

Burst Swimming in Areas of High Flow: Delayed Consequences of Anaerobiosis in Wild Adult Sockeye Salmon

Nicholas J. Burnett^{1,2,*}

Scott G. Hinch²

Douglas C. Braun^{2,3}

Matthew T. Casselman²

Collin T. Middleton²

Samantha M. Wilson²

Steven J. Cooke²

¹Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, Ottawa, Ontario K1S 5B6, Canada; ²Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; ³InStream Fisheries Research, Vancouver, British Columbia V5M 4V8, Canada

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ABSTRACT

Wild riverine fishes are known to rely on burst swimming to traverse hydraulically challenging reaches, and yet there has been little investigation as to whether swimming anaerobically in areas of high flow can lead to delayed mortality. Using acoustic accelerometer transmitters, we estimated the anaerobic activity of anadromous adult sockeye salmon (*Oncorhynchus nerka*) in the tailrace of a diversion dam in British Columbia, Canada, and its effects on the remaining 50 km of their freshwater spawning migration. Consistent with our hypothesis, migrants that elicited burst swimming behaviors in high flows were more likely to succumb to mortality following dam passage. Females swam with more anaerobic effort compared to males, providing a mechanism for the female-biased migration mortality observed in this watershed. Alterations to dam operations prevented the release of hypolimnetic water from an upstream lake, exposing some migrants to supraoptimal, near-lethal water temperatures (i.e., 24°C) that inhibited their ability to locate, enter, and ascend a vertical-slot fishway. Findings from this study have shown delayed post-dam passage survival consequences of high-flow-induced burst swimming in sockeye salmon. We highlight the need for studies to investigate whether

dams can impose other carryover effects on wild aquatic animals.

Introduction

Reproductive migrations are challenging life-history stages, particularly for semelparous species that are limited to a single opportunity to secure lifetime fitness (Dingle 1996). Animals that travel through freshwater to reach their breeding grounds are vulnerable to changes in environmental conditions that are known to dictate their migration success (e.g., river discharge: Rand et al. 2006; water temperature: Farrell et al. 2008; Martins et al. 2012). On a global scale, river systems have become increasingly regulated through the construction of dams, generating highly variable flow and thermal regimes that are energetically demanding environments to traverse (Rosenberg et al. 2000; Preece and Jones 2002; Nilsson et al. 2005). Designed to mitigate these issues, fish passage structures (e.g., fishways and fish locks; Katopodis 1992; Clay 1995) aim to restore connectivity to regulated or constrained watersheds by facilitating the upstream passage of migratory fishes without imposing detrimental effects on fitness (Castro-Santos et al. 2009; Bunt et al. 2011). Much of the fish passage research to date has focused on enumerating passage success at a single dam (Cooke and Hinch 2013), with comparatively little mechanistic research evaluating whether exposure to these velocity barriers can lead to delayed post-dam passage mortality (Caudill et al. 2007).

Anadromous adult Pacific salmon (*Oncorhynchus* spp.) undertake physiologically and energetically challenging migrations from oceanic feeding grounds to natal freshwater spawning sites. Somatic energy conservation plays a central role in this final life-history stage, as these animals cease feeding upon river entry and rely on fixed ocean-accrued energy reserves to fuel their movements and reproduction (Brett 1995; Crossin and Hinch 2005). Energy-conserving traits are strongly selected for; migrants with spawning areas further inland are more streamlined and smaller, exhibit a more efficient swimming gait, have an 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). Fraser River sockeye salmon (*Oncorhynchus nerka*) populations (British Columbia, Canada) are locally adapted to the historic temperature conditions encountered upon river entry (Eliason et al. 2011). Consequently, reductions in whole-animal performance and mortality can result when individuals are exposed to conditions above their optimal temperature for aerobic scope (T_{opt} ; Lee et al. 2003b;

* Corresponding author; e-mail: nich.burnett@gmail.com.

