stress indices resulting in slowed migration rates. Physiological indices were not predictive of failure to reach spawning grounds, but en-route mortalities were characterized by slowed migration rates. Stock and year effects were found for several variables. Overall, my research contributes novel findings on the basic freshwater migration biology of this species by elucidating the interplay among physiology, migration behaviour, thermoregulatory behaviour, environmental conditions, and fate.

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CO-AUTHORSHIP:**Chapter 2: Limited Behavioural Thermoregulation by Adult Up-River****Migrating Sockeye Salmon in the Lower Fraser River Mainstem, British**

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While this study is my own, the work is a collaborative effort and required the valuable assistance of my co-authors. Specifically, the project was conceived by Donaldson, Hinch, Patterson, Farrell, and Cooke. Telemetry and field work was conducted by Donaldson, Robichaud, English, Olsson, Crossin, and Hanson. Telemetry data processing was performed by Donaldson and Robichaud. All data analysis was conducted by Donaldson. Data were interpreted by Donaldson, Patterson, Hanson, and Cooke. All writing was conducted by Donaldson. All co-authors provided comments and feedback on the manuscript. The manuscript is in preparation for submission to *Oecologia*.

Chapter 3: Integrating physiological, behavioural, and environmental indices to understand migration fall back and mortality during the freshwater phase of the sockeye salmon spawning migration in the Fraser River, British Columbia.

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CHAPTER 1: General Introduction

Many organisms from all major taxa in the animal kingdom engage in some form of migration during their life history. Across these taxa there is remarkable variation in the scale of the migrations that are undertaken and many species must overcome spectacular feats of time and space. For example, Arctic tern (*Sterna paradisaea*) annually migrate more than 40,000 km from the Arctic to Antarctica and back again, female green turtles (*Chelonia mydas*) travel 2000 km from feeding areas near the coast of Brazil to deposit eggs on the sandy beaches of Ascension Island, and Pacific salmonids (*Oncorhynchus* spp.) that travel distances > 1400 km to reach natal spawning grounds prior to death. Identifying a simple definition of migration that encompasses the variety of forms and functions that occur in the natural environment has proven problematic. Dingle (1996) defined true migration as movements that are persistent, directional, defined, and must have energy allocated towards specific movements. Regardless of complexity, migration behaviour has evolved and is maintained as a response to the changing availability of resources and variability of environmental conditions. Migratory behaviour has evolved in concert with a suite of physiological and morphological adaptations and is a response to selective pressures that operate on the individual, but ultimately has outcomes at the population level (Åkesson and Hedenström 2007; Dingle and Drake 2007; Ramenofsky and Wingfield 2007).

To date, the majority of migration biology research has focused on individual physiology, behaviour and genetics, as well as population ecology, evolution, timing, and extent (Dingle and Drake 2007). Many of these themes are also prevalent in the fish migration literature (Dodson 1997; Lucas and Baras 2001). Fish species

undertake remarkable migrations in both the marine (i.e., oceanodromous) and freshwater (i.e., potadromous) environments, and in some cases between the two (i.e., diadromous). Diadromous reproductive migrations are sub-categorized as anadromous (i.e., migrations from seawater to freshwater) and catadromous (i.e., migrations from freshwater to seawater). There are a number of costs and benefits associated with each phase of these migrations as individuals must accumulate sufficient energy reserves for growth and maturation and must reach specific locations to be positioned for the subsequent migration phase, all while avoiding predation. Each migration phase requires a specialized suite of physiological, morphological, and behavioural characteristics that accompany these life history characteristics, an important intersection that is becoming a unifying approach in ecology (Ricklefs and Wikelski 2002; Young et al. 2006).

As anadromous sockeye salmon (*O. nerka*) transition between the marine and freshwater environments, they serve a unique seasonal role in both the aquatic and terrestrial ecosystems as food items for piscivorous fish, predatory and scavenging birds, marine and terrestrial mammals, as well as insects (Schindler et al. 2003). As they approach spawning grounds, adult sockeye bring marine derived nutrients to coastal and in-land ecosystems, an important ecological service (Ben-David et al. 1998; Naiman et al. 2002). Fraser River sockeye salmon typically grow and develop in lakes for two years, migrate hundreds to thousands of kilometers to the ocean where they feed for two to three years and finally initiate reproductive migrations to natal spawning grounds. The complex population (i.e., stock) structure of sockeye salmon is a result of fidelity to natal spawning grounds and the fact that sockeye salmon are semelparous. Semelparous species only reproduce once during their life

cycle, meaning that individuals only have one opportunity to spawn. If individuals fail to spawn, they will have zero lifetime fitness, leading to population-level conservation concerns. Since 2003, two Fraser River sockeye populations, Cultus and Sakinaw, have been listed as endangered under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). There is currently a range-wide IUCN Red List assessment underway which will see several Fraser stocks designated as critically endangered (Scott Hinch, personal communication).

The unique life history characteristics, migration strategies, and conservation status of this species have resulted in a growing body of sockeye salmon research. Building on previous studies, it has become apparent that more research is required to examine the physiology, energetics, and behaviour that contribute to en-route mortality versus successfully reaching spawning grounds and the role of environmental conditions in affecting these indices (Hinch et al. 2006). The following paragraphs will describe the previous research on these topics and illustrate how this literature has helped to guide the objectives, hypotheses, and predictions for my dissertation.

Migration Physiology and Energetics

The physiological mechanisms that underlie sockeye salmon migration initiation and homing ability, particularly for adult spawning migrations, has received considerable attention in recent years (reviewed in Hasler and Sholz 1993; Quinn 2005; Hinch et al. 2006; Ueda et al. 2007). The timing of spawning migration initiation is based on both endogenous and exogenous cues. Initiation timing in large rivers is related to migration distance and elevation as well as environmental

conditions (Gilhousen 1990; Hodgson and Quinn 2002). For example, river temperature influences the migration timing of sockeye (Hodgson and Quinn 2002) and Fraser River populations that migrate over short distances will generally time their migration runs in late summer and fall to take advantage of cooler water temperatures (i.e., < 18 °C) and reduced river discharge (Hinch et al. 2006). As migrants transition between the marine and freshwater environments, they reorganize their osmoregulatory and ionoregulatory systems. This transition includes changes in gill and gut transport mechanisms and the upregulation of kidney activity (Wood and Shuttleworth, 1995). Consequently, routine plasma ion concentrations, plasma osmolality, and gill Na⁺/K⁺-ATPase are generally maintained at lower levels upon freshwater entry. During upriver migration, changing levels of reproductive hormones regulate the development of secondary sexual characteristics and gonads (Leonard et al. 2001). This rapid sexual maturation and morphological changes associated with the development of secondary sexual characteristics contributes to the energy depletion that occurs through swimming and spawning behaviours.

Sockeye salmon cease feeding prior to freshwater migration initiation and must rely on endogenous energy reserves to reach spawning grounds, secure a mate, and spawn. For female sockeye, the majority of energy (~55 %) is catabolized to fuel swimming activity and an additional ~23 % is diverted to ripen gonads and reproduce (Brett 1995). Sockeye populations begin their migrations with gross somatic energy (GSE) levels that are proportionate to the distance they must travel to reach spawning grounds. In addition, relative to short-distance migrants, populations that travel longer distances tend to have morphologies adapted for optimal swimming ability and energy conservation (i.e., more fusiform, short and round bodies; Crossin et al. 2004).

Interestingly, long-distance migrants travel at optimal speeds by selecting low current locations where available and exhibit more efficient swimming behaviours, again as a means of energy conversion, relative to short-distance migrants (Bernatchez and Dodson 1987; Standen et al., 2004). Migrants traveling shorter distances also begin migrations with more mature gonads and larger average egg size, relative to long-distance migrants (Brett 1995; Crossin et al. 2004). Mortality tends to occur when GSE levels reach $\sim 4\text{MJ/kg}$ (Crossin et al. 2004). Exposure to high river temperatures and flows can slow migration and accelerate energy depletion to levels below critical threshold, potentially resulting in elevated mortality (Macdonald and Williams 1998; Rand and Hinch 1998).

Exposure to high river temperatures has a number of negative physiological and energetic consequences for adult migrating sockeye salmon. High temperatures can result in elevated indices of physiological stress, potentially resulting in swimming impairments (Macdonald 2000). For example, high plasma lactate levels can reduce recovery following exhaustive exercise (Farrell et al. 1998). Physiological stress may be further elevated due to interactions with fisheries gear (Farrell et al. 2000; Farrell et al. 2001). High temperatures may also lead to increased incidence of infection with a myxosporean kidney parasite, *Parvicapsula minibicornis*, which has been found to lead to additional swimming impairments and physiological alterations (Wagner et al. 2005). The high routine metabolic cost associated with prolonged exposure to high temperatures contributes to the accelerated depletion of energy reserves. Temperature increases metabolic rate exponentially at temperatures higher than 16°C (Brett 1971), suggesting that individuals characterized by low energy reserves upon river entry will have energy stores depleted earlier in the migration than

those with higher energy reserves (Rand and Hinch 1998; Macdonald and Williams 1998; Crossin et al. 2004). The associations between temperatures that approach thermal tolerances and these physiological and energetic indices can result in elevated mortality rates unless individuals are able to behaviourally thermoregulate.

Behavioural thermoregulation can be defined in this sense as individuals actively seeking temperatures that are conducive to optimal energy conservation, reproductive development (Newell and Quinn 2005;), swimming performance (Lee et al. 2003; MacNutt et al. 2006;), and maintenance of aerobic scope (Lee et al. 2003; MacNutt et al. 2006; Farrell et al. 2008).

Migration Behaviour and Swimming Performance

Adult sockeye salmon require a number of behavioural adaptations to reach spawning grounds, which are profoundly influenced by river temperature and discharge conditions. When variable flow conditions are encountered, migrants will seek out river regions with slower river discharge (Standen et al. 2004). Individuals use microscale reverse-flow vortices, where available, to provide forward assists that accelerate migration speed and reduce energetic costs (Vogel 1994; Hinch and Rand 1998; 2000; Liao et al. 2003). Migration delays and slowed migration rates commonly occur due to individuals delaying migration in locations with access to cool water refuge (e.g., cool-water tributaries and thermally stratified lakes; Hyatt et al. 2003; Newell and Quinn 2005; Goniea et al. 2006; Keefer et al. 2008a). Holding behaviours are thought to be linked with behavioural thermoregulation and to facilitate reproductive development (Newell and Quinn 2005). Additionally, migration delays are common in locations of difficult passage (e.g., river constrictions

with high flows, dam passage; Hinch and Rand 2000; Keefer et al. 2006) and can arise due to anomalous migratory behaviours, including overshoot behaviour (i.e., individuals spuriously migrate beyond the tributaries that lead to terminal spawning grounds), potentially as a response to seeking migratory cues (e.g., Keefer et al. 2008b) or cool-water refuge. However, delayed migration initiation and slowed travel rates can be deleterious because migrants are on a fixed energy budget and must spawn prior to the depletion of energy reserves (Crossin et al. 2004). Delayed arrival at spawning grounds results in fewer opportunities for selection of prime spawning sites, shorter time spent on spawning grounds, and fewer opportunities for reproduction (Smoker et al. 1998; Hodgson and Berg 1999; Crossin et al. 2004; Keefer et al. 2006).

The migration speed and swimming performance of Fraser River sockeye varies considerably among stocks and even among individuals (Hinch et al., 2002; Lee et al. 2003; Hanson et al. 2008). A number of metrics of swimming performance are affected by water temperature, including maximum oxygen consumption (MO_2max), critical swimming speed (U_{crit}), and scope for activity (Brett 1995). For Fraser River sockeye, temperature optima for these indices are suggested to be reflective of thermal conditions encountered en-route to natal spawning grounds (Farrell et al. 2003; Lee et al. 2003; Farrell et al. 2008). Optimal temperatures for U_{crit} and maximum MO_2 approach the upper lethal temperature limits for these populations (Brett 1995; Farrell et al. 2008). Consequently, prolonged exposure to abnormally high temperatures that approach thermal tolerances can result in elevated mortality (Farrell et al. 2008). Recently, during a period of abnormally warm Fraser River temperatures, one group of individuals engaged in a holding behaviour in a cool, deep

lake while another group stayed in an adjacent river where temperatures were much higher. High mortality rates were observed for the latter group. A complementary study revealed that prolonged exposure to high, but sublethal river temperatures (18 °C) resulted in mortality rates that were twice as high relative to another group held at 10 °C for a period of 24 d (Crossin et al. 2008). The proposed mechanism of high temperature mortality for migrating sockeye is a collapse of aerobic scope, compounded by other deleterious factors, including an increased likelihood of infection with the *Parvicapsula minibicornis* kidney parasite, for Fraser River sockeye (Crossin et al. 2008; Farrell et al. 2008). From a conservation perspective, this is of particular concern as Fraser sockeye are expected to encounter peak summer river temperatures that exceed current averages by up to 4 °C in the coming decades (Morrison et al. 2002; Rand et al. 2006; Ferrari et al. 2007).

Studying Migration *in situ*

While salmonid migration has been studied intensively in field and laboratory settings, the widespread utilization of biotelemetry has provided considerable insight into migration behaviour and physiology. Biotelemetry enables the tracking of individual fish using a combination of transmitters attached to fish and receivers to track locations, spatial movements, behaviours, estimate travel rates, and also measure physiological indices (e.g., electromyogram telemetry; Cooke et al. 2004a; 2004b). Integrating telemetry technology with tools from other disciplines (e.g., physiological biosampling) has enabled researchers to take an integrated and experimental approach to understanding fish biology in the natural environment (e.g., Donaldson et al. 2008). The integration of biosampling and biotelemetry has been central to a number of

recent studies on adult migrating sockeye salmon (e.g., Cooke et al. 2005; Cooke et al. 2006a; 2006b; Young et al. 2006; Crossin et al. 2007; Cooke et al. 2008; Hanson et al. 2008).

Biotelemetry is well-suited for the study of salmonid migration because these migrations are predictable both spatially and temporally. Fixed receiver stations can be distributed throughout the watershed to detect fish passage intervals to determine migration rate, arrival at spawning grounds, and the location of en-route mortality. For Pacific salmonids that do not feed during their spawning migrations, radio transmitters can be gastrically implanted with generally high retention rates and without the application of anesthesia (e.g., Crossin et al. 2007). Receiver detection efficiency tends to be quite high in these systems (e.g., Robichaud and English 2006; 2007) and the technology provides researchers with simultaneous tracking of multiple individuals with relatively high spatial and temporal resolution. Accordingly, this approach has been used to assess migratory behaviours in a number of salmonid systems. In the Columbia and Snake rivers in the United States, which are both heavily regulated by dams, researchers have used this technology to assess migration rates, holding behaviours, passage through migration barriers, and mortality rates for Pacific salmonids (Naughton et al. 2005; Goniea et al. 2006; Keefer et al. 2008a; 2008b). In the Fraser River, biotelemetry and physiological telemetry have been used to assess migration behaviour, transit through areas of difficult passage, and the factors that contribute to migration failure (reviewed in Hinch et al. 2006). This integrative approach provides opportunities to ask new research questions on salmonid migration.

To assess indices of physiological condition, energetic status, and behaviour of

actively migrating sockeye salmon, Cooke et al. (2005) proposed a novel technique of integrating biosampling and biotelemetry. This approach involves intercepting adult sockeye during their coastal or in-river migrations and taking a minimally invasive blood sample to assess stress indices (e.g., plasma lactate, glucose, and cortisol), reproductive hormones, osmoregulatory indices (e.g., plasma ion concentrations and osmolality), and hematocrit. Gross somatic energy can be calculated based on the reading of a hand-held microwave fat probe that is applied externally to the sampled individual (Crossin and Hinch 2005). Gill Na^+/K^+ -ATPase can be assessed based on a small gill tissue sample. DNA extracted from tissue samples can be used to assess stock complex origins, which is essential for interpreting biotelemetry data (Beacham et al. 2004). Recently, genomic technologies have been applied to this research that utilize cDNA microarrays and quantitative polymerase chain reaction (PCR) to gain greater insight into the expression of genes and gene families involved in the physiological basis of migration outcomes, including mortality (Miller et al. 2007). Laboratory and field approaches can also be combined to gain greater insight into the factors that affect migration under experimental conditions (e.g., Lee et al. 2003; Wagner et al. 2005; Crossin et al. 2008).

Water temperature is considered the abiotic “master” factor of fishes, and influences many aspects of salmonid migration (Brett 1971; Beitinger et al. 2000; Hinch et al. 2006). A number of technological approaches have been proposed to assess the temperatures encountered by individuals en-route to spawning grounds. Temperature probes can be distributed in the river to estimate the ambient thermal conditions encountered by migrants. However, this approach may only provide a

relatively coarse measure of temperatures encountered, as individual behaviour dictates the specific thermal experience of migrants (e.g., use of cool-water regions; Goniea et al. 2006). To gain greater insight into thermoregulatory behaviour, temperature sensors on-board telemetry transmitters or implanted thermal loggers can be used to measure individual body temperatures. Temperature sensors enable data to be transmitted from the individual to the receiver in real time, but require that the individual pass through the detection area in order to record continuously (Berman and Quinn 1991). The advantage of combining positional transmitters with archival temperature loggers is that they permit the collection of complete thermal histories for individual migrants, from release to spawning grounds. However, these loggers must be recovered and downloaded to obtain data, and recovery rates can be quite low (i.e., < 15%; Newell and Quinn 2005). Taken together, combining these interdisciplinary tools is useful to gain greater insight into the complex interplay of physiology, behaviour, and encountered environmental conditions during Pacific salmonid migrations.

