

A Comparison of the Physiological Condition, and Fishway Passage Time and Success of Migrant Adult Sockeye Salmon at Seton River Dam, British Columbia, under Three Operational Water Discharge Rates

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Abstract.—We investigated the effect of changes in water discharge from the Seton River Dam, British Columbia, on the physiological condition, passage time, and passage success of adult migrant sockeye salmon *Oncorhynchus nerka*. Sockeye salmon were intercepted and nonlethally biopsied for blood plasma and energy status. A subset of these fish were fitted with radio transmitters and tracked under three different operational attraction flow levels. Indices of physiological stress and exhaustive exercise (e.g., plasma cortisol, glucose, lactate, osmolality, and hematocrit) did not differ among the attraction flow discharge levels that were examined, nor did they differ appreciably from those of other adult Fraser River sockeye salmon studied during upriver migrations in areas of natural, nonregulated flows. In fact, the fish appeared relatively unstressed after dam passage. Passage time was significantly longer (19.9 h) under intermediate discharge (12.7 m³/s) than under high (15.8 m³/s) or low (11.0 m³/s) discharges (9.3 and 7.0 h, respectively) but did not differ between high- and low-discharge periods. No differences in passage success or fishway ascent time were observed among the three discharges. Though we suspect that unique flow conditions were responsible for the longer passage time during intermediate discharge, a detailed hydraulic analysis is needed to further interpret our results.

The proliferation of dams during the latter half of the 20th century resulted in the alteration of many formerly unconstrained river systems (Dynesius and Nilsson 1994; Rosenberg et al. 2000; Nilsson et al. 2005). At some dam sites, fish bypass systems (e.g., fishways, fish lifts) were installed in order to provide a means of connectivity for fish between upstream and down-

stream habitats (Clay 1961; Odeh 1999). Though the earliest fish bypass structures were often poorly designed for local hydraulic conditions and fish species, designs began to accommodate biologically relevant factors by the early 1900s, and by the middle of the 20th century, design criteria became increasingly based on rigorous fish passage research (Odeh 1999). An important part of effective fishway design is the provision of a means for fish to be able to locate and enter the structure in a timely manner and without undue physiological stress (Andrew and Geen 1960; Clay 1961; Powers et al. 1985; Larinier 1998).

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Water flow velocity is an important factor governing the upstream movements of migrating fish (Banks 1969; Alabaster 1970), and the provision of suitable flow conditions downstream of a dam has been identified as an effective method of improving passage (Andrew and Geen 1960). For fish to be attracted towards a fishway, it is generally held that flows emanating from a point near the fishway entrance should be high relative to those released elsewhere along the dam face (Andrew and Geen 1960; Leman and Paulik 1966; Larinier 1998). However, passage may become hindered if water velocities are too high for fish to navigate through (Leman and Paulik 1966). This may become problematic for many species, but particularly for adult Pacific salmon, whose high fidelity to historic spawning grounds means that passage failure at a dam can result in failure to spawn.

The spawning migrations of Pacific salmon are one of the most physically challenging stages of their lives (Hinch et al. 2006), and many populations must pass dams en route to spawning grounds (up to nine separate dams in some cases; Naughton et al. 2005). During dam passage events, fish exposed to high tailrace water velocities may accrue physiological stress if they are forced to swim with anaerobic efforts. Using electromyogram telemetry, Hinch and Bratty (2000) observed sockeye salmon *Oncorhynchus nerka* commonly swimming above critical swim speeds (U_{crit} ; i.e., anaerobic) downstream of the fishways situated at Hell's Gate on the Fraser River, British Columbia. They found that excessive anaerobic swimming generally led to passage failure. Similarly, Chinook salmon *O. tshawytscha* were observed at times to be swimming at speeds exceeding U_{crit} 26% of the time in the tailrace at Bonneville Dam on the Columbia River (Brown et al. 2006). In fact, swim speeds observed in the tailrace area were higher than those observed within the fishway (Brown et al. 2006). Though both studies were conducted on large rivers, the observations suggest the possibility that fish may become physically exhausted while attempting to locate a fishway entrance. Stress associated with exhaustion can have several adverse effects on migrant salmon, including elevated energy expenditure (Barton and Schreck 1987), the suppression of reproductive hormones (Kubokawa et al. 2001), and even death (Wood et al. 1983).

Observations of sockeye salmon swimming at anaerobic speeds at the Seton River Dam, British Columbia, suggested that there was a potential for fish to incur stress related to dam passage (Pon et al. 2006). To investigate the effect of water discharge on the physiological condition of salmon, we nonlethally assessed several stress metrics in migrating adult

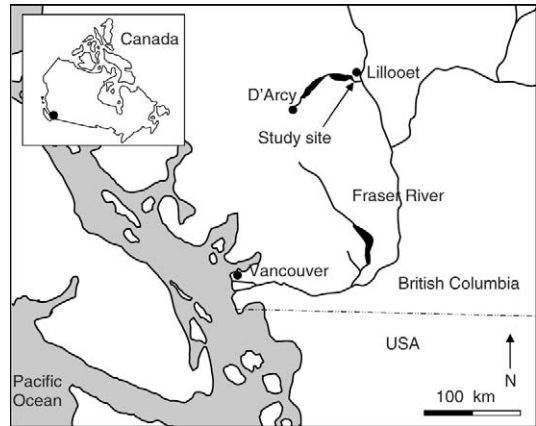


FIGURE 1.—Map of southwestern British Columbia showing the location of the study site along the migration route of Gates Creek sockeye salmon. Fish were captured, tagged, and tracked on the Seton River, which is located near Lillooet. The terminal spawning grounds for this stock are located upstream of the Seton River Dam near D'Arcy.

sockeye salmon from the Gates Creek population during three operational discharge rates at the Seton Dam. A subset of these fish were implanted with radio transmitters and released downstream of the dam to examine passage time and passage success associated with each of the discharge rates. We tested three interrelated hypotheses: (1) that fish would exhibit progressively higher levels of physiological stress with increased discharge, (2) that passage success would be lower under higher discharge, and (3) that passage times among successful fish would be higher with increased discharge.

