REDUCING CARRYOVER EFFECTS ON THE MIGRATION AND SPAWNING SUCCESS OF SOCKEYE SALMON THROUGH A MANAGEMENT EXPERIMENT OF DAM FLOWS

N. J. BURNETT[a]*, S. G. HINCH[a], N. N. BETT[a], D. C. BRAUN[a,b], M. T. CASSELMAN[a], S. J. COOKE[c], A. GELCHU[d],
S. LINGARD[b], C. T. MIDDLETON[a], V. MINKE-MARTIN[a] AND C. F. H. WHITE[a]

[a] *Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences*
University of British Columbia, Vancouver, BC, Canada
[b] *InStream Fisheries Research Inc., Vancouver, BC, Canada*
[c] *Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science*
Carleton University, Ottawa, ON, Canada
[d] *BC Hydro, Burnaby, BC, Canada*

ABSTRACT

Effective dam management requires an understanding of the ecological impact of a facility and its operations on individual fish and fish populations. Traversing high flows downstream of dams is an energetically challenging activity that could influence survival and spawning success following passage. Carryover effects, however, are an underappreciated consequence of dam passage that have been overlooked by researchers and natural resource managers. We conducted a large-scale management experiment to determine if the operation of dam attraction flows could be changed to reduce high sockeye salmon *Oncorhynchus nerka* mortality following passage and increase spawning success. We tested two flow conditions: (i) a baseline condition—currently used by managers—that released high attraction flows directly adjacent to the entrance to a vertical-slot fishway and (ii) an alternative condition that released attraction flows 10 m away from the fishway entrance to reduce the flows fish swim through while approaching the passage structure. We tagged 637 sockeye salmon with telemetry tags to monitor dam passage, post-passage survival to spawning grounds and spawning success under the two flow conditions. Validated fish counters at the exit of the fishway and on spawning grounds were used to generate population level estimates of survival to spawning grounds. Individuals exposed to baseline flow conditions spent two times longer recovering from dam passage and exhibited 10% higher mortality following passage than those exposed to alternative flows. Release of alternative flows for 10 days assisted approximately 550 fish (or 3% of total spawners) in reaching spawning grounds. Once on spawning grounds, female spawning success was strongly influenced by individual spawning characteristics (longevity and date of arrival on spawning grounds) and not dam flow condition. Our findings highlight a cost-effective solution that decreases mortality following passage simply by altering the location of dam flow releases and not reductions in discharge. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS: accelerometry; egg retention; fishway; fitness; delayed mortality; *Oncorhynchus nerka*; telemetry

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INTRODUCTION

Animals move across landscapes to seek viable habitat for survival, feeding or breeding (Dingle and Drake, 2007; Nathan *et al*., 2008). Anthropogenic habitat fragmentation, however, continues to disrupt natural movements that are essential to the viability of populations and health of ecosystems (Fahrig, 2007). Human-made infrastructure can result in the immediate mortality of animals [e.g. collision of birds with offshore wind farms (Drewitt and Langston, 2006) and entrainment of fish at hydropower facilities (Coutant and Whitney, 2000)] as well as sublethal effects, whereby physical injury or an alteration to behaviour and physiology can influence foraging, growth and fitness in the future (Trombulak and Frissell, 2000). River systems throughout the world are fragmented and regulated by dams (Nilsson *et al*., 2005), directly altering riverine biodiversity (Dudgeon *et al*., 2006). Passage structures at dams aim to restore river connectivity by facilitating upstream passage for migratory fishes (Clay, 1995). Fish passage research to date, however, has largely focused on assessing the ability of individuals to pass a single barrier, often considering dam passage as an isolated event (Cooke and Hinch, 2013). Such a focus overlooks the potential for a stressful dam passage event to influence fitness upstream (Caudill *et al*., 2007) and limits our understanding of the absolute ecological impact of dams.

Dam passage, in some instances, can be acutely stressful (Castro-Santos *et al*., 2009) and can manifest into a carryover effect (Burnett *et al*., 2014a). Carryover effects occur

*Correspondence to: N. J. Burnett, Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
E-mail: nich.burnett@gmail.com

when 'an individual's previous history and experience explain their current performance' (O'Connor *et al*., 2014) and have been identified as important drivers of variation in individual fitness, which can influence multiple levels of biological organization (i.e. from individuals to population dynamics; Harrison *et al*., 2011). Few applied ecological studies to date have aimed to identify carryover effects and understand the mechanisms that drive them (O'Connor and Cooke, 2015). Recently, Burnett *et al*. (2014a) showed that high mortality of sockeye salmon following dam passage was closely linked to burst swimming through attraction flows downstream of a dam. Fish that burst swam through these flows increased their *post hoc* oxygen consumption in upstream lakes [known as excess post-exercise oxygen consumption (EPOC); Lee *et al*., 2003a] to re-establish metabolic homeostasis. Mortality associated with high-flow-induced burst swimming and EPOC was two times higher for females than males (Burnett *et al*., 2014a), explaining in part the female-biased migration mortality previously observed for sockeye salmon in this watershed (Roscoe *et al*., 2011). It is possible that reducing the difficulty of passage by providing easier access to the fishway entrance might enable lower EPOC and therefore reduce the carryover effect identified by Burnett *et al*. (2014a). Further, if survival to spawning grounds could be enhanced by a change in water release practices, one might also expect spawning success (female deposition of eggs on spawning grounds) to be enhanced, as spawners could be less stressed by the altered dam flow conditions. Stress can negatively impact the reproductive output of fish (Schreck *et al*., 2001) and other vertebrates (e.g. birds: Wingfield, 1988; mammals: Boonstra *et al*., 1998). Fish experience stressful conditions (e.g. supraoptimal water temperatures and high flows: Caudill *et al*., 2013 and Burnett *et al*., 2014a, respectively) during dam passage; however, no research to date has examined the potential for a stressful dam passage event to influence individual spawning success.