Research Objectives, Hypotheses, and Predictions

I integrated biotelemetry with new research tools from multiple disciplines to gain a greater insight into sockeye salmon spawning migration. The objective of Chapter 2 was to use biotelemetry and thermal loggers to assess behavioural thermoregulation through the Fraser River mainstem migration, a location that is considered to be relatively thermally homogeneous and is known to be one of the warmest segments of the freshwater migration. To date, no studies have explicitly tested for behavioural thermoregulation in this system, yet it is well known that

prolonged exposure to high temperatures here can result in high mortality (Crossin et al. 2008; Farrell et al. 2008). Accordingly, Chapter 2 specifically assessed the differences between fish body temperatures and river temperatures to identify the extent to which individual body temperatures deviate from measured river temperatures. The relationship between temperature deviation and a null relationship where no behavioural thermoregulation is assumed was examined to determine whether or not individuals behaviourally compensate for increasingly high temperatures. Several metrics predicted to be related to thermoregulatory behaviour were compared, including migration speed, river discharge, and run-timing group/stock complex. With predicted increases in peak summer temperatures over the next several decades, understanding thermoregulatory behaviour in this region is essential for in-season environmental management assessments (Morrison et al. 2002).

In chapter 3, I integrated biotelemetry and biosampling of sockeye salmon at the onset of the freshwater phase of their spawning migrations to assess the physiological, behavioural, and environmental factors that characterize (1) fall back (i.e., individuals that engage in anomalous movement down-river following release versus those that continue to migrate up-river, and (2) fate (i.e., individuals that die en-route versus those that survive to reach spawning grounds) both within and between years. The hypothesis here was that individuals that either fall back or die en-route to spawning grounds will be characterized by indices of impaired physiological and energetic status, delayed migration rates, and exposure to higher river temperatures. It was predicted that physiological stress, compromised osmoregulatory status, slowed travel rates, and exposure to high river temperatures

would characterize individuals that fell back following capture relative to those individuals that did not fall back. Further, it was predicted that individuals that failed to reach spawning grounds would have low energetic status, osmoregulatory impairments, be exposed to higher temperatures, and display slowed migration rates. The final prediction was that large stock-specific differences and year effects exist for the relationship between these physiological, behavioural, and environmental indices with fate. There is a growing body of research that examines the interplay between physiology and behaviour of Pacific salmonids, particularly in the marine environment (i.e., fish biopsied and telemetered in the marine environment and then tracked to freshwater spawning grounds). This marine research has yielded insight into correlations among organismal physiology, behaviour, and fate but has failed to provide detailed information on the relationship between fish condition, behaviour, and fate after freshwater entry. Information from the lower Fraser River is essential from a conservation and management perspective since temperature and flow conditions, as well as freshwater gill-net fisheries interactions, pose a new set of challenges for migrants (Hinch et al. 2006; Young et al. 2006).

In this thesis, I integrate new approaches in biotelemetry, temperature logging, and biosampling to understand the physiology, behaviour, and fate of sockeye salmon (*Oncorhynchus nerka*) in relation to environmental conditions encountered during the freshwater phase of their spawning migration in the Fraser River. The ultimate goal of this research is to gain greater insight into the basic migration biology of this species. From an applied perspective, understanding the relationships between environmental conditions, migration behaviour, physiology, and fate is essential to improving in-season management initiatives and developing long-term policies for the

conservation of this commercially and intrinsically valuable species, particularly in the context of climate change.

CHAPTER 2: Limited Behavioural Thermoregulation by Adult Up-River Migrating Sockeye Salmon in the Lower Fraser River Mainstem, British Columbia

Abstract:

The objective of this study was to combine radio telemetry with thermal loggers to assess the extent to which adult migrating sockeye salmon (*Oncorhynchus nerka*) behaviourally thermoregulate during their migration through the Fraser River mainstem, British Columbia. The Fraser mainstem represents a relatively thermally homogeneous region that contains some of the highest average temperatures encountered by sockeye salmon during their life history. I found that, throughout the study area, individual sockeye across stock complexes and run-timing groups maintained mean body temperatures that were consistent with river temperatures except in regions where they had access to thermally stratified waters. In two such study segments, there were moderate mean deviations between body and river temperatures (ΔT). In one of the study segments with the greatest ΔT , body temperatures decreased as river temperatures increased and a positive linear relationship was found between river discharge rate and ΔT . No relationship existed between ΔT and migration rate. This study was conducted during a moderately warm year, but based on my findings and previous research on the causal mechanisms of mortality in this system; I prognosticate that prolonged exposure to elevated mainstem temperatures could potentially lead to high mortality rates through a collapse in aerobic scope. I conclude that there is limited evidence for behavioural thermoregulation while individuals are actively migrating in the lower Fraser River mainstem during a moderately warm year.

Introduction:

Migratory species have evolved some of the most complex behaviours of any group of organisms (Dingle 1996), due in part to adaptations to variable environmental conditions. This is particularly salient for adult anadromous Pacific salmonids (*Oncorhynchus* spp.) that encounter remarkably variable water temperature and flow conditions during their spawning migrations as they return from the ocean to their natal freshwater spawning grounds (Hinch et al. 2006). Water temperature influences migration timing (Hodgson and Quinn 2002; Cooke et al. 2004c; Patterson et al. 2007), migratory behaviour (Berman and Quinn 1991; Goniea et al. 2006; Newell and Quinn 2006; Crossin et al. 2008; Farrell et al. 2008; Keefer et al. 2008b), swimming performance (Lee et al. 2001; MacNutt et al. 2006), migration speed (Hanson et al. 2008; Keefer et al. 2008a), physiology (Young et al. 2006; Crossin et al. 2008), energetics (Hinch and Rand 1998; Crossin et al. 2004; Rand et al. 2006), disease development (Wagner et al. 2005), and survival (Gilhousen 1990; Macdonald 2000; Crossin et al. 2008; Farrell et al. 2008; Keefer, Peery and Heinrich 2008b). In fact, temperature has often been considered the abiotic “master” factor of fishes, and this is particularly evident for salmonids during their spawning migrations (Brett 1971; Beitinger et al. 2000).

Sockeye salmon (*O. nerka*) stocks migrating through the mainstem Fraser River could theoretically encounter river temperatures ranging between 12°C and 22°C (60-year average minima and maxima daily temperatures during the summer migratory season; Patterson et al. 2007). Fraser River maximum summer water temperatures have increased by about 1.8°C over the past 40 years (Patterson et al. 2007), and predictions suggest that this warming trend will continue over the next

century (Morrison et al. 2002; Ferrari et al. 2007). Already, Fraser River temperatures can exceed optimal temperatures for aerobic scope and have approached or exceed lethal limits for certain sockeye populations (i.e., stocks; Lee et al. 2003; Farrell et al. 2008). Such concerns are not unique to the Fraser River, as endangered Snake River sockeye salmon, which are the most southerly distributed sockeye population, migrate over remarkably long durations and high elevations while coping with river temperatures that approach upper tolerance limits, often resulting in high mortality rates, particularly for late-timed migrants (Keefer et al. 2008a). Abnormally high mortality rates (>80%) have been observed for late-run Fraser River sockeye that now enter the Fraser River several weeks earlier than normal (Cooke et al. 2004c). The consequences of this abnormal behaviour is that late-run fish now encounter temperatures that are 4 to 5°C higher than what would have been encountered historically (Patterson et al. 2007).

A growing body of research has examined the thermal associations and thermoregulatory behaviour of adult Pacific salmonids during their freshwater spawning migrations. For example, sockeye salmon will exploit colder depths of thermally stratified Lake Washington prior to spawning further upstream, presumably to conserve energy by reducing exposure to high water temperatures (Newell and Quinn 2005). Snake River Chinook salmon (*O. tshawytscha*) and steelhead (*O. mykiss*) selected for cooler than average river temperatures during coldwater releases from Dworshak reservoir (Clabough et al. 2006). Similarly, Yakima River Chinook salmon maintained an average internal temperature that was 2.5°C cooler than river temperatures during their spawning migrations (Berman and Quinn 1991). Adult Columbia River Chinook salmon delayed migration at high water temperatures and

temporarily exploited refugia from cool-water tributaries (Gonia et al. 2006).

Thus, while holding behaviours in cool-water locations (e.g., deep-water lakes, tributary outflows) are especially important for adult salmon when river temperatures are high, and are thought to be essential for migration success (Cooke and Hinch 2005; Farrell et al. 2008), it is unclear the extent to which individual sockeye salmon behaviourally thermoregulate in the mainstem of the Fraser River, Canada's largest salmon bearing watershed.

The Fraser River mainstem is considered to be relatively thermally homogeneous, containing segments with relatively limited cool water access (Lauzier et al. 1995; Patterson et al. 2007), but represents a migration section with some of the highest average temperatures encountered by Fraser sockeye. No studies have explicitly examined the behavioural thermoregulation of salmonids in this system. Therefore, in the present study, I combined radio telemetry and thermal loggers to assess the temperature associations of adult sockeye salmon during their migration through the Fraser River mainstem. Specifically, differences between fish body temperatures and river temperatures were examined to identify the extent to which individual body temperatures deviate from measured river temperatures. In addition, the relationship between temperature deviation and a null relationship where no behavioural thermoregulation is assumed was examined to determine whether or not individuals behaviourally compensated for increasingly high temperatures. Finally, migration speed, river discharge, and run-timing group/stock complex were also examined to identify the factors that could potentially influence the deviation between body and river temperatures.

Materials and Methods

Fish Capture and Study Sites

This study represents a component of a much larger telemetry project that was conducted to describe the migration biology of Fraser River sockeye salmon. In all, 660 individuals were radio-tagged in the marine environment and a further 378 in the freshwater environment in 2006. Detailed capture methods are described in Robichaud and English (2007). Briefly, marine tagging occurred in coastal British Columbia in Juan de Fuca Strait (Aug 6-10) and Johnstone Strait (sampling occurred over 10 days from Aug 11-27; Figure 2-1). Fish were captured by commercial purse seine. After each net set, 20-30 individuals were selected from the purse seine and transferred by dipnet to on-board holding totes (726 L and 239 L) for tagging as described below. Freshwater tagging occurred in the lower Fraser River mainstem, 69 river kilometres (rkm) from the mouth of the Fraser River (sampling occurred over 22 days from Jul 9-Sep 1). Fish were captured with an 8.9 cm mesh drift gillnet, operated as a tangle net (i.e., the fine mesh of the net entangles the mouths and fins of individuals with minimal damage to the head, body and gills). Captured individuals were immediately hauled aboard the vessel and transferred to on-board holding totes (190 L) that were aerated and constantly supplied with fresh river water, generally with < 6 individuals per tote.

Tagging Procedure and Telemetry Methods

The marine and freshwater components of this study followed a previously established protocol for the non-lethal biosampling and telemetry tagging of unanaesthetized adult sockeye salmon (Cooke et al. 2005). All protocols were

approved by the University of British Columbia and Carleton University Animal Care Committees in accordance with the Canadian Council of Animal Care.

Individuals were rapidly placed supine on a v-shaped tagging trough and a constant flow of clean water was passed through the individual's mouth and gills. As part of a separate physiological study, biopsies were taken [a 2.5 mL blood sample was collected using caudal venipuncture with a 3.81 cm, 21-gauge vacutainer heparinised (lithium heparin) syringe (Houston 1990), a small gill sample (5-8 gill filaments, approximately 0.03 g, McCormick 1993) was collected using sharpened end-cutter pliers and a microwave fat probe was used to assess percent body lipid and gross somatic energy (Crossin and Hinch 2005)]. An adipose fin clip was taken for DNA analysis of stock complexes (as per Beacham et al. 2004). Three scales were collected for aging. An anchor tag or loop tag (Floy Manufacturing, Seattle, WA) was inserted into the dorsal musculature adjacent to the dorsal fin for identification. The radio transmitter was inserted gastrically such that the trailing end of the antenna exited the individual's mouth and was crimped to drift laterally along the individual's body.

Coded radio transmitters (MCFT-3A-3V, Lotek Wireless Inc., Newmarket, ON) were programmed to stop transmitting after 154 d to minimize the chance of interference with other studies. Thermal loggers (iButton DS1921Z [factory stated resolution ± 0.1 °C, accuracy ± 1 °C], Maxim Integrated Products, Inc., Sunnyvale, CA), programmed to record temperatures at 1h intervals (capable of continuous recording for ~ 180 d) were attached to each radio transmitter and waterproofed (Plasti Dip multi-purpose rubber coating, Plasti Dip International, Blaine, MN). Transmitters were 16 mm in diameter, 46 mm long plus an additional 10 mm in

length including the attached thermal logger, and had a 460 mm long antenna. The transmitter/thermal logger complex weighed 17 g in air and 7 g in water. Tags transmitted on the 150 MHz band width on six different frequencies (320, 360, 440, 460, 600 and 800 kHz) with three pulse intervals per frequency (4.5, 5.0, and 5.5 s) to reduce signal collisions.

A total of 24 fixed receiver stations were distributed throughout the Fraser watershed (see Robichaud and English 2007; Figure 2-1) using SRX400, SRX400A, or SRX600 radio receivers (Lotek Wireless Inc.), and 3-element or 4-element Yagi antennas (Maxrad Inc., Hanover Park, IL, or Grant Systems Engineering Inc., King City, ON). Sample sizes vary per study segment based on detection errors at certain fixed receiver stations, resulting in the inability to conclusively assign time of arrival and time of departure from certain study segments. Additionally, segment F had a reduced sample size because it excluded individuals that spawned within the tributaries of the Thompson River.

Environmental Variables

Six study segments of the Fraser mainstem (A-F) were established based on telemetry receiver locations (Table 2-1; Figure 2-1). Locations of hourly Fraser River water temperatures and river discharge are summarized in Table 2-1. River temperatures were collected by Fisheries and Oceans Canada's Fraser River Environmental Watch Program using Vemco data loggers ([resolution ± 0.1 °C, accuracy ± 0.2 °C], Amirix Systems, Inc., Halifax, NS), at Whonock and Lilloet, and Unidatat thermistor probes ([resolution ± 0.15 °C, accuracy ± 0.2 °C], Unidata Pty, Ltd., Australia) at Qualark (Lauzier et al. 1995). Although there are limitations to

measuring temperature from only these three fixed temperature stations, these locations are considered to be representative of the range of temperatures encountered in the upper, middle and lower segments of the study area and have been used by Fisheries and Oceans Canada as long-term temperature monitor locations (see also Hanson et al. 2008). Hourly river discharge data ($\text{m}^3 \cdot \text{s}^{-1}$) was monitored by the Water Survey of Canada at Mission, Hope, and the Thompson River confluence and these data were collated to estimate discharge at each study segment (Table 2-1).

Validation of Thermal Logger Accuracy and Precision

The accuracy and precision of 36 randomly chosen iButtons were tested under laboratory conditions. The sampling rate of the iButtons was set to 10 min intervals. iButtons were waterproofed with Plasti Dip and loosely placed in a fine-mesh net in a water bath. Water temperature was referenced to a digital temperature probe (YSI Model 85 [resolution ± 0.1 °C, accuracy ± 0.1 °C], YSI Inc., Yellow Springs, OH). The fine-mesh net allowed for water flow between iButtons and the temperature probe. The water bath was maintained at constant temperatures that ranged from a minimum of 15 °C to a maximum of 21.5 °C and were representative of the temperatures encountered by sockeye during the study. A total of 104 temperature observations were recorded per thermal logger. Linear regressions were used to assess the temperature deviation of individual iButton thermal loggers and the reference YSI temperature probe. Accuracy was calculated as the mean of the differences between iButton and YSI temperatures and precision was assessed based on their standard deviations (van Marken Lichtenbelt 2006). For all of the 36 iButtons tested under laboratory conditions, the linear regressions between the

thermal loggers and the YSI were highly significant ($P < 0001$; $R^2 > 0.973$). The intercepts ranged between 0.157 and 1.235. The mean iButton accuracy was 0.4 ± 0.3 °C and the mean precision was 0.2 ± 0.0 °C, which was more accurate than the values reported by the manufacturer. However, because this study examines precise values for body temperatures, results should be interpreted cautiously and in relation to the accuracy and precision reported here.

