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FISHWAY PASSAGE AND POST-PASSAGE MORTALITY OF UP-RIVER MIGRATING SOCKEYE SALMON IN THE SETON RIVER, BRITISH COLUMBIA

D. W. ROSCOE,[a]* S. G. HINCH,[a] S. J. COOKE[b] and D. A. PATTERSON[c]

[a] *Centre for Applied Conservation Research and Department of Forest Sciences, University of British Columbia, Vancouver, BC, Canada*
[b] *Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, Ottawa, ON, Canada*
[c] *Fisheries and Oceans Canada, Science Branch, Pacific Region, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, Canada*

ABSTRACT

Adult sockeye salmon (*Oncorhynchus nerka*) were studied to assess the consequences of a dam and vertical-slot fishway on mortality during their spawning migration in the Seton–Anderson watershed, British Columbia, Canada. Since previous research suggests fishway passage may be difficult, our main hypothesis was that the dam and fishway have post-passage consequences that affect subsequent behaviour and survival. Eighty-seven sockeye were caught at the top of the fishway, implanted with an acoustic telemetry transmitter, non-lethally biopsied to obtain a small blood sample and released either upstream or downstream of the dam. Indices of physiological stress (i.e. plasma cortisol, glucose, lactate and ions) indicated that fish were not stressed or exhausted after capture from the fishway, and were not unduly stressed by transportation to release sites or net-pen holding. Of 59 fish released downstream of the dam, 14% did not reach the dam tailrace. Overall passage efficiency at the fishway was 80%. Mortality in two lakes upstream of the dam was greater in fish released downstream of the dam (27%) compared to fish released upstream of the dam (7%; $p = 0.04$) suggesting that dam passage has consequences that reduce subsequent survival. Cumulative mortality of fish released downstream of the dam ($n = 55$) resulted in only 49% survival to spawning areas, compared to 93% of fish released upstream of the dam ($n = 28$). Survival was significantly lower for females (40%) than for males (71%; $p = 0.03$), a finding that has implications for conservation because spawning success of sockeye salmon populations is governed primarily by females. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: fishway; sockeye salmon; migration; mortality; telemetry

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INTRODUCTION

Lifetime reproductive success of anadromous and semelparous Pacific salmon (*Oncorhynchus* spp.) depends on successful completion of a single spawning migration. Consequently, these species are particularly vulnerable to fragmentation of the river corridor by human-made barriers. Dams have contributed to large declines in anadromous salmon throughout North America (Nehlsen *et al*., 1991; Slaney *et al*., 1996). At many dams, fishways have been built to enable passage of fishes over the barrier (Clay, 1995). However, a wide body of literature indicates that fishway passage efficiency is often low and many fishways continue to restrict movements of fish through a barrier (reviewed in Roscoe and Hinch, 2010).

Even successful passage through a fishway can have deleterious effects on fish that could lead to delayed mortality or negatively affect fitness. For example, fishway passage can require high levels of energy-expenditure (Gowans *et al*., 2003; Brown *et al*., 2006), promote increased predation (Pelicice and Agostinho, 2008) or result in long delays (Bunt *et al*., 2000; Keefer *et al*., 2004), all of which could negatively affect fitness. Fishways can also cause injuries or scale loss through fish interactions with infrastructure (Castro-Santos *et al*., 2009). However, research evaluating fishway performance typically only documents usage by certain species or quantifies passage efficiency, and rarely considers post-passage effects or monitors behaviour and survival after passage (Roscoe and Hinch, 2010). In order to completely mitigate the impacts of barriers on fish populations, fishways need to enable passage without subsequent negative effects on fitness (Castro-Santos *et al*., 2009). Indeed, such an outcome is essential to ensuring that fishways do not compromise the welfare status of fish (Schilt, 2007).

Recent work in the Seton River in British Columbia, Canada (i.e. Pon *et al*., 2009a, b), has used electromyogram telemetry (EMG) and physiological biopsy to assess how swimming behaviour, stress physiology and dam-spill discharge affected fishway passage of sockeye salmon (*Oncorhynchus nerka*). The authors found that levels of

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*Correspondence to: D. W. Roscoe, Department of Forest Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada. E-mail: dwroscoe@gmail.com

stress and fishway attraction efficiency did not differ by level of dam-spill discharge but delays were greatest during intermediate flows (Pon *et al.*, 2009a). Fish that failed to pass the fishway were not different from unsuccessful fish in terms of swimming speeds or energy use but unsuccessful fish had depressed plasma sodium levels, suggesting that they might be physiologically stressed (Pon *et al.*, 2009b). However, like most fishway studies, fish were not monitored following passage, therefore the effects of delay and successful passage on migration success were not assessed.

In a recent review of sexual variation in fisheries research (Hanson *et al.*, 2008), the authors concluded that most management programmes are lacking information on the importance of fish gender, and that this could have serious implications for evaluating or assessing management actions. Certainly, large sex differences exist in the migratory behaviour and fate of Pacific salmon. For example, female sockeye salmon swim using less energy per unit distance travelled (Hinch and Rand, 1998) but have higher passage failure rates in Hell's Gate, a constricted and hydraulically challenging area of the Fraser River Canyon, BC (Gilhousen, 1990; Hinch and Bratty, 2000). Moreover, a recent study found that females had higher rates of *en route* mortality and were more susceptible to high temperature stress compared to males (Crossin *et al.*, 2008). Similarly, a holding study manipulating water velocity during simulated spawning migration found that female sockeye salmon suffered higher mortality than males regardless of treatment (Nadeau *et al.*, 2010). Therefore, in cases of passage through tailraces and fishways that are challenging for fish, one might predict poorer passage success and higher mortality in females compared to males. However, few studies evaluating fishway passage have considered the effects of sex on passage success.

