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Alterations to dam-spill discharge influence sex-specific activity, behaviour and passage success of migrating adult sockeye salmon

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ABSTRACT

Delays in the freshwater spawning migrations of anadromous fishes at upstream barriers are well documented, but underlying mechanisms causing slowed migrations are seldom known. Using acoustic accelerometer transmitters and generalized linear models, we investigated how alterations in flow at a diversion dam in British Columbia, Canada, affected the activity, behaviour and passage success of a Fraser River sockeye salmon population (*Oncorhynchus nerka*). Spilling excess water through the radial gate of the dam decreased the attraction efficiency of a vertical-slot fishway by 90% and increased delay below the dam by 2 h, which had adverse effects on passage. Relative to males, female sockeye salmon had significantly lower passage success (73% vs 94%), attraction efficiency (79% vs 100%) and passage efficiency (89% vs 94%) at a fishway, delayed longer in the dam tailrace (mean ± standard error (SE): 20·8 ± 4·1 h vs 14·6 ± 3·2 h), and resorted to anaerobic swimming efforts for a greater percentage of time (0–61·3% vs 0·7–2·7%). Given that the persistence of Pacific salmon populations relies on the spawning success of females, understanding how males and females vary in their response to modified flow regimes will improve the management of complex fish-passage problems.

KEY WORDS dam; fishway; sockeye salmon; delayed migration; accelerometry

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INTRODUCTION

Adult Pacific salmon (*Oncorhynchus* spp.) migrate from oceanic feeding grounds to natal freshwater spawning sites on fixed, endogenous energy reserves. The upriver spawning migration is energetically expensive (Hinch *et al*., 1996), requiring fish to possess a set of behaviours, morphologies and swimming strategies that conserve energy so that they can reach spawning grounds with sufficient energy to spawn (Hinch and Rand, 2000; Liao *et al*., 2003). Consequently, there is a strong selection for energy-conserving traits, wherein migrants from distal spawning areas are more streamlined, smaller, exhibit a more efficient swimming gait, increased aerobic capacity, and produce fewer and smaller eggs than short-distance migrants (Hinch and Rand, 2000; Crossin *et al*., 2004; Eliason *et al*., 2011). During their migration, Pacific salmon encounter a myriad of natural (e.g. rapids and high-gradient reaches) and anthropogenic hydraulic challenges (e.g. dams and weirs) that impede or slow their movement (Keefer *et al*., 2004; Caudill *et al*., 2007) and require elevated swimming speeds to overcome (i.e. hyperactivity; Hinch and Bratty, 2000). Compared to males, female sockeye salmon (*O. nerka*) have lower passage success through hydraulically challenging reaches (Hinch and Rand, 1998; Crossin *et al*., 2008; Roscoe *et al*., 2011) and are more sensitive to natural and anthropogenic stressors, particularly when environmental conditions are difficult for migration (Gilhousen, 1990). Despite a growing understanding of the roles that discharge can have on migration success (Alabaster, 1970; Hinch and Rand, 1998; Rand *et al*., 2006), sex-specific energetic and behavioural responses to altered flow conditions remain poorly studied.

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It is typical for dams to be operated in a manner where minimum discharges are maintained to provide orientation cues for fishes attempting to reach passage facilities (e.g. fishways and fish locks; Clay, 1961; Bunt *et al.*, 2011). Though fishways are designed to restore river connectivity in regulated, constrained systems (Clay, 1961), hydraulically complex and challenging flow regimes downstream of dams often generate a number of confusing migration pathways, causing fish to delay in selecting their optimal path and impeding their ability to locate and ascend fishways (Barry and Kynard, 1986; Naughton *et al.*, 2005). Recent electromyogram (EMG) telemetry research has linked alterations in flow dynamics at dam facilities to the activity (i.e. swimming speed), migration behaviour and energy expenditure of free-swimming adult salmon (Brown *et al.*, 2006; Pon *et al.*, 2009b; Hasler *et al.*, 2012). Research by Brown *et al.* (2006) has demonstrated that Chinook salmon (*O. tshawytscha*) swim above their critical swimming speed (U_{crit}) and exhibit burst swimming in the Bonneville Dam tailrace. Further EMG telemetry work on Chinook salmon in the Puntledge River in British Columbia (BC), Canada, has shown that more of the variability in the activity of fish is attributed to inter-individual variation in swimming strategies than alterations in flow (Hasler *et al.*, 2012). EMG telemetry, however, involves an invasive surgical tagging procedure where electrodes must be inserted into aerobic swimming muscle. Imprecision of electrode placement and variability in the performance of tag components requires the calibration of each tag upon implantation to yield reliable information on fish activity (Brown *et al.*, 2007). In recent years, tri-axial accelerometers have become common tools for studying animal movement given that they do not require the intrusive placement of electrodes (Wilson *et al.*, 2006; Gleiss *et al.*, 2010). Rather than trying to infer tail-beat activity from a proxy (e.g. EMG activity), accelerometers can enable the direct measurement of tail beats. Accelerometer sensors have been incorporated into acoustic telemetry transmitters that can be gastrically implanted in wild fish to monitor fine-scale behaviours and energy expenditure (Wilson *et al.*, 2013). Since the identification of probable mechanisms behind passage success or failure at upstream barriers remains a research challenge (Naughton *et al.*, 2006; Caudill *et al.*, 2007), acoustic accelerometers have the potential of linking habitat-specific activity and migration behaviour to the unique hydraulic conditions fish experience.