Statistical Analyses

Body temperature data were obtained from recovered thermal loggers (N=48). Wilcoxon sign-rank tests were used to test for differences between body temperature (T_B) and river temperature (T_R) at each study segment. Kruskal-Wallis tests followed by sequential Wilcoxon sign-rank *post hoc* tests (a Bonferroni correction of $\alpha = 0.003$ was applied to the *post hoc tests*) were performed to test for differences between body and temperatures ($\Delta T = T_B - T_R$; °C) among the study segments. For each study segment, linear regression analyses were performed separately to assess the relationship between 1) ΔT and river discharge, and 2) ΔT and migration speed. To test for evidence of increased behavioural thermoregulation with increasing temperatures, a Wilcoxon sign-rank test was used to compare the mean differences between the regression coefficients of body versus river temperature with a hypothetical slope of 1 across each study segment. The hypothetical slope of 1 would indicate a 1:1 relationship between body and river temperatures, where significant differences would provide evidence for temperature-dependent selection. Kruskal-Wallis tests were used to assess temperature deviations by run-timing group (i.e., Fraser sockeye are grouped into four broad groups for management purposes, based

on migration timing, called Early Stuart, Early Summer, Summer and Late; Beacham et al. 2004) and for three focal stock complexes (Chilko [a Summer run stock], Stellako [a Summer run stock], and Adams [a Late run stock]) across each study segment. Statistical analyses were conducted using JMP v. 7.0.1 (SAS Institute 2007). The level of significance (α) for all tests was assessed at 0.05 (Zar 1999). For statistical tests with multiple comparisons, a Bonferroni correction of $\alpha = 0.008$ was applied, where noted (see Tables 2-2, 2-3, 2-4 and Figure 2-4). All values presented are means \pm S.D., unless otherwise noted.

Results:

An individual example of a complete thermal history, from marine release to recovery at spawning grounds, can be found in appendix 2-1. An individual example of in-river body temperatures for a sockeye salmon relative to river temperatures is presented in Figure 2-2. This figure traces the thermal conditions experienced by this individual migrating through the Fraser River mainstem from freshwater entry and through each study segment. Upon river entry, mean body temperature was 18.3 ± 0.8 °C at segment A, 18.1 ± 0.7 °C at segment B, 18.1 ± 0.7 °C at segment C, 18.0 ± 0.7 °C at segment D, 17.5 ± 1.6 °C at segment E, and 17.4 ± 1.1 °C at segment F. Within each study segment, mean T_B was not significantly different from mean T_R (Wilcoxon sign-rank tests, all $P > 0.604$). However, mean ΔT varied throughout the study segments (Kruskal-Wallis test, $\chi^2 = 35.594$, d.f. = 5, $P < 0.001$; Figure 2-3). An important finding was that mean ΔT was always less than or equal to zero, albeit by < 0.5 °C. The greatest mean difference in ΔT existed at Segment E (Hell's Gate Canyon to Thompson Confluence; -0.39 ± 0.34 °C). The least mean difference in ΔT

occurred at Segment B (Rosedale to Hope; -0.03 ± 0.41 °C). Large standard deviations for mean ΔT were observed at each study segment (Figure 2-3).

A comparison of the mean differences between the slopes of body versus river temperature regressions and hypothetical slopes of 1 were significantly different for only segment A (Mission to Rosedale) following a Bonferroni correction (Table 2-2; Figure 2-4).

Linear regression analysis yielded a significant positive relationship between ΔT (°C) and river discharge ($\text{m}^3 \text{s}^{-1}$) for segment A only (Table 2-3; Figure 2-5). Linear regression analyses did not yield significant relationships between ΔT and migration speed for any of the study segments (Table 2-4).

The four run-timing groups (i.e., Early Stuart, Early Summer, Summer, and Late) did not differ in ΔT for any of the segments (Kruskal-Wallis tests, all $P > 0.05$). Similarly, there were no significant differences in study segment-specific differences among three major stocks for which reasonable sample sizes were available (Chilko, Stellako, and Adams; Table 2-5).

Discussion:

Body temperatures of Fraser sockeye salmon in the lower Fraser River mainstem routinely exceeded 18°C throughout this study period. Temperatures of this magnitude and higher can elevate basal metabolic rate, cause physiological stress, increase parasite loads for the myxosporean kidney parasite, *Parvicapsula minibicornis*, increase fungal infections, reduce peak aerobic activity, and ultimately result in mortality (Gilhousen 1990; Macdonald 2000; Lee et al. 2003; Wagner et al. 2005; MacNutt et al. 2006; Crossin et al. 2008; Farrell et al. 2008). Even slight

elevations of river temperatures above long-term averages but below thermal maxima, can deleteriously affect migratory behaviour and survival because temperature has such a profound influence on metabolic processes (Berman and Quinn 1991). Indeed, experimentally held adult salmonids at temperatures on either side of their temperature optimum can result in differential mortality rates and migration successes (Crossin et al. 2008).

It follows that the consequences of high river temperature should be countered by behavioural thermoregulation, when possible, to maintain body temperatures conducive to optimal energy conservation, reproductive development, swimming performance, and maintenance of aerobic scope (Lee et al. 2003; MacNutt et al. 2006; Newell and Quinn 2005; Farrell et al. 2008). A growing body of evidence has identified behavioural thermoregulation as a strategy for maintaining optimal temperatures during certain phases of upriver salmonid migrations (Berman and Quinn 1991; Tanaka et al. 2000; Newell and Quinn 2005; Clabough et al. 2006; Goniea et al. 2006; Keefer et al. 2008a). Pacific salmonids have evolved a number of complex behavioural adaptations to reduce migration costs in response to challenging environmental conditions. In fact, a key aspect to stock-specific timing of freshwater migration is the avoidance of deleterious environmental conditions (Hodgson and Quinn 2002; Keefer et al. 2004; Hinch et al. 2006). In addition, migrants will use microhabitat countercurrent flows to minimize energy expenditure (Hinch and Rand 1998; Hinch and Rand 2000) and hold in cooler tributaries and deeper stratified lake water (Newell and Quinn 2005).

The Fraser mainstem represents some of the warmest thermal conditions encountered throughout the entire sockeye spawning migration, yet limited evidence

for behavioural thermoregulation by adult migrating sockeye was found. At each site, mean body temperatures were not statistically different from river temperatures. This may be linked with the fact that most of the segments studied were relatively thermally homogeneous (Lauzier et al. 1995; Patterson et al. 2007). Regardless, body temperatures were on average less than river temperatures for most of the study segments, providing some evidence for limited behavioural thermoregulation in certain segments. While mean differences were < 0.5 °C, this result is given greater importance by the fact that 18 °C is likely above the optimal temperature (T_{opt}) for aerobic scope for these fish and the thermal window between the T_{opt} and the critical temperature (T_{crit} = an aerobic scope of zero) is typically 5-6 °C (Farrell et al. 2008). This means that even a < 1 °C behavioural shift in body temperature represents a large relative shift away from T_{crit} . It should be noted that because the mean ΔT of study segments was found to approach the mean accuracy (i.e., 0.4 ± 0.3 °C) and the mean precision (0.2 ± 0.0 °C) of the thermal loggers used in this study, significant relationships should be interpreted cautiously.

Segment A represents one of the deeper study segments, which may provide access to cooler waters through vertically stratified water temperatures (Patterson, *pers. comm.*) Similarly, near the Thompson confluence (segment E), there may be greater access to vertically stratified waters (Lauzier et al. 1995). Within these segments, mean ΔT were lower relative to other study segments, with a maximum of -0.39 °C at segment E and -0.37 °C at segment A. The regression slope of the difference between T_B and T_R differed from a hypothetical 1:1 relationship at segment A, suggesting that individuals behaviourally compensated for higher temperatures in this segment. This relationship was not apparent in other study segments (i.e., B

through F). These segments receive relatively low volumes of tributary input and have a sufficient volume to surface area ratio to resist the influence of local atmospheric parameters that would create large diurnal variation and vertical thermal stratification within the water column (Patterson et al. 2007). Segment E represents a region that has been shown to be thermally stratified yet behavioural compensation was not recorded in this reach, although mean ΔT was quite cool in this segment (Lauzier et al. 1995). However, an area of difficult migration passage, known as Hell's Gate, is included in this region. Hell's Gate is a river constriction that is characterized by areas of increased flows and turbulent conditions, resulting in mostly homogeneous thermal conditions and a greater challenge for individuals to swim against the strong river flow to seek out any thermal refuge that might be available (Hinch et al. 2006). Previous Fraser River sockeye salmon studies have identified that relative to other segments of the Fraser River mainstem, Hell's gate is energetically costly to navigate and similar to the findings of this study, results in slower migration speeds (Hinch and Rand 1998; Hinch and Bratty 2000; Hanson et al. 2008). From this evidence, I conclude that the additional transit time within this canyon area is not associated with behavioural thermoregulation in seeking cooler water but likely related to overcoming severe hydraulic obstacles.

No relationship was found between run-timing and differences between body and river temperatures. No statistical differences existed among the Chilko, Stellako and Adams stock complexes. Previously, maximum swimming performance, aerobic scope, and thermal optima have been found to vary among Fraser sockeye stocks (Lee et al 2003), as does migration timing (Hinch et al. 2006) and migration mortality in relation to stock-specific T_{crit} (Farrell et al. 2008). The lack of stock specific

differences in ΔT in the present study may simply reflect sockeye migrating within their thermal window for aerobic scope.

River discharge had a positive linear relationship with increasingly positive ΔT in segment A only. With higher river discharge, individuals that hold in cool-water tributary plumes face an energetic cost, as prolonged exposure to high flow conditions is energetically costly and may outweigh the energetic savings that are conferred from cool water exposure (Rand and Hinch 1998; Standen et al. 2002; Standen et al. 2004). Standen et al. (2002; 2004) presented a similar tradeoff for Fraser sockeye exposure to high flow conditions whereby individuals must either take valuable time to seek microscale flow patterns or must invoke fast swimming speeds to move rapidly through areas of difficult passage. The finding that no relationship was observed at segments up-river of segment A may be partially explained by the fact that segments surrounding Hell's Gate and downstream sites receive relatively low tributary input (Patterson et al. 2007). Higher river discharge would suggest more thermal mixing in the water column and less thermal stratification, potentially resulting in reduced access to cool temperatures in most segments of the mainstem (Patterson et al. 2007). My findings suggest that the temperature benefit did not outweigh the cost of exposure to higher flows in most study segments, or the cost of delayed migration rates, at the temperatures examined in this study.

Although travel times varied considerably among many of the study segments, no relationship between body temperature and travel times were observed. During years of moderate Fraser River water temperatures, such as 2006, a tradeoff may have existed between the advantages of traveling through the Fraser mainstem at a rapid speed or slowing migration to seek out cooler water. The lack of behavioural

thermoregulation observed here may be linked with this finding, as individuals may minimize travel times by not holding in regions where limited cool water is available, such as tributary outflows. Individuals may avoid seeking and holding in cool-water locations to travel rapidly through these high temperature segments to accrue less thermal units and minimize the risk of physiological stress and impact of parasites (Wagner et al. 2005; Crossin et al. 2008). Hanson et al. (2008) identified a positive relationship between average maximum water temperatures and sockeye migration speed throughout many segments of the Fraser mainstem. The average river temperature in the Hanson et al. (2008) study was 18.0 °C, and the authors suggested that this temperature range may in fact enable individuals to swim at higher speeds at the peak of aerobic activity. However, as water temperatures approach 20 °C, the peak aerobic activity of Fraser sockeye salmon declines and contributes to mortality (Lee et al. 2003; MacNutt et al. 2006; Farrell et al. 2008). Delayed migration associated with holding in cool water locations has been observed in the Columbia River, where cool-water tributary use has been found to increase exponentially with increasing water temperatures (Hyatt et al. 2003; Goniea et al. 2006). Although the telemetry receiver layout provides excellent spatial coverage, I was unable to determine the extent to which individuals utilize known cool-water locations. However, I infer from individual temperature records and the minimal deviation between river and body temperatures in most study segments, that there is limited evidence of holding behaviours and associated slowed migration rates from use of cool water regions throughout the study area.

While there is limited evidence for behavioural thermoregulation within the lower Fraser mainstem, there is considerable evidence, both in the Fraser and other

river systems, that salmonids exploit cool-water locations including tributaries and lakes as they approach spawning grounds to limit prolonged exposure to high temperatures (Hodgson and Quinn 2002; Cooke and Hinch 2005; Newell and Quinn 2005; Pon et al. 2006; Goneia et al. 2007). Farrell et al. (2008) observed that, during a period of abnormally warm water temperatures, a stock of Fraser sockeye that milled in a cool, deep, oligotrophic lake had a higher survival rate relative to individuals from the same stock that milled in an adjacent river where temperatures were much higher. The latter group failed to complete their migrations, resulting in zero lifetime fitness. To understand the direct consequences of prolonged exposure to high temperatures, a complementary experimental study was conducted on Fraser sockeye and found that exposure at high, but sublethal temperatures (18 °C), resulted in mortality rates twice that of an experimental group held at 10 °C for a period of 24 d. When water temperatures are high, mortality rates are elevated for individuals that are unable to behaviourally thermoregulate to cooler temperatures (i.e., exploit cool water refugia). Taken together, the prevailing mechanism of high temperature mortality for migrating sockeye is a collapse of aerobic scope, compounded by other deleterious factors, including an increased impact of infection with the *Parvicapsula minibicornis* kidney parasite, for Fraser River sockeye (Crossin et al. 2008; Farrell et al. 2008).

With the growing body of evidence that high temperature exposure during the freshwater component of the sockeye salmon spawning migration contributes to mortality, it is necessary to understand how individuals respond to elevated water temperatures (Hinch et al. 2006; Crossin et al 2008). This is particularly warranted because Fraser sockeye are expected to encounter peak summer river temperatures

that exceed current averages by several degrees in the coming decades (Morrison et al. 2002; Rand et al. 2006). The results of this study indicate that there is limited behavioural thermoregulation occurring in the lower Fraser River mainstem by adult up-river migrating sockeye salmon. Combining this result with the evidence that prolonged high temperature exposure leads to increased mortality, under both experimental (Crossin et al. 2008) and field (Farrell et al. 2008) conditions, suggests that high mortality rates can be expected for Fraser sockeye unless they are able to access cool water refugia found in tributaries and deep lakes. Future research must examine how individuals use available thermal refugia in tributaries and lakes (e.g., Harrison Lake) in the upper Fraser watershed to understand the extent to which individuals compensate for prolonged exposure to high temperatures in the Fraser mainstem. Improved knowledge on the interactions between environmental conditions and migration success is of paramount importance to improving the understanding of the basic migration of Pacific salmonids and can be used to further enhance robust management initiatives for the commercial, recreational and First Nations fisheries that operate in the Fraser River watershed.

TABLES:

Table 2-1. Study segment names and corresponding river locations, segment distances, river temperature and river discharge monitoring locations in the Fraser River, British Columbia, Canada.

Study segment	River location	Segment Length (rkm)	River temperature monitoring location	River discharge monitoring location
A	Mission to Rosedale	44	Whonnock	Mission
B	Rosedale to Hope	36	Qualark	Hope
C	Hope to Sawmill Creek	34	Qualark	Hope
D	Sawmill Creek to Hell's Gate Canyon	12	Qualark	Hope
E	Hell's Gate Canyon to Thompson Confluence	55	Qualark	Hope
F	Thompson Confluence to Seton Confluence	57	Lillooet	Hope, excluding Thompson River discharge

Table 2-2. Results of a Wilcoxon Sign-Rank test between the regression slope of river versus body temperature regressions and a hypothetical slope of 1 for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). Bold values denote significant differences, following a Bonferroni correction ($\alpha=0.008$).

Study segment	N	Mean (\pmSD) difference from hypothetical slope of 1	Test statistic	P
Segment A	48	-0.986 (\pm 0.784)	-536.000	<0.001
Segment B	43	-0.445 (\pm 1.343)	178.500	0.9881
Segment C	44	-0.125 (\pm 0.562)	-113.000	0.0876
Segment D	46	-0.136 (\pm 0.749)	-86.500	0.175
Segment E	42	-0.066 (\pm 1.370)	63.500	0.791
Segment F	21	-0.262 (\pm 0.792)	-67.500	0.03

Table 2-3. Regressions of the mean difference between river temperatures and body temperatures (ΔT , °C) with log-transformed river discharge ($\log RDischarge$, $m^3 \cdot s^{-1}$) for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). Bold values denote significant differences, following a Bonferroni correction ($\alpha=0.008$).

Study segment	N	Regression Equation	R ²	Sum of Squares	P
Segment A	49	$\Delta T = -4.252 + 1.140 * \log RDischarge$	0.202	10.677	0.001
Segment B	43	$\Delta T = -1.073 + 0.308 * \log RDischarge$	0.018	7.145	0.391
Segment C	44	$\Delta T = -1.369 + 0.368 * \log RDischarge$	0.029	5.655	0.271
Segment D	46	$\Delta T = -1.839 + 0.491 * \log RDischarge$	0.026	9.411	0.286
Segment E	42	$\Delta T = -1.819 + 0.435 * \log RDischarge$	0.038	4.862	0.214
Segment F	21	$\Delta T = 1.531 - 0.587 * \log RDischarge$	0.019	4.699	0.549

Table 2-4. Regressions of the mean difference (ΔT , °C) between river temperatures and body temperatures with migration speed (MSpeed, km·d⁻¹) for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). No relationships were statistically significant following a Bonferroni correction ($\alpha=0.008$).