We evaluated the consequences of a dam and fishway on sockeye salmon spawning migrations by assessing both success to ascend a fishway and success to reach spawning grounds upstream of the fishway. One challenge in evaluating impacts of dams and fishways is the lack of a 'control' group since passage rates and levels of mortality prior to construction of these facilities are typically unknown (e.g. what would migration success be without the presence of the dam and fishway). To surmount this problem, we used an experimental approach, transporting and releasing fish at locations either immediately up- or down-stream of the dam and comparing mortality and behaviour between these groups. Based on previous work at this dam (Pon *et al.*, 2009a, b), we predicted that some sockeye salmon would fail to pass the fishway. However, because fishway passage is physiologically and behaviourally challenging (Roscoe and Hinch, 2010), we hypothesized that successful fishway ascent would have post-passage consequences. We predicted that fish released downstream of the dam that re-ascended the fishway would have greater mortality *en route* to spawning grounds than fish released upstream of the dam. In light of previous research demonstrating sex differences in sockeye salmon in the Fraser River, we further predicted that fishway passage failure and *en route* mortality would be greater for female fish than male fish. Because transportation by truck can be stressful for salmonids, we evaluated the effects of our handling and transportation approach using non-lethal physiological biopsies. We measured a suite of indicators of stress from blood samples from fish immediately after fishway ascent, and from another group of fish after transportation and a 5-h recovery period in net-pens. In sum, these measures of stress were used to assess physiological condition after fishway ascent, changes due to transportation and holding, and to interpret differences between *en route* mortalities and fish that reached spawning grounds.

METHODS

Study site

We studied the Gates Creek population of sockeye salmon during their migration through the Seton–Anderson watershed in South-Western British Columbia (BC), Canada. Before reaching the study area adult sockeye had already migrated ~320 km from the mouth of the Fraser River to the confluence of the Seton River. Our study area consisted of the final 55 km of their migration route, a migration corridor between the confluence and spawning areas at Gates Creek, which included the Seton River, Seton Lake, Portage Creek and Anderson Lake (Figure 1). A diversion dam spans the Seton River 760 m downstream of Seton Lake and the majority of the flow of the Seton River (up to $125\,m^3\,s^{-1}$) is diverted into a 3.8 km long canal that delivers water to the hydroelectric power station on the Fraser River, 1.2 km downstream of the confluence with the Seton River. A vertical-slot fishway allows passage of fish over the Seton dam. The fishway consists of 32 pools, is 107 m long and has an overall grade of 6.9%. Discharge through the fishway is $1.3\,m^3\,s^{-1}$ throughout the year. Water is discharged at the dam through a sluice gate adjacent to the fishway entrance, intended to attract fish to the fishway, and through any of five siphons. During our study, there were two distinct levels of discharge at Seton dam, $35\,m^3\,s^{-1}$ (21–31 August) and $60\,m^3\,s^{-1}$ (15–20 August). Water temperature in the Seton River was measured using temperature loggers (iButton Thermochrons, DS1921Z, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) and ranged from 13 to 16°C. Water temperature of the Fraser River at Lillooet, BC was obtained from Fisheries and Oceans Canada and ranged from 16 to 18°C during August 2007 (D. Patterson, Personal

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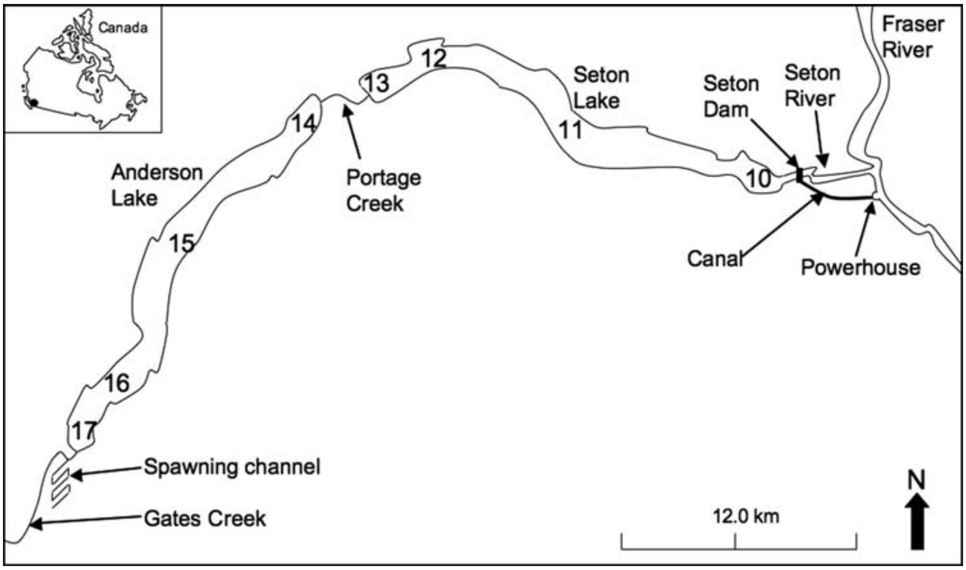

Figure 1. Map of the Seton–Anderson watershed in Southwestern British Columbia, Canada showing the location of hydroelectric facilities on the Seton River and the spawning channel at Gates Creek. Numbers show the approximate location of acoustic telemetry receiver stations in the lakes. The locations of the nine receivers in the Seton and Fraser rivers are shown in Figure 2

Communication, 2008), which is near or slightly cooler than historical averages (Patterson *et al*., 2007).

Fish capture, transport and holding

All fish were captured by dip-net from the top pool of the Seton Dam Fishway, using a removable screen gate to temporarily block the upstream exit. Our general approach was to biopsy sample fish, implant them with acoustic telemetry transmitters and release them either upstream of the dam at the capture site, or transport and release them downstream of the dam. To assess fishway passage efficiency and post-passage consequences, the ideal capture location would have been downstream of the dam in the Seton River, such that study fish would not have previously experienced the tailrace and fishway. However, it was not possible to catch sockeye salmon by dip- or drift-net anywhere in the lower Seton River because of low fish densities and lack of suitable capture locales. Thus, we caught all fish at the top of the fishway and acknowledge the possibility that we were selecting for fish that already demonstrated the ability to locate and ascend the fishway.