In southwestern BC, Canada, the Seton–Anderson watershed is a highly regulated system that offers a unique opportunity to evaluate the effects of a diversion dam on the behaviour and survival of migrating adult Pacific salmonids. Pon *et al.* (2009a, 2009b) used EMG telemetry in conjunction with physiological biopsy to link the total discharge of the Seton Dam to the swimming behaviour and passage success of Gates Creek sockeye salmon. Although energy use within a vertical-slot fishway did not differ among successful and unsuccessful migrants, unsuccessful fish appeared to be physiologically stressed (i.e. depressed plasma Na^+), perhaps because of their time spent in the highly turbulent flows of the tailrace prior to capture (Pon *et al.*, 2009b). Although it has been recognized that Gates Creek sockeye salmon have greater difficulty locating and entering the Seton Dam fishway (i.e. attraction efficiency) compared with passage through the fishway (i.e. passage efficiency; Pon *et al.*, 2009a; Roscoe *et al.*, 2011), a proximate cause for this is unknown. As recommended by Pon *et al.* (2009a), more detailed analyses on the relationship between unique water flows downstream of the Seton Dam and passage success are warranted given that attraction efficiency does not appear to be affected by alterations to the total dam-spill discharge. Additional research in the Seton–Anderson watershed indicated that migration through the dam tailrace and fishway has post-passage consequences for Gates Creek sockeye salmon (Roscoe *et al.*, 2011). Of importance, the authors found that female sockeye salmon demonstrated significantly lower survival (40%) to reach spawning grounds compared with males (71%). In general, it is unclear why there is poor female performance in this watershed and why 20–30% of the annual Gates Creek sockeye salmon run fails to pass the Seton Dam upon reaching the tailrace (Pon *et al.*, 2009a; Roscoe *et al.*, 2011).

The objective of this study was to investigate the effects of managed flow releases at the Seton Dam on the activity, energy use and passage success of sockeye salmon. Building on telemetry data collected in 2007, a secondary study objective was to assess the predictors of passage success, migration delay and attraction efficiency of Gates Creek sockeye salmon at the Seton facility. We hypothesized that alterations in the hydrodynamics below the dam would affect passage success by influencing sockeye salmon activity and behaviour. We predicted that: (1) faster-swimming (i.e. hyperactive), delayed migrants would be more likely to fail in passing the Seton Dam, and (2) female sockeye salmon would exhibit prolonged holding behaviours in the tailrace, impeding their ability to successfully pass the facility. To our knowledge, this research provides some of the first data on the relationship between detailed flow releases from a diversion dam and the passage success of wild, migrating adult Pacific salmon.

METHODS

Study site

Gates Creek sockeye salmon are an ‘early Summer-run’ stock of Fraser River sockeye salmon that migrate ~350 km in July and August from the mouth of the Fraser River to the Seton–Anderson watershed in southwestern BC, Canada. Adult sockeye salmon migrate an additional 50 km through the Seton River, Seton Lake, Portage Creek and Anderson Lake to reach their terminal spawning grounds at Gates Creek and an artificial spawning channel at D'Arcy, BC (Figure 1); spawning takes place between mid-August and mid-September. Approximately 775 m downstream of Seton Lake, the Seton Dam (operated by BC Hydro; Figure 1 inset) spills water down Seton River to attract adult sockeye salmon, in addition to diverting upwards of 125 m^3 s^{-1} down a 3·8 km long power canal to a powerhouse station on the Fraser River. Gates Creek sockeye salmon must negotiate the Seton Dam tailrace and locate and ascend the vertical-slot fishway (32 pools, two turning basins, 107-m-long, 6·9% grade, discharge: 1·0–1·3 m^3 s^{-1}) to reach natal spawning sites. At the Seton facility, flows from the fish water release gate (FWRG) are used to attract adult migrants to the fishway entrance and any excess water spills through the remaining five siphons and/or radial gate spillway. In 2012, there were three distinct periods in the operational regime: (1) a high-discharge period from 17 to 20 August (mean total dam-spill discharge ± standard error (SE): 48·1 ± 2·4 × 10^{-2} m^3 s^{-1}) in which the FWRG (1·7 m^3 s^{-1}) and siphons #1 and #3 were open (45·4 ± 2·8 × 10^{-3} m^3 s^{-1}); (2) a ramp-down event (systematic decrease in total dam-spill discharge) on 21 August in which the FWRG (9·2 ± 1·2 m^3 s^{-1}, range: 1·7–14·0 m^3 s^{-1}) and siphon #1 (29·7 ± 2·5 m^3 s^{-1}, range: 19·9–45·3 m^3 s^{-1}) remained open, siphon #3 was closed and the radial gate spillway was open (7·3 ± 1·7 m^3 s^{-1}, range: 0·8–16·1 m^3 s^{-1}) from 10:00–17:00; and (3) a low-discharge period from 22 August to 2 September (32·3 ± 0·4 m^3 s^{-1}) in which the FWRG (13·7 ± 7·7 × 10^{-3} m^3 s^{-1}) and siphon #1 were open (20·0 ± 1·5 × 10^{-2} m^3 s^{-1}, range: 19·8–21·2 m^3 s^{-1}). Daily water temperatures in the Seton River in 2012 (17·2 ± 0·4 °C, range: 14·7–18·9 °C; YSI model Pro 30 water quality meter, Yellow Springs, OH, USA) were within the thermal optima for Gates Creek sockeye salmon (i.e. 17·5 °C, Lee *et al*., 2003a).

Fish capture, tagging and tracking

Twenty-six Gates Creek sockeye salmon were captured by dipnet between 17 and 28 August 2012 from the top pool of the Seton Dam vertical-slot fishway and immediately transferred to a V-shaped, foam-padded trough containing fresh Seton River water for sampling and tagging. During sampling, a DNA clip was obtained from the adipose fin for stock identification, fork length (FL) was measured (56·9 ± 0·4 cm, range: 53·5–62·0 cm), sex was estimated on the basis of secondary sexual characteristics present at this stage in the freshwater migration (e.g. male hump and kype), and gross somatic energy (GSE; mean +/- SE: 6·3 ± 0·2 MJ kg^{-1}) was obtained through the use of a microwave energy meter (FM 692 Fish Fatmeter, Distell, Scotland, UK; see Crossin and Hinch, 2005).