Study Site

The study was conducted at the Seton River Dam, which is located along a tributary of the Fraser River, 5 km southeast of Lillooet, British Columbia (Figure 1). The Seton River Dam, which is operated by BC Hydro, is a diversion dam that directs a portion of total river discharge down a 4-km artificial channel to a hydroelectric generating station located adjacent to the Fraser River, less than 1 km downstream of the Seton River confluence. The balance of the total discharge is released into the Seton River and is regulated throughout the year, mandated adjustments being made during salmon migration times to meet minimum flow requirements (Andrew and Geen 1958). Between August 10 and 22, 2005, 15.8 m³/s (hereafter, the “high”-discharge period) were spilled from the Seton River Dam. This volume was decreased by approximately 20% to 12.7 m³/s (the “intermediate”-discharge period) for the period of August 23, 2005, to

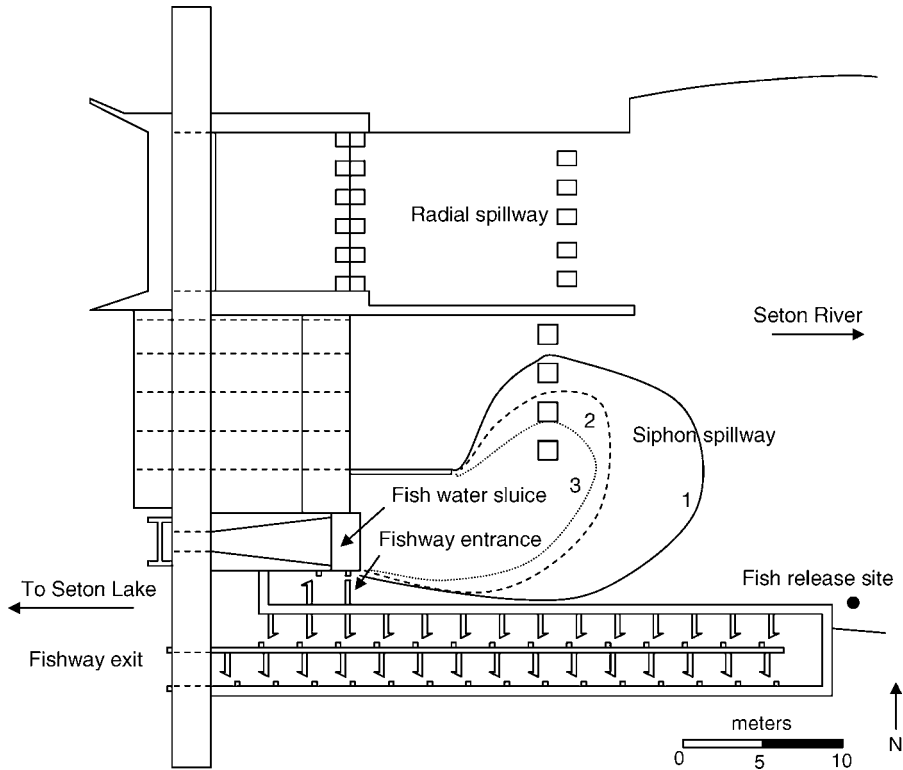


FIGURE 2.—Structural layout of the Seton River Dam and fishway. Throughout the study period, all discharge from the dam was through the fish water sluice, with the exceptions of a consistent flow from the fishway entrance ($1.3 \text{ m}^3/\text{s}$) and minor seepage from the radial spillway gate. Fish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

September 5, 2005, and again by 13.4% to $11.0 \text{ m}^3/\text{s}$ (the “low”-discharge period) from September 6, 2005, until the end of the study period, September 23, 2005. The three discharge levels were set and prescheduled by BC Hydro and were not within our control. Instead, these changes were used in an opportunistic fashion to examine fish attraction under a range of operational discharge levels. Seton River water temperatures were measured using i-button temperature loggers ($\pm 0.5^\circ\text{C}$; Maxim Integrated Products, Inc., Sunnyvale, California). Mean daily water temperatures in the Seton River ranged from a high of 18.0°C to a low of 13.1°C , and gradually declined over the study. Mean daily Fraser River temperatures ranged from a high of 19.3°C to a low of 13.1°C , and followed a gradual decreasing trend (Patterson et al. 2007).

The layout of the Seton River Dam consists of two spillways separated by a concrete wall extending approximately 20 m downstream and perpendicular to the dam face (Figure 2). The radial spillway, located

along the north bank, is approximately 12 m wide, and the siphon spillway, located along the south bank, is about 18 m in width. The fishway entrance is located against the south bank of the Seton River, and released a consistent discharge of $1.3 \text{ m}^3/\text{s}$ throughout the study period. No means of passage is available from the radial spillway. A series of concrete baffles in each of the two spillways are designed to dissipate flow velocities. During the entire study period, discharge from the dam was controlled and released through the fish-water sluice in the siphon spillway, adjacent to the fishway entrance (Figure 2). Minor flows ($<1 \text{ m}^3/\text{s}$) caused by seepage emanated from the radial spillway throughout the study period.

Methods

Sockeye salmon from the Gates Creek population were captured during the period of August 10 to September 21, 2005. Sockeye salmon from this population are classified as an “early summer run”

Fraser River stock, upriver migrations taking place between late July and September of each year. Having already migrated approximately 350 km upstream from the mouth of the Fraser River, Gates Creek sockeye salmon must pass Seton Dam before traveling the final 50 km through Seton and Anderson lakes and arriving on spawning grounds at Gates Creek (Figure 1). Spawning grounds for this stock consist of both natural stream habitat as well as an artificial spawning channel in D'Arcy, British Columbia.

