Physiological Condition Differentially Affects the Behavior and Survival of Two Populations of Sockeye Salmon during Their Freshwater Spawning Migration

M. R. Donaldson[1,2,*]
S. G. Hinch[2]
D. A. Patterson[3]
A. P. Farrell[4]
J. M. Shrimpton[5]
K. M. Miller-Saunders[6]
D. Robichaud[7]
J. Hills[3]
K. A. Hruska[2]
K. C. Hanson[1]
K. K. English[7]
G. Van Der Kraak[8]
S. J. Cooke[1]

[1]Fish Ecology and Conservation Physiology Laboratory, Ottawa-Carleton Institute of Biology, Carleton University, Ottawa, Ontario, Canada; [2]Pacific Salmon Ecology and Conservation Laboratory, Centre for Applied Conservation Research and Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada; [3]Fisheries and Oceans Canada, Science Branch, Pacific Region, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, Canada; [4]Department of Zoology and Faculty of Land and Food Systems, University of British Columbia, Vancouver, British Columbia, Canada; [5]Department of Biology, University of Northern British Columbia, Prince George, British Columbia, Canada; [6]Molecular Genetics Laboratory, Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada; [7]LGL Ltd. Environmental Research, Sydney, British Columbia, Canada; [8]Department of Integrative Biology, University of Guelph, Ontario, Canada

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* Corresponding author. Present address: Centre for Applied Conservation Research and Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; e-mail: mdonald@interchange.ubc.ca.

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ABSTRACT

Recently, a segment of the Adams-Shuswap sockeye salmon (*Oncorhynchus nerka*) population initiated freshwater migration several weeks earlier than historically recorded, resulting in high mortality rates. The comigrating Chilko population maintained their historic river entry timing and did not experience elevated mortality. To test the hypothesis that population-specific differences in physiological condition would differentially influence behavior and survival when exposed to fisheries capture stress, we physiologically sampled individuals from both populations at the onset of the freshwater phase of their reproductive migration and tracked the remainder of their migrations using radio telemetry. Adams-Shuswap individuals had slower migration rates and were less likely to reach natal subwatersheds relative to Chilko individuals. Metabolic and osmoregulatory impairment was related to mortality for Adams-Shuswap individuals but not for Chilko individuals. Similarly, physiological condition correlated with migration rate for Adams-Shuswap but not Chilko fish. Survival to natal subwatersheds was 1.9 times higher for Chilko relative to Adams-Shuswap, a result that did not emerge until individuals approached natal subwatersheds several days after the stressor was applied. We conclude that physiological condition differentially affects the behavior and survival of these two populations, which may be a consequence of the early-entry phenomenon by a segment of the Adams-Shuswap population.

Introduction

Migrations represent some of the most challenging life-history stages for organisms across multiple taxa (Dingle 1996; Dingle and Drake 2007). Reproductive migrations require that individuals be adapted to cope with extreme variability in abiotic conditions while undergoing intrinsic physiological changes associated with reproductive development (Alerstam et al. 2003). Pacific salmonids (*Oncorhynchus* spp.) exemplify the complex interplay between physiology and behavior 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; Hruska et al. 2007; Ueda et al. 2007). Adult anadromous sockeye salmon (*Oncorhynchus nerka*) must transition between the marine and freshwater environments as they home toward natal

spawning areas. This transition requires that individuals remodel their osmoregulatory and ionoregulatory systems in preparation for freshwater (Clarke and Hirano 1995; Shrimpton et al. 2005). During this time, sockeye salmon undergo physiological and morphological changes associated with sexual maturation. The development of secondary sexual characteristics and the partitioning of energy to fuel migration depend solely on endogenous energy reserves, as sockeye salmon cease feeding before entering freshwater (Brett 1995; Hendry and Berg 1999). On freshwater entry, individuals must cope with some of the highest and most variable temperatures that they encounter in their life history, which can increase physiological stress, accelerate energy depletion, increase incidence of disease, and impair migratory behavior (Wagner et al. 2005; Hinch et al. 2006; Crossin et al. 2008; Farrell et al. 2008; Keefer et al. 2008). Prolonged exposure to abnormally high temperatures (i.e., temperatures exceeding population-specific thermal limits) can result in a complete collapse of aerobic scope and mortality (Lee et al. 2003; Farrell et al. 2008), a problem common to all environmental temperature-dependent aquatic animals (Pörtner and Farrell 2008).

Migration timing for long-distance migrating taxa is controlled by endogenous means with some degree of plasticity (Biebach et al. 1986; Berthold 1996), driven largely by broad-scale climatic factors (Tottrup et al. 2008). This paradigm is well exemplified in Pacific salmon spawning migrations, particularly with respect to migration initiation timing (Hodgson and Quinn 2002; Crozier et al. 2008). The onset of the freshwater phase of the sockeye salmon migration and the rate of travel to spawning areas are critical because as a consequence of having a fixed energy budget, sockeye salmon have a limited window of opportunity to reach spawning grounds, secure a mate, and spawn before death by senescence (Brett 1995). Delayed arrival at spawning grounds could result in fewer opportunities for reproduction (Smoker et al. 1998; Keefer et al. 2006).

Although the initiation of the freshwater migration is species and population specific, it generally deviates minimally among years within a given population (Woodey 1987; Hodgson and Quinn 2002). However, since the mid-1990s, a segment of several Fraser River sockeye salmon populations, termed "late-run" populations, has been entering the freshwater environment several weeks earlier than historically recorded (Cooke et al. 2004). This group of fish normally held in the estuary for 4–6 wk before initiating river migration, and it is this holding behavior that has largely disappeared for most late-run populations. Recent evidence from physiological biopsy and telemetry, as well as functional genomics studies, indicates that late-run fish that enter the river early exhibit high levels of physiological stress, are reproductively advanced, are ill prepared osmotically, and are immunosuppressed compared with normal-timed fish (Cooke et al. 2006; Miller et al. 2007; Crossin et al. 2009). The early-entry phenomenon causes late-run individuals to encounter much higher river temperatures than they are adapted for (5°–6°C more than they have historically been exposed to), compounding their already weakened condition, which has contributed to abnormally high mortality rates (i.e., >90% in some years; Cooke et al. 2004; English et al. 2005). This aberrant entry timing has direct implications at the population level, because semelparous sockeye salmon engage in spawning migrations only once in their life history, and individuals that fail to reach spawning grounds and successfully reproduce have zero lifetime fitness (Dingle 1980), forming a major conservation concern for Fraser River sockeye salmon.