Farrell et al. 2008; Eliason et al. 2013). Indeed, it is concerning that Fraser River summer temperatures have increased by 2°C since the 1950s (Patterson et al. 2007) and that this warming trend is anticipated to continue in the future (Hague et al. 2011). Several studies have demonstrated that migrants exposed to high flows can exhibit energy depletion, physiological stress, and migration failure in naturally constrained reaches and regulated watersheds (Rand et al. 2006; Nadeau et al. 2010; Roscoe et al. 2011). Sockeye salmon are both sensitive and vulnerable to river fragmentation, whereby human-made alterations to the migration corridors of this species can affect habitat quality, population sizes, community structure, and ecosystem function (Nehlsen et al. 1991; Slaney et al. 1996). As such, sockeye salmon are an exemplary species for investigating the effects of dam operations on swimming activity and behavior, given that any marked increase in migration difficulty could lead to population-level consequences.

Sex-specific differences in sockeye salmon energy use, behavior, and survival are more apparent in areas with challenging migration conditions (Hinch and Rand 1998; Standen et al. 2002; Roscoe et al. 2011). For example, mortality is exacerbated in females that are exposed to high in-river temperatures and elevated water velocities (Martins et al. 2012 and Nadeau et al. 2010, respectively). In regulated watersheds, female sockeye salmon exhibit lower passage success at dams and suffer exceptionally high levels of en route and prespawn mortality following dam passage (Roscoe et al. 2011; Burnett et al. 2013a). Evidence suggests that high levels of anaerobic swimming by females in areas of high flow may contribute to the female-biased mortality trends often observed post-dam passage (Burnett et al. 2013a). Crossin et al. (2008) hypothesized that female sockeye salmon may be more sensitive to environmental stressors due to their increased energetic investment into gonad development compared to males. Future research aimed at understanding the mechanisms underlying these data will better inform the conservation and management of Pacific salmon. Linking sockeye salmon swimming activity and behavior to detailed flow releases from a dam may shed valuable insight into the individual-level sex-specific responses to challenging migration conditions.

Fish exhibit a diverse set of swimming strategies to facilitate movement over a range of speeds and acceleration rates (Webb 1995). Optimal strategies are selected to reduce the drag and transport costs associated with moving through water (Weihs 1974; Videler 1993). Pacific salmon employ burst-and-coast swimming in areas of fast-flowing water to benefit from significant energy savings and reduced physiological stress (Weihs 1974; Videler and Weihs 1982; Videler 1993). Both aerobic and anaerobic metabolic pathways (slow-red and fast-white muscle fibers, respectively) contribute to the burst-and-coast swimming effort (Burgetz et al. 1998). Anaerobic metabolic pathways exclusively power swimming at speeds exceeding their critical swimming speed (U_{crit}), where short bouts of burst (or sprint) swimming are fueled by the breakdown of glycogen in white muscle fibers (Black et al. 1966). Wild sockeye salmon elicit glycolytic-based burst swimming behaviors to negotiate and

minimize exposure to areas with energetically demanding high flows (Hinch and Bratty 2000; Standen et al. 2002; Brown et al. 2006). Lactate anions and metabolic protons accumulate in the swimming muscle of fish as a result of depleting glycogen reserves, resulting in a cascade of metabolic disturbances (Wood et al. 1983; Wood 1991). Following exhaustive exercise, sockeye salmon require additional oxygen uptake (known as excess postexercise oxygen consumption [EPOC]) and long recovery times to reestablish ion gradients, lactate processing, and pH balance and restore tissue and cellular oxygen levels (Lee et al. 2003a). Furthermore, if sockeye salmon experience temperatures above T_{opt} while swimming at U_{crit} , cardiorespiratory collapse can occur due to an insufficient scope for heart rate (Eliason et al. 2013). Migrants that fail to reestablish metabolic homeostasis can perish hours or even days after prolonged periods of severe muscular exertion (Black 1958; Priede 1977; Wood et al. 1983), although field studies of that phenomenon are lacking. Despite our understanding of the physiological consequences associated with anaerobiosis, there is a growing need to investigate whether burst swimming by sockeye salmon in areas of difficult passage has carryover effects on migratory behavior and survival (Caudill et al. 2007; O'Connor et al. 2014).