Study segment	N	Regression Equation	R ²	Sum of Squares	P
Segment A	49	$\Delta T = -0.120 - 0.194 * \text{MSpeed}$	0.014	10.677	0.427
Segment B	43	$\Delta T = 0.277 - 0.225 * \text{MSpeed}$	0.015	7.145	0.431
Segment C	44	$\Delta T = 0.094 - 0.201 * \text{MSpeed}$	0.022	5.587	0.346
Segment D	46	$\Delta T = -0.199 - 0.025 * \text{MSpeed}$	0.001	9.410	0.935
Segment E	42	$\Delta T = -0.691 + 0.245 * \text{MSpeed}$	0.088	4.862	0.056
Segment F	21	$\Delta T = -1.083 + 0.519 * \text{MSpeed}$	0.080	4.699	0.215

Table 2-5. Results of Kruskal-Wallis tests comparing the temperature deviation (°C) between the Chilko, Stellako and Adams stock complexes for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*).

Study segment	Stock	N	Mean (±SD)	DF	χ^2	F Ratio	P
Segment A	Chilko	9	-0.6 ± 0.6	24	5.947	0.228	0.797
	Stellako	7	-0.4 ± 0.5				
	Adams	9	-0.4 ± 0.5				
Segment B	Chilko	7	0.0 ± 0.3	21	3.487	0.239	0.789
	Stellako	7	0.0 ± 0.5				
	Adams	8	-0.1 ± 0.4				
Segment C	Chilko	9	-0.2 ± 0.3	23	2.849	0.229	0.797
	Stellako	7	-0.1 ± 0.4				
	Adams	8	-0.2 ± 0.4				
Segment D	Chilko	11	-0.3 ± 0.3	26	6.738	0.202	0.818
	Stellako	7	-0.4 ± 0.8				
	Adams	9	-0.2 ± 0.5				
Segment E	Chilko	11	-0.5 ± 0.1	25	1.829	1.747	0.196
	Stellako	7	-0.3 ± 0.4				
	Adams	8	-0.6 ± 0.2				
Segment F	Chilko	9	-1.0 ± 0.4	13	2.19	0.293	0.156
	Stellako	5	-1.2 ± 1.0				

FIGURES:

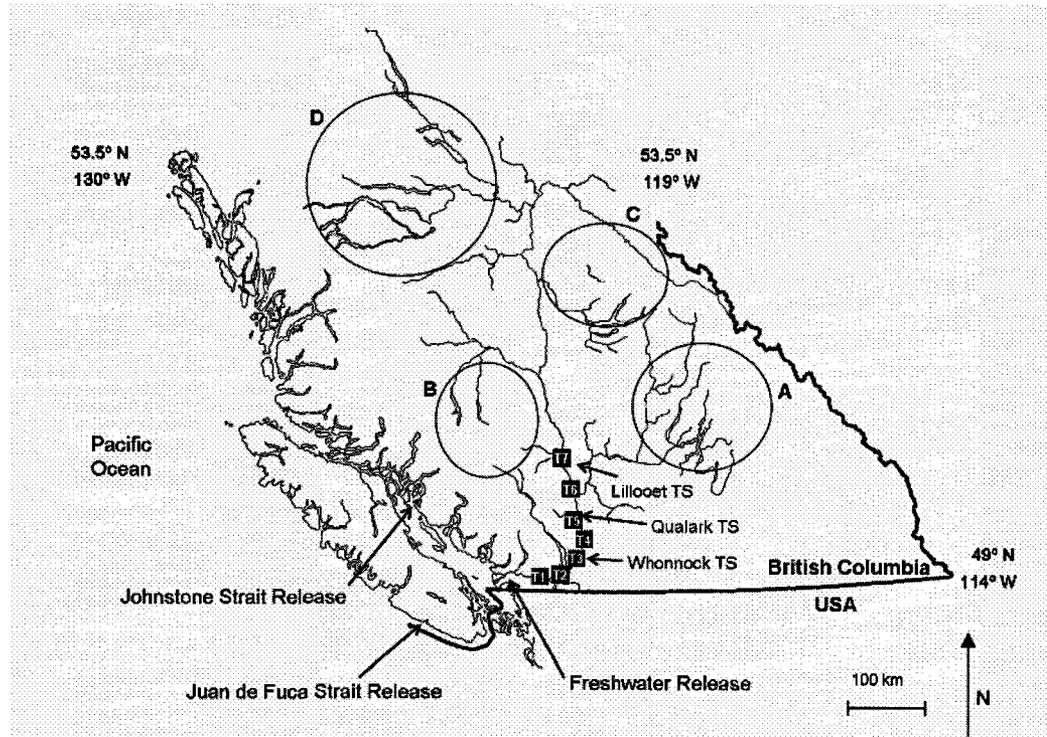


Figure 2-1. A map of the Fraser River watershed, British Columbia. Labels denote marine and freshwater release sites for adult sockeye salmon (*Oncorhynchus nerka*). Fixed receiver stations in the Fraser River mainstem are denoted as Mission (T1), Rosedale (T2), Hope (T3), Sawmill (T4), Hell's Gate (T5), Thompson confluence (T6), and Seton confluence (T7). River temperature monitoring stations are labeled as Whonnock temperature station (TS), Qualark TS and Lillooet TS. Spawning grounds are circled and labeled with letters for each stock complex included in the study as A: Adams, Fennell, Little River, Raft, Scotch, Seymour, and Shuswap, B: Chilko and Gates, C: Bowron and Quesnel, and D: Early Stuart, Stellako, and Nadina.

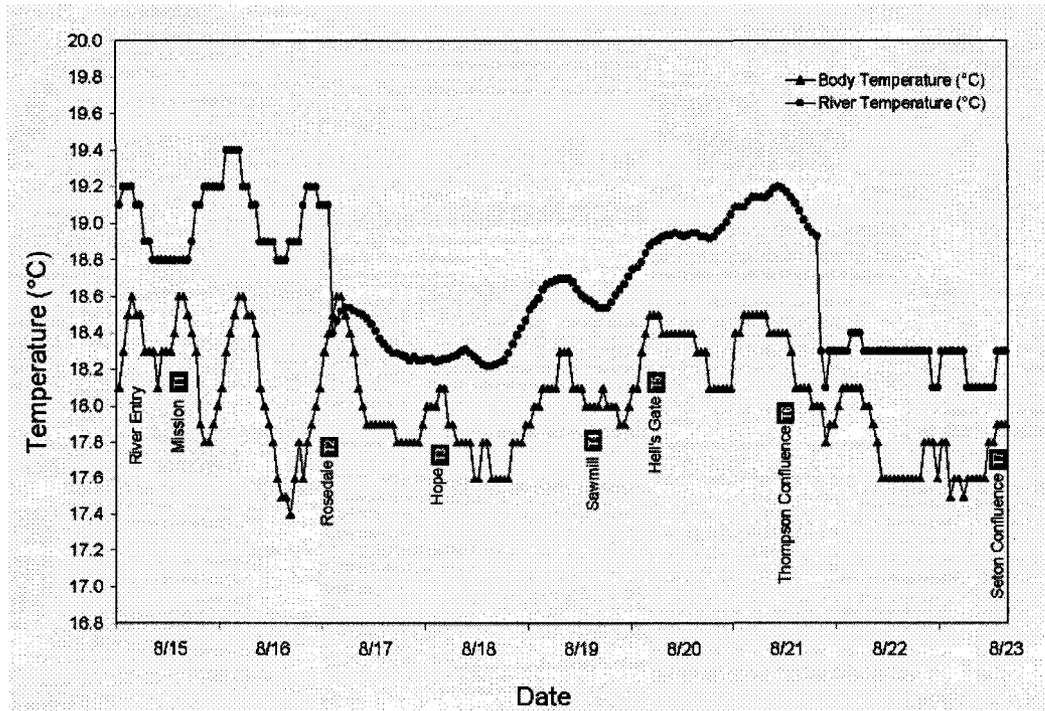


Figure 2-2. An example hourly thermal history figure for an adult migrating sockeye salmon (*Oncorhynchus nerka*) that was released in the marine environment. The figure traces the body temperature recorded for the individual from freshwater entry through each of the study segments, relative to river temperatures. Labels denote freshwater entry and detections at each telemetry receiver station in the Fraser River mainstem, British Columbia.

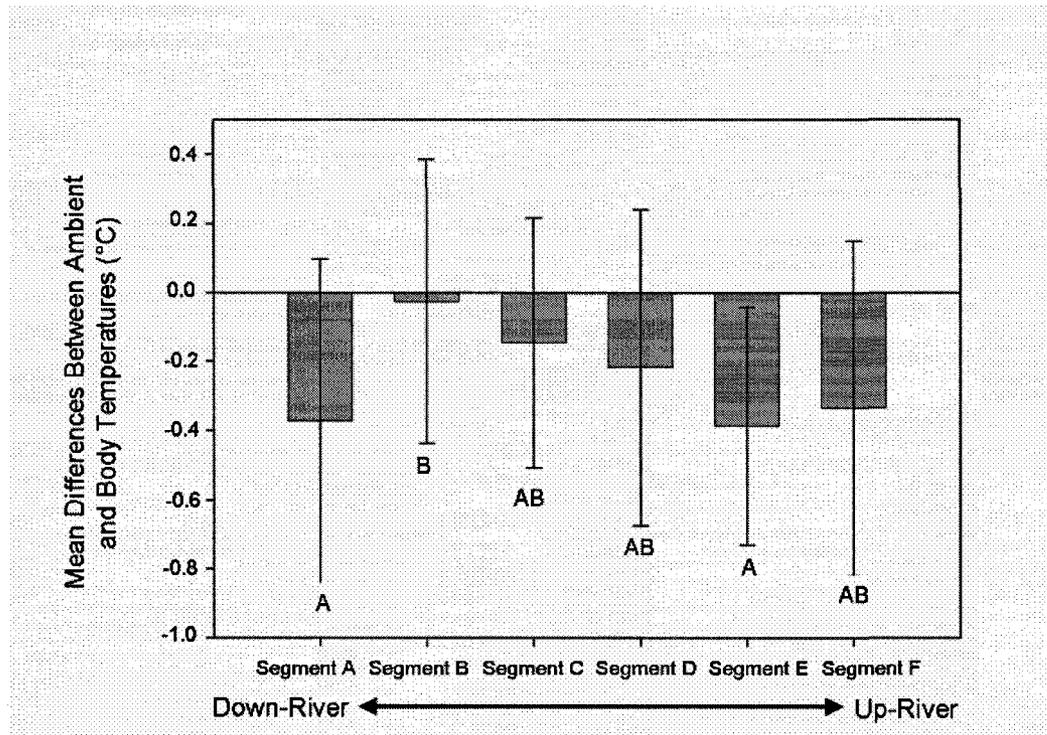


Figure 2-3. Mean differences (\pm SD) between body temperatures and river temperatures ($^{\circ}$ C) for adult Fraser River sockeye salmon (*Oncorhynchus nerka*) at each study segment in the Fraser River mainstem, British Columbia. Dissimilar letter groupings denote significant differences from one another (Kruskal-Wallis test, followed by sequential Wilcoxon sign-rank *post hoc* tests, where $\alpha = 0.003$).

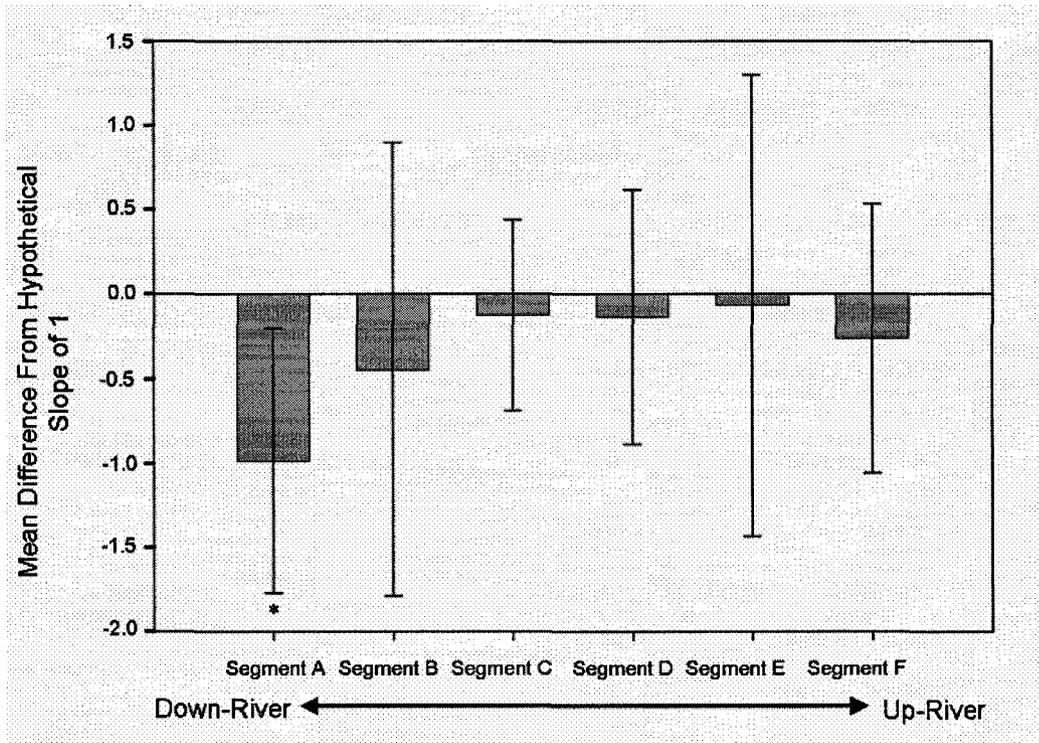


Figure 2-4. Mean differences (\pm SD) between the regression slope of body versus river temperature regressions and a hypothetical slope of 1 for each study segment for adult sockeye salmon (*Oncorhynchus nerka*) in the Fraser River mainstem, British Columbia. Asterisks denote significant differences between the slope of body versus river temperature from 1, following a Bonferroni correction ($\alpha = 0.008$).

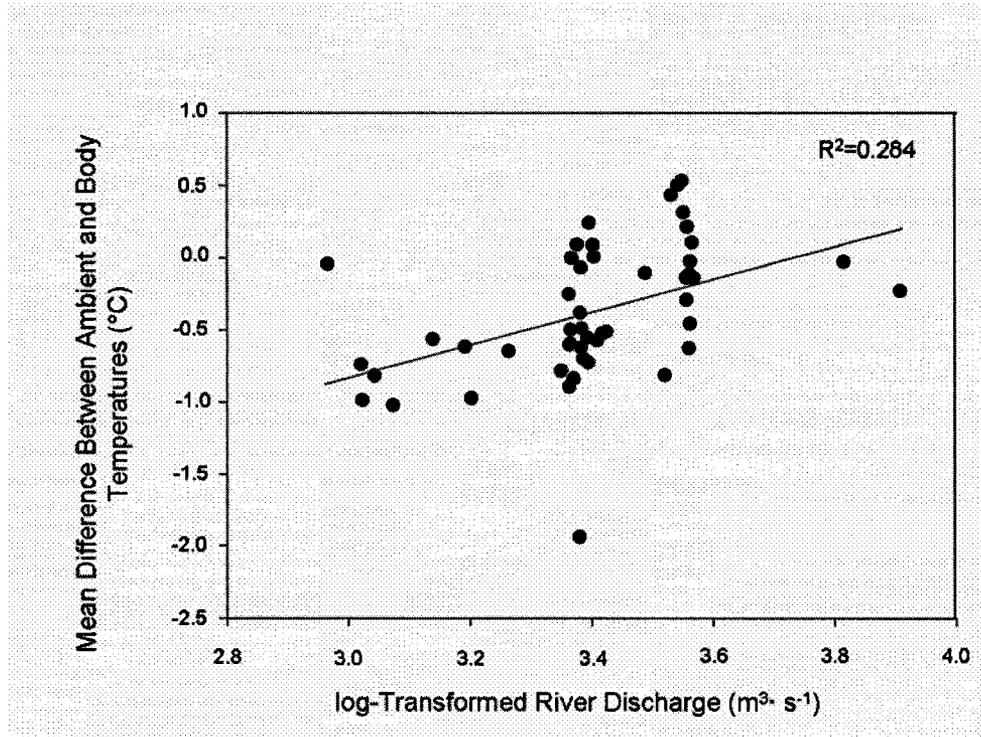
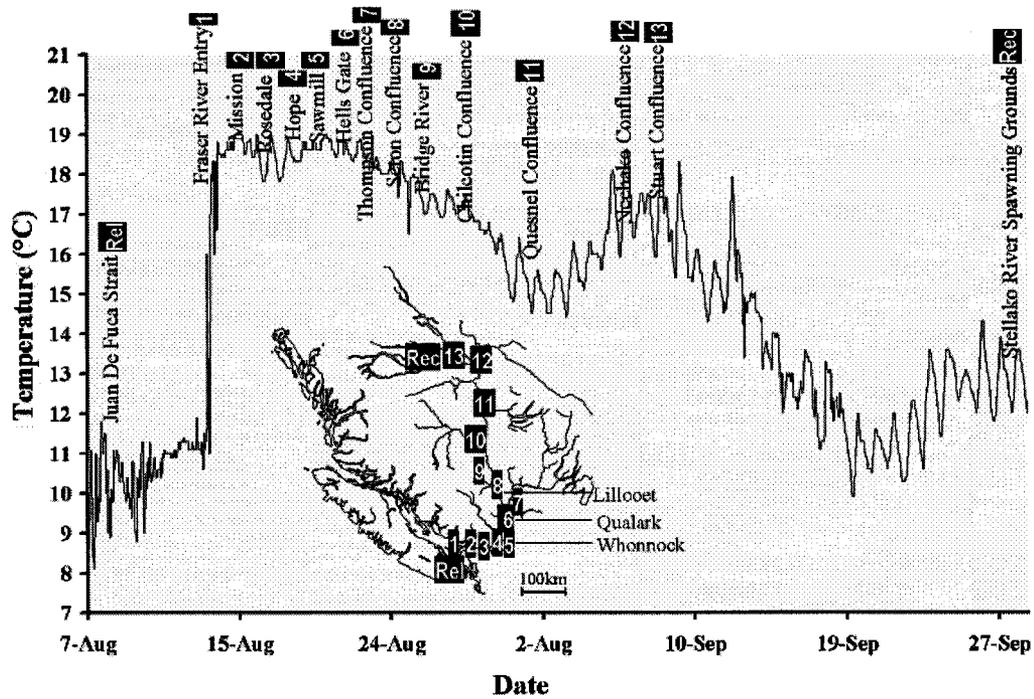


Figure 2-5. Linear regression line of best fit between the difference between body and river temperatures (°C) and river discharges (m³·s⁻¹) at segment A for adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in the Fraser River mainstem, British Columbia.