To date, Fraser River sockeye salmon research has relied on physiological assessments conducted either in the marine environment (Crossin et al. 2009) or near spawning areas (Young et al. 2006*a*). While freshwater entry and migration through the lower Fraser River pose a unique set of physiological and performance challenges, little is known about how physiological condition during this phase of the migration affects behavior and survival among populations with different life histories. This study explores relationships between physiological condition in freshwater with behavior and survival of two comigrating populations of adult sockeye salmon with disparate migratory tactics. Chilko, a "summer-run" population, enters the Fraser River in August when the river temperatures are at their peak. They enter the river directly without holding in the estuary, exhibit rapid freshwater migration (which is energetically efficient; Rand and Hinch 1998), and have high survival rates compared with many other Fraser River sockeye populations (English et al. 2005). Adams-Shuswap, a late-run population complex that comigrates with Chilko during their coastal approach, historically held in the estuary for several weeks before entry in late summer but is now one of the populations that exhibit the anomalous early-entry phenomenon. Because of the known poor condition and survival of early-entry late-run fish, we hypothesized that population-specific differences in physiological condition following the stress applied by gill net capture at the onset of the freshwater phase of the migration would differentially influence behavior and survival for comigrating individuals from early-entry Adams-Shuswap versus Chilko populations. We predicted that the physiological disturbance from capture stress would exert a greater influence on (1) survival and (2) migration rate of early-entry Adams-Shuswap individuals relative to Chilko individuals.

Material and Methods

Fish Capture and Study Site

Sampling occurred in the lower Fraser River mainstem, 69 river km from the mouth of the Fraser River, British Columbia (Fig. 1), from August 1 to September 1, 2006. This sampling period resulted in the collection of Chilko individuals during their normal river entry timing and meant that Adams-Shuswap individuals were exclusively "early-timed" late-run fish since "normal-timed" late-run migrants do not enter the river until mid-September or later (Cooke et al. 2004). These populations, which are genetically distinct, are named according to the natal subwatersheds where they return to spawn. Fish were captured with an 8.9-cm fine-mesh drift gill net (i.e., tangle net), which

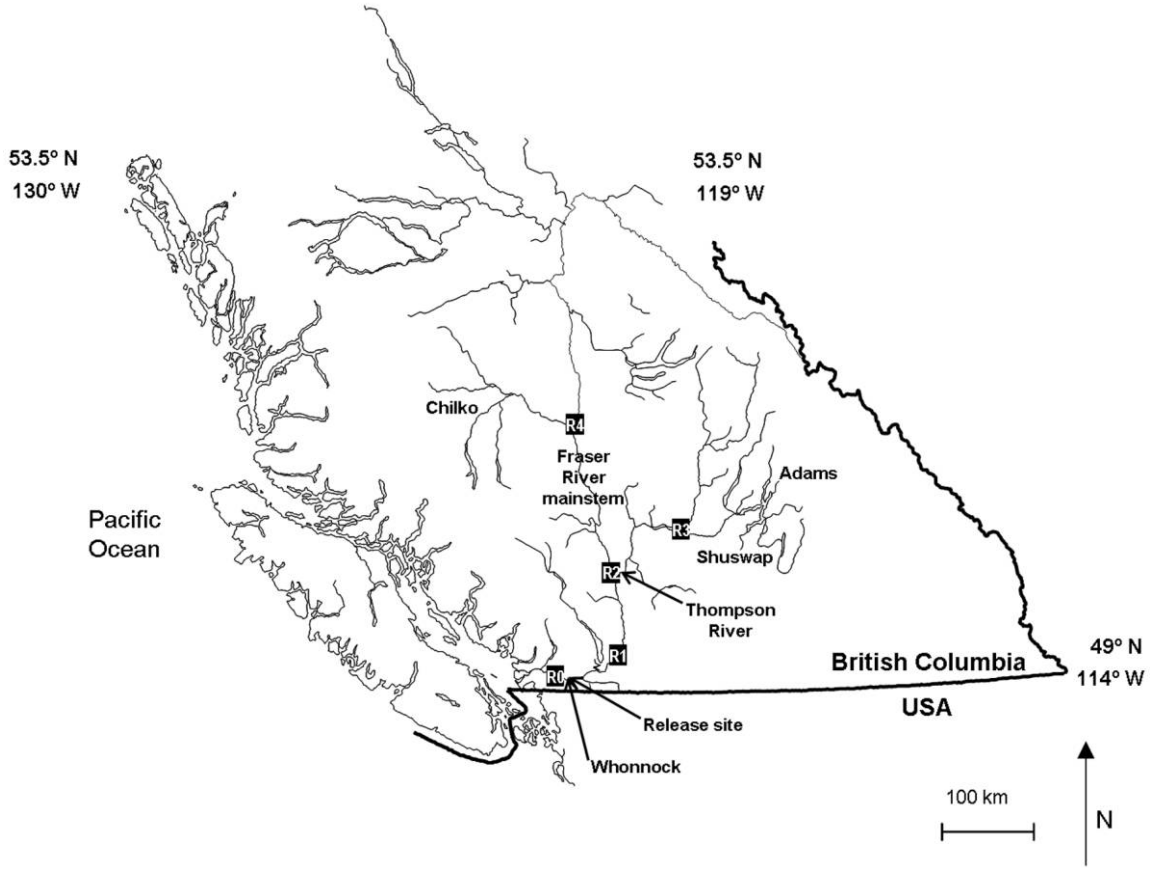

Figure 1. Map of the Fraser River, British Columbia. Fixed receiver stations are denoted as Crescent Island (*R0*), Mission (*R1*), Thompson River confluence (*R2*), Kamloops Lake (*R3*), and Chilcotin River confluence (*R4*). The river temperature monitoring station is at Whonnock. Spawning grounds are labeled for each sockeye salmon population (*Oncorhynchus nerka*) complex included in the study (Chilko, Adams, and Shuswap).