Fish capture, biopsy, and tagging.—Fish were individually captured by dip net at the top pool of the fishway. This location proved to be the only place where we could consistently capture fish. However, by catching fish here we selected a part of the population that had already been able to locate, enter, and ascend the fishway, which may have placed a conservative bias on our estimates of passage time and fishway passage success. Fish for each discharge level were captured at least 24 h following a change to the water discharge rate. Following capture, fish were quickly transferred from the net to a foam-padded, V-shaped trough that was equipped with a constant supply of fresh Seton Creek water directed towards the mouth of the fish. The trough was deep enough that fish could be completely submerged and were only lifted out of water for each of the tagging and sampling procedures. Fish were initially placed ventral side up in the trough and were restrained by two sets of bare, wet hands.

Blood (1.5 mL) was drawn from the caudal vein just posterior to the anal fin using a Vacutainer syringe (1.5-in, 21-gauge needle, 3 mL lithium heparin Vacutainer; Becton Dickson, New Jersey). Blood samples were temporarily held on an ice water slurry. Blood was typically drawn within the first 30 s of restraint; however, if blood was not successfully drawn after 60 s, the fish was excluded and released upstream of the dam. Fork length was measured and a uniquely coded cinch tag (Floy Manufacturing, Seattle, Washington) was attached to the fish anterior of the dorsal fin for external recognition purposes. In order to obtain an indication of the energetic condition of fish, we assessed somatic lipid concentrations using a microwave energy meter (Distell fish fat meter, Model 692; Distell, Inc., West Lothian, Scotland; see Crossin and Hinch 2005). Readings were taken at two locations on the left side of the fish to be later converted to estimates of gross somatic energy density (GSE) using relationships developed by Crossin and Hinch (2005). Fish were not anesthetized for the procedure in order to minimize handling time and related stress, as well as to address the possibility that released fish may be subsequently caught for human consumption. The physiological biopsy procedure we used required less

than 2 minutes and has previously been validated as having no demonstrable effects on the migration success of adult sockeye salmon (Cooke et al. 2005).

We captured and biopsied 36, 16, and 20 fish during the high-, intermediate-, and low-discharge periods, respectively. A subsample of each group were implanted with radio transmitters ($n = 13, 6, \text{ and } 8$, respectively), released downstream of the dam, and tracked as they attempted to locate and pass the fishway. A radio transmitter was gastrically inserted into the fish's stomach using a smooth plastic tube equipped with a plunger device. The antenna trailed posteriorly from the mouth and extended approximately 15–20 cm externally. We used two sizes of positional radio transmitters (Lotek Wireless, Newmarket, Ontario). Larger transmitters were 49 mm in length by 15 mm in diameter, weighed 12.5 g in air, and were inserted into larger sized fish (generally >58 cm). The smaller transmitters were 43 mm in length by 11 mm in diameter, weighed 7.9 g in air, and were inserted into smaller fish (generally <58 cm). In all cases, we followed the rule of less than 2% total fish weight rule with regard to the size of the transmitter (Winter 1996). After inserting the transmitter, the fish was placed in an 80-L container filled with Seton River water and transferred to a point downstream of the fishway where it was released (see Figure 2). Total time from capture to release was typically 3–4 min. All procedures were approved by the University of British Columbia Animal Care Committee in accordance with the policies of the Canadian Council on Animal Care.

Tracking.—Following release, fish movements were manually tracked using radiotelemetry receivers (Model SRX-400; Lotek Wireless, Newmarket, Ontario) and three-element Yagi antennas. Study animals were extensively tracked throughout the study area, which extended from the top of the fishway at the dam to a point approximately 1 km downstream of the dam. Tracking occurred on a daily basis, generally beginning around 0700 hours and concluding at 1800 hours. Tracking efforts rotated among the tagged fish (typically three to four at any given time) and followed individual fish movements for several minutes at a time. During this time period, we recorded the amount of time each fish spent swimming in the more turbulent water (white water) spilled from the fish water sluice (see Figure 2), the time of successful fishway location (i.e., entrance), and the time of fishway passage. Because tracking was conducted manually, there was an equal probability of detecting the fish in a given environment.

For fish that never reentered the fishway following release, we noted the time of last observation within the study area (within 1 km downstream of the dam). Each

evening, receivers were placed at the entrance and exit of the fishway and were set to scan through the frequencies of any tagged fish that had not previously been recorded passing through the fishway. This allowed us to confirm whether these fish were able to enter and pass the fishway, and to record the times of these events. Tracking of all individual fish continued until they either passed through the fishway or moved downstream of the lower bound of our study area, though periodic checks were made to confirm whether fish that moved downstream returned to the dam.

Physiological assays.—To obtain an understanding of the physiological condition of fish, we used several metrics obtained from the blood samples that can be indicative of stress and exhaustive exercise. We examined several metrics of physiological stress which generally show up in the blood plasma within an hour, but persist for several hours after initial response (Postlethwaite and McDonald 1995; McDonald and Milligan 1997; Wendelaar Bonga 1997). Specifically, plasma lactate and glucose were measured as elevated levels of these metabolites are indicative of anaerobic swimming and exhaustive exercise (Wood 1991; Kieffer 2000). Plasma ions (Na^+ , K^+ , Cl^-) and osmolality were measured to determine the osmoregulatory state of fish, a function which can be disturbed following prolonged or exhaustive swimming, as well as other stressors (Postlethwaite and McDonald 1995; McDonald and Milligan 1997). Similarly, hematocrit (Hct; the percent of packed red cell volume) can become elevated following vigorous aerobic exercise (Gallaughan et al. 1992). We also examined plasma cortisol, as increased concentrations may occur following exposure to a stressor or vigorous swimming activity (Wendelaar Bonga 1997), although it also increases naturally during spawning migrations of salmon (Carruth et al. 2000).