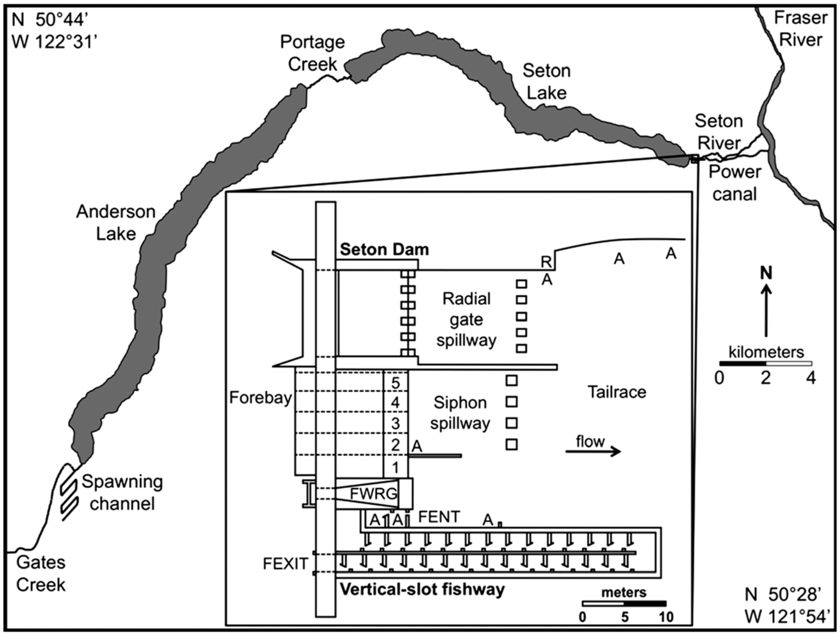

Figure 1. A map depicting the Seton–Anderson watershed in southwestern British Columbia, Canada, the terminal spawning grounds for Gates Creek sockeye salmon (*O. nerka*), as well as the location of the Seton Dam and fishway (inset). Minimum flows at the Seton facility are released through the fish water release gate (FWRG) to attract migrating sockeye salmon to the fishway entrance (FENT). Seven sentinel acoustic receivers (A) were placed within the tailrace area to capture activity data. A single fixed radio receiver (R) with a five-element Yagi antenna was positioned at the dam to quantify tailrace delay before eventual pass through the fishway exit (FEXIT) or fallback out of the Seton system. Schematic of the Seton Dam and fishway was adapted from Pon *et al*., 2009a and used with permission.

Three tagging configurations were established: (1) eight individuals (three male and five female sockeye salmon) received a gastrically inserted (Cooke *et al.*, 2005) acoustic accelerometer (Model V13A-1x, 69 kHz, 16 × 52 mm; VEMCO, Halifax, NS, Canada) as well as a radio transmitter (Pisces 5, 15 × 50 mm; Sigma Eight Inc., Newmarket, ON, Canada) externally attached posterior to the dorsal fin as a 'backpack' using stainless-steel wiring inserted through the dorsal musculature; (2) eight individuals (one male and seven female sockeye salmon) received only gastrically-inserted acoustic accelerometers to test the effects of the external-backpack method; and (3) ten individuals (three male and seven female sockeye salmon) received a gastrically-inserted radio transmitter to provide supplementary behavioural data. Acoustic accelerometers measure acceleration in three axes (range: 0–4·901 m s^{-2}) for 10 s at a sampling frequency of 10 Hz; acceleration data is then averaged for that 10 s period (root mean square (RMS) acceleration = $(X^2 + Y^2 + Z^2)^{0\cdot5}$) and transmitted every 13–17 s to sentinel receivers. RMS acceleration can further be converted to swimming speed and oxygen consumption as described in the succeeding text. The sampling and tagging procedure took less than 2 min to complete, and fish were not anaesthetized to minimize handling time and related stress (Cooke *et al.*, 2005). After tagging and sampling, fish were transported in an oxygenated, insulated 1000-l transport tank and released individually or in groups (maximum of six individuals) 350 m downstream of the Seton Dam on the southern bank of the Seton River (50°40′N, 121°58′W).

To monitor the activity and movement of free-swimming sockeye salmon in real-time, we used a combination of fixed and mobile acoustic and radio telemetry methods. An acoustic array consisting of nine single-channel receivers (VR2W, 69 kHz; VEMCO) was installed in the Seton River to remotely record the activity of fish tagged with acoustic accelerometers. Prior to the study period, the detection ranges of acoustic receivers were tested (e.g. 10 m in the radial gate spillway and <1 m along the fishway outer wall) to ensure that no single transmission was detected on multiple receivers (i.e. overlap). Seven receivers were placed in the Seton Dam tailrace (Figure 1 inset), a single acoustic receiver was positioned in the dam forebay to capture the time that fish exited the fishway, and a single receiver was located at the release site to monitor immediate post-release activity and behaviour. Two fixed radio receivers (SRX_400; Lotek Wireless Inc., Newmarket, ON, Canada) with five-element Yagi antennas were used throughout the 2012 study period. One was positioned at the dam to monitor the total amount of time any given fish spent within the tailrace area before eventual pass or fallback (hereafter, tailrace delay) and one fixed station located in the dam forebay to confirm the passage success of radio-tagged fish. Additionally, two SRX_400 radio receivers with three-element Yagi antennas were used for manual tracking purposes along the northern bank of the Seton River to provide detailed movement data from the release site to the dam tailrace.

Data analysis and statistics

RMS acceleration data were converted to a representative swimming speed (BL s^{-1}) using the calibrations and relationships described in Wilson *et al.* (2013). Acceleration data were further converted to estimates of oxygen consumption (MO_2, mg O_2 kg^{-1} min^{-1}) for Fraser River 'early Summer-run' sockeye salmon (S. Wilson, unpublished data), based on the equation

$$\begin{aligned} MO_2 = {} & [2.81 + (0.89 \times \text{RMS acceleration}) \\ & + (0.05 \times \text{Water temperature } (^\circ\text{C})) - (0.03 \times \text{FL}) \\ & + 1.21 - (\text{RMS acceleration} \times 0.32)]^2 \end{aligned} \tag{1}$$