We studied sockeye salmon migration through a dam tailrace and vertical-slot fishway in southwestern British Columbia, Canada, to determine the effects of anaerobiosis on dam passage success and postpassage survival. We hypothesized that dam operations would provide a significant hydraulic challenge for migrating sockeye salmon to overcome, requiring individuals to use burst swimming behaviors to negotiate high flows surrounding the fishway entrance. We predicted that (1) increased use of anaerobic metabolic pathways would reduce post-dam passage survival and (2) females would exhibit a higher degree of failure in dam passage and ability to reach natal sites compared to males. To our knowledge, this research is the first field-based study to reveal the delayed consequences of burst swimming on the spawning migrations of wild adult Pacific salmon.

Methods

Study Site

We studied the swimming activity and behavior of adult Gates Creek sockeye salmon below Seton Dam (operated by BC Hydro) in the Seton-Anderson watershed, British Columbia, Canada. At a distance of 350 km from the Pacific Ocean, migrants encounter Seton Dam, a diversion dam that spills excess water down the Seton River and redirects upward of 125 m³ s⁻¹ down a 3.8-km-long power canal to a powerhouse station on the Fraser River (fig. 1). Adult sockeye salmon must locate and ascend a vertical-slot fishway (32 pools, 2 turning basins, 107 m long, 6.9% grade, discharge [mean ± SE]: 1.2 ± 2.0 × 10⁻³ m³ s⁻¹) to pass the dam and complete the remaining 55 km of their reproductive migration. Flows from the fish water release gate (FWRG) and siphon 1 are used to attract fish toward the fishway entrance, while excess water spills through