Because capture and transport of sockeye can cause certain blood metabolite and stress hormone levels to be elevated (Kubokawa *et al*., 1999) and some fish would be released at the capture site and others would be transported then released, we needed to evaluate and control for the effects of transportation. We held 67 of the study fish for a 5-h in-river recovery period at the release sites before biopsy sampling, tagging and release (hereafter 'net-pen held' fish). During this holding period the metabolite levels should have returned to near baseline (Milligan *et al*., 2000; Portz *et al*., 2006). An additional 20 sockeye were biopsy sampled, tagged and released immediately after capture from the top of the fishway (hereafter 'control' fish) to compare initial physiology of fish that were held to those not held. Transported fish were placed in an aluminium transport tank (1 m × 1 m × 1.5 m) filled with river water and continuously aerated with a 30 cm long air diffuser to maintain 100% oxygen saturation. Fish were then transported to one of the release sites where they were held in enclosures for 5-h, then biopsied, tagged and released. A 4 m × 8 m × 4 m enclosure consisting of aluminium tubing frame, vinyl sides and bottom and nylon mesh ends was used to hold fish during the recovery period. The enclosure was placed in the river at the release site such that a steady current of water passed through it, requiring fish to swim slowly to maintain position but without becoming exhausted. A maximum of 12 fish were transported in the tank and then held in the enclosure at one time.

Tagging, physiological biopsy and tracking

Tagging and biopsy procedures followed those of Cooke *et al.* (2005). Fish were restrained in a V-shaped foam-padded trough continuously supplied with fresh river water. A 1.5 ml blood sample was taken from the caudal vasculature (Houston, 1990) using a heparinized Vacutainer syringe (1.5 inches, 21 gauge; lithium heparin). Blood samples were centrifuged for 6 min to separate plasma from red blood cells, and plasma was temporarily stored in liquid nitrogen before transfer to an −80°C freezer. Fork length was measured to the nearest 5 mm. A small tissue sample was removed from the adipose fin using a hole punch and stored in ethanol for subsequent DNA analysis to confirm population of origin (Beacham *et al.*, 2004). Somatic lipid concentration was measured using a hand-held microwave energy meter (Fatmeter model 692, Distell Inc., West Lothian, Scotland, UK) and converted to estimates of gross somatic energy (GSE) using relationships described by Crossin and Hinch (2005). Fish were marked with an external tag (FT-4 Cinch up, Floy Tag Inc., Seattle, WA, USA) attached through the dorsal musculature immediately anterior to the dorsal fin using a hollow needle. The external tag permitted visual identification of study sockeye on spawning grounds or if they were caught by fisheries. An acoustic telemetry transmitter (V16-1H-R64K coded tags, Vemco Inc., Shad Bay, NS, Canada; 16 mm diameter, 54 mm length, all weighed less than 2% of the body mass of the fish) was inserted gastrically using a tag applicator consisting of a hollow plastic tube and plunger to expel the tag. The entire tagging and biopsy procedure lasted less than 3 min, after which fish were held for recovery in a net-pen. No fish regurgitated transmitters during this holding period, which is consistent with other studies that have shown high levels of transmitter retention in migratory adult sockeye salmon (i.e. 100%, Cooke *et al.*, 2005). After the holding period, fish were released at one of three locations (Figure 2): (1) Powerhouse tailrace on the Fraser River (site D), (2) lower Seton River at confluence of Cayoosh Creek (site C) or (3) Seton Lake near outflow (site A). The 20 control fish sampled immediately after capture and released without a recovery period were released directly upstream of the dam into the Seton River (site B).

A fixed array of acoustic telemetry receivers (VR2, Vemco Inc., Shad Bay, NS, Canada) was used to monitor fish movements. Seventeen receivers were deployed underwater in strategic locations along the migration route including one in the Fraser River at the powerhouse tailrace, two in the lower Seton River, two in the tailrace of Seton dam, one in the upper Seton River and four in each of Seton and Anderson Lakes (Table I). In addition, receivers were placed near the bottom, middle and top of the fishway to detect entrance into and ascent of the fishway.

Physiological analysis

We measured a suite of variables from blood plasma samples that were used as indices of physiological stress or exhaustion. Plasma lactate and glucose concentrations were measured using YSI 2300 STAT Plus glucose and lactate analyser (YSI Inc., Yellow Springs, OH, USA). Plasma chloride concentrations were measured in duplicate using a model 4425000 digital chloridometer (Haake Buchler Instruments, Saddle Brook, NJ, USA). Concentrations of plasma sodium and potassium ions were measured in duplicate using a model 410 Cole-Palmer flame photometer (Vernon Hills, IL, USA) calibrated to a 4-point standard curve prior to use and after every 10 samples. Plasma osmolality was measured using a model 3320 freezing point osmometer (Advanced Instruments, Norwodd, MA, USA). Cortisol, 17-*ß* estradiol and testosterone concentrations were measured in duplicate using enzyme-linked immunosorbent assay (ELISA) kits (Neogen Co., Lexington, KY, USA). Plasma testosterone and 17-*ß* estradiol were ether-extracted according to kit directions prior to assaying. Measurements were repeated if the coefficient of variation between replicates was greater than 10%. To determine the sex of individual fish 17-*ß* estradiol was plotted versus testosterone resulting in two distinct clusters of points, which corresponded with males and females.

Data analysis

To evaluate the ability of the telemetry receiver array to detect fish we calculated detection efficiency using the method of Jolly (1982) as described by Welch (2007).