was used to tangle individuals by the mouth and fins and minimize injuries associated with the head and gills that can occur when using a larger-mesh-size conventional gill net (Vander Haegan et al. 2004). Gill net capture is a necessary technique to rapidly obtain adult sockeye salmon in the lower Fraser River but may represent a considerable physiological stressor when compared to other capture methods, such as dip net (Young et al. 2006*a*). Individuals that were injured or in poor condition (e.g., had visible wounds from predatory marine mammals or excessive scale loss) were excluded from the study. Captured individuals were immediately removed from the net and transferred to onboard holding totes (190 L) that were aerated and constantly supplied with fresh river water.

Biopsy and Tagging Procedure

Established protocols were used to biopsy and gastrically implant radio transmitters in unanesthetized sockeye salmon. This approach has been validated in the marine environment and upper portions of the Fraser River by demonstrating that these methods do not compromise sockeye salmon behavior or survival (Cooke et al. 2005, 2006; Young et al. 2006*a*; Crossin et al. 2009). 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. Onshore, 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. The following samples were collected: (*a*) a 2-mL blood sample using caudal venipuncture with a 1.5-in., 21-gauge needle and a vacutainer (lithium heparin, 3 mL, Becton-Dickson, Franklin Lakes, NJ) to assess plasma physiological indices; (*b*) a small gill sample (5–8 gill filaments, ~0.03 g) obtained with sharpened end-cutter pliers for quantification of gill tissue Na^+/K^+-ATPase activity (Shrimpton et al. 2005); (*c*) a 0.5-g adipose fin clip for DNA identification of stock complexes (Beacham et al. 2004); and (*d*) three scales for aging. An anchor tag (Floy Manufacturing, Seattle, WA) was inserted into the dorsal musculature adjacent to the dorsal fin for visual identification. A microwave fat probe (Distell Fish Fatmeter model 692, Distell, West Lothian, Scotland) was used to quantify gross somatic energy levels (GSE; Crossin and Hinch 2005), and body length (BL) measurements were made. The radio transmitter was in-

serted gastrically with the trailing end of the antenna exiting the mouth and crimped to drift laterally along the individual's body. The mean time between capture and sampling did not vary between populations (Adams-Shuswap: mean = 25.6 min ± 0.8 SD; Chilko: mean = 26.0 min ± 0.8 SD, *t*-test $P = 0.986$). The entire biopsy and tagging procedures were always completed in ≤3 min.

Laboratory Assays and Calculation of Physiological and Energetic Variables

Individual population origin was determined from DNA analysis of fin clips and scales (Beacham et al. 2004). Plasma ions (K^+, Cl^-, and Na^+), glucose, lactate, and osmolality were quantified from blood plasma samples based on procedures described in Farrell et al. (2001), except analyses were conducted using an AI 3320 freezing-point osmometer (Advanced Instruments, Norwood, MA) and a model 410 single-channel flame photometer (Cole Parmer, Montreal, Quebec). Plasma reproductive hormones (testosterone [T] and 17β-estradiol [E2]) were extracted according to Scott et al. (1983) and were assayed with EIA in duplicate after suitable dilution (Carey and McCormick 1998). Hematocrit was measured using a hematocrit centrifuge to compare the proportion of packed cells to plasma. Gill Na^+/K^+-ATPase activity was determined from the gill samples by kinetic assay (McCormick 1993). GSE was calculated based on a conversion formula derived for adult sockeye salmon (Crossin and Hinch 2005). Sexes were assigned based on plasma reproductive hormone values.

Telemetry Methods

Coded radio transmitters (MCFT-3A-3V, Lotek Wireless, Newmarket, Ontario) were 16 mm in diameter and 46 mm long, with a 460-mm-long antenna. Coded transmitters enabled the identification of individual fish as they were detected at receiver stations. As part of another study, a thermal logger was attached to each transmitter and waterproofed using Plasti Dip multipurpose rubber coating (Plasti Dip, Blaine, MN), adding ~10 mm in length (Donaldson et al. 2009). The transmitter/thermal logger complex weighed 17 g in air and 7 g in freshwater. Tags transmitted on the 150-MHz band on six unique 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.

Fixed receiver stations were strategically distributed throughout the Fraser watershed (Fig. 1; Robichaud and English 2006, 2007). SRX400, SRX400A, or SRX600 radio receivers (Lotek Wireless) were used with three-element or four-element Yagi antennas (Maxrad, Hanover Park, IL; Grant Systems Engineering, King City, Ontario). A public awareness campaign was launched to offer a reward for recovered transmitters to avoid spuriously assigning fisheries harvest to natural mortality.

Determination of Survival and Migration Rate

Detections by fixed station telemetry receivers in tributaries en route to spawning grounds (i.e., the Chilcotin/Fraser River confluence for Chilko fish and the inflow of the North Thompson River into Kamloops Lake for Adams-Shuswap fish) were used to indicate whether individuals successfully reached terminal spawning tributaries, herein referred to as "natal subwatershed" (Fig. 1). En route mortalities were categorized by the failure of the individual to reach subsequent telemetry receiver locations (Robichaud and English 2006, 2007). Individuals that were reported as fisheries harvest were excluded from this study. For statistical analyses, we evaluated survival to Mission, Thompson, and natal subwatersheds (Fig. 1).

Interpopulation comparisons revealed that mean BL differed between populations (Table 2), so all correlations were conducted on migration rates, measured as body lengths per second between the release site ("Release") and Mission and between Mission and the Thompson River confluence. Migration rate from Release to Mission included fish that "fell back" downriver following release. Migration rate from Release to Mission and from Mission to the Thompson River confluence was calculated because all sockeye salmon in this study must migrate past each of these locations to reach natal subwatersheds. If an individual was not detected by a receiver because of mortality or detection failure, it was excluded from migration rate analyses.