APPENDIX:



Appendix 2-1. An example hourly thermal history figure for an adult migrating sockeye salmon (*Oncorhynchus nerka*) that was released in the marine environment at Juan de Fuca Strait. Labels denote marine release (Rel) and recovery (Rec) locations and numbered labels denote additional telemetry receiver detection locations throughout the Fraser River watershed. River temperature monitoring stations are labeled as Whonnock, Qualark and Lillooet.

CHAPTER 3: Integrating Physiological, Behavioural, and Environmental Indices to Understand Migration Fall Back and Mortality During the Freshwater Phase of the Sockeye Salmon Spawning Migration in the Fraser River, British Columbia

Abstract:

To gain greater insight into the interplay of physiology and behaviour in salmonid spawning migrations, I intercepted sockeye salmon (*Onchorhynchus nerka*) at the onset of the freshwater phase of their migration in the lower Fraser River, British Columbia. Individuals were sampled for physiological indices of stress, osmoregulatory status, and energy content, then gastrically implanted with radio telemetry transmitters to assess migration behaviour and fate (i.e., en-route mortality versus survival to spawning grounds). I found ~24 % of individuals fell back down-river immediately following capture. Individuals that fell back were characterized by elevated hematocrit and plasma sodium concentrations. Fall back resulted in slowed migration rates. I did not find a relationship between fall back and fate. Overall, individuals that died en-route to spawning grounds had slower migration rates between the release site and the Thompson River confluence. Contrary to predictions, none of the physiological or environmental variables measured here affected migration fate. Stock specific differences were observed in many of the physiological (hematocrit, plasma lactate, glucose, sodium), behavioural (migration rate) and environmental (river temperature) indices examined in this study, reflecting the phenotypic differences and genetic variation associated with semelparous Pacific salmonid migrations. I found differences between years for plasma lactate, sodium, chloride, and osmolality, yet none of these factors contributed to year-specific fate. I

conclude that multiple factors contribute to ultimate migration fate and further targeted research is necessary to unravel the complex relationship between the physiology and behaviour of Pacific salmonid migration.

Introduction:

Reproductive migrations represent some of the most challenging life history stages for organisms across multiple taxa (Dingle 1996; Dingle and Drake 2007). For these migrations to be successful, organisms must undergo a suite of physiological and behavioural changes. Pacific salmonids (*Oncorhynchus* spp.) exemplify the complexity of this interplay between physiology and behaviour throughout their spawning migrations, from the perception of cues that initiate migration to the factors that affect mating systems at the spawning grounds (Quinn and Adams 1996; Hinch et al. 2006; Ueda et al. 2007; Hruska et al. 2007). Within species, there is remarkable population (i.e., stock)-specific variation reflecting the phenotypic differences and underlying genetic variation associated with homing to natal spawning grounds (Bernatchez and Dodson 1987; Hinch et al. 2006). The timing of the onset of the freshwater component of the migration is species and stock-specific, but within a stock, migration initiation generally deviates minimally between years (Woodey 1987; Hodgson and Quinn 2002). For some sockeye salmon (*O. nerka*) stocks, the freshwater component of the migration can exceed 1400 km in distance and 2000 m in elevation (Brett 1995; Burgner et al. 1991; Keefer et al. 2008a). Since sockeye salmon only engage in spawning migrations once in their life cycle, individuals that fail to reach spawning grounds and successfully reproduce will have zero lifetime fitness (Dingle 1980).

In addition to the physiological and morphological changes associated with migration and maturation, sockeye salmon must cope with challenging environmental conditions, including high water temperatures and interactions with fisheries gear. The transition from marine to freshwater requires that individuals remodel their osmoregulatory and ionoregulatory systems in preparation for the freshwater environment (Clarke and Hirano 1995; Shrimpton et al. 2005). As sockeye salmon approach spawning grounds, they undergo physiological and morphological changes associated with sexual maturation. All of these changes, as well as the spawning migration, are fuelled by endogenous energy reserves because sockeye salmon do not feed during their spawning migrations (Brett 1995; Hendry and Berg 1999). While sockeye salmon migrations are intrinsically challenging, high temperature exposure can result in physiological stress, accelerated energy depletion, increased incidence of disease, and impaired migratory behaviour (Wagner et al. 2005; Hinch et al. 2006; Farrell et al. 2008; Crossin et al. 2008; Keefer et al. 2008a). Prolonged exposure to abnormally high temperatures (i.e., temperatures approaching thermal tolerances) can result in a complete collapse of aerobic scope and high mortality rates (Farrell et al. 2008). In addition, interactions with fisheries gear can further elevate physiological stress and can potentially lead to behavioural impairments even for individuals that are able to free themselves from gear entanglement or are released as non-target species (Farrell et al. 2000; 2001).

Migration behaviour and travel rate in Pacific salmon are affected by differences in energetic status, physiological condition, swimming performance, and sex (Lee et al. 2003; Crossin et al. 2004; Crossin et al. 2008; Farrell et al. 2008; Hanson et al. 2008). Migrants use a number of behavioural adaptations, such as

selection of migration pathways, exploitation of forward assists, and engaging in holding behaviours in response to elevated river temperatures and variable flow conditions (Brett 1995; Hinch and Rand 1998; Hinch and Rand 2000; Hyatt et al. 2003; Newell and Quinn 2005; Goniea et al. 2006; Keefer et al. 2008a). Migration can be delayed due to movement through areas of difficult passage (e.g., river constrictions with high flows, dam passage; Hinch and Rand 2000; Keefer et al. 2006), holding and thermoregulatory behaviours (e.g., Newell and Quinn 2005; Farrell et al. 2008) or anomalous migratory behaviours, such as overshoot behaviour (e.g., Keefer et al. 2008b). Migration timing and travel rate are critical because the salmon not only have a limited energy budget, but they also have a limited amount of time to reach spawning grounds, secure a mate, and spawn prior to death (Brett 1995; Hendry and Berg 1999; Crossin et al. 2004). Delayed arrival at spawning grounds could result in reduced reproductive success due to less time spent on spawning grounds and fewer opportunities for reproduction, which could potentially result in a reduction of overall population fitness (Smoker et al. 1998; Keefer et al. 2006; Hruska et al., unpublished data).

Despite the growing body of research on the physiology and behaviour of salmonid migrations, many knowledge gaps remain (Hinch et al. 2006; Young et al. 2006). Previous Fraser sockeye salmon research has involved intercepting fish in the ocean, ~ 200 km from the mouth of the Fraser River (e.g., Cooke et al. 2006a; *in press*; Crossin et al. 2007). These studies provided insight into correlations among physiology, behaviour, and fate during the marine and coastal phases of the adult spawning migration. However, data are lacking on the relationships between fish condition and migratory behaviour and fate after freshwater entry, a migration phase

that is known to be particularly challenging for migrants (e.g., prolonged exposure to high temperatures; Farrell et al. 2008). In the marine environment, it is difficult to make behavioural assessments at a fine spatial scale immediately following release. Accordingly, the objective of the present study was to gain greater insight into the freshwater migration biology of this species by characterizing whether or not individuals engaged in anomalous movement down-river following release and by assessing the factors that contribute to ultimate fate. I hypothesized that for sockeye salmon at the onset of their freshwater spawning migrations, individuals characterized by indices of impaired physiological and energetic status, delayed migration rates, and exposure to higher river temperatures were more likely to (1) fall back following capture or continue migrating up-river, and (2) die en-route or survive to reach spawning grounds both within and between years. Based on previous research conducted in the marine environment, I predicted that physiological stress, compromised osmoregulatory status, slowed migration rates, and exposure to high river temperatures would characterize individuals that fell back following capture relative to those individuals that did not. Further, I predicted that individuals that failed to reach spawning grounds would have low energetic status, osmoregulatory impairments, be exposed to higher temperatures and display slowed migration rates. My final prediction was that large stock-specific differences and year effects would be observed for the relationship between these physiological, behavioural, and environmental indices with fate due to the complex life history and population structure of sockeye salmon.

Materials and Methods:

Fish Capture and Study Site

Established protocols were used to biosample and gastrically implant radio transmitters in unanesthetized sockeye salmon in this study. A large body of previous research has validated this approach in the marine environment and upper portions of the Fraser River by demonstrating that these methods do not compromise the behaviour or survival of adult up-river migrating sockeye salmon (e.g., Cooke et al. 2005; Cooke et al. 2006a; 2006b; Young et al. 2006; Crossin et al. 2007; Cooke et al. in press). This study was one component of a larger radio telemetry project conducted in 2005 and 2006. Part of this project was undertaken not only to gain better insight into the migration biology of this species in a critical component of their migrations, but also to validate the freshwater capture methods used to biosample and tag sockeye salmon in the lower Fraser River, an area where the live-sampling of fish using other gear types is inherently difficult. Detailed capture methods are described in Robichaud and English (2006; 2007). Briefly, tagging occurred in the lower Fraser River mainstem, 69 river kilometres (rkm) from the mouth of the Fraser River. Sampling occurred over 6 days from Aug 2–Sep 8 in 2005 and over 22 days from Jul 9–Sep 1 in 2006. River temperatures varied between 16.6 and 20.2 °C throughout the tagging period in 2005 and between 16.9 and 20.6 °C in 2006. Fish were captured with an 8.9 cm mesh drift gillnet, operated as a tangle net. The tangle net was used to tangle individuals by the mouth and fins in an effort to reduce gill damage and expedite the removal of individuals from the net. Once caught, individuals were immediately removed from the net and transferred to on-board holding totes (190 L) that were aerated and constantly supplied with fresh river water. Individuals that appeared to be injured or in poor condition were not included in the study.

Tagging Procedure and Telemetry Methods

This study followed a previously established protocol for the non-lethal biosampling and telemetry tagging of unanaesthetized adult sockeye salmon (Cooke et al. 2005). It must be noted that this procedure inevitably imparts physiological stress on all individuals; however, because the sampling protocol was followed in the exact same manner for all individuals, I assume that the degree of stress imparted is of similar magnitude for all individuals in the study. All biopsy and tagging protocols were approved by the University of British Columbia and Carleton University Animal Care committees in accordance with the Canadian Council of Animal Care. On shore, fish were individually transferred by hand from the holding totes and placed supine in a flow-through v-shaped tagging trough supplied with a constant flow of clean river water passing through the individual's mouth and gills. A 2.5 mL blood sample was collected using caudal venipuncture with a 1.5", 21-gauge vacutainer heparinised (lithium heparin) syringe to assess plasma physiological indices (Houston 1990). A small gill sample (5-8 gill filaments, ~ 0.03 g) was collected using sharpened end-cutter pliers for quantification of gill tissue Na^+ , K^+ -ATPase activity (McCormick 1993; Shrimpton et al. 2005). A microwave fat probe (Distell Fish Fatmeter model 692, Distell, Inc., West Lothian, Scotland, UK) was used to quantify gross somatic energy levels (GSE, Crossin and Hinch 2005). A 0.5 g adipose fin clip was taken for DNA analysis of stock complexes (Beacham et al. 2004). Three scales were collected for aging and fork length measurements were made. An anchor tag (Floy Manufacturing, Seattle, WA) was inserted into the dorsal musculature adjacent to the dorsal fin for visual identification. The radio transmitter was inserted gastrically with

the trailing end of the antenna exiting the mouth and crimped to drift laterally along the individual's body. Sampling times were standardized to ≤ 3 min.

Coded radio transmitters (MCFT-3A-3V, Lotek Wireless Inc., Newmarket, ON) were programmed to stop transmitting after 154 d to minimize the chance of interference with other studies. Transmitters were 16 mm in diameter, 46 mm long and had a 460 mm long antenna. The transmitter/thermal logger complex weighed 17 g in air and 7 g in water. In 2006, a thermal logger was attached to each transmitter and waterproofed using Plasti Dip multi-purpose rubber coating (Plasti Dip International, Blaine, MN), adding <10 mm in length. Tags transmitted on the 150 MHz band on six different frequencies (320, 360, 440, 460, 600 and 800 kHz) with three pulse intervals per frequency (4.5, 5.0, and 5.5 s) to reduce the occurrence of signal collisions.

A total of 19 and 24 fixed receiver stations were distributed throughout the Fraser watershed in 2005 and 2006, respectively (see Robichaud and English 2006; 2007). Figure 3-1 shows the locations for the seven telemetry receiver stations that were the focus of the present study. SRX400, SRX400A, or SRX600 radio receivers (Lotek Wireless Inc.) were used with 3-element or 4-element Yagi antennas (Maxrad Inc., Hanover Park, IL, or Grant Systems Engineering Inc., King City, ON).

Laboratory Assays and Calculation of Physiological and Energetic Variables

Individual stock origin was determined from DNA analyses (Beacham et al. 1995, 2004). Plasma ions (K^+ , Cl^- and Na^+), glucose, lactate and osmolality were quantified by procedures based on Farrell et al. (2001). Gill Na^+, K^+ -ATPase activity was determined by kinetic assay (McCormick 1993). Hematocrit was measured using

a hematocrit centrifuge to measure the proportion of packed cells to plasma (Archer 1965). GSE was calculated based on a previously established conversion formula validated for sockeye salmon (Crossin and Hinch 2005).

Determination of Fall backs, Mortalities, Arrival at Spawning Grounds, and Migration Rate

Any individual that was known to be caught by in-river fisheries after tagging were excluded from all analyses. The term “fall back” was used to describe any individual that was detected at least once at a fixed receiver stationed at Crescent Island, a location 1 rkm down-river from the release site. Downstream movements detected in the upper reaches of the study area were not considered fall backs; only those individuals that moved downstream as far as Crescent Island were considered fall backs in this study. En-route mortalities were categorized by the failure of the individual to be detected at sequential fixed receiver stations based on criteria described by Robichaud and English (2006; 2007). Detections by fixed station receivers at the lower end of natal spawning grounds were indicative of whether or not individuals reached spawning grounds. The term “fate” was used to describe whether an individual survived to reach spawning grounds or died en-route.

Migration rate was calculated by dividing the distance (rkm) between successive receiving stations by the time interval (hrs) from the first detection at the downstream receiver station and the first detection at the subsequent upstream station. Migration rate is a relative measure, as it assumes linear movement based solely on distance traveled and the timing of telemetry receiver detections and does not account for local environmental variability, migration timing, or subtle behavioural variability

(e.g., holding behaviours, selection for “forward assists”; Hinch and Rand 2000; Goniea et al. 2006). For the purposes of this study, I calculated migration rate between the release location and the receiver located at the Thompson River confluence, as all sockeye salmon stocks in this study migrate through this segment of the river. Individuals that were not detected by the fixed station receiver at the Thompson River confluence were excluded from migration rate analyses. Migration rate included the delayed time for individuals that fell back below the release site prior to returning up-river.

River Temperature Monitoring

River temperatures were collected by Fisheries and Oceans Canada’s Fraser River Environmental Watch Program using Vemco data loggers ([resolution $\pm 0.1^{\circ}\text{C}$, accuracy $\pm 0.2^{\circ}\text{C}$], Amirix Systems, Inc., Halifax, NS), near the release site, at Whonnock. Although there are limitations to measuring temperature from one fixed temperature station, these locations are considered to be representative of the range of temperatures encountered by all individuals during the capture and tagging procedure.

Statistical Analyses

All physiological, behavioural and environmental data were \log_{10} -transformed to reduce heteroscedasticity. Homogeneity of variance was assessed using Levene’s tests for each variable. Sexes were pooled in all analyses to conserve sample sizes for response variables and stock complexes. To assess the relationships between predictor variables with both fall back and fate, the Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap stock complexes were examined using 2006 data only.

Two-way multivariate analysis of variance (MANOVA) was used to assess broad differences between all physiological, behavioural, and environmental variables for fall back, stock, and fall back x stock interaction terms. Subsequent two-way analysis of variance (ANOVA) was used to test the relationship between each variable in relation to fall back, stock and fall back x stock interaction terms. A Fisher's exact test was used to test for a relationship between fall back and fate for all stocks combined, due to low sample sizes among categories.