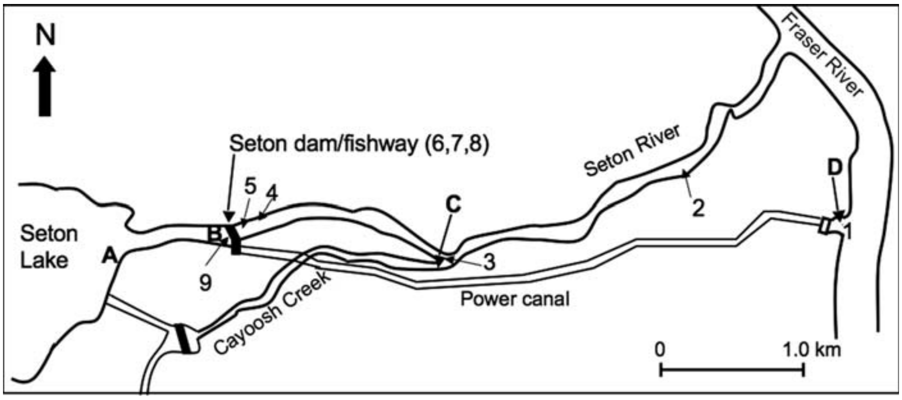

Figure 2. Map of Seton River showing four release locations of telemetered sockeye salmon in 2007: Seton Lake near outlet (A), Seton River directly upstream of dam (B), lower Seton River at Cayoosh Creek (C) and powerhouse tailrace on the Fraser River (D). Numbers show the approximate location of acoustic telemetry receivers

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Table I. Location and detection efficiency of acoustic telemetry receivers used to track Gates Creek sockeye migrations in 2007. Receivers 4 and 5 were considered redundant, so that fish detected at either receiver were known to have reached the dam, and hence, the receivers worked as one station with a single detection efficiency. Figures 1 and 2 show the location of telemetry receivers

ID #	Approximate location	Detection efficiency	Number of fish detected on receiver
1	Powerhouse tailrace (Fraser River)	n/a	24
2	Seton River, ~1.3 km upstream from mouth	74%	38
3	Seton River at Cayoosh Creek	48%	25
4 5	Seton River, ~80 m downstream of dam Below dam, end of radial gate channel	95%	49
6	Fishway, bottom (Pool 3)	91%	41
7	Fishway, 1/2 way, (Pool 17)	75%	31
8	Fishway, top (Pool 32)	100%	61
9	Seton River, ~160 m upstream of dam	98%	60
10	Outflow of Seton Lake	100%	64
11	Seton Lake, middle	100%	65
12	Seton Lake, West end	100%	65
13	Seton Lake, inflow	100%	64
14	Anderson outflow	100%	60
15	Anderson Lake, middle	100%	58
16	Anderson Lake, West end	100%	53
17	Anderson Lake, inflow	n/a	53

Fishway entrance efficiency was calculated by the number of fish detected in the fishway (either of receivers 6 or 7) divided by the number of fish detected in the tailrace of the dam (either of receivers 4 or 5). Fishway passage efficiency was calculated as the number of fish that reached the top pool of the fishway divided by the number of fish known to have initially entered the fishway (i.e. detected on receiver 6). Gates Creek sockeye salmon spawn in natural areas in Gates Creek, as well as in an artificial spawning channel ~1 km from the mouth of Gates Creek, and reception of acoustic telemetry receivers would be poor in both of these areas. Therefore, fish that were detected on the receiver in Anderson Lake at the mouth of Gates Creek (#17; Table I) were considered to be successful migrants. Travel speed between the outflow of Seton Lake and the inlet of Anderson Lake was calculated by the distance divided by the difference in time of first detection at these two locations.

The proportion of individuals surviving to spawning grounds was compared between males and females and fish released up- and down-stream of the dam using χ^2 contingency test, or in cases where expected cell sizes were less than five, Fisher's exact test. Measures of blood biochemistry (lactate, glucose, ions, osmolality, hormones), GSE, fork length and travel speeds were compared between net-pen held and control fish and between sexes using two-way analysis of variance (ANOVA). Two-way ANOVA was also used to assess differences in blood biochemistry, GSE and fork length between fish that reached spawning grounds (successful migrants) and those that did not (mortalities) while accounting for sex differences. The variables lactate, glucose, Na^+, K^+, Cl^-, osmolality, testosterone and travel speed needed to be log-10 transformed to meet assumptions of normality and homoscedasticity (Zar, 1999). In cases where there was a significant interaction between factors, a Tukey–Kramer multiple comparison test was used to compare recovery treatments ('net-pen held' or 'control') or fate groups (successful migrant or mortality) for both males and females. A significance level of 0.05 was used for statistical tests but Bonferroni corrections were made for ANOVA models, because there were multiple comparisons, resulting in a significance level of 0.005. Analyses were carried out in SAS v.9.1.3 (SAS Inc., Cary, NC, USA).

RESULTS

High detection efficiencies at most receiver stations indicated a good ability to detect fish movements and determine individual fate of fish (Table I). Detection efficiencies at receivers in Seton and Anderson lakes were all 100%. Efficiencies at the first two receivers in the lower Seton River (#2 and 3) were lower (48% and 75%) and therefore we could not confidently detect fish movements between the mouth of the Seton River and the dam. However, the two redundant receivers in the dam tailrace had a detection efficiency of 95% suggesting a good ability to detect whether or not fish reached the tailrace of the dam. Receivers in the fishway had efficiencies of 100%, 74% and 91% for stations at the top, middle and bottom, respectively. Thus, the ability to detect fish that entered the fishway was high (91%) and if the bottom and middle fishway receivers

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were used together (redundantly) to detect fishway entrance, efficiency improved to 95%.

Eighty-eight sockeye were caught, biopsied and tagged between 15 and 24 August, 2007. Fish were tagged and released at site A on 20 August, at site B on 15–16 August, at site C on 17, 21 and 23 August, and site D on 18–19, 22 and 24 August. DNA analyses indicated that 87 of the fish were from the Gates Creek population and one was a stray from the Chilko population, which was eliminated from all analyses. In total, there were 32 fish released into the powerhouse tailrace on the Fraser River (site D), 27 fish released into the lower Seton River at Cayoosh Creek (site C), 8 fish released into Seton Lake near the mouth (site A) and 20 fish released upstream of the dam without a recovery period (site B). When analysing the telemetry data, we observed that three fish ascended the fishway and arrived at the top pool at times when we had blocked the upstream exit in order to capture and tag fish. These fish descended and moved downstream and were not subsequently detected the fishway. These three fish were included in estimates of fishway passage (i.e. they were successful in passing fishway) but excluded from analyses of fate. One fish that was released into the lower Seton River was caught by fisheries in Portage Creek and was also excluded from mortality comparisons but used in fishway passage estimates. Samples sizes and sex ratios were not equal among release groups because of logistic difficulties when capturing fish. We discuss how these potential biases may have affected our results.