River Temperature Monitoring

Thermal data loggers (resolution ±0.1°C, accuracy ±0.2°C, Vemco-Amirix Systems, Halifax, Nova Scotia) were deployed near the release site at Whonnock (Fig. 1). This location represents the range of temperatures encountered by all individuals during the capture and tagging procedure, as the Fraser River is a large, well-mixed system (Patterson et al. 2007) and temperatures in the lower river are generally correlated with upper river temperatures (Hague et al. 2008). However, we cannot exclude minor variations in temperature exposures that may have been exploited by behaviors that cannot be resolved at the resolution of our telemetry array (Donaldson et al. 2009). To assess population-specific differences in physiological indices, tagging date was included as a covariate to account for seasonal variation throughout the sampling period, as river temperatures at the time of tagging were significantly correlated with tagging date ($R^2 = 0.171$; $P < 0.001$).

Statistical Analyses

Homogeneity of variance was assessed using Levene's test, and physiological, behavioral, and environmental data were $\log_{10}$ transformed to reduce heteroscedasticity where necessary. MANOVA was used to compare physiological variables between populations and to compare population-specific physiological variables in relation to survival. Where MANOVAs were significant, ANCOVAs that used tagging date as a covariate were conducted for each physiological variable. Correlation analyses

Table 2: Population-specific comparisons at time of capture, with tagging date as a covariate for Fraser River sockeye salmon (*Oncorhynchus nerka*)

			Population	Tagging Date (Covariate)
Physiological Variables	Adams-Shuswap (*N*)	Chilko (*N*)	*P*	*P*
Gross somatic energy (MJ/kg)	8.7 ± 2.1 (70)	9.1 ± 1.7 (60)	.129	.113
Hematocrit (%)	49.4 ± 4.5 (70)	49.1 ± 4.4 (60)	.737	.066
Plasma lactate (mmol/L)	16.6 ± 4.6 (70)	15.9 ± 4.3 (60)	.365	.324
Plasma glucose (mmol/L)	9.3 ± 1.8 (70)	9.4 ± 1.7 (60)	.865	**<.001**
Plasma Na^+ (mmol/L)	169.9 ± 8.6 (69)	169.2 ± 8.0 (59)	.591	.734
Plasma Cl^- (mmol/L)	137.3 ± 3.6 (70)	136.9 ± 3.3 (60)	.493	.709
Plasma osmolality (mOsm/kg)	359.5 ± 13.5 (70)	357.2 ± 12.6 (60)	.142	**.002**
Na^+/K^+-ATPase (μmol ADP mg protein^{-1} h^{-1})	2.8 ± .9 (66)	3.1 ± 1.2 (58)	.383	.514
Body length (cm)	60.9 ± 2.6 (70)	59.0 ± 2.7 (60)	**<.001**	.019*
Plasma [T] (ng/mL):				
Female	43.6 ± 20.6 (11)	62.7 ± 36.1 (23)	.103	.313
Male	23.0 ± 15.3 (38)	32.8 ± 16.1 (25)	.007*	.460
Plasma [E2] (ng/mL):				
Female	2.1 ± 1.2 (11)	3.7 ± 2.5 (23)	.017*	.586
Male	n/a (n/a)	n/a (n/a)	n/a	n/a

Note. Reproductive hormones analyzed by sex. Sexes were pooled for other comparisons because they did not differ significantly between groups at the time of sampling. Individuals that were reported to be harvested by fisheries were excluded from analysis. Values were adjusted to account for covariation with tagging date (ANCOVA). Variables were $\log_{10}$ transformed before analysis, if needed. Boldfaced values indicate significance at Bonferroni-corrected α values: 0.005. T = testosterone; E2 = 17β-estradiol; n/a = not available.

* Significance at $\alpha = 0.05$.

were used to test for relationships between physiological variables and migration rates for each population. Additional statistical tests are summarized in "Results." All known fisheries-related captures were excluded from statistical analyses (i.e., fish that were released as part of the study and subsequently recaptured by recreational, commercial, or First Nations fisheries that operate in the Fraser River). Statistical analyses were conducted using JMP, version 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, we 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 that they consider to be most biologically relevant (Cabin and Mitchell 2000). All values presented here represent means ± SD, unless otherwise noted.

Results

Population Comparisons

Postrelease survival to the first telemetry receiver location at Mission did not differ between populations ($\chi^2 = 0.352$, $P = 0.553$, $N = 130$; Table 1). Similarly, survival to the Thompson River confluence, the last receiver location that both populations migrate past, did not differ between populations ($\chi^2 = 0.453$, $P = 0.501$, $N = 130$; Table 1). However, survival to natal subwatersheds did differ significantly between populations, where Chilko individuals had a survival rate 1.9 times higher than Adams-Shuswap ($\chi^2 = 6.194$, $P = 0.013$, $N = 130$; Table 1).

Migration rate (BL s^{-1}) between Release and Mission did not differ significantly between populations (Adams-Shuswap: mean = 0.31 ± 0.15 SD; Chilko: mean = 0.31 ± 0.16 SD; *t*-test: $P = 0.869$, $N = 97$). Migration rate between Mission and the Thompson River confluence was significantly different between populations, where Chilko individuals traveled 30% faster than Adams-Shuswap individuals (Adams-Shuswap: mean = 0.45 ± 0.09 SD; Chilko: mean = 0.61 ± 0.09 SD; *t*-test: $P < 0.001$, $N = 64$). Mean water temperature at the time of sampling of individual fish did not differ between populations (*t*-test: $P = 0.552$, $N = 130$; Table 1).

Population-Specific Physiology at the Time of Capture

Analysis of the physiologic, energetic, and BL variables (i.e., GSE, HCT, plasma [Na^+], [Cl^-], [glucose], [lactate], osmolality, gill Na+/K+-ATPase activity, and BL) were not significantly different between sexes for either population (Adams-Shuswap: MANOVA, $P = 0.264$; $N = 43$; Chilko: MANOVA, $P = 0.645$; $N = 46$). For subsequent analyses, males and females were pooled for all variables except reproductive hormones (i.e., plasma [T] and [E2]).