Two-way MANOVA was used to assess broad differences among all predictor variables for fate, stock, and fate x stock interaction terms. The fate x stock interaction term was not significant and was excluded from further analysis (see Results). Subsequent two sample *t* tests or Mann-Whitney *U* tests (when data were non-normal) were used to test the relationship between each variable in relation to fate. One-way analysis of variance (ANOVA) or Kruskal-Wallis tests (when data were non-normal) were used to test the relationship between each variable in relation to stock.

Sample sizes for the Chilko stock enabled a multi year comparison of migratory fate. To examine between year (2005 and 2006) differences for the Chilko stock, two-way MANOVA was used to assess broad differences between all physiological variables for fate, year, and fate x year interaction terms. The fate and fate x year interaction terms were not significant and were excluded from further analysis. Subsequent two sample *t* tests or Mann-Whitney *U* tests (when data were non-normal) were used to assess the relationship between predictor variables and fate for the year term. Note that hematocrit and Na^+, K^+ -ATPase were not compared between years because these data were not available for 2005.

Statistical analyses were conducted using JMP v. 7.0.1 (SAS Institute 2007). For statistical tests that used multiple comparisons, the level of significance (α) was Bonferroni corrected, where noted (Zar 1999). However, I also denote significance for α at 0.05 in data tables using an asterisk (*), to enable readers to use their discretion to define for themselves the values which they consider to be most biologically relevant (Cabin and Mitchell 2000). All values presented here represent means \pm S.D., unless otherwise noted.

Results:

In 2006, the proportion of individuals that fell back following release was 23.8% overall. The proportion of individuals that died en-route was 59.0%. This study examined the following possible outcomes for individuals; (1) did not fall back and reached spawning grounds (31.4%) or did not fall back and died en-route (68.6%) and (2) fell back and reached spawning grounds (29.6%) or fell back and died (70.4%; Tables 3-1; 3-2). The proportion of individuals from both the fall back and non-fall back groups that reached spawning grounds was remarkably similar (~70%). Accordingly, there was no significant relationship between fall back and fate when stocks were pooled (Fisher's exact test, $\chi^2 = 0.109$; $df = 1$; $P = 0.440$).

Assessing Fall Back Among Stocks

Fall back varied among stocks, ranging from a low of 11.8% for Adams to a high of 46.5% for Stellako. Of the fish that fell back, 13 (22.4%) never returned to the study area, 16 (27.6%) died below the Thompson River confluence, 9 (15.5%) died above the Thompson River confluence, and 16 (27.6%) reached spawning

grounds. Multivariate analysis of physiological, behavioural, and environmental variables among stock (Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap, all from 2006) and fall back (i.e., individuals that fell back versus those that did not) was significant for the whole model (MANOVA; Wilk's lambda = 0.06, $F_{110, 791.61} = 3.26$, $P < 0.001$), the fall back term (MANOVA; Wilk's lambda = 0.68, $F_{10, 104} = 7.04$, $P < 0.001$); the stock term (MANOVA; Wilk's lambda = 0.23, $F_{50, 477.68} = 3.66$, $P < 0.001$), and the fall back x stock interaction term (MANOVA; Wilk's lambda = 0.58, $F_{50, 477.68} = 1.22$, $P = 0.049$). Subsequent two-way ANOVAs on the response variables revealed significant differences with the fall back (i.e., elevated hematocrit, elevated plasma sodium, and slowed migration rate for fish that fell back) and stock terms (i.e., plasma lactate, plasma sodium, migration rate, and river temperature), and one fall back x stock interaction term (i.e., plasma sodium; Tables 3-3; 3-4). There were marginally significant effects of elevated gross somatic energy, elevated plasma glucose and elevated Na^+/K^+ -ATPase for fish that fell back and plasma chloride on stock, but significance was lost following Bonferroni corrections.

Assessing Fate Among Stocks

Migration mortality varied widely among individual stocks, ranging from a low of 58.1% for Chilko to a high of 80.6 % for Stellako. A multivariate analysis of physiological, behavioural, and environmental variables with fate (i.e., en-route mortality versus reaching spawning grounds) yielded a significant multivariate effect on the whole model (MANOVA; Wilk's lambda = 0.08, $F_{110, 731.75} = 2.69$, $P < 0.001$), the fate term (MANOVA; Wilk's lambda = 0.21, $F_{10, 96} = 2.02$, $P = 0.039$), the stock term (MANOVA: Wilk's lambda = 0.16, $F_{50, 441.19} = 4.37$, $P < 0.001$) but not the fate x

stock term (MANOVA; Wilk's lambda = 0.56, $F_{50, 441.19} = 1.19$, $P = 0.183$).

Subsequent *t* tests or Mann-Whitney *U* revealed significant differences for migration rate on fate. One-way analysis of variance (ANOVA) or Kruskal-Wallis tests (if data were non-normal) revealed significant differences for several variables for the stock term (i.e., hematocrit, plasma lactate, plasma glucose, migration rate, and river temperature). River temperatures were marginally significantly elevated for the fate term and plasma chloride had a marginally significant effect for the stock term, but significance was lost following Bonferroni corrections (Tables 3-5; 3-6).

Assessing Fate Among Years

Overall, 59.1 % of Chilko individuals died en-route in 2005 and 50.0% died in 2006 (Table 3-2). A multivariate analysis of physiological variables for the Chilko stock among fate and years (2005 and 2006) yielded a significant effect for the whole model (MANOVA; Wilk's lambda = 0.12, $F_{24, 119.5} = 5.38$; $P < 0.001$) and the year term (MANOVA; Wilk's lambda = 3.89, $F_{8, 41} = 3.89$; $P < 0.001$). Non-significant effects were found for the fate term (MANOVA; Wilk's lambda = 0.36, $F_{8, 41} = 1.85$; $P = 0.096$) and the fate x year (MANOVA; Wilk's lambda = 0.41, $F_{8, 41} = 0.72$; $P < 0.671$). Subsequent two sample *t* tests or Mann-Whitney *U* tests revealed significant differences for several physiological variables with the year term (i.e., plasma lactate, plasma sodium, plasma chloride and plasma osmolality; Tables 3-7; 3-8).

Discussion:

The purpose of this chapter was to assess the physiological, behavioural, and environmental factors that contribute to fall back and fate in sockeye salmon

following entry into the Fraser River. While I observed high fall back rates following capture (~24%), I found that regardless of whether or not individuals fell back, ~30 % reached spawning grounds and no statistical relationship existed between fall back and ultimate fate.

Assessing Fall Back Among Stocks

Individuals that fell back were characterized by elevated hematocrit which is an indicator of blood loss and stress, as well as elevated plasma sodium concentration which is an indicator of ionic and osmoregulatory balance and stress (Farrell et al. 2001). Acute stress, including exhaustive exercise, struggling and capture, generally result in short-term elevation of plasma sodium, and often chloride levels (Farrell et al. 2001), due to fluid shifts between intracellular and extracellular space (McDonald and Milligan 1992). In contrast, depressed concentrations of plasma ions in the freshwater environment would be indicative of chronic stress (Pickering and Pottinger 1995), suggesting that the levels observed here are reflective of capture and handling stress. Elevated hematocrit may also be related to the stress associated with capture and net entanglement (Farrell et al. 2000). Elevations in hematocrit and plasma ion concentrations occurring with exhaustive swimming could be linked with muscle fatigue (Wood et al. 1983). This muscle fatigue can result in behavioural impairments and reduced swimming ability, ultimately contributing to post-exhaustion mortality in extreme cases (Wood et al. 1983). Mean plasma sodium concentrations were much higher here than previous mean (\pm SE) values obtained for exhaustively exercised sockeye that were held in freshwater in the laboratory ($159 \pm 3 \text{ mmol}\cdot\text{L}^{-1}$; Hinch et al. 2006). Although not significantly different between groups in this study, I also noted

that the values here were much higher relative to mean (\pm SE) values obtained for exhaustively exercised sockeye held in freshwater in the laboratory for plasma lactate ($5 \pm 1.5 \text{ mmol}\cdot\text{L}^{-1}$) and glucose ($7.1 \pm 0.4 \text{ mmol}\cdot\text{L}^{-1}$; i.e., indicators of stress and metabolic loading) and osmolality ($334 \pm 17 \text{ mmol}\cdot\text{L}^{-1}$) and chloride ($121 \pm 3 \text{ mmol}\cdot\text{L}^{-1}$; i.e., indicators of ion-osmoregulatory balance; Hinch et al. 2006). Values for plasma lactate and glucose as well as indicators of osmoregulatory status were also higher here relative to sockeye that were caught in the Thompson River at comparable temperatures by dip net, which is a rapid capture technique that does not require entanglement and minimizes exercise and struggling (Young et al. 2006). Taken together, this suggests that individuals in this study were severely stressed.

Although this study was not specifically designed to measure the effects of gill net entanglement, these data may provide insight into the physiological consequences of contact with freshwater fisheries gear. Previous research has found that interactions with fisheries gear can contribute to elevated physiological stress, metabolic exhaustion, ion-osmoregulatory disturbances, and impaired swimming ability (Kreiberg and Blackburn 1994; Farrell et al. 2000). The capture methods used in this study were comparable to those in the freshwater commercial gill net fishery, except that I used a fine-mesh gill net operated as a tangle net to minimize gill injury and promote survival. In addition, the individuals collected for this study were immediately retrieved from the net and placed in an onboard aerated holding tote for several minutes, as opposed to being held in the net for the entire net soak duration as is the case with commercial gill net fisheries. As discussed above, there was evidence of acute stress associated with capture and entanglement, evidenced by high glucose and lactate levels in all fish and the fall back fish had elevated hematocrit and plasma

sodium levels, which may also be associated with an acute stress response. Fall back was linked to slowed migration rate. If this slowed migration results in a delay in arrival at spawning grounds it could ultimately reduce reproductive success by reducing longevity on the spawning grounds and reducing the number of spawning opportunities (Smoker et al. 1998; Keefer et al. 2006; Hruska et al., unpublished data).

Assessing Fate Among Stocks

Despite the physiological differences and slowed migration rate associated with falling back, I did not find a statistical relationship between fall back and ultimate fate. While this lack of a significant effect suggests that many individuals were able to recover after capture and resume up-river migration, more than 22% of fall back fish were never detected again in the study area and were considered to be en-route mortalities. Migration rate was the only factor that was a significant predictor of fate, where en-route mortalities had slower migration rates between release and the Thompson River confluence.

Contrary to predictions, I did not find any differences in physiological or environmental variables between the group that reached spawning grounds versus the group that died en-route. The rationale for developing these predictions was based on previous assessments of Fraser River sockeye salmon migration physiology and energetics. For example, work by Young et al. (2006) found differences in GSE, plasma lactate and plasma glucose for fate between dip-net caught Fraser sockeye sampled and tagged in the Thompson River, a location nearly 270 km up-river from the mouth of the Fraser. I suggest that the physiological disturbances in this study may be so severe for all individuals that it is difficult to distinguish between the fates

of individuals based solely on the variables measured here. The finding that GSE had no relationship with fate was surprising, but it may be partially explained by the allocation of somatic energy reserves towards gonadal development that occurs during freshwater migration, resulting in a potential relationship with fate being masked (Patterson et al. 2004; Cooke et al. 2006a).

Contrary to predictions, river temperature was not found to affect fate after Bonferroni corrections. En route mortality in Pacific salmonids has been linked with exposure to high river temperatures that approach tolerance thresholds through concomitant physiological and behavioural impairments as well as accelerated energy depletion and parasite and disease development (Servizi and Jensen 1977; Macdonald et al. 2000; Lee et al. 2003; Wagner et al. 2005; Naughton et al. 2006; Crossin et al. 2008; Keefer et al. 2008a). For example, a recent study of Snake River sockeye salmon revealed that late-season migrants had slower migration times and higher mortality rates relative to river temperatures that approached the upper temperature threshold (Keefer et al. 2008a). Ultimately, the mechanism for mortality is likely due to a complete temperature-mediated and stock-specific collapse in aerobic scope, which has been observed for a Fraser River sockeye stock that experienced abnormally high river temperatures as they approached spawning grounds (Farrell et al. 2008). The fish in this study encountered moderate temperatures (i.e., mean temperatures for each stock was between 17-19 °C), which may not have been high enough to impede migration. River temperatures even a few degrees higher than those observed here could lead to physiological and behavioural impairments that would contribute to migration delays and elevated mortality (Crossin et al. 2008; Farrell et al. 2008; Keefer et al. 2008b).

I found considerable stock-specific variability in a number of physiological parameters in both fall back and fate analyses. Differences in migration timing, migration routes, and environmental variability encountered during migration have been observed between stocks (Hinch et al. 2006). Previous research has similarly identified stock-specific differences in physiology and behaviour of Fraser river sockeye (Brett 1995; Lee et al. 2003; Cooke et al. 2006a; 2006b; Crossin et al. 2007; Farrell et al. 2008; Hanson et al. 2008). In this study, analyses of fall back and fate focused on six Fraser River sockeye stock complexes that, for management purposes, are grouped into Early Stuart, Summer (Chilko, Quesnel, and Stellako), and Late-run (Adams and Shuswap) based on migration timing. These stocks exemplify the variation among Fraser sockeye with respect to migration distance, elevation, river entry timing and associated physiological, energetic, and behavioural variability. For example, the Early Stuart stock spawns >1000 km from the Fraser River mouth, and has higher GSE density at the onset of river migration compared to the Adams and Shuswap stocks that spawn <500 km from the coast (Crossin et al. 2004). Early Stuart sockeye, due in part to the distance they must migrate to reach spawning grounds and also to avoid peak river temperatures, are among the first stocks to begin river migration. In contrast, late-run stocks, including the Adams and Shuswap stock complexes, exhibit a coastal holding behaviour for several weeks and enter the Fraser River later in the migration period after peak river temperatures have occurred, although in recent years, abnormal entry timing has become an increasing concern for late-run stocks (Cooke et al. 2004c).

Assessing Fate Among Years

To determine whether or not the relationship between physiology and fate varies by year, I examined the Chilko stock complex using data collected with similar methods in 2005 and 2006. Similar to the 2006 analysis of fall back and fate, I did not find any interannual relationships between physiological indices and whether or not individuals reached spawning grounds. However, I uncovered a year effect for plasma lactate, sodium, chloride, and osmolality. I suggest that between-year differences may be linked with factors that were not measured here, including variable conditions encountered during the marine phase of the migration, holding duration in the coastal environment, or conditions encountered following freshwater entry. Further investigation of this finding is required as it has implications for between year data comparisons for other studies and is also relevant for annual in-season management initiatives.

This study demonstrates that there are many intrinsic and extrinsic factors that affect fall back rates and fate for adult migrating sockeye in the Fraser River. I found sockeye that fell back had elevated hematocrit and plasma sodium concentrations. While the results of this study suggest that fisheries capture stress may be linked with fall back, future research needs to investigate whether or not fall back is also associated with natural factors (e.g., searching for olfactory cues, behavioural associations with temperature and flow) and how it may be linked with, and magnified by, fisheries gear interactions. One approach to answering these questions is to use telemetry receivers at a fine spatial scale and comparing fall back rates immediately after release versus fall back rates several days post-release at up-river telemetry stations. While none of the physiological indices examined here were related to fate, I did find that slower migration rates were related to en route mortality.

I also found considerable stock-specific differences in several of the variables measured, which may be a reflection of the differences in migration routes, timing and environmental variables encountered. The relatively moderate river temperatures observed here had only a limited effect on rates of fall back and en-route mortality. However, I anticipate that the physiological and behavioural consequences of contact with fisheries gear will be exacerbated by prolonged exposure to temperatures that approach upper tolerance limits, which are predicted to occur in the Fraser River in the coming decades (Morrison et al. 2002; Rand et al. 2006; Ferrari et al. 2007; Patterson et al. 2007). To yield novel insights into salmonid migration biology, future work will require adopting an approach that combines comparative laboratory studies (e.g., Crossin et al. 2008) with new approaches in the study of migration physiology and biotelemetry in the field (e.g., Hruska et al. 2007; Miller et al. 2007; Cooke et al. *in review*).

TABLES:

Table 3-1. Summary fall back and fate data for each of the sockeye salmon (*Oncorhynchus nerka*) stocks studied in 2006 in the Fraser River, British Columbia.

Stock	Fall Back		Fate	
	En-route mortality (N [%])	Reached spawning grounds (N [%])	En-route mortality (N [%])	Reached spawning grounds (N [%])
Early	3 (60.0)	2 (40.0)	10 (55.6)	8 (44.4)
Stuart				
Chilko	8 (53.3)	7 (47.7)	36 (58.1)	26 (41.9)
Quesnel	0 (0.0)	2 (100.0)	13 (61.9)	8 (38.1)
Stellako	13 (72.2)	5 (27.8)	30 (76.9)	9 (23.1)
Adams	5 (100.0)	0 (0.0)	33 (80.5)	8 (19.5)
Shuswap	9 (100.0)	0 (0.0)	22 (75.9)	7 (24.1)
Total	38 (70.4)	16 (29.6)	144 (68.6)	66 (31.4)

Table 3-2. Summary data for the fate of sockeye salmon (*Oncorhynchus nerka*) that were radio-tagged from the Chilko stock in 2005 and 2006 in the Fraser River, British Columbia.