White muscle fibers start to be recruited at ~80% of the critical swimming speed (U_{crit}) in migratory Pacific salmonids (Burgetz *et al.*, 1998). Swimming speeds in the present study that were less than 80% U_{crit} (Gates Creek $U_{\text{crit}} = 2{\cdot}10 \pm 0{\cdot}05$ BL s^{-1}; Lee *et al.*, 2003a) represent purely aerobic swimming efforts. Oxygen consumed as a result of swimming at speeds less than 80% U_{crit} can be estimated using Equation 1. Swimming speeds from 80 to 100% U_{crit} (1·66–2·10 BL s^{-1}) have both an aerobic (Equation 1) and anaerobic portion, typical of a burst-and-coast swimming gait commonly found in migrating adult sockeye salmon (Weihs, 1974). We applied an anaerobic 'tax' of 50·5% to all swimming speeds greater than 80% U_{crit} to account for the oxygen consumed post-exercise (i.e. excess post-exercise oxygen consumption, EPOC) in Gates Creek sockeye salmon (Lee *et al.*, 2003b). Oxygen consumed as a result of swimming at speeds $\geq U_{\text{crit}}$ was assumed to be the maximum oxygen consumption ($MO_{2\ \text{max}}$) for Gates Creek sockeye salmon (15·10 mg O_2 kg^{-1} min^{-1}; Lee *et al.*, 2003a) with the additional tax to account for EPOC. Given the amount of oxygen consumed during aerobic swimming efforts and the amount consumed during EPOC, we were able to quantify the percentage of detected swimming efforts that recruited anaerobic muscle fibers. Acceleration data collected from the three acoustic receivers on the northern bank of the Seton River adjacent to the radial gate spillway (Figure 1 inset) were pooled and represent the swimming speeds and oxygen consumption data from the 'radial gate spillway' habitat (~300 m^2; non-turbulent flows unless radial gate opened). Data from all four acoustic receivers in and around the fishway entrance (Figure 1 inset) represent the swimming speed and oxygen consumption of Gates Creek sockeye salmon in the 'fishway entrance' habitat (~400 m^2; consistently turbulent).

We incorporated telemetry data collected in 2007 from a previous study (Roscoe *et al.*, 2011) on Gates Creek sockeye salmon at the Seton Dam to allow for more robust analyses. Information regarding the operational regime in 2007 is described in detail in Roscoe *et al.* (2011); however, it must be noted that the radial gate spillway was open ($16{\cdot}0 \pm 3{\cdot}1\ \mathrm{m^3\,s^{-1}}$, range: $0{\cdot}7$–$30{\cdot}6\ \mathrm{m^3\,s^{-1}}$) during the tagging and tracking period on 20 August 2007 from 11:00–20:00. Fish were collected in an identical procedure in 2007 and 2012 and were all released downstream of the Seton Dam to monitor migration behaviour and passage success. We constructed three generalized linear models (GLM) to predict the passage success and attraction efficiency (family: binomial; link: logit) and tailrace delay (family: Gaussian; link: identity) of Gates Creek sockeye salmon. Nine explanatory variables were used: (1) sex; (2) tailrace delay (in h); (3) number of detected, unique efforts to cross the turbulent tailrace area from the radial gate spillway towards the fishway entrance (hereafter, tailrace crossings); (4) GSE; and (5) study year to account for potential inter-annual differences in passage success and behaviour. Mean discharges from the (6) fishway, (7) FWRG and (8) siphon spillway were calculated for each individual fish while present in the dam tailrace, as well as (9) whether or not (binomial) an individual was in the tailrace at the time of the radial gate opening on 20 August 2007 and 21 August 2012. All nine explanatory variables were included in each of the three models unless that variable was in fact the response variable (i.e. tailrace delay). Attraction efficiency was not included as an explanatory variable because of high passage efficiencies in 2007 and 2012 (93% and 89%, respectively). Multicollinearity among explanatory variables was tested, and no variables possessed a variance inflation factor greater than four, indicating that the explanatory variables were not highly correlated (O'Brien, 2007). A total of 63 adult Gates Creek sockeye salmon (2007: 47 total, 14 males, 33 females; 2012: 16 total, 4 males, 12 females) were included in the three models. Twelve individuals tagged and released downstream of the Seton Dam in 2007 were removed from the analyses because of a failure to reach the tailrace post-release. Similarly, all ten individuals tagged with only radio transmitters in 2012 were omitted because of a lack of sufficient detection data in the tailrace. We generated the top five candidate models using the R (Version 2.15.0; R Core Team, 2012) package 'glmulti' (Calcagno, 2012) and then compared them by using the bias-corrected, second-order information criterion (AIC_c) to determine the most parsimonious models (Sugiura, 1978). After the most parsimonious models were identified, F-tests were used to calculate significance levels of all retained variables to assess the relative importance among explanatory variables. Models were further analyzed using AIC_c weights (w_i), which describe the relative weighting of each candidate model based on the amount of information lost (Wagenmakers and Farrell, 2004). One-way analysis of variance (ANOVA) and Tukey post hoc tests were used to compare the activity, energy expenditure, migration behaviour and flow conditions experienced by successful and unsuccessful, male and female Gates Creek sockeye salmon. In some cases, data were log transformed to meet the normality and homoscedasticity assumptions of parametric tests. Non-parametric tests (Kruskal–Wallis and Mann–Whitney U) were used when the assumptions of normality were not met. Data are presented as mean ± SE, and all statistical analyses were performed at $\alpha = 0{\cdot}05$.

RESULTS

Individuals were pooled from the three tagging configurations, as there were no significant differences among these groups in tailrace delay (ANOVA $F = 0{\cdot}11$, df = 24, $p = 0{\cdot}75$), fork length (ANOVA $F = 0{\cdot}49$, df = 24, $p = 0{\cdot}49$), GSE (Kruskal–Wallis $H = 4{\cdot}80$, df = 2, $p = 0{\cdot}091$), mean discharge experienced from the fishway (Kruskal–Wallis $H = 5{\cdot}11$, df = 2, $p = 0{\cdot}08$), FWRG (Kruskal–Wallis $H = 3{\cdot}45$, df = 2, $p = 0{\cdot}18$), siphon spillway (Kruskal–Wallis $H = 0{\cdot}87$, df = 2, $p = 0{\cdot}65$) and radial gate spillway (Kruskal–Wallis $H = 1{\cdot}18$, df = 2, $p = 0{\cdot}55$). We also found no difference in mean swimming speed at the release site (ANOVA $F = 0{\cdot}31$, df = 7, $p = 0{\cdot}60$) and within the tailrace (ANOVA $F = 0{\cdot}02$, df = 13, $p = 0{\cdot}90$) between fish that possessed an acoustic tag only and fish that were acoustically- and radio-tagged.