MANOVAs examining population-specific physiology (i.e., GSE, HCT, plasma [Na^+], [Cl^-], [glucose], [lactate], osmolality, gill Na^+/K^+-ATPase activity, and BL) at capture were significant ($P = 0.004$, $N = 121$). ANCOVA, with tagging date as a co-

Table 1: Number of tagged individuals and mean (±SD) survival rates, migration rate, tagging date, and water temperature for individuals from the Adams-Shuswap and Chilko populations of Fraser River sockeye salmon (*Oncorhynchus nerka*)

Population	No. Tagged (*N*)	Survived to Mission (*N*, % of Tagged)	Mean ± SD Migration Rates (BL s^{-1}) from Release to Mission	Survived to Thompson (*N*, % of Tagged)	Mean ± SD Migration Rates (BL s^{-1}) from Mission to Thompson	Survived to Natal Subwatershed (*N*, % of Tagged)	Mean ± SD Tagging Date	Mean ± SD Water Temperature at Time of Sampling (°C)
Adams-Shuswap	70	63, 90.0	.31 ± .15	46, 65.7	.45 ± .09	16, 22.9	14.6 ± 10.3	18.7 ± .6
Chilko	60	52, 86.7	.31 ± .16	36, 60.0	.61 ± .09	26, 43.3	11.5 ± 9.0	18.8 ± .4

Note. BL = body length.

variate, showed that the variable driving MANOVA significance was BL ($P < 0.001$, $N = 127$; Table 2). As such, all correlations with migration rates were calculated as BL per second, to account for the significant influence of body length in population-level differences. When BL was removed from the MANOVA model, physiology at the time of capture did not differ significantly between populations ($P = 0.104$, $N = 121$). A MANOVA model of the sex-specific variables was significant for both males ($P = 0.043$, $N = 62$) and females ($P = 0.019$, $N = 34$). ANCOVA, with tagging date as a covariate, showed that the population-level variables that were significantly different were male [T] ($P = 0.007$, $N = 62$) and female [E2] ($P = 0.017$, $N = 34$), but these differences were not apparent following Bonferroni corrections.

Relationship between Physiology and Fate

MANOVAs examining population-specific differences in physiology and survival to Mission revealed significant models for Adams-Shuswap ($P = 0.015$, $N = 64$) but not Chilko populations ($P = 0.079$, $N = 57$). ANCOVA, with tagging date as a covariate, found that the variables driving MANOVA significance for the Adams-Shuswap population were elevated plasma lactate and osmolality, and Bonferroni corrections resulted in elevated hematocrit and plasma sodium no longer being significant (Table 3). MANOVA models examining sex-specific variables by population were not significant for Adams-Shuswap males ($P = 0.507$, $N = 37$) and females ($P = 0.511$, $N = 11$) or Chilko males ($P = 0.620$, $N = 25$) and females ($P = 0970$, $N = 23$).

MANOVAs testing population-specific differences in physiology and survival to Thompson were not significant for Adams-Shuswap ($P = 0.259$, $N = 64$) or Chilko ($P = 0.175$, $N = 57$). MANOVAs examining sex-specific variables by population were not significant for Adams-Shuswap males ($P = 0.395$, $N = 37$) and females ($P = 0.193$, $N = 11$) or Chilko males ($P = 0.789$, $N = 25$) and females ($P = 0.319$, $N = 23$).

MANOVAs examining population-specific differences in physiology and survival to natal subwatersheds were not significant for either Adams-Shuswap ($P = 0.252$, $N = 64$) or Chilko ($P = 0.554$, $N = 57$). MANOVAs testing sex-specific variables by population were not significant for Adams-Shuswap males ($P = 0.592$, $N = 37$) and females ($P = 0.260$, $N = 11$) or Chilko males ($P = 0.288$, $N = 25$) and females ($P = 0.074$, $N = 23$).

Correlations between Physiology and Migration Rate

Migration rates from Release to Mission revealed that Adams-Shuswap fish that reached natal subwatersheds had significantly faster mean migration rates (*t*-test: $t = 5.01$, $P = 0.032$, $N = 35$) than those that did not (Table 1). There was no relationship between migration rate and survival for Chilko fish (*t*-test: $t = 0.09$, $P = 0.754$, $N = 30$). For Adams-Shuswap, migration rates from Release to Mission were negatively correlated with plasma osmolality but no other physiological variables (Table 4). Migration rates for Adams-Shuswap from Mission to Thompson were negatively correlated with GSE, plasma osmolality, and plasma estradiol (for females) and positively correlated with gill Na^+/K^+-ATPase activity (Table 5). No correlations were evident between migration rates and physiological variables for Chilko fish (Tables 4, 5).

Discussion

Population-Specific Physiology and Stress at River Entry

At the time of capture, BL was the only variable that differed significantly between populations, reflecting known morphological differences between these populations (Hinch et al. 2006). Population-specific differences among Pacific salmon species emerge because of a combination of phenotypic plasticity and local adaptation of a suite of life-history, physiological, and behavioral traits (Taylor 1991; Hutchings 2004; Crozier et al. 2008). Fraser River sockeye populations that spawn relatively long distances from the ocean generally have higher GSE density at the onset of river migration compared with short-distance migrating populations (Crossin et al. 2004). Population-specific differences in physiology (Cooke et al. 2006; Crossin et al. 2009), behavior (Hanson et al. 2008; Crossin et al. 2009), and survival (English et al. 2005) have been identified for Fraser River sockeye salmon. Furthermore, swimming performance studies in adult Fraser salmon indicate that optimal performance and thermal tolerance is finely tuned, adaptive, and population specific (Lee et al. 2003; Farrell et al. 2008).