Dam-induced carryover effects could be particularly problematic for anadromous, semelparous species that swim upstream on a fixed energy budget with only a single opportunity to reproduce (Groot and Margolis, 1991). Pacific salmon, for example, are susceptible to significant fitness costs in regulated river systems, especially considering the prevalence of dams in salmon-bearing watersheds (Nehlsen *et al*., 1991; Slaney *et al*., 1996). And yet, there has been a complete lack of research investigating the potential for dam passage to result in delayed or carryover effects on salmon (Caudill *et al*., 2007). Previous research has demonstrated close linkages between migration success and reproductive investment and discharge at a whole-river scale (e.g. Rand *et al*., 2006; Braun *et al*., 2013) and between swimming behaviours and hydrodynamics at a sub-metre scale (e.g. Liao *et al*., 2003). Burst swimming (recruitment of anaerobic

muscle fibres) by sockeye salmon in areas of difficult passage has been attributed to failure in passing fishways (Hinch and Bratty, 2000) and reaching natal spawning grounds post-passage (Burnett *et al*., 2014a). Historically, regulated watersheds that support salmon were managed with little consideration for the impact of dams on migration behaviour and survival (McLain and Lee, 1996; Lichatowich and Lichatowich, 2001), but longitudinal assessments of flow requirements for salmon productivity are being applied to regulated river systems (Bradford *et al*., 2011). Ultimately, there is a need to develop a more comprehensive understanding of both the immediate and carryover effects of dam passage on this ecologically, culturally and economically important group of fishes.

Passage conditions at dams can be readily controlled through alterations to water release practices, making dams ideal model systems for testing management options in the field (Memmott *et al*., 2010) through large-scale experiments (Walters and Holling, 1990). In this study, we conducted a field-based management experiment in an attempt to reduce the high mortality of sockeye salmon identified by Burnett *et al*. (2014a). We tagged and tracked fish from below a diversion dam to natal spawning grounds in a regulated watershed in British Columbia, Canada. Two flow conditions were tested: (i) a baseline condition—currently used by managers—that released attraction flows directly adjacent to the entrance to a vertical-slot fishway and (ii) an alternative condition that released attraction flows 10 m away from the fishway entrance. Based on a physiological understanding of individual fish mortality under baseline flow conditions (Burnett *et al*., 2014a), we hypothesized that the proportion of the population that reaches spawning grounds and successfully deposits eggs could increase by reducing the flows fish swim through while approaching the passage structure. We predicted that post-dam passage survival would be higher for individuals exposed to alternative flows. Once on spawning grounds, we predicted that spawning success would also be higher for individuals exposed to alternative flows. Support for either of these predictions would provide evidence for our hypothesis. Our findings emphasize that information gained from management experiments can provide natural resource managers with cost-effective strategies that reduce the impacts of dams on populations of fish.

METHODS

Study site

We studied dam passage, post-passage survival to spawning grounds and spawning success in Gates Creek sockeye, a wild population of Fraser River salmon (British Columbia, Canada). Adult Gates Creek sockeye salmon swim 400 km

upstream from the mouth of the Fraser River to natal spawning grounds (Figure 1), encountering a single physical barrier (Seton Dam, operated by BC Hydro) during their migration. Consequently, passage of Seton Dam represents a significant migration challenge for this interior population of Fraser River sockeye. Fish must locate and ascend a vertical-slot fishway (32 pools, 2 turning basins, 107 m long, 6.9% grade) to pass the facility and complete the remaining 55 km of their freshwater migration through two natal lakes. Operated in a manner consistent with dams and fish passage structures around the world, flows from the fish water release gate (FWRG) and siphon #1 (collectively known as 'attraction flows') at Seton Dam are used to attract fish towards the fishway entrance (Figures 1 and 2). BC Hydro has used this operational protocol for 60 years to facilitate the upstream passage of salmon (hereafter, 'baseline flow condition').

In this study, we evaluated migration and spawning success under two flow conditions (Figure 1 inset). Baseline flows (via the FWRG and siphon #1; total dam-spill discharge: $26 \, m^3 \, s^{-1}$) were released from 2 to 7 August 2014 and 20 August to 7 September 2014. Alternative flows (total dam-spill discharge: $31 \, m^3 \, s^{-1}$) were tested from 9 to 18 August 2014, whereby water was spilled through the FWRG and siphon #4, which is located 10 m away from the fishway entrance (Figures 1 and 2). We highlight that the nature and timing of this flow experiment were limited by BC Hydro's Water Use Plan requirements and that the alternative flow condition is a potentially viable operational change at this facility.