Following tagging and release of the fish, a small amount of the stored blood sample was transferred from the Vacutainer to a capillary tube to determine Hct using a Readacrit centrifuge (4.5 min at $5,900 \times$ gravity; Clay Adams, New York). The balance of the blood sample was centrifuged using a Compact II centrifuge (6 min at $1,163 \text{ g}$; Clay Adams, New York). Plasma was transferred into three separate 0.8-mL containers and locally stored on dry ice until they could be transferred to a -80°C freezer. Measurements of plasma concentrations of ions (Na^+ , K^+ , Cl^-), osmolality, cortisol, lactate, and glucose were made following the methods outlined in Farrell et al. (2001). 17β -estradiol (E2) was measured following the methods described Carey and McCormick (1998) and was used to assign sex to individual fish. Measures of E2 were compared with those from another set of

Gates Creek sockeye salmon caught in 2005 for which sex was confirmed, females generally having E2 values greater than 1.0 ng/mL (J. Hills, Fisheries and Oceans Canada, personal communication).

Data analysis.—One-way analysis of variance (ANOVA) was used to compare mean daily water temperatures experienced by migrants during the three discharge periods. To check for differences in the physiological condition of fish that were subsequently tagged or untagged, two-way ANOVAs were used with discharge and tag status as effects. When no differences were found, the model was reduced to a one-way ANOVA with discharge as the effect. Wilcoxon–Kruskal–Wallis tests were used where data did not meet parametric assumptions. Exploratory analysis of data revealed a sex-specific difference in cortisol, a hormone which changes over the course of migration with sexual maturity (Carruth et al. 2000, 2002) and has previously been reported to be higher in mature female sockeye salmon (Kubokawa et al. 1999). Therefore, cortisol measures were compared separately by sex among each of the three discharges. Because we had sampled a disproportionately low number of females during the low-discharge period ($n = 1$), cortisol was only compared across the high and medium discharges for females. As no differences were observed for any of the other physiological measures, sexes were pooled for the remainder of analyses. This is consistent with previous studies on migrating adult sockeye salmon where sex-related differences have only been found in hormone levels and measurements of GSE taken at early stages in the migration (Cooke et al. 2006; Young et al. 2006). Data for plasma lactate, glucose, and cortisol were \log_{10} transformed to meet parametric test assumptions.

Because time of day can affect passage rates at dams (Naughton et al. 2005), we compared release times of tagged fish among the discharge periods using a Wilcoxon–Kruskal–Wallis test, and conducted a Spearman's rank correlation analysis between release time of day and passage time. Passage times, which were normally distributed under each discharge period (Kolmogorov–Smirnov test; all $P > 0.15$) were compared with a one-way ANOVA. A chi-square test compared the relative proportion of time that fish spent in turbulent water released from the dam (see Figure 2). This was used in order to get an indication of the extent to which fish were actively searching for a way upstream. To calculate this, we divided the amount of time we recorded fish swimming in turbulent water in the tailrace by the total amount of time fish were manually tracked within the tailrace area. The proportions of fish that successfully relocated the fishway entrance under each of the three discharge periods were

examined using a χ^2 test. We used a one-way ANOVA to compare the average fishway ascent time among the three discharge periods. All statistical analyses were conducted with SAS, version 9.1 (SAS Institute, Cary, North Carolina). Results are reported as significant at $\alpha = 0.05$, sequential Bonferroni corrections being applied to groupings of statistical comparisons relevant to each prediction.

Results

Mean daily water temperature at the Seton Dam significantly differed among the three discharge periods ($F = 11.798$; $df = 42$; $P < 0.001$). Temperatures during the low-discharge period (mean daily average [SE], 14.5°C [0.2]) were cooler than those in both the high- and intermediate-discharge periods ($t = 3.919$, $df = 30$, $P < 0.001$; $t = 4.294$, $df = 30$, $P < 0.001$, respectively); however, temperatures did not differ between the high- and intermediate-discharge periods (mean daily average [SE], 16.1°C [0.5] and 16.2°C [0.2], respectively; $t = 0.323$, $df = 26$, $P = 0.725$).

No physiological differences were detected among tagged and untagged fish groups (all $P > 0.05$), which suggested that tagged fish were physiologically representative of sockeye salmon migrating past the Seton Dam. Among the three discharge periods, no differences were found in the measured physiological variables, energy condition, or size (Table 1). Specifically, we found no differences among groups for plasma lactate, glucose, Hct, ionic status (Na^+ , Cl^- , K^+ , osmolality), gross somatic energy, or fork length (all $P > 0.05$; Table 1). Among male fish, no differences were detected in cortisol levels among the three groups ($F = 0.842$; $df = 44$; $P = 0.439$). For female fish, we found no difference in cortisol among the high- and the intermediate-discharge groups ($F = 0.289$; $df = 21$; $P = 0.593$).

All fish that entered the fishway successfully passed the fishway. No differences were found among the proportions of fish to successfully pass under the high- (77%), intermediate- (100%), and low-discharge periods (63%) ($\chi^2 = 3.841$; $df = 25$; $P = 0.147$). Two fish released under the high-discharge period were excluded from the passage time analysis; both made a successful passage. One was excluded as it was the only fish to move downstream of our study for several days, before returning to the dam and passing after 107 h following release (roughly 12 times the average passage time for all other fish released under the high-discharge period). The other fish was also released under high discharge and was detected upstream of the fishway but was excluded because we were unable to calculate a passage time estimate.