Of the 26 Gates Creek sockeye salmon tagged and tracked in 2012, 16 individuals [overall: 62%; males: 71% (5/7); females: 58% (11/19)] successfully re-ascended the fishway and passed the Seton Dam. A single female successfully passed the dam, only to descend the fishway at a later time; this individual was considered to have failed in passing the facility. All 26 sockeye salmon swam volitionally in schools up to the dam tailrace ($1{\cdot}1 \pm 0{\cdot}1$ h, range: $0{\cdot}4$–$3{\cdot}2$ h) along the southern shore of the Seton River immediately post-release and delayed there for $16{\cdot}1 \pm 4{\cdot}9$ h (range: $0{\cdot}5$–$114{\cdot}8$ h) until eventual pass or fallback. Attraction efficiency (69%, 18/26) was considerably lower than passage efficiency (89%, 16/18) in 2012. We only captured $10{\cdot}8 \pm 2{\cdot}7$% (range: $1{\cdot}2$–$39{\cdot}2$%) of the activity of the acoustically tagged Gates Creek sockeye salmon within the tailrace (comparing total number of 10 s acoustic detections to tailrace delay for each fish). Overall, Gates Creek sockeye salmon used anaerobic swimming efforts $12{\cdot}0 \pm 4{\cdot}4$% (range: 0–$61{\cdot}3$%) of their detected time within the tailrace.

Comparison between successful and unsuccessful migrants

Successful ($n = 50$; 17 males, 33 females) and unsuccessful ($n = 13$; 1 male, 12 females) fish (2007 and 2012 pooled) did not differ with respect to their GSE (Mann–Whitney *U*-test W = 338, $p = 0{\cdot}83$), the mean discharge experienced within the fishway (Mann–Whitney *U*-test W = 419·5, $p = 0{\cdot}11$), FWRG (Mann–Whitney *U*-test W = 437, $p = 0{\cdot}06$) nor siphon spillway (Mann–Whitney *U*-test W = 330·5, $p = 0{\cdot}93$). However, unsuccessful fish experienced significantly higher mean discharges ($2{\cdot}92 \pm 1{\cdot}40\,\mathrm{m^3\,s^{-1}}$) from the radial gate spillway compared with successful fish ($0{\cdot}64 \pm 0{\cdot}45\,\mathrm{m^3\,s^{-1}}$; Mann–Whitney *U*-test W = 241, $p = 5{\cdot}3 \times 10^{-3}$). Successful fish (1·4 ± 0·1 times, range: 0–5 times) crossed the tailrace towards the fishway entrance area significantly more times (Mann–Whitney *U*-test W = 508·5, $p = 2{\cdot}03 \times 10^{-4}$) than unsuccessful fish (0·5 ± 0·2 times; range: 0–2 times).

One-way ANOVA and Tukey post hoc tests revealed that the mean swimming speeds of successful fish in the fishway entrance area in 2012 were significantly higher than the mean swimming speeds of successful and unsuccessful fish in the radial gate spillway (Table I). While in the fishway entrance area in 2012, both successful ($1{\cdot}8 \pm 0{\cdot}1\,\mathrm{BL\,s^{-1}}$, range: $1{\cdot}30$–$2{\cdot}28\,\mathrm{BL\,s^{-1}}$) and unsuccessful ($1{\cdot}9 \pm 0{\cdot}3\,\mathrm{BL\,s^{-1}}$, range: $1{\cdot}57$–$2{\cdot}13\,\mathrm{BL\,s^{-1}}$) fish recruited anaerobic muscle fibers while exhibiting a burst-and-coast swimming strategy. Mean oxygen consumption (MO_2) did not differ between successful and unsuccessful fish in 2012 among locations (ANOVA $F = 1{\cdot}51$, df = 27, $p = 0{\cdot}22$). No significant differences were found among successful ($n = 12$) and unsuccessful ($n = 4$) fish in the relative proportion of the activity our acoustic array captured within the tailrace (ANOVA $F = 5{\cdot}79$, df = 1, $p = 0{\cdot}14$). As such, we were able to compare the anaerobic contribution to swimming efforts among successful (13·2 ± 5·4%, range: 0·2–61·3%) and unsuccessful (5·5 ± 3·1%, range: 0–14·2%) and found no significant difference (ANOVA $F = 1{\cdot}46$, df = 1, $p = 0{\cdot}44$).

All five candidate models contained tailrace delay and tailrace crossings as significant predictors of passage success (Table II). Each tailrace-crossing event increased the odds of passing the Seton Dam by ~25% ($e^{3{\cdot}21}$; Table II). The predicted probability of Gates Creek sockeye salmon passing the Seton Dam was visualized by fitting a logistic regression to the tailrace delay (Figure 2A) and tailrace crossings (Figure 2B) of successful and unsuccessful migrants using the R package 'popbio' (Stubben and Milligan, 2007). A migrant that possessed a GSE $1\,\mathrm{MJ\,kg^{-1}}$ higher than other individuals delayed within the tailrace for 18% less time ($e^{-0{\cdot}20}$; Table II).

Sex-specific differences

Male Gates Creek sockeye salmon in 2007 and 2012 had a higher passage success (94%; 17/18) compared with females (73%; 33/45). Attraction efficiency and passage efficiency in male sockeye salmon [100% (18/18) and 94% (17/18), respectively] were higher than in females [79% (37/45) and 89% (33/37), respectively]. Sex was retained within the attraction efficiency GLM and contributed significantly to all top-five candidate models. Female sockeye salmon delayed significantly longer (20·8 ± 4·1 h; range: 0·5–114·8 h) than males (14·6 ± 3·2 h; range: 1·0–48·5 h) in the tailrace (ANOVA $F = 4{\cdot}87$, df = 16, $p = 0{\cdot}04$). Although there was no significant difference in the number of tailrace crossings between male (1·5 ± 0·3 times) and female (1·1 ± 0·1 times) Gates Creek sockeye salmon (Mann–Whitney *U*-test W = 479, $p = 0{\cdot}18$), males exhibited a larger range (range: 0–5 times) in the number of tailrace crossings compared with females (range: 0–3 times). Male and female sockeye salmon did not differ with respect to their GSE (Mann–Whitney *U*-test W = 385·5, $p = 0{\cdot}77$), the mean discharge experienced within the fishway (Mann–Whitney *U*-test W = 450·5, $p = 0{\cdot}49$), FWRG (Mann–Whitney *U*-test W = 457·5, $p = 0{\cdot}43$), siphon spillway (Mann–Whitney *U*-test W = 452·5, $p = 0{\cdot}47$) and radial gate spillway (Mann–Whitney *U*-test W = 381, $p = 0{\cdot}48$).