Tagging

Upstream migrating sockeye salmon were captured from 2 August to 7 September 2014 by means of a full-spanning fence (*c*. 50-m long) and trap located 200-m downstream of Seton Dam and held temporarily in a flow-through pen prior to tagging and sampling. Fish were individually transferred to a *V*-shaped, foam-padded trough containing continuously flowing water directed towards the gills.
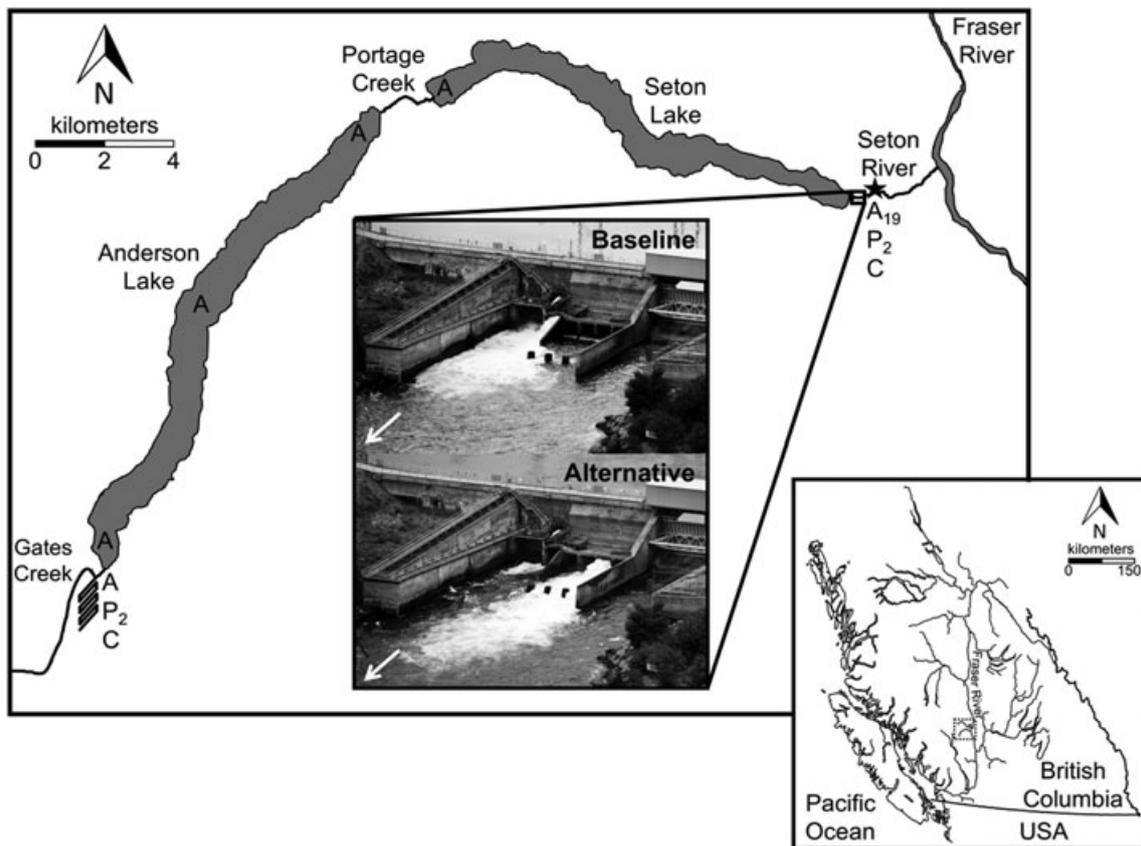
Figure 1. Baseline and alternative flow conditions at Seton Dam in British Columbia, Canada. Subscripted numbers represent the quantity of acoustic receivers (*A*) or PIT antennas (*P*) at a given locale. A detailed schematic of the acoustic telemetry array at Seton Dam (A_{19}) is depicted in Figure 2. *C* is the validated resistivity counter; star is the capture, tagging and release site; white arrow is the flow direction. Photographer: Nicholas Burnett. Insert map depicts the Fraser River Basin, with the study area enclosed within a box
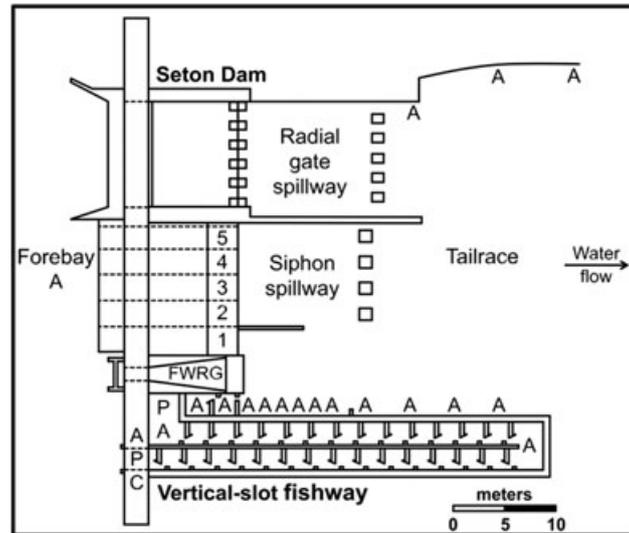
Figure 2. Acoustic receivers (*A*), PIT antennas (*P*) and a validated resistivity counter (*C*) surrounding Seton Dam and the vertical-slot fishway. FWRG, fish water release gate

Forty-five individuals were gastrically tagged with an acoustic accelerometer transmitter (Model V13A-1x, 69 kHz, 16 × 52 mm; VEMCO, Halifax, NS, Canada; Wilson *et al*., 2013 and Burnett *et al*., 2014a) to monitor the swimming speed and behaviour of sockeye salmon in the dam tailrace and forebay. Of these 45 individuals, 30 (13 males and 17 females) were released under baseline flow conditions (15 fish from 4 to 7 August 2014, and 15 fish from 27 August to 4 September 2014), and 15 (seven males and eight females) were released under alternative flow conditions (10 to 13 August 2014). All fish were fitted with an external spaghetti tag (Floy Manufacturing, WA, Seattle, USA) attached posterior to the dorsal fin for visual identification. A half-duplex passive integrated transponder (PIT) tag (32 × 3.65 mm; Texas Instruments Inc., Dallas, TX, USA) was inserted into the dorsal musculature using a six-gauge needle. An additional 592 sockeye salmon were tagged with spaghetti and PIT tags only (hereafter, 'PIT-tagged' fish) to supplement the dam passage and post-passage survival to spawning grounds data from acoustic-tagged sockeye salmon. We also present survival from release to spawning grounds to examine the cumulative effect of releasing alternative flows on the survival of tagged fish.

Fork length was measured (to nearest 5 mm) for use in swimming speed analyses, and sex was determined on the basis of secondary sexual characteristics present at this stage in the freshwater migration (e.g. male hump and kype). Tagging and sampling took less than 3 min to complete, and fish were not anaesthetized to (i) minimize handling time and related stress (Cooke *et al*., 2005) and (ii) avoid potential consumption of anaesthetizing agents by anglers (Roscoe *et al*., 2011). Notably, there was no fishery on Gates Creek sockeye salmon downstream or upstream of

Seton Dam because of a low abundance in 2014. All fish were released directly above the full-spanning fence immediately after tagging and sampling and were captured, handled and tagged in accordance with guidelines of the Canadian Council on Animal Care and approved animal use protocols (University of British Columbia; AUP A11-0125).

Tracking

A fixed telemetry array consisting of 19 single-channel acoustic receivers (VR2W, 69 kHz; VEMCO) was installed in the dam tailrace and vertical-slot fishway to remotely record the swimming speed and behaviour of acoustic-tagged fish (Figure 2). An additional four acoustic receivers were positioned in two upstream lakes (Seton and Anderson lakes; Figure 1) to monitor post-passage survival to spawning grounds.

Two pass-through PIT antennas (2.2 × 0.7 m) were positioned on the upstream-facing side of the vertical-slot baffles at the entrance and exit of the fishway. PIT antennas were constructed out of 3.8 cm polyvinyl chloride pipe with 12-gauge stranded electrical wire; each antenna was connected to a remote tuner box (Oregon RFID, Portland, OR, USA), and both antennas were connected to a multiplexor unit (Oregon RFID) via twin-axial cable. PIT antennas within the fishway were manually tuned and tested prior to daily tagging to ensure maximum read range (*c*. 0.5 m) and tag-reading performance. A two-antenna PIT array was also installed at Gates Creek to determine if tagged sockeye salmon had reached spawning grounds. Detection efficiencies of acoustic receivers and PIT-telemetry arrays were all exceptionally high (all > 93%; Table I).