No difference was found in the time of release among successful tagged fish from each discharge period ($\chi^2 = 1.431$; $df = 17$; $P = 0.48$), and no relationship was found between release time of day and passage time ($r_s = 0.175$; $df = 17$; $P = 0.437$). Among fish that successfully passed the dam, the mean (SE) passage time under the high-discharge flow was 9.3 (2.1) h, 19.9 (4.8) h under the intermediate discharge, and 7.0 (1.7) h under the low discharge. A significant difference among the passage times for the three discharge regimes ($F = 4.616$; $df = 17$; $P = 0.026$). Post hoc Tukey tests revealed significant differences between the high- and intermediate-discharge periods ($t = 2.492$; $df = 12$; $P = 0.022$), and among the low- and the intermediate-discharge periods ($t = 2.691$; $df = 9$; $P = 0.015$), but not between the high- and low-discharge periods ($t = 0.497$; $df = 11$; $P = 0.617$).

Under all discharge levels fish were generally observed alternating between holding in calm waters approximately 30–50 m downstream of the fishway entrance, and actively swimming near the source of attraction flow. No difference in the average proportion of time spent in turbulent water was detected among the high (27%), intermediate (16%), and low (15%) discharges ($F = 1.100$; $df = 24$; $P = 0.356$). No difference was found in terms of fishway passage time (high = 42 [6.6] min, intermediate = 49 [6.5] min, low = 42 [3.8] min; $F = 0.531$, $df = 11$, $P = 0.602$).

Discussion

It is generally held that fish passage systems should be designed to minimize energetic cost, or “undue effort” associated with ascent (Powers et al. 1985; Odeh 1999; Bunt 2001). However, few efforts have been made to quantitatively assess the impact of passage on the physiological condition of fish. Our results suggest that changes to discharge, within the operational range studied, did not affect the physiological condition of migrating sockeye salmon. The prediction of higher levels of physiological stress in fish that experienced the highest attraction flows proved unfounded despite an approximately 30% difference in discharge between the high and low periods.

Anadromous salmonid migrations can be physiologically stressful events (see Hinch et al. 2006). Thus, it is important to consider the stress levels we observed relative to what could normally be expected for the spawning migration life history stage. Plasma ion concentrations were consistent with those previously reported in migrating adult Fraser sockeye salmon which had not encountered dams or fishways (Shrimpton et al. 2005; Crossin et al. 2008). Glucose and lactate levels were lower than those reported for other

TABLE 1.—Means, SEs, and sample sizes for physiological and condition variables of sockeye salmon under three discharge levels. Comparisons with nonparametric Wilcoxon–Kruskal–Wallis tests are indicated by daggers. Statistical significance was assessed at a Bonferroni-corrected $\alpha = 0.05$ for groupings of variables: for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions, hematocrit), for fish condition $\alpha = 0.025$ (gross somatic energy and fork length). Measures marked with asterisks were \log_{10} transformed prior to analysis, but the untransformed means and SEs are presented.

Measure	Discharge	Mean \pm SE	<i>n</i>	<i>F</i> or χ^2	<i>P</i>
Plasma lactate (mmol/L)*	High	2.90 \pm 0.32	36	0.025	0.975
	Medium	2.33 \pm 0.31	15		
	Low	2.62 \pm 0.20	20		
Plasma glucose (mmol/L)*	High	4.76 \pm 0.16	34	0.786	0.460
	Medium	4.49 \pm 0.27	16		
	Low	4.53 \pm 0.21	20		
Plasma cortisol (ng/mL) (males)*	High	237.64 \pm 43.38	21	0.842	0.439
	Medium	187.793 \pm 41.21	8		
	Low	171.93 \pm 43.37	18		
Plasma cortisol (ng/mL) (females)*	High	348.97 \pm 46.37	12	0.289	0.593
	Medium	317.39 \pm 62.78	11		
	Low				
Plasma Na ⁺ (mmol/L)	High	148.51 \pm 1.43	36	2.304	0.108
	Medium	143.84 \pm 1.28	16		
	Low	147.65 \pm 1.39	20		
Plasma Cl ⁻ (mmol/L)†	High	136.48 \pm 1.85	36	0.421	0.658
	Medium	134.23 \pm 2.26	16		
	Low	135.10 \pm 1.44	20		
Plasma K ⁺ (mmol/L)	High	2.57 \pm 0.14	36	2.387	0.099
	Medium	2.73 \pm 0.26	16		
	Low	3.11 \pm 0.18	20		
Osmolality (mosmol/L)†	High	304.68 \pm 2.10	36	1.627	0.443
	Medium	303.25 \pm 2.36	16		
	Low	307.13 \pm 2.08	20		
Hematocrit (%)	High	39.94 \pm 0.60	36	0.801	0.453
	Medium	39.56 \pm 0.52	16		
	Low	38.70 \pm 0.94	20		
Gross somatic energy (MJ/kg)	High	6.42 \pm 0.14	36	2.903	0.062
	Medium	5.88 \pm 0.27	16		
	Low	5.72 \pm 0.35	20		
Fork length (cm)	High	57.72 \pm 0.40	36	1.170	0.317
	Medium	56.50 \pm 0.69	16		
	Low	56.98 \pm 0.79	20		

stocks of wild migrating Fraser sockeye salmon, caught under similar circumstances as those used in our study (e.g., ~ 4.5 mmol/L and ~ 5 mmol/L, respectively; Young et al. 2006). In fact, lactate concentrations were closer to values observed in captive adult sockeye salmon at rest in a swim tunnel respirometer (~ 2 mmol/L) than those observed following exercise to U_{crit} (6 mmol/L; Jain et al. 1998; Wagner et al. 2006). Plasma cortisol levels were elevated relative to what would be considered an unstressed condition, though this was to be expected as cortisol plays an important role in reproductive maturation and is naturally elevated during spawning migrations (Carruth et al. 2000, 2002). Indeed, plasma cortisol levels were consistent with those reported in other sockeye salmon populations nearing spawning grounds (Crossin et al. 2008), as were Hct levels (Magnoni et al. 2006). Collectively, the measures of stress suggested that fish were not becoming physiologically exhausted while approaching or passing the Seton River Dam.