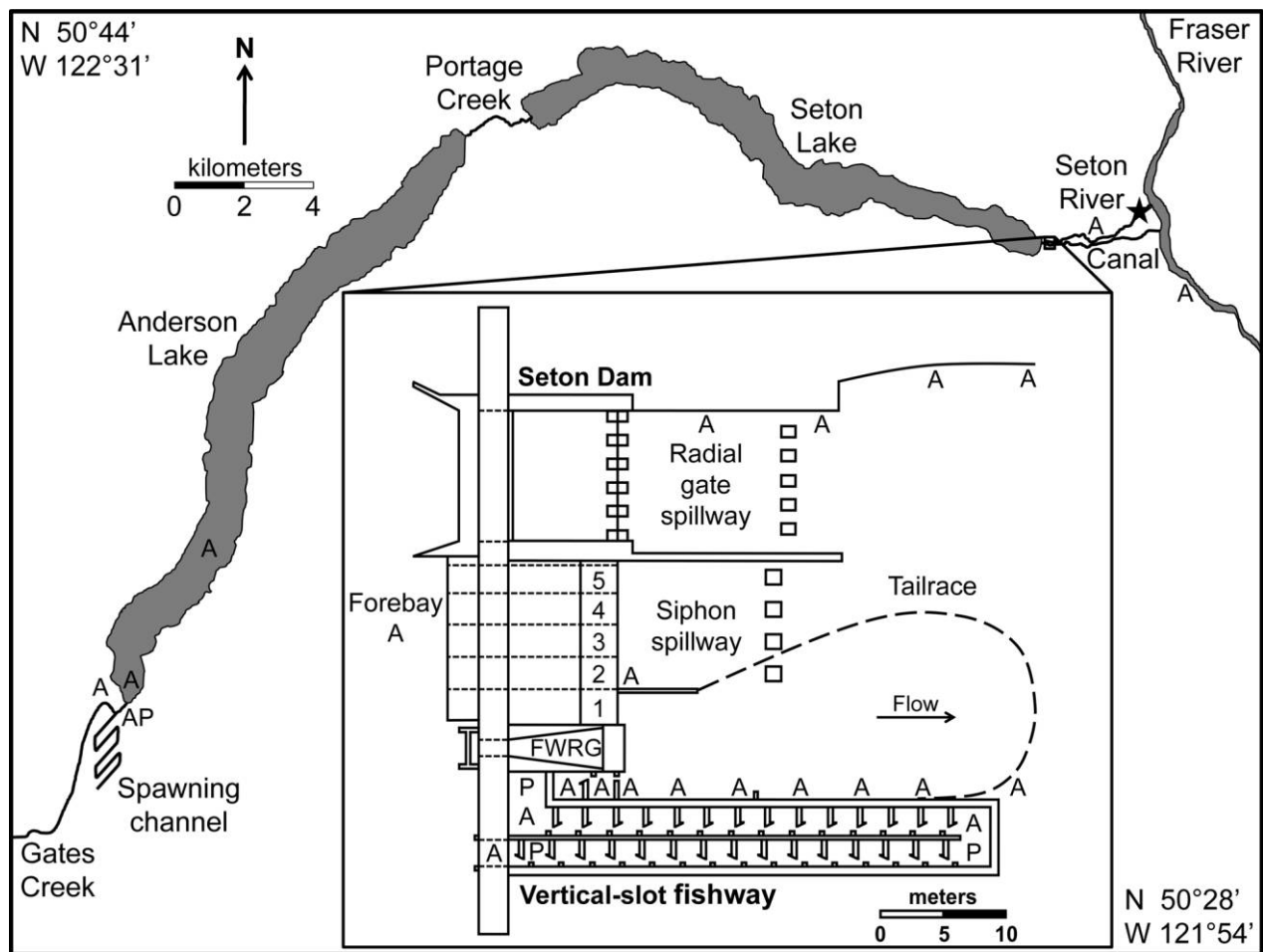


Figure 1. Map of the Seton-Anderson watershed in southwestern British Columbia, Canada; the natal spawning streams of Gates Creek sockeye salmon (*Oncorhynchus nerka*); and the location of Seton Dam and vertical-slot fishway (inset). Dashed trace within the inset represents the high flows from the fish water release gate and siphon 1. A = acoustic receiver; P = pass-through passive integrated transponder antenna; star = release site for fishway-nonnaive individuals.

the remaining four siphons and/or radial gate spillway (fig. 1, inset).

Fish Capture, Tagging, and Tracking

All fish were captured, handled, and tagged in accordance with the guidelines of the Canadian Council on Animal Care administered by the University of British Columbia Committee (A11-0125) and Carleton University Animal Care Committee (B12-6). Sixty-three adult Gates Creek sockeye salmon were captured, tagged, and released from August 3 to August 27, 2013. Twenty-eight individuals (14 males, 14 females) were dip-netted from the top pool of the fishway (hereafter, fishway nonnaive), transported 50 m off of the dam in an oxygenated, insulated 1,000-L transport tank, and held for upward of 2 h in a 5,000-L holding tank prior to sampling and tagging. Thirty-five individuals (18 males, 17 females) were captured by means of a full-spanning fence and trap (ca. 50 m long) located 200 m downstream of the dam in the Seton River (hereafter, fishway

naive) and were held temporarily in a flow-through holding pen prior to sampling and tagging. Fish were individually transferred to a V-shaped, foam-padded trough containing continuously flowing Seton River water directed toward the gills.

Triaxial accelerometers have become common tools in ecology to monitor energy use and behavior in wild animals (Wilson et al. 2006; Gleiss et al. 2010; Brown et al. 2013). Of late, accelerometer sensors have been incorporated into acoustic telemetry transmitters that can be gastrically implanted into anadromous fishes that have ceased feeding (Wilson et al. 2013). In the stomach, transmitters are positioned at the center of mass to avoid large errors generated by centripetal acceleration (Videler 1993). Acoustic accelerometer transmitters (model V13A-1x, 69 kHz, 16 mm × 52 mm; VEMCO, Halifax) were inserted into the stomach cavity of all 63 sockeye salmon by means of a plastic plunger (Cooke et al. 2005). A DNA clip was obtained from the adipose fin for stock identification, fork length (FL) was measured to the nearest 5 mm (57.7 ± 0.4