Table I. Detection efficiency of acoustic receivers and PIT-telemetry arrays depicted in Figures 1 and 2

	Location of receiver or array	Detection efficiency
Acoustic telemetry	Radial gate spillway$_3$	100% (44/44)
	Fishway entrance$_{11}$	93% (42/45)
	Within fishway$_4$	100% (44/44)
	Dam forebay$_1$	100% (43/43)
	Portage Creek outflow$_1$	100% (33/33)
	Portage Creek inflow$_1$	100% (33/33)
	Middle of Anderson Lake$_1$	100% (33/33)
	Gates Creek outflow$_1$	100% (33/33)
PIT-telemetry	Within fishway$_2$	99% (579/587)
	Artificial spawning channel at Gates Creek$_2$	98% (447/455)

PIT, passive integrated transponder.
Subscripted numbers represent the quantity of acoustic receivers or PIT antennas pooled to calculate the detection efficiencies. Numbers in parentheses represent the number of individuals detected out of the total number of individuals known to have passed by acoustic receivers or through PIT antennas.

We quantified the total amount of time (in h) acoustic-tagged fish spent in the dam tailrace (0–60 m downstream of dam face) before eventual passage or fallback, as passage time can strongly influence dam passage (Burnett *et al*., 2014b) and survival to spawning grounds (Caudill *et al*., 2007). We developed a ratio between the amount of time acoustic-tagged fish spent near the fishway entrance and in the radial gate spillway (30 m away from fishway entrance; Figure 2) to determine if fish spent a disproportionate amount of time in one area of the dam tailrace. Using acoustic-telemetry and PIT-telemetry data, we quantified the number of times acoustic-tagged sockeye salmon crossed the tailrace from the radial gate spillway to the fishway entrance (hereafter, tailrace crossings). Tailrace crossings have previously been linked to passage success at Seton Dam (Burnett *et al*., 2014a, 2014b). Finally, we quantified the total amount of time (in h) acoustic-tagged fish spent in the dam forebay following dam passage using a single acoustic receiver (Figure 2).

Seton River water temperatures were recorded hourly from the top pool of the fishway using a TidbiT v2 Water Temperature Data Logger (0.2 °C accuracy; Onset HOBO Data Loggers, Bourne, MA, USA) and were used for the swimming speed and oxygen consumption analyses. Fraser River water temperature and discharge was monitored throughout the study period using the Water Survey of Canada gauge station at Texas Creek (Station No. 08MF040; 10 km from Seton River).

Resistivity counters in fishway exit

We estimated the number of sockeye salmon that migrated through the Seton Dam fishway using two Logie 2100c resistivity electronic fish counters (Aquantic Ltd., Scotland, UK). Each counter was connected to four independent sensor tubes installed at the top of the fishway (Figure 2). Fish passing upstream and downstream through the sensor tubes show consistent changes in resistance and can be used to visually determine if the counter correctly counted a fish; this includes both false positives (counted fish that did not pass) and false negatives (missed fish that passed).

Digital underwater video cameras were attached to camera mounts just upstream of the fish counter. Field of view of the cameras allowed for all eight tubes to be validated simultaneously. Video was recorded from 13 August to 10 September 2014 and was saved to a digital-video recorder at 15 frames per second. Video recordings of fish passage were used to validate the counter detections and estimate the accuracy of each sensor tube. Recordings of fish passing through the counter were matched with the counter detections to determine the daily proportion of detections that were correctly recorded (i.e. counter accuracy). We also used graphical outputs of the change in resistance to validate additional up counts from the counter.

We validated a total of 3020 fish using both validation methods. Daily sensor tube accuracies were consistent throughout the migration and ranged from 90% to 100%; therefore, we pooled all daily count data across the migration to estimate an accuracy for each tube. One tube's accuracy, however, was not consistent throughout the migration, and daily accuracies were typically low. Thus, we used the daily accuracies for the tube with variable and low accuracy. Using the same video data, we estimated the proportion of up counts that were sockeye salmon (i.e. 1078 of the 1106 fish observed on video were sockeye salmon) and calculated the abundance of sockeye salmon through the counter as follows:

$$S = \sum_{i=1}^{7} \left(\frac{P_i U_i - V_i}{A_i} \right) \qquad (1)$$

where S is the total number of sockeye salmon that migrated through the fishway counter, U_i is the total number of up counts recorded by the counter for all species for sensor tube i (from tubes one to seven), P is the proportion of counts that were sockeye salmon for the sensor tube i, V_i is the number of sockeye salmon that were validated for sensor tube i and A_i is the accuracy of the sensor tube. We used Equation 1 for the eighth tube; however, A, U and V were daily values, and P was the mean over the migration. We estimate that 27 192 sockeye salmon migrated past the fishway from 25 July to 10 September 2014.

Mechanical counters on spawning grounds

We estimated the number of sockeye salmon that reached spawning grounds (Gates Creek and the artificial spawning

channel at Gates Creek) using two mechanical counters and visual counts in the first 1 km of the river. While some fish spawn downstream of the artificial spawning channel, the vast majority (>95%) are diverted into either the artificial spawning channel or upper reaches of Gates Creek by a diversion fence. Mechanical counters were video validated and had an accuracy of 87%, where the only source of error was false positives (i.e. over counting). Using Equation 1, we estimated that 16 929 sockeye salmon reached spawning grounds at Gates Creek.

Estimating population level survival to spawning grounds

To estimate the number of additional survivors, we applied the difference in the mean estimates of post-passage survival to spawning grounds from PIT-tagged fish under baseline and alternative flows (baseline: 81% vs alternative: 88%) to daily estimates of abundance through the fishway. PIT-tagged sockeye salmon are the ideal group of study subjects to provide this population level estimate, as these individuals were tagged and handled less invasively than acoustic-tagged fish (i.e. no gastric implantation of a transmitter).