Though not significantly different, there was some

indication of lower energy status (GSE) in fish caught later in the study period than in those caught earlier. This is not surprising as fish caught later in the season would have already invested more energy into reproductive development than those caught earlier (Crossin et al. 2004). Nevertheless, the trend in GSE did not appear to be related to passage time as this was longest under the intermediate-discharge period.

The lack of exercise-induced stress in fish caught at Seton River Dam may be attributed, in part, to the relatively favorable environmental conditions present in both the Fraser and Seton rivers during the course of the Gates Creek sockeye salmon run. In 2005, water temperature and discharge in the lower Fraser River were consistent with long-term averages, and were not unusual for the time of year coinciding with our study period (Patterson et al. 2007). Average water temperatures in the Seton River were 16.3°C and 15.0°C during the months of August and September, respectively. These values are very close to the optimal temperature for aerobic scope in adult Gates Creek

sockeye salmon (16.5°C; Lee et al. 2003). Thus, the environmental conditions experienced by the sampled fish in 2005 may have minimized migration-related stress, particularly in the lead up to capture at Seton River Dam. As a consequence, the comparisons we made of fish physiology should be indicative of the relative effect the three discharges had on exercise-related stress levels.

Though previous observations of sockeye salmon swimming in the tailrace of the Seton Dam suggested that fish would occasionally reach anaerobic speeds (Pon et al. 2006), the physiological assessments suggested that little exercise-related stress was incurred in fish. The ability of fish to use reverse flows or upwellings created by structures downstream of the dam may have helped to minimize swimming efforts. Such behaviors have previously been observed in upriver migrating sockeye salmon (Hinch et al. 2002) and have been shown to allow fish to hold position in flowing water while expending little energy (Liao et al. 2003). Indeed, in the present study, fish were commonly observed swimming near concrete baffles designed to interrupt and dissipate flow emanating from the dam, suggesting that they may have been using reverse-flow fields to reduce swimming efforts (e.g., Hinch and Rand 2000).

The observation of longer passage times under the intermediate flow conditions was surprising and one which we cannot immediately explain. Passage time at dams along the Columbia and Snake rivers have been strongly related to time of day as migrant salmon have been observed to overwinter in the tailrace prior to passage (Naughton et al. 2005; Caudill et al. 2007). However, this did not appear to explain the difference in passage times we observed at Seton Dam as there was no difference in release times among the three discharge periods. Furthermore, we did observe sockeye salmon passing through the fishway during night hours as recorded on the telemetry array setup at the entrance and exit of the fishway. Indeed, the notion of resting at night may not be the case with sockeye salmon which have been observed to move through difficult reaches such as Hell's Gate on the Fraser River at night (S. G. Hinch, personal observation).

Though water temperature declined over the course of the study, it did not appear to be a significant factor affecting passage time as we found no difference in temperature between the high- and intermediate-discharge periods, despite a difference in passage time between them. Water temperatures were slightly cooler (an average decline of ~2°C) during the lowest, and final, discharge period, yet passage time was the same as that observed during the highest, and first, discharge period. The fact that water temperatures throughout the

study were close to the optimal range for maximum aerobic scope in adult Gates Creek sockeye salmon (Lee et al. 2003) may partially explain this lack of effect, and why fish were in relatively good physiological condition following passage. Although there was a seasonal decline in discharge in both the Fraser and Seton rivers, there did not appear to be an interaction between temperature and discharge, suggesting that seasonal changes in river flow and temperature did not confound our results.

Shoreline orientation behavior can be an important factor in dam passage on larger river systems such as the Columbia (Reischel and Bjornn 2003; Keefer et al. 2006), but it did not appear to be present among salmon moving up the Seton River (a likely consequence of the relatively low discharges). Had fish oriented along the south shoreline, they would have arrived directly at the fishway entrance upon reaching the dam face. Instead, fish were found to approach the dam from various routes, which included the center of the channel where turbulent flow patterns were present. It is possible that complex flows and turbulence unique to the intermediate discharge may have disrupted directional cues for salmon (Hinch and Rand 1998) or caused them to avoid such areas (Smith et al. 2005; Cotel et al. 2006). A subsequent examination of passage at the Seton Dam showed that passage times were similar to the high and low discharges examined here despite much higher discharge conditions (35 m³/s), highlighting the fact that hydraulic challenges may be an important factor to consider at the Seton Dam (Roscoe and Hinch 2008). To fully address these issues, a thorough investigation of flow hydraulics and fish migration pathways is needed under different discharge levels at the study site.

Across the three discharge periods, we observed a passage failure rate of 22%. However, by selectively capturing fish that already demonstrated the ability to locate and pass the fishway, this may be a conservative estimate and may have proved higher if we had been able to capture "fishway-naïve" fish. Other studies of adult migrating salmon have reported both lower and higher rates of passage failure than in our study (e.g., Gowans et al. 1999; Hinch and Bratty 2000; Keefer et al. 2007). However, comparisons of studies may be difficult to make due to variation in the migration stage of fish, fish handling procedures, and unique hydraulic conditions. Further investigation may reveal the extent to which capture location (i.e., within versus downstream of a fishway) may affect estimates of passage success.

Within the operational range of flows that were studied, discharge did not appear to affect the physiological condition of migrating sockeye salmon,

although it may have influenced passage time. Although there are many variables that dam managers must consider in selecting adequate flows, it is important to minimize the impact of dam passage on migrant fish. Physiological assessments of passing fish may reveal the extent to which fish incur stress during dam passage, but they do not account for passage time. Where this is important, telemetry studies may be necessary, though we caution that studies should be conducted at a scale appropriate for identifying potential effects. Furthermore, as the hydraulic characteristics of each dam site are largely unique, discharge assessments should be conducted in a site specific manner.