The mean swimming speeds of female sockeye salmon in the fishway entrance area were significantly greater (ANOVA $F = 6{\cdot}5$, df = 35, $p = 6{\cdot}28 \times 10^{-5}$) than the mean swimming speeds of females at all other locations (Tukey post hoc test; release site: $p = 0{\cdot}030$; radial gate spillway: $p = 3{\cdot}30 \times 10^{-5}$; forebay: $p = 0{\cdot}018$) and males at the release site ($p = 4{\cdot}40 \times 10^{-3}$) and in the radial gate spillway ($p = 3{\cdot}60 \times 10^{-5}$) (Figure 3). An ANOVA ($F = 6{\cdot}6$, df = 35, $p = 5{\cdot}31 \times 10^{-5}$) and Tukey post hoc tests revealed that the mean oxygen consumption of female sockeye salmon was

Table I. Mean swimming speeds ($\mathrm{BL\,s^{-1}}$; ± standard error) of successful and unsuccessful Gates Creek sockeye salmon (*O. nerka*) at the release site, radial gate spillway and fishway entrance area.

	Location		
Fate	Release site	Radial gate spillway	Fishway entrance area
Successful	$1{\cdot}4 \pm 0{\cdot}1\ (6)^{ab}$	$1{\cdot}1 \pm 0{\cdot}1\ (11)^{a}$	$1{\cdot}7 \pm 0{\cdot}1\ (8)^{b}$
Unsuccessful	$1{\cdot}1 \pm 0{\cdot}1\ (3)^{ab}$	$1{\cdot}1 \pm 0{\cdot}1\ (4)^{a}$	$1{\cdot}7 \pm 0{\cdot}5\ (2)^{ab}$

Numbers within parentheses represent sample sizes (*n*) and lowercase letters represent significant differences ($p < 0{\cdot}05$) from a one-way analysis of variance (ANOVA) and Tukey post hoc tests.

Table II. Candidate generalized linear models to predict passage success, attraction efficiency and tailrace delay of Gates Creek sockeye salmon (*O. nerka*).

Response variable	Model	k	ΔAIC_c	w_i
Passage success	Tailrace delay* (−3·13), tailrace crossings* (3·21), sex* (1·81) and year* (−2·40)	4	0·00	0·24
	Tailrace delay*, tailrace crossings*, sex*, siphon spillway and FWRG	5	0·29	0·21
	Tailrace delay*, tailrace crossings*, siphon spillway and FWRG	4	0·35	0·20
	Tailrace delay*, tailrace crossings* and year	3	0·47	0·19
	Tailrace delay*, tailrace crossings*, siphon spillway*, FWRG and fishway	5	0·64	0·17
Attraction efficiency	Sex* (17·97) and radial gate spillway* (−2·35)	2	0·00	0·31
	Sex*, radial gate spillway and tailrace delay	3	0·92	0·20
	Sex*, siphon spillway*, radial gate spillway, FWRG, tailrace delay and year	6	1·12	0·18
	Sex*, radial gate spillway, siphon spillway, FWRG and tailrace delay	5	1·23	0·17
	Sex*, radial gate spillway* and siphon spillway	3	1·41	0·15
Tailrace delay	Radial gate spillway* (0·62), GSE* (−0·20) and FWRG (0·05)	3	0·00	0·30
	Radial gate spillway*, GSE*, FWRG and tailrace crossings	4	0·07	0·29
	Radial gate spillway*, FWRG* and tailrace crossings	3	1·25	0·16
	Radial gate spillway*, GSE*, FWRG and fishway	4	1·61	0·13
	Radial gate spillway*, GSE*, FWRG*, tailrace crossings and fishway	5	1·93	0·11

Models are ranked from lowest to highest ΔAIC_c (highest to lowest AIC_c weight, w_i).
Explanatory variables that contribute significantly ($p < 0{\cdot}05$; one-way analysis of variance (ANOVA)) to a generalized linear model are marked with an asterisk. Numbers within parentheses represent the slope coefficients of the explanatory variables from the top-ranked models.
FWRG, fish water release gate; GSE, gross somatic energy.
k is the number of model parameters.

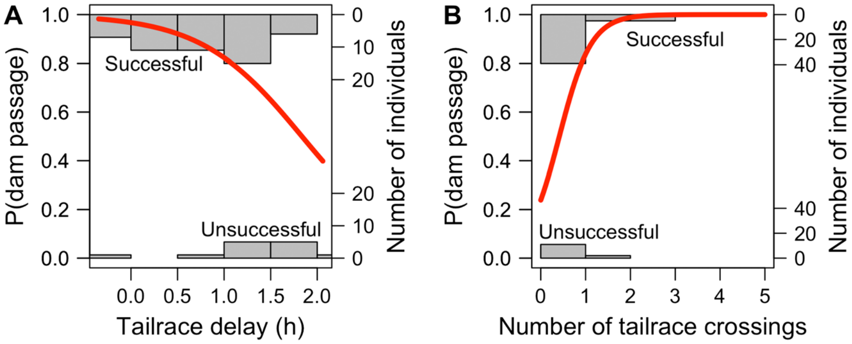

Figure 2. Logistic regression fitted to the tailrace delay [log transformed; (A)] and number of tailrace crossings (B) of successful and unsuccessful migrants. The red line shows the predicted probability of Gates Creek sockeye salmon (*O. nerka*) passing the Seton Dam.

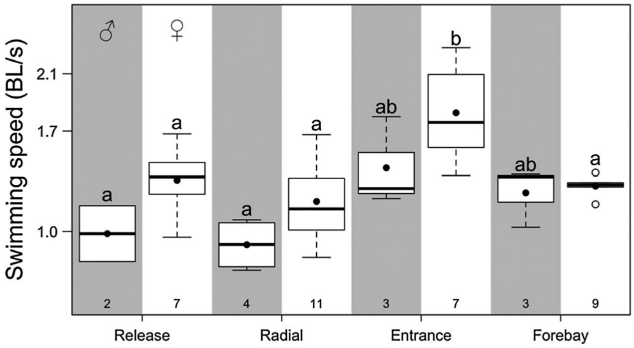

Figure 3. Box-and-whisker plot (median: solid line, mean: closed circle, extreme value: open circle, 25% and 75% quartiles) comparing the swimming speed ($BL\,s^{-1}$) of male (shaded grey) and female (white) Gates Creek sockeye salmon (*O. nerka*) at the release site, radial spillway, fishway entrance area and forebay. Optimal (~$1\,BL\,s^{-1}$) and critical (U_{crit}; $2{\cdot}10\,BL\,s^{-1}$) swimming speeds of Gates Creek sockeye salmon are shown along the y-axis; the swimming speed at which anaerobic muscle fibers start to be recruited (~$1{\cdot}7\,BL\,s^{-1}$) is also shown. Sample sizes (n) are presented below each box and whisker, and lowercase letters represent significant differences ($p < 0{\cdot}05$) from ANOVA and Tukey post hoc tests.