Swimming speed and oxygen consumption analyses

Acoustic accelerometer transmitters measure acceleration in three axes (range: 0–4.901 m s^{-2}) for 10 s at a sampling frequency of 10 Hz. Acceleration data are then averaged for that 10-s period [root mean square (RMS) acceleration = $\sqrt{X^2 + Y^2 + Z^2}$] and transmitted every 13–17 s to receivers. RMS acceleration data were converted to swimming speed in units of body lengths per second (BL s^{-1}) following the calibrations of 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 (intermediate difficulty category; Wilson *et al.*, 2014) using corresponding hourly Seton River temperatures in the following equation:

$$MO_2 = [2.81 + (0.89{\bullet}A) + (0.05{\bullet}T) - (0.03{\bullet}L) + 1.21 - (0.32{\bullet}A)]^2 \tag{2}$$

where A is RMS acceleration, T is water temperature and L is fork length. We calculated the degree to which anaerobic metabolism contributed to swimming in the dam tailrace (hereafter, 'anaerobic recruitment') for acoustic-tagged fish. To do this, we divided the amount of oxygen consumed after anaerobic swimming efforts (i.e. EPOC; Lee *et al.*, 2003a) by the total amount of oxygen consumed as a result of aerobic and anaerobic contributions to swimming. Anaerobic recruitment is expressed as a percentage, where higher values reflect the greater EPOC required to restore tissue and cellular oxygen

levels and re-establish metabolic homeostasis following burst swimming.

Acceleration data collected from three acoustic receivers on the northern bank of the Seton River adjacent to and in the radial gate spillway (Figure 2) were pooled and represent the swimming speeds from the 'radial gate spillway' area of the dam tailrace. Data from 10 acoustic receivers along the outer fishway wall and the receiver in the first pool of the fishway were combined and represent the swimming speed of sockeye salmon in the flows surrounding the fishway entrance. Within-fishway swimming speeds were pooled from four acoustic receivers positioned in the fishway (Figure 2). One acoustic receiver in the dam forebay provided swimming speeds upstream of the dam (Figure 2).

Spawning success assessment

We examined the gonads of PIT-tagged females that attempted to or spawned in the artificial spawning channel at Gates Creek. Dead fish in the channel were examined daily for spaghetti tags to locate PIT-tagged females. Once located, we recorded the date of death after attempted spawning. Knowing the date each fish arrived in the channel (via PIT-telemetry) and the date of death, we were able to quantify the length of time (in days) each female survived on spawning grounds (hereafter, longevity; Hruska *et al.*, 2011).

Most females had clearly spawned (virtually no eggs in body cavity) or had not spawned at all (eggs held tightly in the skein membrane). Using the same stock assessment techniques employed by Fisheries and Oceans Canada, we qualitatively assessed a female to have spawned if less than half of her eggs remained in the body cavity upon examination. Conversely, an unspawned female retained the majority (i.e. >90%) of her eggs. Acoustic-tagged sockeye salmon were sacrificed on spawning grounds via cerebral percussion to permit the re-deployment of acoustic accelerometer transmitters; thus, acoustic-tagged fish were not assessed for spawning success.

Statistical analyses

All data were examined for homoscedasticity, normality and independence. Welch's two-sample *t*-tests were used to compare the exposure of fish released under the two flow conditions with water temperatures and discharges in the Fraser River prior to dam passage. Non-parametric tests were used when assumptions of normality and homoscedasticity were not met. Mann–Whitney *U*-tests were used to compare the swimming speed and behaviour of acoustic-tagged sockeye salmon under the two flow conditions. We used Monte Carlo simulations to generate posterior distributions (95% credible intervals) around the

survival estimates (i.e. dam passage, post-passage survival to spawning grounds and survival from release to spawning grounds) of PIT-tagged sockeye salmon. Simulations drew 1000 samples from a binomial beta distribution.

We used a generalized linear model to predict the spawning success (family: binomial, link: logit) of the PIT-tagged females that entered the artificial spawning channel at Gates Creek. We were interested in the relative effect of dam flow condition on spawning success compared with the effects of individual spawning characteristics [i.e. longevity (Hruska *et al.*, 2011) and date of arrival (Dickerson *et al.*, 2005) on spawning grounds] that are known to contribute to egg retention in sockeye salmon. Our full model included three explanatory variables: (i) flow condition (alternative or baseline), (ii) longevity (in days) and (iii) Julian date of arrival on spawning grounds. All variables were tested for multicollinearity using variance inflation factors; all variables had a variance inflation factor <2 (Zuur *et al.*, 2010).

All candidate models were generated using the R (version 3.0.2; R Core Team, 2013) package 'MuMIn' (Barton, 2012) and compared using AICc (for small sample sizes) to determine the most parsimonious models. Relative effect sizes presented herein are from the top model from the candidate set that was well supported (i.e. AICc weight (w_i) two to three times that of other models). Model fits were evaluated using adjusted-R^2 values. All data are presented as means $\pm$ SEM unless otherwise noted. Statistical analyses were considered significant at $p < 0.05$.

RESULTS

Environmental conditions

Sockeye salmon exposed to alternative flows (9 to 18 August 2014) experienced significantly higher water temperatures ($t_{1099} = -28.1$, $p < 2.2 \times 10^{-16}$) and discharges ($t_{4229} = -86.4$, $p < 2.2 \times 10^{-16}$) in the Fraser River compared with fish exposed to baseline flows (20 August to 15 September 2014; Figure. 3). Gates Creek sockeye salmon exposed to alternative flows experienced water temperatures in the Fraser River consistently higher (range: 17.8–20.5 °C; Figure. 3) than the thermal optimal for aerobic scope for this population (i.e. >17.5 °C; Lee *et al.*, 2003b).