cm, range: 49.0–62.5 cm), and sex was estimated on the basis of secondary sexual characteristics present at this stage in the freshwater migration (e.g., male hump and kype). DNA analyses confirmed that all study subjects were of Gates Creek origin (Beacham et al. 2004). Fish were fitted with an external spaghetti tag (Floy Manufacturing, Seattle) attached posterior to the dorsal fin to aid in visual identification. A half-duplex passive integrated transponder (PIT) tag (32 mm × 3.65 mm; Texas Instruments, Dallas) was inserted into the dorsal musculature of each fish using a sterile 6-gauge needle. Tagging and sampling took less than 2 min to complete, and fish were not anesthetized to minimize handling time and related stress (Cooke et al. 2005). Fishway-nonnaive fish were transported and released 4 km downstream (50°40'N, 121°55'W) of Seton Dam (fig. 1, star); fishway-naive fish were released directly above the fish fence.

A fixed acoustic array consisting of 18 single-channel receivers (VR2 and VR2W, 69 kHz; VEMCO) was installed in the Seton Dam tailrace to remotely record the swimming activity and behavior of tagged fish (fig. 1, *inset*). Prior to the study period, the detection ranges of acoustic receivers were tested to ensure that no single acoustic transmission was detected on multiple receivers. Three pass-through PIT antennas (2.2 m × 0.7 m) were positioned on the upstream-facing side of the vertical-slot baffles at the entrance, second turning basin, and exit of the fishway (fig. 1, *inset*). PIT antennas were constructed out of 3.8-cm watertight polyvinyl chloride pipe with 12-gauge stranded electrical wire; each antenna was connected to a remote tuner box (Oregon RFID, Portland, OR), and all three antennas were connected to a multiplexor unit (Oregon RFID) via twin-axial cable (see Burnett et al. 2013b). PIT antennas within the fishway were manually tuned and tested prior to daily tagging to ensure optimal read range (~0.5 m) and tag-reading performance (see “Results”). A three-antenna PIT array was also installed at the Gates Creek spawning channel to determine whether migrants had reached spawning grounds. Two VR2W receivers were installed in Gates Creek and were positioned at the channel entrance to ensure optimal tag-reading performance. Detection efficiencies of acoustic- and PIT-telemetry arrays were calculated using the methods of Burnett et al. (2013b) and have been presented in “Results.”

Fishway attraction efficiency (number of fish that located and entered the fishway divided by the total number of fish that reached the dam tailrace postrelease) and passage efficiency (number of fish that passed the fishway divided by the number of fish that located and entered the structure) were determined using a combination of acoustic- and PIT-telemetry data. Following Burnett et al. (2013a), we quantified the total amount of time (in h) each fish spent within the dam tailrace before eventual pass or fallback (hereafter, tailrace delay), as well as the number of times each individual crossed the tailrace from the radial gate spillway toward the fishway entrance (hereafter, tailrace crossings). Hourly Seton River water temperatures were recorded from the top pool of the fishway using a TidbiT v2 water temperature data logger (Onset HOB0 data loggers, Bourne, MA).

Swimming Activity Analyses

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 are then averaged for that 10-s period (root mean square [RMS] acceleration = $(X^2 + Y^2 + Z^2)^{0.5}$) 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 and relationships of Wilson et al. (2013). Acceleration data were further converted to estimates of oxygen consumption (Mo₂, mg O₂ kg⁻¹ min⁻¹) for Fraser River early summer run sockeye salmon using corresponding hourly Seton River temperatures. We strove to develop a model that incorporated a metric of the physiological differences of sockeye salmon populations, as well as acceleration, to predict Mo₂. Swimming speed data from Eliason et al. (2011) were used to estimate acceleration values based on a previously developed model (Wilson et al. 2013). Predicted acceleration values from Early Stuart, Chilko, Nechako, Quesnel, Lower Adams, Bowron, and Raft populations (Eliason et al. 2011) and actual acceleration values from acoustic-tagged Harrison River sockeye salmon (Wilson et al. 2013) were correlated with Mo₂ values from swim trials using a mixed-effects model. RMS acceleration, temperature, FL, tunnel, acclimation rate, instrumentation, and either run timing group, population, or migration difficulty index (see Wilson et al. 2014) were used as possible fixed effects to build candidate models. Subject ID was held as a random factor to account for nonindependence of data, and a 95% confidence set was used (all models with cumulative summed second-order Akaike Information Criterion [AIC_c] weights [w_i] ≥ 0.95; Burnham and Anderson 2002). Mo₂ for Gates Creek sockeye salmon (intermediate difficulty category) was predicted using the simplified model:

$$\begin{aligned} \text{Mo}_2 = & [2.81 + (0.89 \times \text{RMS acceleration}) \\ & + (0.05 \times \text{water temperature } (^{\circ}\text{C})) \\ & - (0.03 \times \text{FL}) + 1.21 \\ & - (\text{RMS acceleration} \times 0.32)]^2. \end{aligned}$$

For each study subject, we calculated the degree to which anaerobic glycolysis contributed to swimming in high flows surrounding the fishway entrance (hereafter, anaerobic recruitment). To do this, we divided the amount of oxygen consumed after anaerobic swimming efforts (i.e., EPOC; see Lee et al. 2003a) by the total amount of oxygen consumed as a result of aerobic and anaerobic contributions to swimming (see Burnett et al. 2013a for a detailed description). Anaerobic recruitment is expressed as a percentage, where higher values reflect the greater EPOC required to restore tissue and cellular oxygen levels and reestablish metabolic homeostasis following anaerobiosis. Acceleration data collected from four acoustic receivers on the northern bank of the Seton River adjacent to and in the radial gate spillway (fig. 1, *inset*) were pooled and represent the swimming speeds from the “radial gate spillway” habitat (ca. 300 m²; low flow area). Data from seven 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 high flows surrounding the fishway entrance (ca. 400 m²). Within-fishway swimming speeds were pooled from four acoustic receivers positioned in the fishway (fig. 1, inset).

Model Selection, Multimodel Averaging, and Inference

Generalized linear models (GLMs) were used to predict dam passage (family: binomial, link: logit), anaerobic recruitment (family: Gaussian, link: identity), and tailrace crossings (family: Poisson, link: log) by Gates Creek sockeye salmon. A final GLM was used to predict the ability of migrants who successfully passed Seton Dam to reach spawning grounds in Gates Creek (family: binomial, link: logit). Seven explanatory variables (biotic and abiotic) were included in each of the four model sets unless that variable was in fact the response variable. Biotic explanatory variables included (1) sex (male [1], female [0]), (2) anaerobic recruitment (%), (3) tailrace delay (h), and (4) tailrace crossings. Abiotic explanatory variables included (5) the maximum Seton River temperature (°C) and (6) mean flows (m³ s⁻¹) from siphon 1 each individual fish experienced while present in the dam tailrace. Cooke and Hinch (2013) reason that capture location (i.e., use of fishway-naïve and fishway-nonnaïve fish) affects the ability of migrants to locate, enter, and ascend a fishway. Therefore, we included capture location (7; fence caught [1] or fishway caught [0]) as a fixed factor in all models to account for its effects when testing our main hypothesis. However, we do present the relative effect of capture location on all response variables to show the importance of

considering capture location when conducting and interpreting the results of fish passage studies (Cooke and Hinch 2013). All variables were tested for multicollinearity using variance inflation factors (VIFs); flows from the FWRG were collinear (VIF > 3) with the maximum Seton River water temperature fish experienced (Zuur et al. 2010). Consequently, FWRG was removed as an explanatory variable, as the discharge from siphon 1 provided the vast majority of encountered flows below the dam during the study period. We did not model attraction efficiency because only one individual failed to pass the fishway after locating and entering the structure (i.e., 98% passage efficiency); therefore, results would be nearly identical to those of the dam passage model. Tailrace crossings was not included as an explanatory variable in the dam passage model, as it was highly collinear with both attraction and passage efficiency. Nine individuals (two males, seven females) were omitted from the analyses due to a failure to reach the tailrace postrelease; thus, a total of 54 Gates Creek sockeye salmon (fishway non-naïve: 19 total, 12 males, 7 females; fishway naïve: 35 total, 18 males, 17 females) were included in the four models.