significantly higher in the fishway entrance area compared with male ($p = 3{\cdot}43 \times 10^{-5}$) and female sockeye salmon ($p = 9{\cdot}53 \times 10^{-4}$) in the radial gate spillway and males at the release site ($p = 0{\cdot}012$). The mean oxygen consumption of male sockeye salmon in the radial gate spillway was significantly higher compared with males in the fishway entrance area ($p = 0{\cdot}011$) and females at both the release site ($p = 0{\cdot}018$) and in the forebay ($p = 0{\cdot}045$). Although it appears as if females exhibited higher mean oxygen consumption compared with males at all locations (Table III), no differences were found in the mean oxygen consumption between male and female sockeye salmon at the same location. No significant differences were found among male and female sockeye salmon in 2012 in the relative proportion of the activity that our acoustic array captured within the tailrace (ANOVA $F = 0{\cdot}32$, df = 2, $p = 0{\cdot}63$). Though there was no significant difference (ANOVA $F = 0{\cdot}023$, df = 2, $p = 0{\cdot}89$) in the anaerobic contribution to swimming efforts between male (1·7 ± 0·5%) and female sockeye salmon (14·4 ± 5·2%), females exhibited a much larger range (0–61·3%) in detected anaerobic swimming efforts compared with males (0·7–2·7%).

Effects of the operational regime

All 26 Gates Creek sockeye salmon tagged in 2012 delayed (range: 0·5–114·8 h) in the radial gate spillway on the northern bank of Seton River. However, all individuals [9 total; $n = 3$ (2007), $n = 6$ (2012)] that experienced the opening of the radial gate failed to pass the Seton Dam. Opening the radial gate (hereafter, distraction flow) in 2007 and 2012 decreased attraction efficiency by 90% ($e^{-2{\cdot}35}$; Table II) and increased tailrace delay by 2 h ($e^{0{\cdot}62}$; Table II).

DISCUSSION

Gates Creek sockeye salmon tagged with acoustic accelerometers in 2012 had habitat-specific and flow-dependent activity patterns in the Seton Dam tailrace. Contrary to our hypothesis and previous research on migrating Fraser River sockeye salmon (Hinch and Bratty, 2000), the hyperactivity observed in these fish does not appear to contribute to failure in passing the dam. We found that all sockeye salmon that passed through the turbulent waters of the fishway entrance area recruited anaerobic muscle fibers while exhibiting a burst-and-coast swimming strategy, consistent with previous observations in the Seton Dam tailrace (Pon *et al.*, 2009b) and hyperactivity reported in other tailraces (Brown *et al.*, 2006; Enders *et al.*, 2008). Burst swimming may not be required to ascend the Seton Dam fishway (Pon *et al.*, 2009b); however, anaerobically fueled locomotion (11·3 ± 4·1%, range: 0–61·3%) is typically needed to locate and enter the fishway entrance in a timely manner. Anaerobiosis is potentially costly, but whether or not it contributes to the observed failure of Gates Creek sockeye salmon to reach natal spawning sites (Roscoe *et al.*, 2011) is unclear.

Table III. Mean oxygen consumption (mg O_2 kg^{-1} min^{-1}; ± standard error) of male and female Gates Creek sockeye salmon (*O. nerka*) at the release site, the radial gate spillway, the fishway entrance area and the forebay.

Location	Males	Females
Release site	10·9 ± 1·0 (2)	12·8 ± 0·5 (7)
Radial gate spillway	10·3 ± 0·5 (4)	11·8 ± 0·4 (11)
Fishway entrance area	13·5 ± 0·4 (3)	14·3 ± 0·2 (7)
Forebay	12·3 ± 0·9 (3)	12·6 ± 0·1 (6)

Numbers within parentheses represent sample sizes (*n*).

Female sockeye salmon delayed significantly longer within the Seton Dam tailrace than male sockeye salmon, and yet, male and female sockeye salmon did not differ with respect to GSE at the time of tagging and the flows encountered from the fishway, FWRG, siphon spillway, and radial gate spillway. Therefore, we infer that the reduced overall performance of female Gates Creek sockeye salmon at the dam may be the result of being sensitive to certain discharge conditions and associated flow patterns downstream of the facility. Crossin *et al.* (2008) hypothesized that greater energetic investment to gonad development in female sockeye salmon might render them more sensitive to environmental stressors such as warming temperatures and high flows in constricted passes or regulated systems. The results from the present study suggest that greater passage success in male sockeye salmon may be attributable to behavioural differences, as female sockeye salmon had a lower range in tailrace crossings and a lower attraction efficiency, which resulted in longer delays in the tailrace and a lower overall passage success. Moreover, female sockeye salmon appeared to have higher swimming speeds compared with males at all locations in the Seton River in 2012. Female sockeye salmon consistently swam above the optimal swimming speed and in some cases above the critical swimming speed (U_{crit}) of Gates Creek sockeye salmon (Lee *et al.*, 2003a, 2003b). Consequently, female sockeye salmon possessed a larger range of detected anaerobic swimming efforts compared with males and may support the notion that increased levels of lactate accumulation and EPOC may contribute to the observed sex-specific differences in dam passage and survival to spawning grounds (Roscoe *et al.*, 2011). Certainly, it is possible that the significantly longer delays and higher mean activity levels present in female sockeye salmon may contribute to energy depletion within the tailrace and impede their ability to pass the facility.