Dam passage

Tagging effort was in proportion to the sockeye salmon run, where the release of tagged fish mirrored the number of individuals passing through the fishway (Figure 4). We note that all tagged fish passed Seton Dam under the same flow condition they were released. Dam passage was 7% higher for acoustic-tagged (Table II) and 9% higher for PIT-tagged (Table III) sockeye salmon under the alternative flow condition. Both male and female PIT-tagged fish showed increased dam passage under alternative flows (8% and 10% increases, respectively; Table III). Under the alternative flow condition, acoustic-tagged sockeye salmon exhibited significantly more tailrace crossings (Mann–Whitney U-test, $p = 0.001$) and spent significantly more time below the dam ($p = 0.022$; Table II). Compared with baseline flow conditions, fish appeared to spend more time around the fishway entrance under alternative flows (Table II), although this difference was not significant (Mann–Whitney U-test, $p = 0.252$). Fish that experienced the baseline flow condition spent significantly more time in the dam forebay (Mann–Whitney U-test, $p = 0.001$; Table II) following dam passage. Anaerobic recruitment in the dam tailrace did not differ between the two flow conditions (Mann–Whitney U-test, $p = 0.350$; Table II). No significant differences were found when comparing the swimming speed of acoustic fish in the radial gate spillway
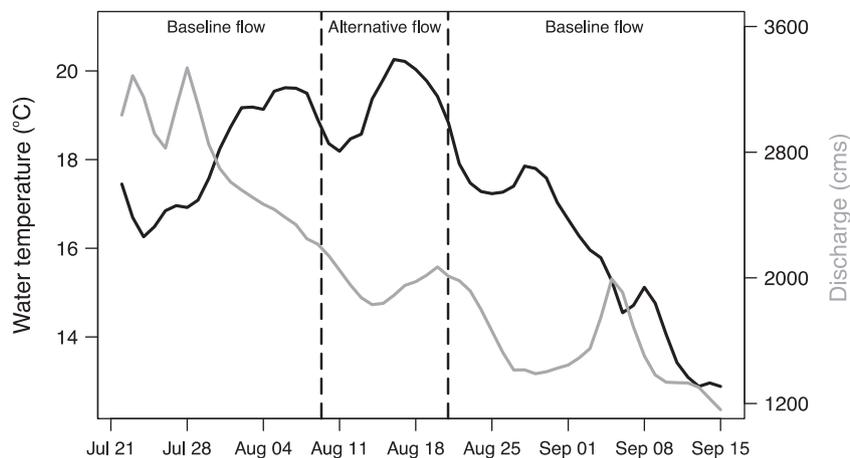
Figure 3. Mean daily Fraser River water temperature (black) and discharge (grey) at Texas Creek (10 km from Seton River) throughout the study period. Vertical lines denote the date that flow conditons were changed
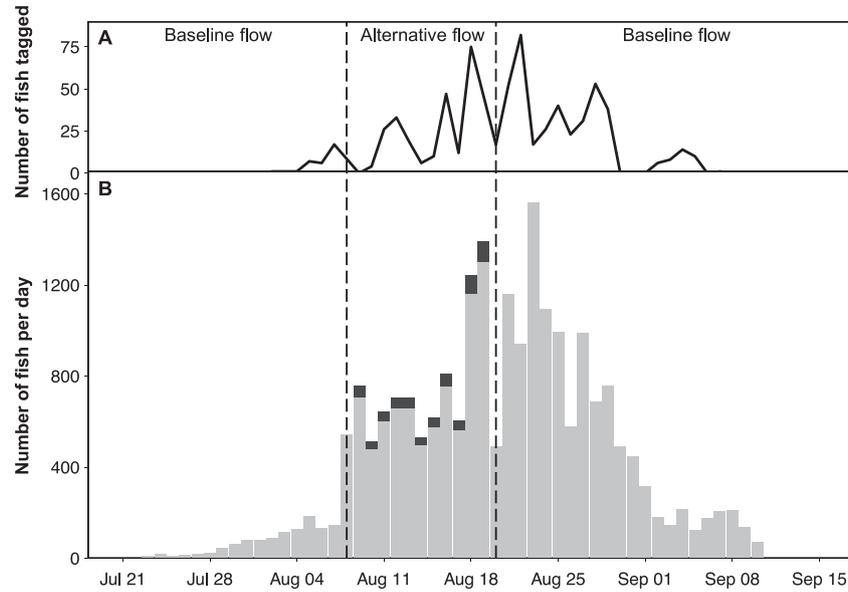
Figure 4. A. Number of sockeye salmon *Oncorhynchus nerka* tagged (acoustic and PIT) throughout the study period; B. Estimated number of fish that migrated from the top of the fishway to natal spawning grounds under baseline flows (grey) and the estimated number of additional survivors to spawning grounds (black) because of the testing of alternative flows. Vertical lines denote the date that flow conditons were changed

(Mann–Whitney U-test, $p = 0.404$), near the fishway entrance ($p = 0.516$), within the fishway ($p = 0.447$) and in the dam forebay ($p = 0.357$) under the two flow conditions (Figure 5).

Post-passage survival to spawning grounds

Post-passage survival to spawning grounds was 52% higher for acoustic-tagged (Table II) and 7% higher for PIT-tagged (Table III) sockeye salmon under the alternative flow condition. Both male and female PIT-tagged fish showed increased survival to spawning grounds under alternative flows (12% and 4% increases, respectively; Table III). Of the 27 192 sockeye salmon that passed the fishway, only 16 929 (62%) successfully migrated to natal spawning grounds. A 7% higher estimate

of post-passage survival to spawning grounds for PIT-tagged fish under alternative flows (Table III) assisted approximately 557 additional fish in reaching spawning grounds (Figure 4).

Survival from release to spawning grounds was 55% higher for acoustic-tagged (Table II) and 14% higher for PIT-tagged (Table III) fish under the alternative flow condition. Survival of acoustic-tagged sockeye salmon—that experienced baseline flows—through Seton Lake was 67% (18/27) and 72% (13/18) through Anderson Lake.

Spawning success

Once fish were on spawning grounds, dam flow condition did not significantly contribute to the model explaining

Table II. Behaviour and survival of acoustic-tagged sockeye salmon *Oncorhynchus nerka* under the baseline and alternative flow conditions

	Flow condition	
	Baseline	Alternative
Dam passage	93% (28/30)	100% (15/15)
Post-passage survival to spawning grounds	48% (13/27)	100% (15/15)
Survival from release to spawning grounds	45% (13/29)	100% (15/15)
Tailrace crossings	2.0 ± 0.2 times (1–4 times)	4.5 ± 0.8 times[a] (1–12 times)
Time in dam tailrace	10.0 ± 1.3 h (0.7–25.9 h)	18.8 ± 3.5 h[a] (1.6–50.9 h)
Entrance time: radial gate time	1.6 ± 0.2 (0.2–4.9)	5.4 ± 1.8 (0.3–20.4)
Anaerobic recruitment in tailrace	6.9 ± 1.6% (0.2–43.5%)	8.2 ± 2.1% (0.7–28.0%)
Time in dam forebay	1.1 ± 0.3 h[a] (0.3–8.7 h)	0.6 ± 0.3 h (0.2–5.4 h)

Values are given in means ± standard error; ranges are presented in parentheses.
[a]Significant differences ($p < 0.05$; Mann–Whitney U-test).