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References

- Alabaster, J. S. 1970. River flow and upstream movements and catch of migratory salmonids. *Journal of Fish Biology* 2:1–13.
- Andrew, F. J., and G. H. Geen. 1958. Sockeye and pink salmon investigations at the Seton Creek hydroelectric installation. International Pacific Salmon Fisheries Commission, Progress Report 4, Vancouver.
- Andrew, F. J., and G. H. Geen. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. International Pacific Salmon Fisheries Commission Bulletin 11.
- Banks, J. W. 1969. A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology* 1:85–136.
- Barton, B. A., and C. B. Schreck. 1987. Metabolic cost of acute physical stress in juvenile steelhead. *Transactions of the American Fisheries Society* 116:257–263.
- Brown, R. S., D. R. Geist, and M. G. Mesa. 2006. Use of electromyogram telemetry to assess swimming activity of adult Chinook salmon migrating past a Columbia River dam. *Transactions of the American Fisheries Society* 135:281–287.
- Bunt, C. M. 2001. Fishway entrance modifications enhance fish attraction. *Fisheries Management and Ecology* 8:95–105.
- Carey, J. B., and S. D. McCormick. 1998. Atlantic salmon smolts are more responsive to an acute handling and confinement stress than parr. *Aquaculture* 168:237–253.
- Carruth, L. L., R. M. Dores, T. A. Maldonado, D. O. Norris, T. Ruth, and R. E. Jones. 2000. Elevation of plasma cortisol during the spawning migration of a landlocked kokanee salmon (*Oncorhynchus nerka kennerlyi*). *Comparative Biochemistry and Physiology* 127C:123–131.
- Carruth, L. L., R. E. Jones, and D. O. Norris. 2002. Cortisol and Pacific salmon: a new look at the role of stress hormones in olfaction and home-stream migration. *Integrative and Comparative Biology* 42:574–581.
- Caudill, C. C., W. R. Daigle, M. L. Keefer, C. T. Boggs, M. A. Jepson, B. J. Burke, R. W. Zabel, T. C. Bjornn, and C. A. Peery. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality. *Canadian Journal of Fisheries and Aquatic Sciences* 64:979–995.
- Clay, C. H. 1961. Design of fishways and other fish facilities. Department of Fisheries and Oceans, Canada, Ottawa.
- Cooke, S. J., G. T. Crossin, D. A. Patterson, K. K. English, S. G. Hinch, J. L. Young, R. Alexander, M. C. Healey, G. Van Der Kraak, and A. P. Farrell. 2005. Coupling noninvasive physiological assessments with telemetry to understand interindividual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *Journal of Fish Biology* 67:1–17.
- Cooke, S. J., S. G. Hinch, G. T. Crossin, D. A. Patterson, K. K. English, M. C. Healey, J. M. Shrimpton, G. Van Der Kraak, and A. P. Farrell. 2006. Mechanistic basis of individual mortality in Pacific salmon during spawning migrations. *Ecology* 87:1575–1586.
- Cotel, A. J., P. W. Webb, and H. Tritico. 2006. Do brown trout choose locations with reduced turbulence? *Transactions of the American Fisheries Society* 135:610–619.
- Crossin, G. T., and S. G. Hinch. 2005. A nonlethal method for assessing the somatic energy content of freely migrating adult Pacific salmon. *Transactions of the American Fisheries Society* 134:184–191.
- Crossin, G. T., S. G. Hinch, S. J. Cooke, D. W. Welch, A. G. Lotto, D. A. Patterson, R. A. Leggett, M. T. Mathes, J. M. Shrimpton, G. Van Der Kraak, and A. P. Farrell. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migrations. *Canadian Journal of Zoology* 86:127–140.
- Crossin, G. T., S. G. Hinch, A. P. Farrell, D. A. Higgs, A. G. Lotto, J. D. Oakes, and M. C. Healey. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology* 65:788–810.
- Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266:753–762.
- Farrell, A. P., P. E. Gallagher, and R. Routledge. 2001. Rapid recovery of exhausted adult coho salmon after commercial capture by troll fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2319–2324.