Table 3: Comparisons between physiological variables and survival to Mission, with tagging date as a covariate for the Adams-Shuswap population of Fraser River sockeye salmon (*Oncorhynchus nerka*)

			Fate	Tagging Date (Covariate)
Physiological Variables	Died before Mission (*N*)	Survived to Mission (*N*)	*P*	*P*
Gross somatic energy (MJ/kg)	8.4 ± 1.8 (7)	8.7 ± 2.1 (63)	.769	.143
Hematocrit (%)	52.7 ± 3.6 (7)	49.0 ± 4.6 (63)	.044*	.169
Plasma lactate (mmol/L)	22.5 ± 3.8 (7)	15.9 ± 4.2 (63)	**<.001**	.482
Plasma glucose (mmol/L)	10.3 ± 2.3 (7)	9.2 ± 1.7 (63)	.304	**.001**
Plasma Na^+ (mmol/L)	178.3 ± 3.7 (6)	169.2 ± 8.6 (63)	.013*	.657
Plasma Cl^- (mmol/L)	135.3 ± 3.0 (7)	137.5 ± 3.6 (63)	.127	.330
Plasma osmolality (mOsm/kg)	375.6 ± 9.3 (7)	357.7 ± 12.8 (63)	**.002**	.012*
Na^+/K^+-ATPase (μmol ADP mg protein^{-1} h^{-1})	2.9 ± 1.2 (6)	2.8 ± .9 (60)	.948	.213
Body length (cm)	59.3 ± 1.7 (7)	61.1 ± 2.7 (63)	.127	.760
Plasma [T] (ng/mL):				
Female	n/a (0)	43.6 ± 20.6 (19)	n/a	n/a
Male	24.2 ± 12.6 (7)	22.7 ± 15.9 (31)	.536	.141
Plasma [E2] (ng/mL):				
Female	n/a (0)	.3 ± .2 (11)	n/a	n/a
Male	n/a (n/a)	n/a (n/a)	n/a	n/a

Note. Reproductive hormones analyzed by sex. Sexes were pooled for other comparisons because they did not differ significantly between groups at the time of sampling. Individuals that were harvested by fisheries were excluded from analyses. Values were adjusted to account for covariation with tagging date of sampling (ANCOVA). Variables were $\log_{10}$-transformed before analysis, if needed. Boldfaced values indicate significance at Bonferroni-corrected α values: 0.005. T = testosterone; E2 = 17β-estradiol; n/a = not available.

* Significance at $\alpha = 0.05$.

That physiological variables did not differ between populations in this study reflects the fact that individuals from both populations were sampled at the same locale at the same time and that both groups of fish migrate similar distances up the Fraser River to spawning areas.

While the physiological response to capture was the same for both populations, it was apparent from the plasma ion, lactate, and glucose values that the capture event was a considerable acute stressor. Compared with values in other studies in which adult sockeye were exercised to exhaustion in freshwater laboratory situations (reviewed in Hinch et al. 2006), our plasma lactate and glucose values, indicators of metabolic loading, were ~325% and 32% higher, respectively, and osmolality and sodium levels, indicators of ion-osmoregulatory balance, were ~6%–8% higher. Our lactate and glucose values were more than 20% higher than those obtained from freely migrating Adams-Shuswap sockeye captured in the Thompson River (several hundred kilometers upriver of our capture site) by dip net (Young et al. 2006*a*). Dip net is a rapid capture technique that does not require entanglement and thus minimizes exercise and struggling, which enables sampling to occur within 2 min of capture (Young et al. 2006*a*). The mean time between capture and sampling in this study was ~25 min for both populations, a time lag that may explain the magnitude of these responses, as many of the physiological variables measured here would have been increasing toward peak concentrations by this time (Mazeaud et al. 1977). Because the physiological response to capture did not differ between populations, this study design provides an excellent platform for an interpopulation comparison that tests the limits of physiological tolerance to a major stressor.

Relationship between Population-Specific Physiology and Survival

Late-run Adams-Shuswap fish historically enter the Fraser River in September and October and encounter relatively cool water temperatures, whereas the summer-run Chilko fish, with their peak river entry timing in August, encounter much warmer water in the Fraser River main stem before reaching cool-water glacial-fed spawning areas (Burgner et al. 1991). For early-entry late-run fish such as Adams-Shuswap, the mechanism of mortality has been proposed to be mediated at least in part by these fish encountering environmental conditions for which they are not adapted (Cooke et al. 2004; Farrell et al. 2008). Because of the known poor condition and survival of early-entry late-run fish, we had predicted that population-specific differences in physiological condition following capture stress at the onset of the freshwater phase of the migration would exert a greater influence on the survival of early-entry Adams-Shuswap relative to Chilko individuals. We found that physiological stress and osmoregulatory impairment had a greater influence on survival for Adams-Shuswap fish relative to Chilko fish shortly after release, which suggests that the former was less able to tolerate a significant acute stressor. We had expected that Adams-Shuswap fish would perish at relatively high levels, as there is

Table 4: Correlations between physiological variables and migration rate (body length s^{-1}) from release point to Mission, for individuals from the Adams-Shuswap ($N = 70$) and Chilko ($N = 60$) populations of Fraser River sockeye salmon (*Oncorhynchus nerka*)

	Adams-Shuswap			Chilko		
Physiological Variables	Correlation	*P*	*N*	Correlation	*P*	*N*
Gross somatic energy (MJ/kg)	.203	.186	44	.164	.347	35
Hematocrit (%)	−.207	.178	44	−.167	.339	35
Plasma lactate (mmol/L)	−.221	.154	43	−.231	.182	35
Plasma glucose (mmol/L)	−.260	.088	44	−.180	.301	35
Plasma Na^+ (mmol/L)	.031	.843	44	−.039	.828	34
Plasma Cl^- (mmol/L)	.011	.942	44	.227	.190	35
Plasma osmolality (mOsm/kg)	−.307	**.043**	44	−.213	.220	35
Na^+/K^+-ATPase (μmol ADP mg protein^{-1} h^{-1})	−.118	.456	42	.049	.785	33
Plasma [T] (ng/mL):						
Female	.665	.072	8	.245	.468	11
Male	−.321	.135	23	−.287	.300	15
Plasma [E2] (ng/mL):						
Female	.297	.475	8	.086	.802	11
Male	n/a	n/a	n/a	n/a	n/a	n/a

Note. Reproductive hormones analyzed by sex. Sexes were pooled for other comparisons because they did not differ significantly between groups at the time of sampling. Boldfaced values indicate significance at Bonferroni-corrected α values: 0.005. T = testosterone; E2 = 17β-estradiol; n/a = not available.

a growing body of evidence that individuals from this population complex are in relatively poor condition. Functional genomics studies have revealed that early-entry late-run fish from the Adams-Shuswap population are in a state of poorer health compared to Chilko individuals. Specifically, they are immunosuppressed, have a coagulative blood disorder, are in a poor nutritional state, and show signs of advanced senescence, which could contribute to the mortality observed here (Miller et al. 2007; Cooke et al. 2008).