Table III. Survival of PIT-tagged sockeye salmon *Oncorhynchus nerka* under baseline and alternative flow conditions

	Flow condition					
	Baseline			Alternative		
	Males	Females	Combined	Males	Females	Combined
Dam passage	89%; 137/154	88%; 207/234	89%; 344/388 (85–92%)[a]	97%; 83/86	98%; 116/118	98%; 199/204 (94–99%)[a]
Post-passage survival to spawning grounds	77%; 105/137	84%; 174/207	81%; 279/344 (77–85%)	89%; 74/83	88%; 102/116	88%; 176/199 (83–92%)
Survival from release to spawning grounds	68%; 105/154	74%; 174/234	72%; 279/388 (67–76%)[a]	86%; 74/86	88%; 102/118	86%; 176/204 (81–90%)[a]

PIT, passive integrated transponder.
95% credible intervals from Monte Carlo simulations are presented in parentheses.
[a]Non-overlapping 95% credible intervals.
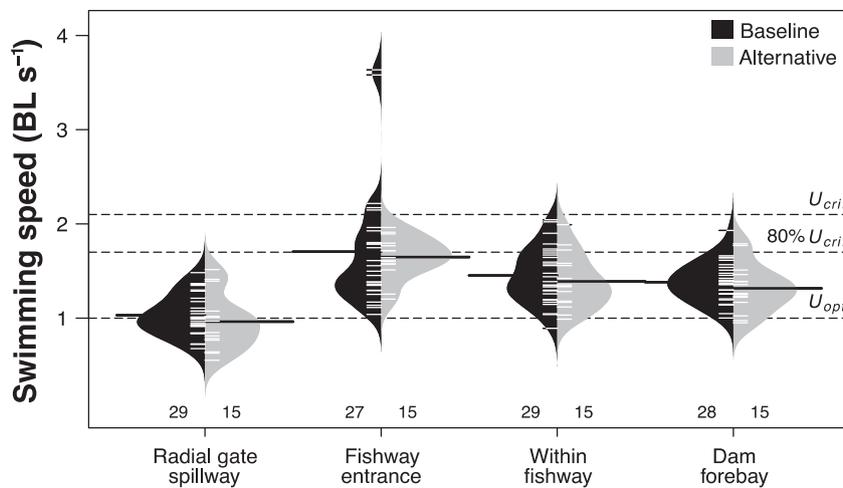
Figure 5. Swimming speed (BL s^{-1}) of acoustic-tagged sockeye salmon *Oncorhynchus nerka* under the baseline (black) and alternative flow conditions (grey) in the radial gate spillway, surrounding the fishway entrance, within the fishway and dam forebay. Shaded curved polygons (beans) depict the estimated density of the distribution of individual swimming speed values (white horizontal lines; mean: black horizontal line). Optimal (U_{opt}; 1.0 BL s^{-1}) and critical (U_{crit}; 2.1 BL s^{-1}) swimming speeds (Lee *et al.*, 2003a) are shown as dashed horizontal lines; the swimming speed at which anaerobic muscle fibres are recruited (80% U_{crit}) is also shown. Sample sizes (n) are presented below each bean. No statistical differences ($p > 0.05$; Mann–Whitney U-tests) were detected between the two flow conditions at the four sites

Table IV. AICc 95% confidence set of models relating longevity, date of arrival and dam flow condition to the spawning success of PIT-tagged female sockeye salmon *Oncorhynchus nerka*

Response variable	Model	log Lik	AICc	ΔAICc	w_i	adj-R^2
Spawning success	Longevity + date of arrival	−11.43	29.20	0.00	0.75	0.76
	Longevity + date of arrival + dam flow condition	−11.42	31.50	2.23	0.25	0.76

ΔAICc is the difference in AICc values between model *i* and the best model of those considered and w_i is the probability that a model is the best model of the set.

spawning success (Table IV). Instead, longevity and date of arrival on spawning grounds explained 76% of the variation in the spawning success data (Table IV). Longevity had two times the effect on spawning success compared with date of arrival on spawning grounds [relative effect size (95% confidence intervals): 11.8 (5.5–23.9) vs 5.4 (2.3–10.8)].

DISCUSSION

Flows from a diversion dam were experimentally altered to reduce water velocities around the entrance to a vertical-slot fishway during the upriver migration of sockeye salmon. Individuals exposed to alternative flows showed reduced recovery time following dam passage and significantly

higher post-passage survival to spawning grounds. Once on spawning grounds, female spawning success was largely governed by longevity and date of arrival on spawning grounds and not the flow condition an individual experienced during dam passage. However, this finding does not dispute our hypothesis, as releasing alternative flows resulted in a higher proportion of tagged fish surviving to spawning grounds.

Acoustic-tagged fish exhibited different behavioural responses to the two flow conditions tested herein. Sockeye salmon exposed to alternative flows made significantly more crossing attempts and spent more time downstream of the dam. Fish that make multiple approaches are more likely to pass this facility (Burnett *et al.*, 2014a, 2014b) and fish passage structures elsewhere (Gowans *et al.*, 1999). Laine (1995) suggests that this behaviour may allow individuals to become more accustomed to the entrances, flows and lowest pools of fishways. Regardless, more crossing attempts and time spent downstream of the dam under alternative flows clearly did not come at a cost to the upstream survival of acoustic-tagged fish, suggesting that the conditions may have been more benign. Notably, this finding challenges the concept that increased passage time or 'delay' downstream of migration barriers may have negative consequences for upstream survival (Caudill *et al.*, 2007). Following dam passage, acoustic-tagged sockeye salmon exposed to baseline flows spent significantly more time in the dam forebay (64.8 vs 38.4 min) compared with fish exposed to alternative flows. For context, using a swim tunnel respirometer, Lee *et al.* (2003a) found that Gates Creek sockeye salmon took 78.0 min to return to a routine metabolic rate ($MO_{2routine}$) following exhaustion at U_{crit}. Acoustic-tagged fish exposed to baseline flows showed a significantly longer recovery time after burst swimming through attraction flows. While we consistently observed swimming speeds exceeding U_{crit} in the tailrace (i.e. burst swimming), we found no differences in mean swimming speeds under the two flow conditions. It is possible that this finding is attributable to different detection ranges of acoustic receivers around the fishway entrance under high (baseline) and low (alternative) flow conditions. Collection of absolute swimming speed data may have only been possible if the location of flow releases was held constant throughout the study period.