Comparisons of blood physiology, body length and energy between net-pen held and control fish and between sexes revealed a significant interaction between sex and recovery holding treatment for the variables glucose and K^+ ($p < 0.05$, two-way ANOVA; Table II). Tukey–Kramer tests indicated that glucose was significantly higher in net-pen held versus control fish for both males ($p = 0.0009$) and females ($p < 0.0001$), and that K^+ was higher in net-pen held versus control females ($p < 0.0001$) but not different between net-pen held and control males ($p = 0.7$). Net-pen held fish had significantly lower testosterone and Cl^-, and shorter fork length compared to control fish although Cl^- was not significant after Bonferroni correction (Table II). Females had significantly higher cortisol, testosterone and GSE, and lower Na^+ compared to males (Table II). The sex-specific hormone 17-*ß* estradiol was not different between net-pen held and control females ($p = 0.42$).

To assess differences in physiology, size and energy between successful migrants and mortalities we conducted a series of two-way ANOVAs with fate and sex as factors. In these models, only fish released downstream of the dam were included because so few fish released upstream were mortalities (see below). Glucose was higher in mortalities than successful migrants ($p = 0.027$), though the difference

Table II. Results of two-way ANOVA comparing blood biochemistry, energy and length between male and female sockeye salmon sampled immediately after capture from the fishway (control) or sampled following 5-h recovery period in a net-pen (net pen held). Means (± SE), sample sizes and *p*-values are shown. Analyses were conducted on log10-transformed data for variables that did not initially meet model assumptions but untransformed means are presented

Variable	Male—Control	*n*	Male—net pen held	*n*	Female—Control	*n*	Female—net pen held	*n*	*p*-value Holding	*p*-value Sex	*p*-value Interaction
Cortisol (ng ml^{-1})	198.0 ± 13.8	11	216.2 ± 15.9	22	323.0 ± 40.3	6	389.9 ± 12.8	43	0.0599	<0.0001*	0.28
Testosterone (ng ml^{-1})	9.98 ± 2.3	10	3.79 ± 0.4	22	22.9 ± 4.0	5	10.4 ± 1.9	42	<0.0001*	0.0006*	0.5
Estradiol (ng ml^{-1})	n/a	10	n/a	22	1.71 ± 0.07	5	1.48 ± 0.1	43	0.42	n/a	n/a
Lactate (mmol L^{-1})	1.66 ± 0.2	11	1.30 ± 0.1	22	2.20 ± 0.4	6	1.93 ± 0.1	43	0.095	**0.0354**	0.74
Glucose (mmol L^{-1})	4.42 ± 0.2	11	5.86 ± 0.2	22	4.89 ± 0.7	6	8.4 ± 0.2	43	<0.0001*	0.0003*	0.0063 *
Na^+ (mmol L^{-1})	163.6 ± 1.2	11	162.2 ± 1.4	22	155.2 ± 6.3	6	157.2 ± 1.3	43	0.82	0.0035*	0.4
K^+ (mmol L^{-1})	2.54 ± 0.1	11	2.37 ± 0.1	22	3.81 ± 0.7	6	2.39 ± 0.1	43	<0.0001*	0.0005*	0.0006*
Cl^- (mmol L^{-1})	134.1 ± 0.9	11	129 ± 0.7	22	130.3 ± 5.7	6	128.3 ± 0.6	43	**0.038**	0.1	0.23
Osmolality (mOsm kg^{-1})	310.1 ± 2.5	11	303.8 ± 0.9	22	303.5 ± 13.0	6	307.1 ± 1.0	43	0.86	0.43	0.068
GSE (MJ kg^{-1})	5.62 ± 0.1	11	5.95 ± 0.1	21	6.49 ± 0.1	8	6.43 ± 0.1	43	0.33	<0.0001*	0.16
Length (cm)	62.1 ± 1.1	11	58.8 ± 0.9	22	59.8 ± 1.0	9	57.6 ± 0.4	45	0.0013*	**0.03**	0.5

Note: Values in bold text were significant at 0.05 and values marked by an asterisk were significant after Bonferroni correction ($\alpha = 0.0005$).

was not significant after Bonferroni correction. In all other models, fate was not a significant factor, suggesting that successful migrants were not different from mortalities in terms of GSE, length and most measures of blood biochemistry. The female hormone 17-β estradiol was not different between fate groups ($p = 0.9$).

Survival to spawning grounds was much lower for the fish released downstream of the dam (49% of 55 fish) than for fish released upstream of the dam (93% of 28 fish; $p < 0.0001$). Of fish released upstream of the dam, survival to spawning grounds was not significantly different between fish released immediately after capture (95% of 20 fish) and those released after transportation and net-pen holding (88% of 8 fish; $p = 0.5$). Similarly, survival was not different between fish released at the two sites downstream of the dam (52% of 25 fish and 47% 30 fish; $p = 0.7$). Among fish released downstream of the dam, females had significantly lower survival to spawning grounds (39% of 38 fish) than males (71% of 17 fish; $p = 0.03$). There was a higher proportion of females in the downstream release group (69%) compared to the upstream release group (50%); however, survival to spawning grounds was significantly lower in fish released downstream compared to fish released upstream for both males (71 and 100%, respectively; $p = 0.03$) and females (86 and 39%, respectively; $p = 0.003$; Table III).