Year	En-route mortality (N [%])	Reached spawning grounds (N [%])
2005	13 (59.1)	9 (40.9)
2006	36 (50.0)	26 (36.1)

Table 3-3. Results of a series of two-way ANOVAs with fall back, stock and the fall back x stock interaction comparing the physiological indices of six sockeye salmon stocks (*Oncorhynchus nerka*) only (Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap) sampled in the Fraser River, British Columbia, in 2006. Significant values following Bonferroni corrections ($\alpha = 0.005$) are presented in bold. An asterisk indicates values that are considered significant at the $\alpha = 0.05$ threshold.

Variable	Fall back			Stock			Fall back x stock		
	Test	df	P	Test	df	P	Test	df	P
	statistic			statistic			statistic		
Gross somatic energy (MJ/kg)	F, 4.01	1, 11	0.047*	F, 0.83	5, 11	0.527	F, 1.73	5, 11	0.129
Hematocrit (%)	F, 9.39	1, 11	0.002	F, 1.52	5, 11	0.186	F, 0.48	5, 11	0.788
Plasma lactate (mmol/L)	F, 2.40	1, 11	0.123	F, 4.04	5, 11	0.001	F, 0.77	5, 11	0.569
Plasma glucose (mmol/L)	F, 5.04	1, 11	0.026*	F, 2.07	5, 11	0.070	F, 1.04	5, 11	0.392
Plasma Na ⁺ (mmol/L)	F, 11.08	1, 11	0.001	F, 4.29	5, 11	<0.001	F, 5.13	5, 11	<0.001
Plasma Cl ⁻	F, 0.68	1, 11	0.409	F, 3.10	5, 11	0.009*	F, 1.06	5, 11	0.385

(mmol/L)

Plasma	F, 3.23	1, 11	0.074	F, 0.78	5, 11	0.564	F, 0.985	5, 11	0.428
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osmolality

(mOsm/kg)

Na ⁺ /K ⁺ -	F, 4.51	1, 11	0.035*	F, 2.34	5, 11	0.043	F, 1.926	5, 11	0.091
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ATPase

(μmol

ADP·mg

protein⁻¹·h⁻¹)

Migration	F, 35.95	1, 11	<0.001	F, 13.33	5, 11	<0.001	F, 1.33	5, 11	0.255
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rate (km·d⁻¹)

River	F, 0.17	1, 11	0.682	F, 11.21	5, 11	<0.001	F, 0.517	5, 11	0.763
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temperature

(°C)

Table 3-4. Mean values of physiological indices among six sockeye salmon stocks (*Oncorhynchus nerka*; Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap) for individuals that fell back and individuals that migrated up the Fraser River, British Columbia in 2006.

Variable	Stock	Fall back			Migrated up-river		
		Mean	SD	n	Mean	SD	n
Gross somatic energy (MJ/kg)	Early	9.9	0.3	5	9.4	0.9	14
	Stuart						
	Chilko	9.1	1.9	16	9.1	1.7	56
	Quesnel	9.7	0.	2	8.8	1.9	24
	Stellako	9.1	1.6	20	8.6	1.9	23
	Adams	8.5	1.8	6	8.7	2.1	45
	Shuswap	10.2	0.4	9	7.9	2.2	24
Hematocrit (%)	Early	50.8	5.9	5	45.1	4.1	14
	Stuart						
	Chilko	51.0	2.3	16	47.8	7.9	56
	Quesnel	47.0	1.4	2	47.0	5.0	24
	Stellako	49.7	12.0	20	49.9	6.1	23
	Adams	51.0	7.0	6	48.3	4.3	45
	Shuswap	52.6	3.9	9	48.5	4.5	24
Plasma lactate (mmol/L)	Early	13.69	4.86	5	10.14	3.87	14
	Stuart						
	Chilko	16.06	3.73	16	16.12	4.57	56
	Quesnel	19.00	4.67	2	16.69	4.27	24

							70
	Stellako	15.38	5.22	20	15.49	4.32	23
	Adams	16.33	6.47	6	15.89	4.62	45
	Shuswap	17.47	4.09	9	16.45	3.89	24
Plasma glucose (mmol/L)	Early	8.78	1.42	5	7.98	1.66	14
	Stuart						
	Chilko	10.32	1.95	16	9.26	1.75	56
	Quesnel	9.10	0.59	2	7.67	1.72	24
	Stellako	10.15	1.72	20	9.42	2.42	23
	Adams	8.57	1.91	6	9.41	1.67	45
	Shuswap	10.07	1.93	9	8.90	1.82	24
	Early	188.3	11.4	5	170.6	9.7	14
Plasma Na ⁺ (mmol/L)	Stuart						
	Chilko	168.2	8.9	16	170.2	8.5	55
	Quesnel	183.6	6.1	2	169.4	5.9	24
	Stellako	168.6	8.8	20	171.9	8.3	23
	Adams	168.5	6.8	6	168.9	7.1	44
	Shuswap	176.3	13.2	9	168.7	7.8	24
	Early	139.7	5.2	5	137.9	4.1	14
Plasma Cl ⁻ (mmol/L)	Stuart						
	Chilko	135.9	3.5	16	137.1	3.3	56
	Quesnel	141.5	2.7	2	137.1	4.5	24
	Stellako	138.9	3.1	20	139.6	4.7	23
	Adams	136.5	2.4	6	137.7	3.5	45
	Shuswap	137.4	4.5	9	136.9	3.5	24

Plasma osmolality (mOsm/kg)	Early	360.4	15.7	5	350.7	10.5	14
	Stuart						
	Chilko	357.7	11.2	16	357.5	13.6	56
	Quesnel	371.3	10.9	2	357.3	13.2	24
	Stellako	359.4	15.8	20	361.0	11.3	23
	Adams	357.5	15.5	6	358.6	13.3	45
	Shuswap	364.5	13.7	9	357.9	13.3	24
Na ⁺ /K ⁺ -ATPase (μ mol ADP·mg protein ⁻¹ ·h ⁻¹)	Early	3.08	1.29	4	3.30	1.23	14
	Stuart						
	Chilko	3.58	1.64	16	2.97	1.03	54
	Quesnel	7.02	1.52	2	2.97	0.89	23
	Stellako	3.43	1.54	19	2.93	1.20	23
	Adams	2.62	0.85	5	2.79	0.94	42
	Shuswap	2.67	0.95	8	2.80	0.96	23
Migration rate (km·d ⁻¹)	Early	26.1	5.4	3	34.3	5.7	11
	Stuart						
	Chilko	23.1	5.0	8	28.9	4.2	33
	Quesnel	24.9	4.2	2	30.6	3.9	12
	Stellako	19.6	1.6	7	22.9	4.6	10
	Adams	12.9	6.4	2	21.9	4.9	26
	Shuswap	17.8	3.2	4	23.2	3.1	13
River temperature (°C)	Early	17.4	0.4	5	17.8	0.9	14
	Stuart						

Chilko	18.7	0.4	16	18.8	0.5	72 56
Quesnel	18.4	0.0	2	18.4	0.6	24
Stellako	18.8	0.5	20	18.8	0.5	23
Adams	18.8	0.5	6	18.7	0.6	45
Shuswap	18.7	0.3	9	18.7	0.6	24

Table 3-5. Results of *t* tests or Mann-Whitney *U* tests (when data were non-normal) testing the relationship between each physiological, behavioural, and environmental variable in relation to fate and results of a one-way analysis of variance (ANOVA) or Kruskal-Wallis tests (if data were non-normal) to test the relationship between each variable in relation to sockeye salmon (*Oncorhynchus nerka*) stocks (Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap) sampled in the Fraser River, British Columbia, in 2006. Significant values following Bonferroni corrections ($\alpha=0.005$) are presented in bold. An asterisk represents values that are considered significant at the $\alpha=0.05$ threshold.

Variable	Fate			Stock		
	Test	df	P	Test	df	P
	statistic			statistic		
Gross somatic energy (MJ/kg)	<i>U</i> , 0.97	1, 11	0.328	χ^2 , 3.87	5, 11	0.568
Hematocrit (%)	<i>U</i> , -1.44	1, 11	0.151	χ^2 , 21.73	5, 11	<0.001
Plasma lactate (mmol/L)	<i>U</i> , -0.22	1, 11	0.829	χ^2 , 24.37	5, 11	<0.001
Plasma glucose (mmol/L)	<i>U</i> , -0.30	1, 11	0.762	χ^2 , 26.0	5, 11	<0.001
Plasma Na ⁺ (mmol/L)	<i>t</i> , 0.49	1, 11	0.621	<i>F</i> , 1.45	5, 11	0.206
Plasma Cl ⁻ (mmol/L)	<i>t</i> , 0.03	1, 11	0.860	<i>F</i> , 2.53	5, 11	0.029*
Plasma osmolality	<i>t</i> , -0.34	1, 11	0.733	<i>F</i> , 0.869	5, 11	0.502

(mOsm/kg)						
Na ⁺ /K ⁺ -ATPase	<i>U</i> , 0.64	1, 11	0.523	χ^2 , 8.39	5, 11	0.136
($\mu\text{mol ADP}\cdot\text{mg}$ $\text{protein}^{-1}\cdot\text{h}^{-1}$)						
Migration rate	<i>U</i> , -3.51	1, 11	<0.001	χ^2 , 48.13	5, 11	<0.001
($\text{km}\cdot\text{d}^{-1}$)						
River temperature	<i>U</i> , -2.47	1, 11	0.013*	χ^2 , 34.22	5, 11	<0.001
(°C)						

Table 3-6. Mean values of physiological, behavioural, and environmental indices among six sockeye salmon (*Oncorhynchus nerka*) stocks (Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap) for individuals that died en-route and individuals that reached spawning grounds in the Fraser River, British Columbia in 2006.

Variable	Stock	En-route mortality			Reached spawning grounds		
		Mean	SD	n	Mean	SD	n
Gross somatic energy (MJ/kg)	Early Stuart	9.3	1.1	10	9.9	0.3	8
	Chilko	8.9	1.8	36	9.3	1.6	26
	Quesnel	8.5	2.2	13	9.5	0.6	8
	Stellako	8.7	1.8	30	8.7	1.8	9
	Adams	8.5	1.9	33	9.5	2.2	8
	Shuswap	8.9	1.8	22	7.4	2.8	7
Hematocrit (%)	Early Stuart	47.0	6.2	10	46.3	4.2	8
	Chilko	49.9	4.5	36	47.9	3.9	26
	Quesnel	47.0	4.3	13	46.5	3.5	8
	Stellako	49.3	11.2	30	51.2	4.7	9
	Adams	48.3	4.7	33	50.6	4.9	8
	Shuswap	50.9	3.9	22	48.3	4.7	7
Plasma lactate (mmol/L)	Early Stuart	11.87	5.36	10	10.45	2.89	8
	Chilko	15.96	4.64	36	15.85	3.90	26

	Quesnel	16.11	4.75	13	17.85	4.34	8
	Stellako	15.59	4.98	30	16.08	4.04	9
	Adams	15.90	4.96	33	17.63	5.58	8
	Shuswap	17.59	3.96	22	15.30	3.33	7
Plasma glucose	Early Stuart	8.52	1.83	10	8.06	1.15	8
(mmol/L)							
	Chilko	9.37	1.56	36	9.43	1.83	26
	Quesnel	7.72	1.61	13	8.34	1.79	8
	Stellako	9.64	2.44	30	10.15	0.99	9
	Adams	9.29	1.83	33	8.99	1.03	8
	Shuswap	9.53	1.82	22	8.59	1.84	7
Plasma Na ⁺	Early Stuart	175.1	11.3	10	176.6	15.3	8
(mmol/L)							
	Chilko	169.6	9.2	35	169.2	7.2	26
	Quesnel	169.3	4.9	13	173.9	9.2	8
	Stellako	169.9	9.6	30	169.9	6.7	9
	Adams	168.3	7.6	32	170.8	4.8	8
	Shuswap	172.6	10.6	22	168.5	9.0	7
Plasma Cl ⁻	Early Stuart	138.2	3.7	10	137.9	5.5	8
(mmol/L)							
	Chilko	136.8	2.9	36	137.1	3.7	26
	Quesnel	136.1	4.4	13	138.4	4.2	8
	Stellako	139.2	4.4	30	138.3	2.5	9
	Adams	137.5	3.6	33	136.9	3.2	8

	Shuswap	137.5	3.7	22	136.5	4.2	7
Plasma osmolality (mOsm/kg)	Early Stuart	353.6	12.9	10	353.8	13.1	8
	Chilko	357.4	13.0	36	356.5	11.9	26
	Quesnel	353.5	15.6	13	364.9	8.9	8
	Stellako	360.3	14.8	30	361.7	11.3	9
	Adams	358.5	14.1	33	357.5	12.9	8
	Shuswap	364.1	12.4	22	351.9	12.9	7
Na ⁺ /K ⁺ -ATPase ($\mu\text{mol ADP}\cdot\text{mg}$ $\text{protein}^{-1}\cdot\text{h}^{-1}$)	Early Stuart	3.23	1.48	9	3.43	0.91	8
	Chilko	3.05	1.18	35	3.09	1.22	25
	Quesnel	2.89	0.79	12	3.85	2.29	8
	Stellako	3.02	1.24	29	3.00	1.19	9
	Adams	2.85	1.02	31	2.83	0.96	8
	Shuswap	2.84	1.05	20	2.41	0.55	7
Migration rate ($\text{km}\cdot\text{d}^{-1}$)	Early Stuart	29.4	6.5	6	34.9	5.8	8
	Chilko	28.0	3.2	11	28.0	5.7	26
	Quesnel	31.7	5.2	4	29.3	4.4	8
	Stellako	21.1	4.0	7	21.9	4.3	9
	Adams	20.3	4.8	21	26.4	3.7	6
	Shuswap	20.9	4.6	10	23.4	1.7	7
River temperature	Early Stuart	17.78	0.87	10	17.41	0.37	8

(°C)

Chilko	18.81	0.52	36	18.71	0.49	26
Quesnel	18.41	0.65	13	18.56	0.39	8
Stellako	18.83	0.56	30	18.77	0.36	9
Adams	18.79	0.57	33	18.31	0.90	8
Shuswap	18.82	0.42	22	18.36	0.79	7

Table 3-7. Results of two sample *t* tests or Mann-Whitney *U* tests by year comparing the physiological, behavioural and environmental indices for one focal sockeye salmon (*Oncorhynchus nerka*) stock (Chilko) sampled in the Fraser River, British Columbia, in 2005 and 2006. Significant values following Bonferroni corrections ($\alpha = 0.006$) are presented in bold.

Variable	Year		
	Test statistic	df	<i>P</i>
Gross somatic energy (MJ/kg)	<i>U</i> , -1.56	1, 3	0.119
Plasma lactate (mmol/L)	<i>t</i> , 3.61	1, 3	<0.001
Plasma glucose (mmol/L)	<i>t</i> , 1.61	1, 3	0.118
Plasma Na ⁺ (mmol/L)	<i>t</i> , 6.56	1, 3	<0.001
Plasma Cl ⁻ (mmol/L)	<i>t</i> , -4.37	1, 3	<0.001
Plasma osmolality (mOsm/kg)	<i>t</i> , 7.22	1, 3	<0.001
Migration rate (km·d ⁻¹)	<i>U</i> , 0.03	1, 3	0.605
River temperature (°C)	<i>U</i> , -1.57	1, 3	0.115

Table 3-8. Mean values of physiological, behavioural, and environmental indices among two years (2005 and 2006) for individuals from the Chilko sockeye salmon (*Oncorhynchus nerka*) stock that died en-route and individuals that reached spawning grounds in the Fraser River, British Columbia in 2006.