We observed carryover effects of dam passage on survival and found that these effects were mediated by flow conditions. More specifically, sockeye salmon survival following passage was significantly lower under the baseline flow condition. We believe that this difference in survival is an underestimate, as fish that were exposed to alternative flows (early arriving fish) experienced significantly higher water temperatures (supraoptimal for aerobic scope; Lee *et al.*, 2003b) and discharges in the Fraser River. Further,

we might have observed a larger difference in survival had the fish that were released under both flow conditions experienced comparable migration conditions prior to dam passage. Research into carryover effects occurring in migratory animals is still in its infancy (Norris and Taylor, 2006), and despite decades of research examining fish passage at dams and other impediments, research continues to focus almost exclusively on short-term phenomena such as attraction and passage efficiency (Caudill *et al.*, 2007; Cooke and Hinch, 2013) and not survival following passage. Even if a fish passage structure is 'effective' at passing fish, researchers should consider monitoring upstream survival to improve the information provided to natural resource managers and conservation practitioners. Conclusions and management recommendations of the current study would have been much different had survival to spawning grounds not been assessed. We may have concluded that baseline flows were more suitable for passing fish given the reduced time spent below the dam. Our estimates of post-passage survival to spawning grounds suggest that the opposite is true—that the release of alternative flows benefits salmon. With the potential for dam passage to manifest into a carryover effect, we caution applied practitioners about only using estimates of dam passage as measures of success in fish passage studies and emphasize the need to monitor upstream survival, especially for migratory species with challenging migrations.

We estimate that of the 27 192 sockeye salmon that passed the fishway, only 16 929 (62%) successfully migrated to natal sites in 2014. Indeed, this mortality is significant when one considers the proximity of Seton Dam to natal spawning grounds (55 km) and the relatively benign migration conditions fish encounter in upstream lakes. Given that approximately 7% more fish survived to spawning grounds under the alternative flow condition, we estimate that this would translate into 557 additional survivors (3% of total spawners) to natal sites. Of course, this estimate describes the number of fish that were assisted during the current management experiment, where alternative flows were tested for only 10 days near the peak of a 5- to 6-week-long migration. Had these flow conditions been in place throughout the entire run, we estimate that up to 1517 sockeye salmon (applying 7% difference over migration period) could have been assisted to spawning grounds. Further, we believe that the number of additional survivors presented herein is a conservative estimate for four key reasons: (i) we applied the mean survival of PIT-tagged fish to daily estimates of abundance through the fishway and not the extreme estimates from either side of the credible range; (ii) survival estimates from PIT-tagged fish were consistently lower than those generated from acoustic-tagged fish; (iii) our estimate of additional survivors does not take into account the significant difference in dam passage under

each flow condition, as only the post-passage survival to spawning grounds data from PIT-tagged fish can be extrapolated to resistivity counter data; and (iv) fish released under alternative flows experienced significantly higher water temperatures and discharges in the Fraser River prior to dam passage. Regardless of the absolute number of fish assisted to spawning grounds under alternative flows, that migration success could be enhanced without affecting downstream flow requirements is an important finding. Considering this has no negative implications on hydropower operation, and that the alternative flow condition is a potentially viable operational change at this facility, managers could consider implementing this flow condition to mitigate physiological stress in years when fish encounter challenging migration conditions (non-optimal water temperatures and discharges) prior to dam passage. Finally, by enabling more fish to pass the dam, this provides additional opportunities for harvest in the future.

As a final carryover effect, we examined the potential for dam passage to influence female spawning success, as stress can impair the reproductive output of vertebrates. Dam passage can be acutely stressful (Burnett et al., 2014a) and could reduce the energy available to females for reproduction. Biotelemetry studies on migratory fish species often use spawning grounds (Roscoe et al., 2011), or even natal watersheds (e.g. Donaldson et al., 2011), as migration end-points, failing to account for the mortality that occurs in natal streams prior to spawning (up to 90% in some Fraser River sockeye salmon; reviewed by Hinch et al., 2012). Little research has linked migratory stressors to individual reproductive consequences on spawning grounds (Hruska et al., 2011). Despite an improvement in upstream survival, we found no evidence that dam flow condition influenced the spawning success of females that successfully reached spawning grounds. McConnachie et al., (2012) exhaustively exercised and air-exposed pink salmon (*Oncorhynchus gorbuscha*) upon arrival on spawning grounds and found no evidence that these acute stressors impaired female spawning success. Maternal exposure to an acute stressor close to (current study) and on spawning grounds (McConnachie et al., 2012) does not appear to influence the ability of females to spawn. Instead, our results suggest that spawning success is strongly influenced by the length of time a female can survive on spawning grounds (Hruska et al., 2011) and the date of arrival (Dickerson et al., 2005). Females with greater longevity have considerably more time to locate mates and suitable habitat for redds and defend the nest from later spawning females. And yet, with greater longevity comes an increased likelihood of physical injury or immediate mortality from terrestrial and avian predators. Stressful dam passage could have intergenerational effects on the life history and survival traits of juvenile salmon, with recent research suggesting that female sockeye salmon forced to burst swim can rear emergent fry with superior burst swimming capacity (Sopinka et al., 2014). Dam flow condition did not influence female spawning success in the current study; however, baseline flows effectively reduced the number of spawners and thus the potential productivity of the population.

Managing dynamic ecosystems is a constantly evolving, iterative process that must reflect our best scientific knowledge (Walters and Hilborn, 1978). Natural resource managers often rely on applied ecological research to make responsible environmental management decisions. Current approaches, novel technologies, interdisciplinary communication and collaborative partnerships among stakeholders should be employed to effectively address management objectives (McLain and Lee, 1996; Memmott et al., 2010). Recent and significant advances in biotelemetry technology have provided aquatic ecologists with effective tools to investigate the mechanisms underlying post-release behaviour and survival (Wilson et al., 2015). We used multiple biotelemetry and enumeration techniques in the current study, allowing us to cross-validate technologies and determine if trends scale up from individual animals to the population level (Cooke and Hinch, 2013). We acknowledge that the alternative flow condition tested herein may not be the 'best case scenario' for fish passage, but simply a less-impactful operation out of a suite of possible management options. Continued flow manipulation experiments are required to understand if further improvements can be made.

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