All candidate models were generated using the R (ver. 3.0.2; R Development Core Team 2012) package “MuMIn” (Barton 2012) and compared using AIC_c to determine the most parsimonious models. 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). Average parameter estimates were calculated using the natural average method (Grueber et al. 2011) and a 95% confidence set (Burnham and Anderson 2002). We standardized all data by centering (subtracting the mean) and dividing by 2 SD (Gelman 2008), allowing for the

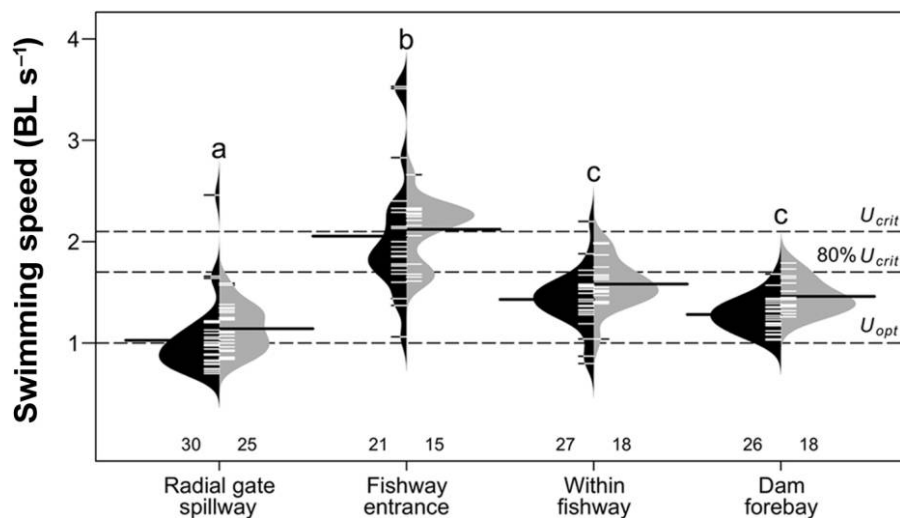


Figure 2. Beanplot (black horizontal lines = means) comparing the swimming speed (body lengths per second [BL s⁻¹]) of male (black) and female (gray) Gates Creek sockeye salmon (*Oncorhynchus nerka*) in the radial gate spillway, surrounding the fishway entrance, within the fishway, and in the dam forebay. Shaded curved polygons (beans) depict the estimated density of the distribution of individual swimming speed values (white horizontal lines). Optimal (U_{opt} ; 1.0 BL s⁻¹) and critical (U_{crit} ; 2.1 BL s⁻¹) swimming speeds are shown as dashed horizontal lines; the swimming speed at which anaerobic muscle fibers start to be recruited (80% U_{crit}) is also shown. Sample sizes (n) are presented below each bean, and lowercase letters represent significant differences ($P < 0.05$) from one-way ANOVA and Tukey post hoc tests.