There was no one single area that unsuccessful migrants failed to pass through. Migration failure occurred in all sections of the migration route including the lower Seton River prior to reaching the dam, at the dam and fishway, and in Seton and Anderson lakes (Table IV). Of 59 fish released downstream of the dam, 14% were not detected at, and likely did not reach the tailrace of the dam. Because detection efficiency was poor in the lower Seton River and at the powerhouse tailrace on the Fraser, the fate of these fish is unknown. Three of the eight fish were never detected anywhere on the receiver array, and, since all tags were known to be functioning properly, are presumed to have moved back into the Fraser River. The mean time from release of fish to when they were first detected a short distance upstream of the fishway (receiver 9) was 2.7 ± 0.4 days (range 0.5–5.8 days) for fish released at site C and 2.8 ± 0.2 (range 1.6–4.7 days) for fish released at site D.

Twenty per cent of fish that reached the dam tailrace failed to pass the fishway. Attraction efficiency of the fishway was 85%, since 44 of 51 fish detected in the dam tailrace located and entered the fishway. Only three fish that entered the fishway failed to ascend the entire length, therefore, the

Table III. Survival to spawning grounds of male and female sockeye salmon released upstream or downstream of a dam and fishway, and released immediately (control) or after transportation and holding in a netpen. Data are the number of fish that survived to spawning grounds out of the total number of fish released. See Figure 2 for location of release sites (letters)

	Upstream vs. downstream release site comparison		Control vs. netpen comparison (upstream release sites only)	
	Upstream (sites A and B)	Downstream (sites C and D)	Control (site B)	Netpen (site A)
Male	14 of 14 (100%)	12 of 17 (71%)	11 of 11 (100%)	3 of 3 (100%)
Female	12 of 14 (86%)	15 of 38 (39%)	8 of 9 (89%)	4 of 5 (80%)
Sexes combined	26 of 28 (93%)	27 of 55 (49%)	19 of 20 (95%)	7 of 8 (88%)

Table IV. Fate of Gates Creek sockeye salmon captured from Seton Dam Fishway and released either up- or down-stream of the dam. Release site locations are shown in Figure 2. Data are not included for three sockeye released downstream of the dam that successfully ascended the fishway but descended while a gate was blocking the exit at the top of the fishway during sampling

Fate	Upstream of dam		Downstream of dam	
	#	%	#	%
Successful migrant	26	93	27	48
Failed in Anderson Lake	1	3.5	6	11
Failed in Seton Lake	1	3.5	4	7
Failed at fishway	n/a	n/a	10	18
Did not reach dam	n/a	n/a	8	14
Fishery removal	0	0	1	2
Total	28		56	

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passage efficiency was 93%. Of fish that reached the dam tailrace, 15 of 16 males (94%) and 26 of 35 females (74%) passed the fishway but this difference in passage efficiency was not statistically significant ($p = 0.14$). Water discharge from the dam was $35\,m^3\,s^{-1}$ from 21–31 August and $60\,m^3\,s^{-1}$ from 15–20 August. Only five fish were detected at the receivers near the tailrace of the dam during the high discharge period ($60\,m^3\,s^{-1}$) and of these, only two (20%) successfully passed the fishway during the high discharge (one passed several days later during the lower discharge and two fell back and were not detected again).

In Seton and Anderson lakes, there was greater mortality of fish released downstream of the dam (27% of 37 fish that passed dam) compared to those released upstream (7% of 28 fish; $p = 0.04$). Only one fish (released in lower Seton River) was known to be caught by the small subsistence fishery in Portage Creek, the stream connecting the two lakes, and this fish was not included in our comparison of mortality between release sites. The rest of in-lake mortalities died of unknown causes. Travel speed through the lakes was not different between fish that were released downstream of the dam and fish released upstream of the dam ($p = 0.11$).

DISCUSSION

We assessed indices of physiological stress measured from blood samples to evaluate whether our methods of transporting fish below the dam as a means to ultimately study post-passage consequences had any effects on sockeye salmon in our study. There were some differences in stress physiology between fish sampled immediately after fishway ascent (control) compared to fish sampled after transportation and a 5-h net-pen holding period (Table II). For instance, glucose was higher and testosterone was lower in net-pen held fish compared to control fish, differences that were likely related to confinement stress during transportation and holding. The non-specific stress response in salmonids involves an initial increase in catecholamines and cortisol, often referred to as the primary stress response, followed by increases in glucose and other metabolites known as the secondary stress response (Mazeaud *et al.*, 1977; Barton, 2002; Portz *et al.*, 2006). Other studies have reported primary and secondary stress responses to confinement in sockeye (Kubokawa *et al.*, 1999) and other salmonids (Wedemeyer and Wydoski, 2008). High levels of stress are also associated with depressed reproductive hormones including testosterone (Kubokawa *et al.*, 1999; Hinch *et al.*, 2006). In our study, cortisol may not have been significantly different at the time of sampling (5 h after confinement) because it is a fast and transient response that can return to normal levels in salmonids after 60 min of confinement (Portz *et al.*, 2006). Females had initially higher levels of stress than males, as indicated by concentrations of cortisol, glucose and lactate, and larger changes in glucose and testosterone after net-pen confinement. Both of these findings are consistent with previous research concerning sex-specific stress levels and responses in sockeye salmon (Kubokawa *et al.*, 1999; Hinch *et al.*, 2006).

There were also modest differences in plasma ion concentrations, including higher K^+ in net-pen held than control females. Muscle contraction during exercise can cause an efflux of potassium from muscle into the plasma in rainbow trout (*Oncorhynchus mykiss*; Nielsen *et al.*, 1994; Van Ginneken *et al.*, 2004). Thus, K^+ may have been elevated due to swimming through the tailrace and fishway, and returned to normal concentration after net-pen holding. Net-pen held fish also had lower plasma Cl^- concentrations than control fish, although the difference was not significant after Bonferroni correction. Loss of plasma ions in response to stress results mostly from increased efflux across the gills (Macdonald and Milligan, 1997) and in this study could have been related to confinement stress previously mentioned. Although there were some differences in plasma ion concentrations between net-pen held and control fish there were not changes in total osmolality, or in Na^+, and values of K^+ and Cl^- were not critically high or low. Therefore, the changes in ion concentrations were not deemed to be physiological significant or such that changes in behaviour or survival would be expected.