- Gallaughan, P., M. Axelsson, and A. P. Farrell. 1992. Swimming performance and haematological variables in splenectomized rainbow trout, *Oncorhynchus mykiss*. *Journal of Experimental Biology* 171:301–314.
- Gowans, A. R. D., J. D. Armstrong, and I. G. Priede. 1999. Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology* 54:713–726.
- Hinch, S. G., and J. M. Bratty. 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Transactions of the American Fisheries Society* 129:604–612.
- Hinch, S. G., S. J. Cooke, M. C. Healey, and A. P. Farrell. 2006. Behavioural physiology of fish migrations: salmon as a model approach. Pages 239–295 in K. Sloman, S. Balshine, and R. Wilson, editors. *Fish physiology*, volume 24. Behaviour and physiology of fish. Academic Press, New York.
- Hinch, S. G., and P. S. Rand. 1998. Swim speeds and energy use of river-migrating adult sockeye salmon: role of local environment and fish characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1821–1831.
- Hinch, S. G., and P. S. Rand. 2000. Optimal swim speeds and forward assisted propulsion: energy conserving behaviours of upriver-migrating salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2470–2478.
- Hinch, S. G., E. M. Standen, M. C. Healey, and A. P. Farrell. 2002. Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. *Hydrobiologia* 165:147–160.
- Jain, K. E., I. K. Birtwell, and A. P. Farrell. 1998. Repeat swimming performance of mature sockeye salmon following a brief recovery period: a proposed measure of fish health and water quality. *Canadian Journal of Zoology* 76:1488–1496.
- Keefer, M. L., C. C. Caudill, C. A. Peery, and T. C. Bjornn. 2006. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:1752–1762.
- Keefer, M. L., C. A. Peery, T. C. Bjornn, M. A. Jepson, K. R. Tolotti, R. R. Ringe, and L. C. Stuehrenberg. 2007. Adult salmon and steelhead passage through fishways and transition pools at the Dalles dam, 1997–2001. Idaho Cooperative Fish and Wildlife Research Unit, Technical Report 2007-2, Moscow.
- Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology* 126A:161–179.
- Kubokawa, K., T. Watanabe, M. Yoshioka, and M. Iwata. 1999. Effects of acute stress on plasma cortisol, sex steroid hormone, and glucose levels in male and female sockeye salmon during the breeding season. *Aquaculture* 172:335–349.
- Kubokawa, K., M. Yoshioka, and M. Iwata. 2001. Sex-specific cortisol and sex steroids responses in stressed sockeye salmon during spawning period. *Zoological Science* 18:947–954.
- Larinier, M. 1998. Upstream and downstream fish passage experience in France. Pages 127–145 in M. Jungwirth, S. Schmutz, and S. Weiss, editors. *Fish migration and fish bypasses*. Blackwell Scientific Publications, Oxford, UK.
- Lee, C. G., A. P. Farrell, A. G. Lotto, M. J. MacNutt, S. G. Hinch, and M. C. Healey. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology* 206:3239–3251.
- Leman, B., and G. J. Paulik. 1966. Spill-pattern manipulation to guide migrant salmon upstream. *Transactions of the American Fisheries Society* 95:397–407.
- Liao, J. C., D. N. Beal, G. V. Lauder, and M. S. Triantafyllou. 2003. Fish exploiting vortices decrease muscle activity. *Science* 302:1566–1569.
- Magnoni, L. J., D. A. Patterson, A. P. Farrell, and J. M. Weber. 2006. Effects of long-distance migration on circulating lipids of sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:1822–1829.
- McDonald, G., and L. Milligan. 1997. Ionic, osmotic, and acid–base regulation in stress. Pages 119–144 in G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B. Schreck, editors. *Fish stress and health in aquaculture*. Cambridge University Press, Cambridge, UK.
- Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, L. C. Stuehrenberg, and C. A. Peery. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 62:30–47.
- Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's largest river systems. *Science* 308:405–408.
- Odeh, M. 1999. Innovations in fish passage technology. American Fisheries Society, Bethesda, Maryland.
- Patterson, D. A., J. S. Macdonald, K. M. Skibo, D. P. Barnes, I. Guthrie, and J. Hills. 2007. Reconstructing the summer thermal history for the lower Fraser River, 1941 to 2006, and implications for adult sockeye salmon (*Oncorhynchus nerka*) spawning migration. *Canadian Technical Report of Fisheries and Aquatic Sciences* 2724.
- Pon, L. B., S. J. Cooke, and S. G. Hinch. 2006. Passage efficiency and migration behaviour of salmonid fishes at the Seton Dam fishway. Final report for the Bridge Coastal Restoration Program, Project 05.Se. 01, Burnaby, British Columbia.
- Postlethwaite, E. K., and D. G. McDonald. 1995. Mechanisms of Na⁺ and Cl⁻ regulation in freshwater-adapted rainbow trout (*Oncorhynchus mykiss*) during exercise and stress. *Journal of Experimental Biology* 198:295–304.
- Powers, P. D., J. F. Orsborn, T. W. Bumstead, S. Klinger-Kingsley, and W. C. Mih. 1985. Fishways: an assessment of their development and design. Bonneville Power Administration, DOE/BP-36523-4, Portland, Oregon.
- Reischel, T. S., and T. C. Bjornn. 2003. Influence of fishway placement on fallback of adult salmon at Bonneville Dam on the Columbia River. *North American Journal of Fisheries Management* 23:1215–1224.
- Roscoe, D. W., and S. G. Hinch. 2008. Fishway passage, water diversion, and warming temperatures: factors limiting successful spawning migration of Seton–Anderson watershed sockeye salmon. Final report for the

- Bridge Coastal Restoration Program, Project 07.BRG01, Burnaby, British Columbia.
- Rosenberg, D. M., P. McCully, and C. M. Pringle. 2000. Global-scale environmental effects of hydrological alternations: introduction. *BioScience* 50:746–751.
- Shrimpton, J. M., D. A. Patterson, J. G. Richards, S. J. Cooke, P. M. Schulte, S. G. Hinch, and A. P. Farrell. 2005. Ionoregulatory changes in different populations of maturing sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia, during ocean and river migration. *Journal of Experimental Biology* 208:4069–4078.
- Smith, D. L., E. L. Brannon, and M. Odeh. 2005. Response of juvenile rainbow trout to turbulence produced by prismatic shapes. *Transactions of the American Fisheries Society* 134:741–753.
- Wagner, G. N., L. J. Kuchel, A. Lotto, D. A. Patterson, M. Shrimpton, S. G. Hinch, and A. P. Farrell. 2006. Routine and active metabolic rates of migrating adult wild sockeye salmon (*Oncorhynchus nerka* Walbaum) in seawater and freshwater. *Physiological and Biochemical Zoology* 79:10–108.
- Wendelaar Bonga, S. E. 1997. The stress response in fish. *Physiological Reviews* 77:591–625.
- Winter, J. 1996. Advances in underwater biotelemetry. Pages 555–590 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Wood, C. M. 1991. Acid–base and ion balance, metabolism, and their interactions after exhaustive exercise in fish. *Journal of Experimental Biology* 160:285–308.
- Wood, C. M., J. D. Turner, and M. S. Graham. 1983. Why do fish die after severe exercise? *Journal of Fish Biology* 22:189–201.
- Young, J. L., S. J. Cooke, S. G. Hinch, G. T. Crossin, D. A. Patterson, A. P. Farrell, G. Van Der Kraak, A. G. Lotto, A. Lister, M. C. Healey, and K. K. English. 2006. Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon in the Thompson River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 63:1067–1077.