Variable	Year	En-route mortality			Reached spawning grounds		
		Mean	SD	n	Mean	SD	n
Gross somatic energy (MJ/kg)	2005	9.7	0.8	13	9.7	0.5	9
	2006	8.9	1.8	36	9.3	1.6	26
Plasma lactate (mmol/L)	2005	12.86	2.52	13	12.49	2.04	9
	2006	15.96	4.64	36	15.85	3.90	26
Plasma glucose (mmol/L)	2005	8.80	2.29	13	8.56	1.59	9
	2006	9.37	1.55	36	9.42	1.83	26
Plasma Na ⁺ (mmol/L)	2005	158.3	5.2	13	155.1	8.9	9
	2006	169.6	9.2	35	169.2	7.2	26
Plasma Cl ⁻ (mmol/L)	2005	142.2	5.3	13	140.7	3.7	9
	2006	136.7	2.9	36	137.1	3.7	26
Plasma osmolality	2005	335.1	11.5	13	334.8	12.8	9

(mOsm/kg)							
	2006	357.4	13.0	36	356.5	11.9	26
Migration rate	2005	24.4	7.2	8	30.1	3.9	9
(km·d ⁻¹)							
	2006	28.2	3.3	10	28.0	5.7	26
River	2005	18.4	1.3	13	18.3	1.2	9
temperature (°C)							
	2006	18.8	0.5	36	18.7	0.5	26

FIGURES:

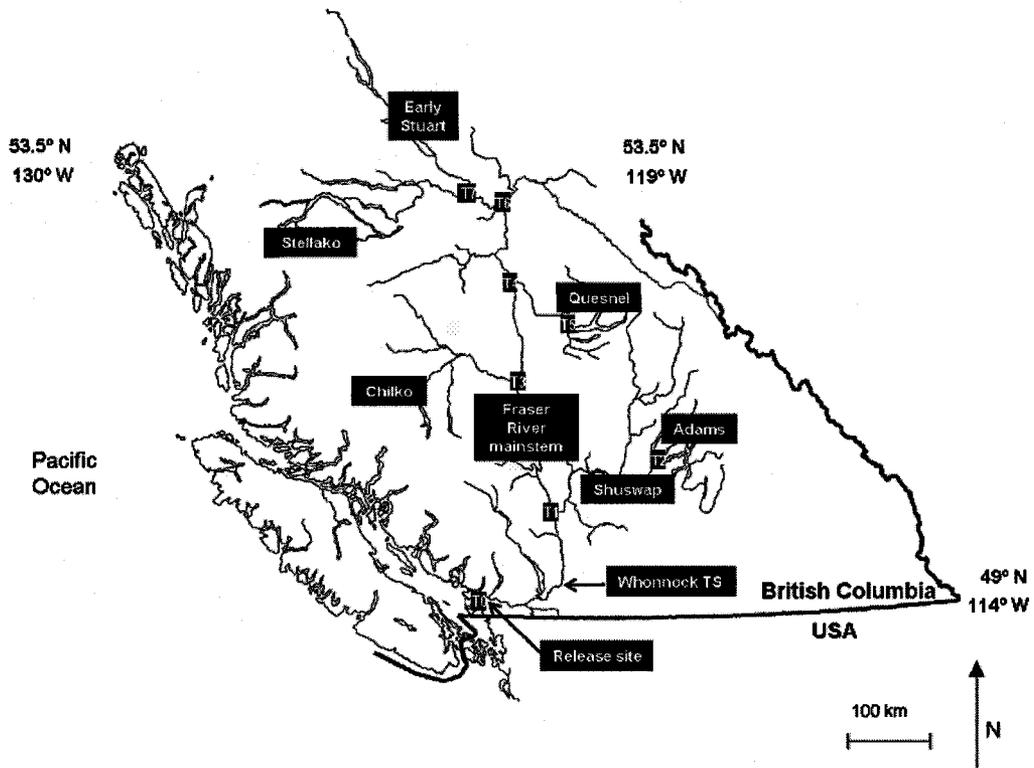
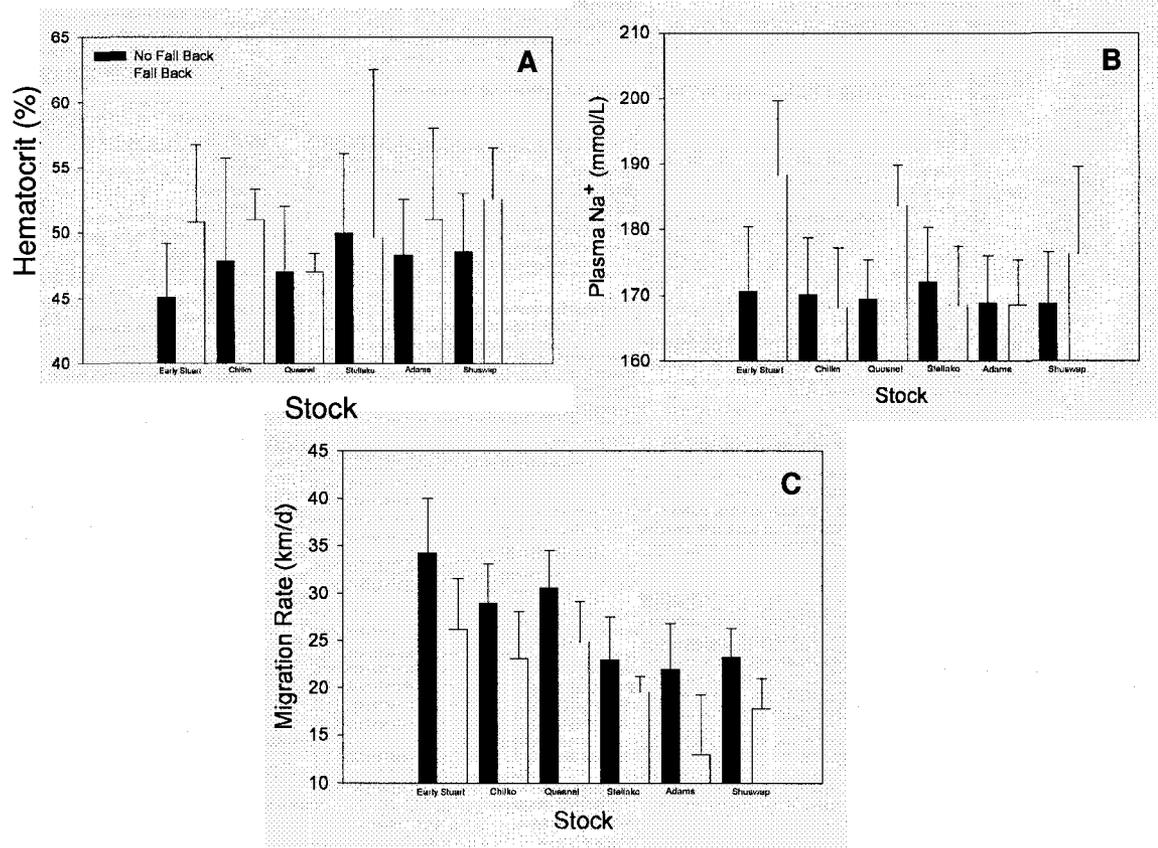


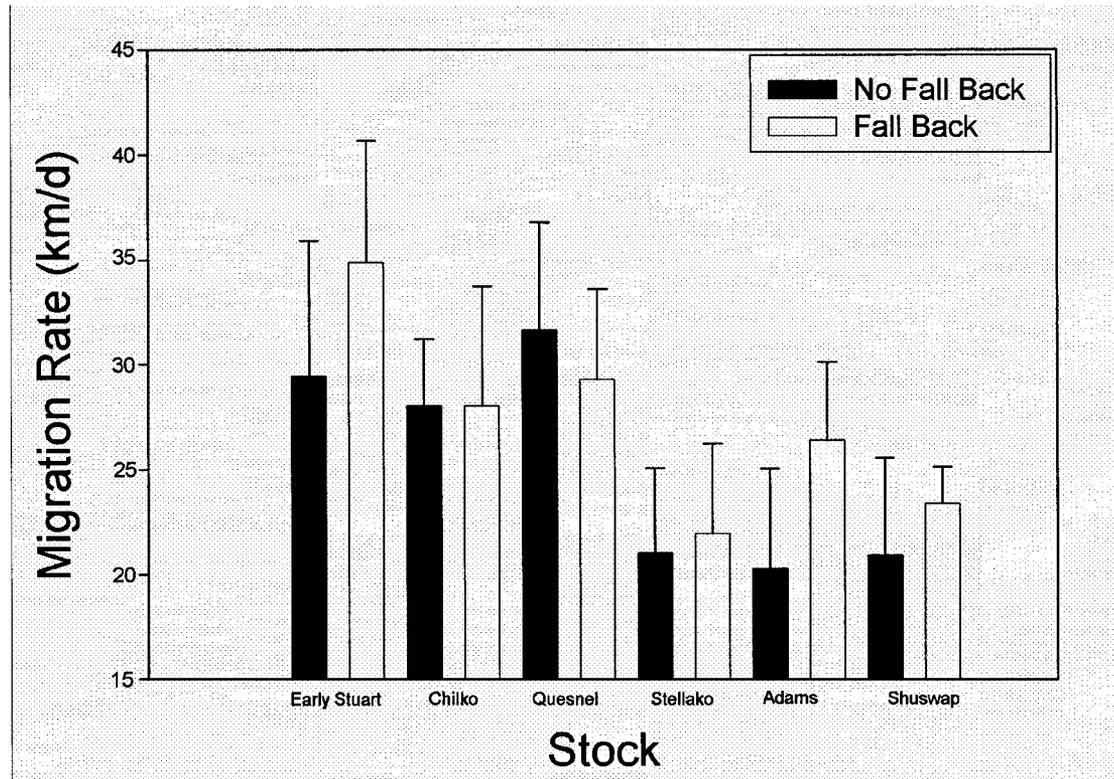
Figure 3-1. A map of the Fraser River, British Columbia. Fixed receiver stations are denoted as Crescent Island (T0), Thompson River confluence (T1), Adams Lake (T2), Chilcotin River confluence (T3), Quesnel River confluence (T4), Quesnel Lake (T5), Nechako River confluence (T6), and Stuart River (T7). The river temperature monitoring station is labeled as Whonnock TS. Spawning grounds are labeled for each sockeye salmon (*Oncorhynchus nerka*) stock complex included in the study (Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap).

APPENDICES:

Appendix 3-1. Mean values of hematocrit (A), plasma sodium (B), and migration rate (C) among six sockeye salmon stocks (*Oncorhynchus nerka*; Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap) for individuals that fell back and individuals that migrated up the Fraser River, British Columbia in 2006.



Appendix 3-2. Mean migration rates among six sockeye salmon stocks (*Oncorhynchus nerka*; Early Stuart, Chilko, Quesnel, Stellako, Adams, and Shuswap) for individuals that died en-route versus survived to reach spawning grounds in the Fraser River, British Columbia in 2006.



CHAPTER 4: General Discussion

This thesis integrated tools from multiple disciplines to gain greater insight into sockeye salmon migration during the freshwater phase of their spawning migrations. In chapter 2, I used biotelemetry and thermal loggers to identify thermoregulatory behaviour as individuals migrate through the Fraser River mainstem, a location that is relatively thermally homogeneous and is known to be one of the warmest segments of the freshwater migration. In chapter 3, I integrated biotelemetry and biosampling to assess the physiological, behavioural, and environmental factors that characterize individuals that fall back following capture versus those that continue migrating up-river, and individuals that die en-route relative to those that survive to reach spawning grounds both within and between years. Taken together, the results of this thesis contribute to the understanding of the basic freshwater migration biology of this species by elucidating the relationships between environmental conditions, migration behaviour, physiology, and fate. These findings are essential for the improvement of in-season management initiatives and for the development of long-term policies for the conservation of sockeye salmon populations.

Findings and Implications:

Prior to the findings described in chapter 2, little was known about the extent to which migrating sockeye salmon engage in behavioural thermoregulation in the Fraser River mainstem. However, understanding the thermal experience during the freshwater phase is fundamental to salmonid migration research because there is considerable evidence that prolonged exposure to high temperatures here can magnify

mortality rates (Crossin et al. 2008; Farrell et al. 2008). I found that throughout the study area, individual sockeye salmon across stock complexes and run-timing groups maintained mean body temperatures that were not significantly different from river temperatures, leading to my novel conclusion that there is limited evidence for behavioural thermoregulation of active migrants in the lower Fraser River mainstem. Due to this finding, I surmise that prolonged exposure to elevated mainstem temperatures could lead to high mortality rates through a collapse in aerobic scope, particularly during abnormally warm years (Farrell et al. 2008). Predicted increases in peak summer temperatures over the next several decades necessitate this understanding of thermoregulatory behaviour in the Fraser mainstem to improve in-season environmental management assessments that are conducted by Fisheries and Oceans Canada.

Chapter 3 provided new knowledge on the interplay between physiology and behaviour of adult migrating Pacific salmonids by focusing on the factors in the freshwater environment that contribute to migration fall back and fate. I sampled individuals at the onset of their freshwater migrations and I found that ~24 % of individuals fell back down-river following release. Individuals that fell back had elevated hematocrit and plasma sodium concentrations, indicating physiological stress. Although fall back resulted in slowed migration rates, I did not find a relationship between fall back and fate. Overall, none of the physiological or environmental variables measured here affected migration fate, yet stock-specific differences were observed in many of these indices, reflective of the genetic variation among sockeye salmon populations. I found differences between years for plasma lactate, sodium, chloride, and osmolality, yet none of these factors contributed to

year-specific fate. My results demonstrate the complex relationship between the physiology and behaviour associated with Pacific salmonid migration biology in the freshwater environment. While uncertainties remain, characterizing the factors that affect fall back and fate is essential from a conservation perspective because freshwater entry poses a number of intrinsic (e.g., remodeling of osmoregulatory apparatus) and extrinsic (e.g., high temperature and flow conditions, freshwater fisheries) challenges for migrants, potentially resulting in fitness consequences through high mortality rates (Hinch et al. 2006).

In general, I found that as sockeye salmon migrate through the Fraser River mainstem, they exhibit limited behavioural thermoregulation. During the freshwater migration phase, fall back is associated with physiological stress and delayed migration rates, while fate is associated with delayed migration rates but no statistical relationship was found between fall back and fate. These findings were the result of combining field techniques from a number of disciplines to integrate measures of physiology, energetics, body temperature, migration behaviour, and environmental indices to characterize the freshwater spawning migration of adult sockeye salmon. These techniques provide novel insights into the basic migration biology of this species in the freshwater environment and contribute new knowledge on thermoregulatory behaviour and the factors characterizing fall back and fate, which is essential from an applied perspective.

Future Research:

In addition to the contributions to research identified here, this dissertation illuminates several opportunities for future research. Chapter 2 provided unique

insight into the thermal experience of migrating sockeye salmon in the Fraser River mainstem. However, little is known about the thermal experience of fish in the upper Fraser River mainstem, particularly once individuals enter the tributaries and lakes that lead to spawning grounds. Accordingly, future research, based in part on the data collected in this thesis, needs to focus on multiple stocks to determine the extent to which individuals utilize cool-water refugia in the upper Fraser River watershed. It is well known that prolonged exposure to high temperatures can result in high mortality rates through a collapse in aerobic scope if individuals are unable to eventually access cool-water refuge (Farrell et al. 2008). However, understanding how and the extent to which these fish utilize thermal refuge remains unknown. Because Fraser River temperatures are expected to increase with climate warming, understanding the thermoregulatory behaviour of individuals in the upper Fraser watershed will be critical to estimating temperature-mediated mortality (Ferrari et al. 2007). This information may also feed in to the designation of temperature-dependent fisheries closures, as it remains unclear the extent to which cumulative high temperature exposure (i.e., higher than the temperatures observed in chapter 3) and fisheries gear interactions contribute to mortality.

This dissertation provided further evidence that the physiological, behavioural and environmental factors that characterize salmonid freshwater migrations are clearly multifaceted and difficult to discern. Accordingly, there is an opportunity for improvement of the tools used here by integrating new and multidisciplinary approaches to this research. For example, an exciting new method for interpreting the physiology of migrants is to incorporate cDNA microarrays (or quantitative polymerase chain reaction [qPCR]) based on non-lethally biopsied tissue with the

behavioural assessments made using biotelemetry (Miller et al. 2007). This novel approach in genomics enables the monitoring of expression profiling of thousands of genes simultaneously to identify a subset of genes or gene families that are differentially expressed among groups (i.e., en-route mortalities versus individuals that reach spawning grounds). The genes thought to be involved with thermal stress and acclimation, including CIRP, HSPs, and CERPA2, can be examined to provide more insight into gene expression in relation to thermal tolerances and temperature-mediated mortality (Mosser and Bols 1998; Aho and Vornanen 1998; Iwama et al. 1999). Migration mortality and behaviour can be assessed by combining this approach with biotelemetry since tissue samples for gene expression analyses can be collected non-lethally from actively migrating fish. To address the concern over high temperature and fisheries gear interactions, simulated gear entanglement experiments can be conducted in the laboratory to understand the physiological mechanisms contributing to mortality at the gene expression level.

Building on the results of this thesis, there are many opportunities for future research on Pacific salmonid migration biology by integrating new and multidisciplinary approaches. Gaining greater insight into the thermoregulatory behaviour of sockeye salmon during their spawning migrations and understanding and utilizing genomics tools to elucidate the physiological mechanisms associated with fate in relation to temperature and fisheries-related stressors are important and novel directions for future research. This thesis provides important context for developing novel studies that further elucidate the basic migration biology of sockeye salmon and also contribute to improving the management and conservation of this commercially and intrinsically valuable Pacific salmonid species.

Afterword and Summary:

The objective of this thesis was to acquire an improved understanding of the physiology, behaviour, and fate of up-river migrating sockeye salmon in relation to environmental conditions encountered during the freshwater phase of their migrations in the Fraser River, British Columbia. The research has made a number of novel contributions to knowledge: 1) limited behavioural thermoregulation occurs in the Fraser River mainstem; 2) physiological stress contributes to fall back and slowed migration rates; 3) slowed migration rates contribute to elevated en-route mortality; and 4) there is a large amount of stock-specific and year specific variation in the indices measured here. In addition, I have identified a number of opportunities for future research stemming from these findings, including an assessment of the consequences of exposure to elevated water temperatures and interactions with fisheries gear. As Fraser River temperatures continue to warm, this research will be increasingly relevant from both the basic and applied research perspectives.

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