Although there were some physiological differences between control and net-pen held fish, when compared to literature values for 'healthy' up-river migrating sockeye salmon, neither control nor net-pen held fish in our study showed signs of severe stress or anaerobic exhaustion. Plasma lactate (1.3–2.2 mmol) and glucose levels (4.4–8.4 mmol) levels were similar to or lower than levels previously reported for adult sockeye in the late stages of migration (e.g. Young *et al.*, 2006), except for net-pen held females who had elevated glucose levels likely due to confinement. Plasma ion concentrations and total osmolality were also very similar to values reported in previous work on adult sockeye in freshwater (Young *et al.*, 2006; Crossin *et al.*, 2008; Pon *et al.*, 2009b). Cortisol levels were within the range reported by other studies of sockeye (Cooke *et al.*, 2006; Pon *et al.*, 2009b) although cortisol titres can vary considerably during migration (Hinch *et al.*, 2006) and among populations (Cooke *et al.*, 2006).

Overall, we found little evidence that fishway passage or previous experience in the tailrace of the dam resulted in physiological stress or exhaustion. Indices of stress in sockeye salmon sampled immediately after dam passage were low compared to several previous reports of blood biochemistry in the same species. After transportation and net-pen holding fish were in good condition although higher glucose and lower testosterone compared to control fish suggests that there was a mild stress response to confinement. We cannot be sure of the consequences of confinement stress but because there were not severe changes in metabolites or osmoregulatory function we would not expect subsequent behaviour or survival to be affected. As further evidence that our handling and transportation approaches were relatively benign, we found that net-pen held and control fish released upstream of the dam did not differ in their survival rates to spawning grounds, although sample sizes were small for this comparison. This finding corroborates other telemetry studies that involved transporting Fraser River sockeye salmon among sites or holding facilities (Hinch and Bratty, 2000; Crossin *et al*., 2008).

Our results indicate that passage through the Seton River, dam tailrace and fishway had a significant impact on successful spawning migration of sockeye salmon, as approximately half of migrating adults released downstream of the dam failed to reach spawning areas. Migration failure occurred not only at the dam and fishway, but also in the lower Seton or Fraser River prior to reaching the dam, and in Seton and Anderson lakes. Similar patterns of passage failure at several different locales along the migration route resulting in high cumulative mortality have been observed by others studying Pacific salmon (Naughton *et al*., 2005; Keefer *et al*., 2008) and Atlantic salmon (*Salmo salar*; Gowans *et al*., 2003; Lundqvist *et al*., 2008). These studies suggest a need to assess cumulative impacts in systems with several passage facilities or locales of difficult passage. In some years in the Fraser River, high levels (e.g. 20–90%) of migrating adult sockeye salmon can perish *en route* to spawning grounds (Macdonald, 2000; Macdonald *et al*., 2000; Cooke *et al*., 2004; Quinn, 2005), often as a result of high river temperatures or discharge. The high levels of migration failure observed in our study (~50% of fish released downstream of dam) are alarming because river temperatures and discharge were not unusually high that year (Patterson *et al*., 2007) and because migration failure occurred over a very short spatial scale.

It was surprising that some fish failed in the lower Seton River before reaching Seton Dam as these individuals were initially able to reach and ascend the fishway where they were first captured. The distances from each of the release sites to the dam were relatively short (~5 km from the powerhouse tailrace and 1.3 km from lower Seton release site) and probably not hydraulically challenging for strong swimming fish like sockeye salmon. One factor that could have contributed to *en route* losses in this section is attraction of fish to water discharge at the powerhouse tailrace. Discharge from the powerhouse consists of pure ‘homestream’ Seton Lake water whereas flows in the Seton River are an engineered mixture of Seton Lake water spilled at the dam and water from Cayoosh Creek, a tributary joining the Seton River 1.3 km downstream of the dam. Fretwell (1989) previously reported that when Seton River flows consisted of greater than 20% Cayoosh Creek water sockeye were more attracted to discharges from the powerhouse, resulting in significant delay before entering the Seton River. Based on these studies Seton River flows are maintained at less than 20% Cayoosh Creek water during the spawning migration period. In our study, because detection efficiency of the receiver in the tailrace was poor, it is difficult to determine whether tailrace attraction may have caused delay and contributed to migration failure.

A large portion of the total migration failure (~20%) occurred at the dam and fishway, a finding consistent with a previous telemetry study at the Seton Fishway (Pon *et al*., 2006) confirming that this locale is a limiting factor for sockeye migrations in the watershed. In both the present and Pon *et al.* (2006) studies passage efficiency was much higher (93% in this study, 100% in Pon *et al*., 2006) than attraction efficiency (86% in this study, 77% in Pon *et al*., 2006) suggesting that most of passage failure was associated with failure to locate the fishway entrance and not passage itself. In comparison, total efficiency at individual dams on the Columbia River ranged from 90 to 100% for radio-tagged Chinook salmon (Bjornn *et al*., 2000). Many studies of Atlantic salmon have reported low passage efficiencies at fishways (23%, Karppinen *et al*., 2002; 63%, Gowans *et al*., 2003; 0%, Thorstad *et al*., 2003; 21%, Lundqvist *et al*., 2008). Although passage efficiency of anadromous salmonids is lower at many fishways compared to at Seton Dam, the fact that ~20% of all sockeye salmon migrants were unable to pass the Seton fishway suggests a need to improve passage at this location. Furthermore, all fish in our study were captured at the top of the fishway and had therefore already demonstrated the ability to locate and ascend the fishway, whereas some fish never initially located the fishway and were not represented in our estimates of passage efficiency. Therefore, passage efficiency in at the Seton fishway may in fact be lower than our estimates of ~80% (Pon *et al*., 2006 and this study). Because only five fish reached the tailrace of the dam during the period when discharge was 60 $m^3 s^{-1}$, and the rest of the fish passed when discharge was 35 $m^3 s^{-1}$, it is difficult to draw conclusions regarding the effect of discharge level on passage. However, the fact that only two of five fish passed during the high discharge suggests that passage may be more difficult during high flows.