Crossin et al. (2009) found that physiological indices of stress (i.e., levels of plasma lactate, sodium, chloride, and osmolality) of sockeye salmon measured in the marine environment indicated whether Adams-Shuswap individuals entered the Fraser River, yet physiological stress had no relationship with river entry for Chilko fish. In our study, Adams-Shuswap individuals that failed to reach Mission had elevated plasma lactate and elevated plasma osmolality concentrations relative to those that survived to Mission. Elevated plasma lactate concentrations indicate physiological stress and metabolic loading, while higher plasma osmolality concentrations indicate physiological stress and osmoregulatory imbalance. Similarly, elevated hematocrit and plasma sodium concentrations, which were significantly higher for mortalities before Bonferroni corrections, have been linked with physiological stress and osmoregulatory imbalance, respectively, in wild-migrating Pacific salmon (Farrell et al. 2000). In freshwater, acute stress generally results in short-term elevations of ion concentrations due to fluid shifts between intracellular and extracellular space (McDonald and Milligan 1992; Farrell et al. 2001), whereas depressed concentrations of plasma ions would indicate chronic stress (Pickering and Pottinger 1995). A laboratory-derived threshold for maximum plasma lactate has been proposed at 12.2 mmol L^{-1} (Jain and Farrell 2003). However, Crossin et al. (2009) found that survival to river entry for marine-sampled sockeye salmon depended on a threshold concentration of ~18–20 mmol L^{-1}. The results of this study corroborate this relationship in general, although one Chilko and two Adams-Shuswap fish that reached spawning grounds had plasma lactate concentrations exceeding 20 mmol L^{-1}.

Our finding that Chilko individuals had higher survival rates to natal subwatersheds relative to Adams-Shuswap is not surprising, given that early-river entry by segments of late-run sockeye salmon populations has resulted in mortality rates exceeding 90% in certain years (Cooke et al. 2004; English et al. 2005). It was not until fish had passed the Thompson River confluence that we observed Adams-Shuswap fish exhibiting ~60% lower survival than Chilko fish. The survival rates here were much lower relative to a sockeye salmon telemetry tagging project carried out in the marine environment (i.e., fish captured in cooler ocean waters by purse seine) during the same time period, where 64.5% of Chilko fish and 43.6% of late-run Shuswap fish that survived to Mission reached natal subwatersheds (Robichaud and English 2007). Higher mortality here (i.e., on fish tagged in the lower river) may be related to the fact that fish from both populations were captured at river temperatures that were warm relative to cooler marine capture temperatures (e.g., Robichaud and English 2007). Because we did not find a direct relationship between physiological condition at the time of capture and survival to natal subwatersheds, the acute stress does not appear to have contributed

Table 5: Correlations between physiological variables and migration rate (body length s^{-1}) from Mission to Thompson, for individuals from the Adams-Shuswap ($N = 70$) and Chilko ($N = 60$) populations of Fraser River sockeye salmon (*Oncorhynchus nerka*)

	Adams-Shuswap			Chilko		
Physiological Variables	Correlation	*P*	*N*	Correlation	*P*	*N*
Gross somatic energy (MJ/kg)	−.416	**.013**	35	.269	.149	30
Hematocrit (%)	.129	.457	35	.051	.789	30
Plasma lactate (mmol/L)	−.306	.078	34	.142	.455	30
Plasma glucose (mmol/L)	−.042	.811	35	−.002	.990	30
Plasma Na^+ (mmol/L)	−.279	.104	35	.0485	.803	29
Plasma Cl^- (mmol/L)	−.158	.364	35	.069	.714	30
Plasma osmolality (mOsm/kg)	−.357	**.036**	35	.101	.597	30
Na^+/K^+-ATPase (mol ADP mg protein^{-1} h^{-1})	.425	**.015**	32	.034	.863	28
Plasma [T] (ng/mL):						
Female	−.419	.261	9	.141	.739	8
Male	.009	.977	14	.173	.555	14
Plasma [E2] (ng/mL):						
Female	−.691	**.039**	9	−.181	.668	8
Male	n/a	n/a	n/a	n/a	n/a	n/a

Note. Reproductive hormones analyzed by sex. Sexes were pooled for other comparisons because they did not differ significantly between groups at the time of sampling. Boldfaced values indicate significance at Bonferroni-corrected α values: 0.005. T = testosterone; E2 = 17β-estradiol; n/a = not available.

directly to a carryover, or legacy, effect, although indirect effects of the acute stress are possible (i.e., delayed physiological recovery, which we could not measure postrelease). A carryover effect has been described for migratory birds, in which an event that occurs at a discrete time point influences subsequent migratory and reproductive outcomes (Norris and Taylor 2006; Sorenson et al. 2009). Chilko fish encounter cooler water as they migrate past the Thompson River confluence, while Adams-Shuswap fish encounter warm water as they migrate through the Thompson River toward spawning grounds (Patterson et al. 2007). Untangling the role of an acute stress, such as the one applied here, on survival is challenging because the mechanism of mortality is likely caused by a combination of factors, including a temperature-mediated and population-specific collapse in aerobic scope (Farrell et al. 2008). Preliminary results of studies under way to quantify the optimal temperatures for aerobic scope for Chilko reveal that this population, compared with individuals from late-run populations, has a broader thermal tolerance for aerobic scope (e.g., Gates Creek and Weaver Creek populations; Lee et al. 2003; E. Eliason, University of British Columbia, personal communication). The apparent lower thermal tolerance of Adams-Shuswap could contribute to the higher mortality observed for this population.