Migration delay in the Seton Dam tailrace has a negative effect on passage. Tailrace delay was a significant predictor of passage success, with an apparent threshold tailrace delay of ~6 h in which the probability of passing the dam was 80%. Although successful fish were able to pass after short and long bouts of delay, 12 of the 13 individuals that failed to pass the Seton Dam in 2007 and 2012 delayed for greater than 6 h. Passage probability diminished with tailrace delays greater than 6 h, lowering to 50% with a delay of 60 h. This finding is of interest as Gates Creek sockeye salmon are known to delay in the Seton Dam tailrace for up to 5 days and may be applicable to other regulated watersheds in which migrants are known to spend several days downstream of a barrier prior to eventual pass or fallback (Bjornn and Peery, 1992; Geist *et al*., 2000; Caudill *et al*., 2007). On the Columbia River, Caudill *et al*. (2007) found that unsuccessful migrants delayed longer at nearly all encountered dams. Our finding that migrants with a higher GSE delayed for significantly less time in the tailrace and had a higher passage probability provides some insight into a biological mechanism for migrating adult salmon passage success or failure at the Seton Dam. Previous work has shown that adult Pacific salmon (sockeye salmon, Chinook salmon and steelhead *O. mykiss*) with lower GSE travel slower through energetically demanding reaches and are less likely to successfully complete their spawning migration (Young *et al*., 2006; Caudill *et al*., 2007).

We found that successful migrants crossed the turbulent flows of the tailrace towards the fishway entrance significantly more times than unsuccessful fish. This finding suggests that unsuccessful Gates Creek sockeye salmon may be unable to cross the tailrace enough times to locate the fishway entrance or decide to search for alternate migration routes after limited attempts at locating the fishway. Although the opposite behaviour was observed in actively migrating sockeye salmon attempting to locate the Hell's Gate fishway in the Fraser River Canyon, BC (Hinch and Bratty, 2000), research on Atlantic salmon (*Salmo salar*) found that successful adult migrants approached the fishway entrance upwards of ten times (Gowans *et al*., 1999). Some believe this behaviour allows fish to become accustomed with the entrances, flows and lowest pools of fishways (Laine, 1995), whereas others have suggested it may be the result of confusion in selecting the desired migration path in areas with complex, convoluted flow patterns (Hinch *et al*., 2002). We are uncertain whether multiple, repeated attempts at crossing these energetically demanding areas contribute to the failure of migrants to reach natal spawning sites (Roscoe *et al*., 2011) given that Gates Creek sockeye salmon recruit anaerobic muscle fibers within these areas of the tailrace. Capturing Gates Creek sockeye salmon that have previous migration experience in the Seton Dam tailrace and fishway (Pon *et al*., 2009a; Roscoe *et al*., 2011; present study) could very well affect their ability to relocate the fishway entrance and pass the dam. To account for this, future passage studies at this facility should consider using dam- and fishway-naive fish when generating efficiency estimates (Cooke and Hinch, 2013).

MANAGEMENT IMPLICATIONS

Opening the radial gate spillway at the Seton facility had adverse effects on Gates Creek sockeye salmon in both years that were examined. Spilling excess water from this portion of the dam decreased attraction efficiency by 90% and increased tailrace delay by 2 h. Interestingly, soon after the Seton Dam was constructed (i.e. 1956), Andrew and Geen (1958) observed that no serious migration delay occurred within the tailrace unless the radial gate was opened. Given that the radial gate spillway is located nearly 30 m from the fishway entrance on the opposite bank of the Seton River, we believe that flows emanating from the radial gate generate multiple pathways for sockeye salmon to choose, which likely distracts and confuses fish (Bunt, 2001; Reischel and Bjornn, 2003; Bunt *et al*., 2011). Further, Gates Creek sockeye salmon appeared to be equally affected when the ratio of the attraction to distraction flows released from the Seton Dam was 1 : 1 (2007) and even 2 : 1 (2012). By generating a number of confusing migration pathways, it is likely that the multidirectional currents downstream of the Seton Dam caused adult migrants to be less successful in selecting their optimal migration path as they were naturally attracted to the distraction flows released from the radial gate (Andrew and Geen, 1958; Barry and Kynard, 1986). Gates Creek sockeye salmon are known to delay within the closed radial gate spillway around the concrete baffles (Pon *et al*., 2009b), perhaps as an effort to use reverse flow fields to maintain their position in the tailrace while expending minimal energy (Bunt, 2001; Liao *et al*., 2003). Releasing excess water through the radial gate not only attracts migrants to this part of the spillway but also does not allow holding to occur, reducing attraction efficiency and overall passage success (Pon *et al*., 2009a; Roscoe *et al*., 2011; present study). Yet, the radial gate is typically used to spill excess water once during the annual Gates Creek sockeye salmon run in a single ramp-down event and thus, likely only affects fish immediately downstream of the Seton Dam at the time of the operational change. Research conducted elsewhere has shown that alterations to the operational regime during the migration period of anadromous fishes can adversely affect migration rates and passage success (Bjornn and Peery, 1992). Modifying the Seton Dam operational regime to improve attraction efficiency should be considered, particularly during the latter parts of the sockeye salmon migration period when energy levels are lower, and subsequent delays within the tailrace are longer. Alterations to the flow regimes at the Seton facility would not result in a loss of power generation, but at hydroelectric dams, the power generated could be affected by altering the specific location and magnitude of flow releases. Ultimately, the operating strategies that mitigate delays in upstream migration would need to be balanced with other water-use goals for environmental protection, flood control and irrigation.

Although it is widely recognized that the hydraulic conditions downstream of dam facilities are site specific (Bunt, 2001; Pon *et al*., 2009a), we feel that the results from the current study demonstrate a clear need for more detailed hydraulic analyses when addressing complex fish-passage problems. Several studies evaluating the effects of dam operations on the upriver spawning migrations of Pacific salmonids have found that changes in the total dam-spill discharge at a facility can increase delay and decrease passage success at individual dams and through multi-dam reaches (e.g. Caudill *et al*., 2006; Caudill *et al*., 2007). However, others using this approach have been unable to understand the influence of managed flow releases on the migration behaviour and passage success of migrants (Pon *et al*., 2009a, 2009b; Roscoe *et al*., 2011). Linking the total discharge at an upstream barrier to passage success or failure does not reflect the complex flow patterns fish negotiate downstream. We highlight the importance of transitioning from using the total dam-spill discharge in analyses to more detailed flow releases. Improving our understanding of the interactions between anadromous fishes and hydrodynamics at natural and man-made barriers will aid in the management of fish passage.

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