Mortality in the lakes was higher for fish that were released downstream of the dam (27%) than for fish released upstream of the dam (7%), supporting the hypothesis that dam passage has post-passage consequences on survival. All fish were caught at the top of the fishway, and had therefore already ascended the fishway once. However, passing through the lower Seton River, dam tailrace and fishway a second time had some effect on fish that resulted in subsequent high mortality *en route* to spawning grounds. The mechanism of this high in-lake mortality is not clear. If mortality was related to exhaustion or physiological stress caused by dam and fishway passage, we would expect fish that died before reaching spawning grounds to exhibit higher levels of stress at release compared to successful migrants. We did find that fish that died before reaching spawning grounds had higher glucose than successful migrants. However, none of the other physiological measures differed by fate and glucose levels of mortalities were still lower than wild sockeye from other studies (e.g. Cooke *et al.*, 2006; Crossin *et al.*, 2007) and not critically high such that mortality would be expected. Therefore, mortality in the lakes following dam passage did not appear to be related to high levels of acute physiological stress.

Other researchers have hypothesized that low initial energy levels and depletion of energetic reserves may contribute to migration failure in anadromous salmon (Cooke *et al.*, 2004; Caudill *et al.*, 2007). In our study, all individuals had GSE levels at the time of release that were at least 25% greater than proposed threshold energy level required to sustain life ($4\,\mathrm{MJ\,kg^{-1}}$; Crossin *et al.*, 2004). Furthermore, GSE was not initially lower in in-lake mortalities compared to successful migrants. Although fishway ascent was not energetically demanding at Seton Dam, observations of burst swimming in the tailrace suggest that energy use could be high at this locale (Pon *et al.*, 2009b). Others have also reported that swim speeds were highest in tailraces compared to in fishways or forebays (Brown *et al.*, 2006; Scruton *et al.*, 2007; Enders *et al.*, 2008). We did not find direct evidence of energy limitation in our study. However, it is possible fish that were delayed below the fishway or at the powerhouse tailrace exhausted their energy reserves or ran out of time before reaching spawning grounds and we cannot rule out the role of energy depletion in *en route* mortality.

The issue of delayed migration of fish at hydroelectric facilities is often difficult to address because it is not known how long a delay is likely to have negative consequences for migrants. In our study, fish caught in the fishway that were transported and released downstream took, on average, less than 3 days to re-ascend the lower Seton River and pass the dam and fishway a second time. All fish in our study were tagged and released within a 10-day period and we would not expect differences in mortality or behaviour across this relatively short time frame. We did observe greater levels of mortality in the fish released downstream but it is not possible to say whether this was related to the migration delay and resulting later timing, or some other legacy effect of dam passage. The fact that successful migrants and mortalities did not differ in levels of energy or reproductive hormones suggests that mortality was not necessarily related to later timing or premature senescence caused by migration delay.

As predicted, we found that female sockeye suffered greater *en route* mortality than males. Fishway passage failure was also higher in females although the difference was not significant. Greater passage failure of female compared to male sockeye salmon has previously been reported in years of difficult migration conditions in the Fraser River Canyon (Gilhousen, 1990). Patterson *et al.* (2004) and Nadeau *et al.* (2010) both found that mortality was greater for females than males in holding studies of sockeye salmon near the end of freshwater migration. Similarly, Crossin *et al.* (2008) found that female sockeye were more physiologically stressed in response to temperature holding treatments and suffered higher mortality than males during subsequent migration to spawning grounds. A study of anadromous brown trout (*Salmo trutta*) in the river Eman, Sweden found that more males than females successfully passed upstream of a series of hydroelectric power plants, although the difference was not statistically significant (Calles and Greenberg, 2009). All these results contrast with studies of Pacific salmon migration through the hydroelectric system in the Columbia River, which found no differences in mortality (Keefer *et al.*, 2008) or passage success (Naughton *et al.*, 2005; Caudill *et al.*, 2007) between the sexes, although these studies were carried out at sites much further away from spawning areas. The reasons for higher female mortality are not clear although Crossin *et al.* (2008) hypothesized that greater energetic investment in reproductive development make females less able to buffer against the effects of environmental stressors. Whatever the mechanisms involved, the finding that females suffer higher *en route* mortality has important implications for conservation and management. Estimates of *en route* mortality that pool sexes may underestimate female mortality. Population level effects of higher female *en route* mortality could be significant since total spawning success of a population is governed mostly by female success whereas loss of males has little effect on subsequent generations (Gilhousen, 1990). Because male and female sockeye salmon may differ in physiology, energetics and survival it is important to include sex as a factor in future research and management programmes, as was recently suggested by Hanson *et al.* (2008).

This study demonstrates the importance of monitoring fish after they pass dams and fishways to incorporate potential post-passage consequences in evaluations of fishway performance. In addition, consequences of dam passage such as physiological stress, energy use or physical injury are likely to be associated with fitness costs (Castro-Santos *et al.*, 2009) although no previous studies have assessed effects of passage on reproductive success. We did not assess spawning success of fish in our study but because passage through the lower river, tailrace and fishway was associated with relatively high levels of post-passage mortality, it is possible there could also be consequences for reproductive success. For instance, Gates Creek sockeye suffer high levels of pre-spawn mortality (i.e. dieing on spawning grounds without reproducing) relative to many other Fraser River populations (Gilhousen, 1990) but it is not known whether hydroelectric facilities may be a contributing factor. Finally, we found that our transportation and holding approaches resulted in some changes to stress indices measured from blood samples, although these did not seem to affect survival or behaviour. Others have found that net-pen holding can cause significant physiological stress (Wedemeyer and Wydoski, 2008) or alter migration behaviour (Bromaghin *et al*., 2007). We recommend that future studies of migrating fish which involve transport or net-pen confinement should assess their methodologies, and utilize as part of their interpretations, the physiological status of their fish.

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