Correlations between Physiology and Migration Rate

Consistent with our second prediction, physiological stress and osmoregulatory impairment had a greater effect on the migration rate of Adams-Shuswap fish relative to Chilko fish. The strong negative correlation between GSE and migration rate for Adams-Shuswap is consistent with previous research that migrating sockeye salmon with higher energy stores generally take longer to reach spawning grounds (Crossin et al. 2004; Hanson et al. 2008). The strong negative correlations between plasma osmolality and migration rate observed through both river segments is consistent with physiological stress and osmoregulatory impairment. Interestingly, migration rates from Release to Mission revealed that Adams-Shuswap fish that failed to reach natal subwatersheds had significantly slower migration rates than successful fish, yet no such relationship was found for Chilko. This slower migration rate could be related to exercise stress and associated muscle fatigue (Wood et al. 1983). The negative correlation between migration rate and plasma estradiol for Adams-Shuswap females was surprising given the known relationships between elevated reproductive hormones stimulating upriver migration in salmonid species (Munakata et al. 2001). The correlations observed between migration rate and physiological indices of acute stress for Adams-Shuswap individuals provides further evidence that tolerance to stress is compromised for early-entry late-run fish relative to the Chilko population.

The positive correlation between gill Na^+/K^+-ATPase activity and migration rate was unexpected since gill Na^+/K^+-ATPase activity generally declines as fish approach spawning grounds (Shrimpton et al. 2005). Surprisingly, the mean gill Na^+/K^+-ATPase activity of both populations was much higher than previously recorded for sockeye salmon in freshwater, generally measured hundreds of kilometers upriver, as these fish approach spawning areas. These values were comparable in magnitude to enzyme activity measured during the coastal approach

(Hinch et al. 2006). This suggests that these fish were still undergoing the osmoregulatory transition between marine and freshwater and are doing so during their migration through the warm Fraser River mainstem. That these fish may not have been completely osmotically prepared for freshwater, combined with the warm waters associated with river entry, could mean that the capture event was a cumulative stressor that served to further exacerbate the level of stress for individuals from both populations.

To reach natal subwatersheds, Adams-Shuswap travel distances <500 km from the river mouth and elevations of <400 m, while Chilko fish travel >600 km in distance and >1,100 m in elevation. The faster migration rates exhibited by Chilko relative to Adams-Shuswap individuals reflect known differences among life-history and morphological traits between summer-run and late-run sockeye salmon in the Fraser River (Crossin et al. 2004; English et al. 2005). In fact, Chilko are considered superoptimal migrants because they achieve higher ground speeds for a given tail-beat frequency and conserve more energy relative to other sockeye populations in the Fraser River (Hinch and Rand 2000). Even before river entry, Adams and other late-run populations travel slower through coastal areas and take a longer time to enter freshwater relative to summer-run populations such as Chilko (Crossin et al. 2004). These population-specific differences in migration rate were likely further differentiated because the early-entry Adams-Shuswap fish encountered higher river temperatures than those that they are historically adapted for, a finding consistent with interpopulation and interspecies comparisons among swimming performance and migration rates in Fraser River salmon (MacNutt et al. 2006; Hanson et al. 2008). If this slowed migration results in delayed arrival at spawning grounds, it could ultimately affect reproductive success by reducing longevity on the spawning grounds and by reducing the number of spawning opportunities (Smoker et al. 1998; Keefer et al. 2006). Concomitant with delayed arrival at spawning grounds, slower migration rates result in a longer duration spent migrating through regions with high water temperatures (e.g., Mission to Thompson; Patterson et al. 2007; Donaldson et al. 2009).

Conclusions

With expected increases in Fraser River peak summer river temperatures, early-entry late-run fish could encounter temperatures several degrees higher than they are historically adapted for, in addition to the ~5°C increase in temperature that late-run fish already experience because of the early-entry phenomenon (Morrison et al. 2002; Rand et al. 2006; Ferrari et al. 2007; Patterson et al. 2007). Sockeye salmon in this study encountered moderate temperatures for the Fraser River (i.e., mean temperatures for each population was ~18.5°C; Table 1), and temperature had no statistical relationship to survival. In high-temperature years, these population-specific differences in physiological tolerance, behavior, and survival may be magnified, resulting in fitness consequences for early-entry late-run fish. The ultimate consequences of climate change on population persistence are uncertain but have the potential to differentially select for individuals within a population that have wide windows for coping with physiological stress and variable environmental conditions (Pörtner and Farrell 2008). Even at the moderate temperatures observed here, the imposed stressor had a greater effect on the behavior and survival of early-entry late-run Adams-Shuswap fish.

Consistent with predictions, metabolic (e.g., elevated plasma lactate concentrations) and osmoregulatory (e.g., elevated plasma osmolality concentrations) impairment was significantly and negatively associated with survival of individuals from the early-entry late-run Adams-Shuswap population but not the summer-run Chilko population. Similarly, correlations between physiological condition and migration rate were found for Adams-Shuswap fish but not Chilko fish. Overall, Adams-Shuswap individuals had slower migration rates and were less likely to reach natal subwatersheds relative to Chilko individuals. Together, this evidence suggests that Chilko fish respond to stress in a manner similar to Adams-Shuswap fish, yet Chilko fish are potentially better able to cope with the stressor relative to Adams-Shuswap fish. We conclude that physiological condition differentially affects the behavior and survival of these two populations of sockeye salmon, potentially as a consequence of the early-entry phenomenon by a segment of the Adams-Shuswap population. This information is relevant for management models to predict population-specific variation in migration success relative to environmental conditions (Young et al. 2006*b*), an outcome that is at the heart of applied evolutionary physiology (Feder et al. 2000). Disentangling the many intrinsic and extrinsic factors that influence the migration success of vulnerable Fraser River sockeye salmon, particularly with respect to the early-entry late-run phenomenon, is paramount to the management and conservation of this species.

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