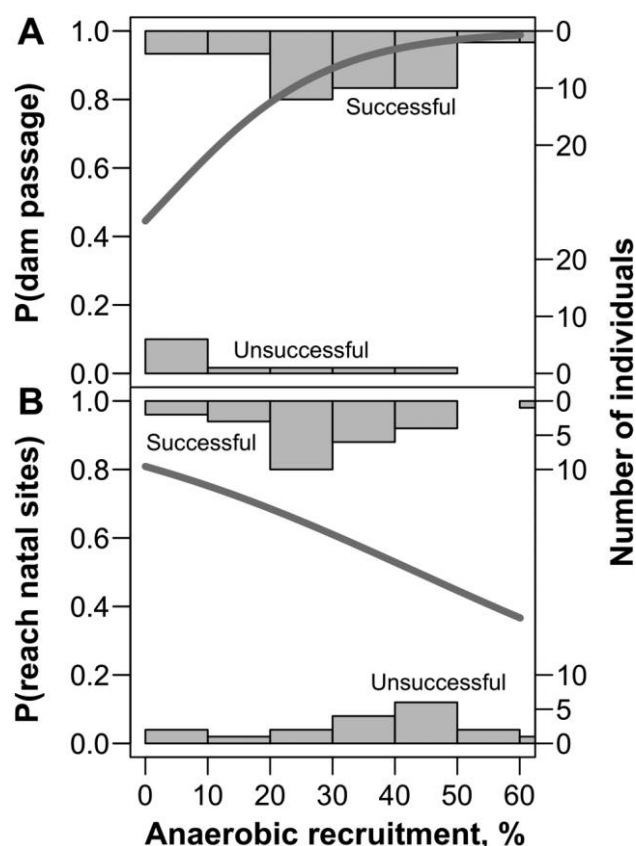


Figure 3. Predicted probability of Gates Creek sockeye salmon (*Onchorhynchus nerka*) passing Seton Dam (A; $n = 54$) and reaching natal spawning streams (B; $n = 44$), visualized by fitting a logistic regression to the anaerobic recruitment of successful and unsuccessful migrants. A color version of this figure appears online.

direct comparison of the relative effect sizes of explanatory variables. Model-averaged standardized coefficients for binary explanatory variables were exponentiated to provide an interpretable odds ratio. Model fits were evaluated using the percentage and significance of deviance explained by a GLM (Kindt and Coe 2005). A one-way ANOVA and Tukey post hoc tests were used to compare the swimming speeds of male and female Gates Creek sockeye salmon. Residuals were examined for homoscedasticity, normality, and independence. Data are presented as mean $\pm$ SE throughout, and statistical analyses were considered significant at $\alpha = 0.05$.

Results

Seton River temperatures during the study period ($19.3^\circ \pm 0.1^\circ\text{C}$, range: 16.0° – 23.7°C) were consistently above the thermal optima for Gates Creek sockeye salmon (i.e., 17.5°C ; Lee et al. 2003b). Acoustic receivers in the radial gate spillway (100% [$n = 54$]), fishway entrance area (80% [$n = 45$]), within the fishway (100% [$n = 45$]), and in the dam forebay (100% [$n = 44$]) were all effective at detecting acoustic-tagged sockeye salmon. PIT arrays within the Seton Dam fishway and at the

Gates Creek spawning channel had high detection efficiencies ($91.7\% \pm 6.1\%$ [$n = 44$] and $89.6\% \pm 1.6\%$ [$n = 25$], respectively).

Dam Passage

Anaerobiosis was required to reach the fishway entrance (fig. 2) and pass the dam (fig. 3A; table 1). Fish exposed to warmer water temperatures while in the dam tailrace were less likely to locate, enter, and ascend the fishway (fig. 4; table 1). Compared to females, male Gates Creek sockeye salmon were 17% ($e^{2.85}$) more likely to locate and enter the fishway and 9% ($e^{2.24}$; fig. 5A) more likely to pass the dam. Males made significantly more crossing events (1.37 ± 0.16 times, range: 0–4 times) toward the fishway entrance compared to females (0.88 ± 0.13 times, range: 0–2 times; fig. 5C). Anaerobic recruitment, maximum Seton River temperature, and sex formed the top-ranked dam passage model, explaining 50% of the variation in the data after accounting for capture location (table 1). Capture location, anaerobic recruitment, sex, and maximum temperature had similar effect sizes (fig. 5A). Fishway-naïve individuals were 15% ($e^{2.68}$) more likely to locate and enter the fishway entrance and 16% ($e^{2.74}$; fig. 5A) more likely to pass Seton Dam.

Anaerobiosis in Areas of High Flow

Fish that experienced higher flows from siphon 1 showed higher anaerobic recruitment near the fishway entrance (fig. 5B). Individuals that traversed the high flows multiple times used more anaerobic effort compared to fish that made fewer crossings of the tailrace (fig. 5B). Females swam with more anaerobic effort in areas of high flow compared to males (fig. 5B; table 1). Fishway-naïve individuals relied more on anaerobic glycolysis near the fishway entrance compared to fishway-nonnaive individuals (fig. 5B). Flows from siphon 1, sex, and tailrace crossings formed the top-ranked anaerobic recruitment model, explaining 46% of the variation in the data after accounting for capture location (table 1). Swimming at their U_{crit} (2.1 BL s^{-1}), fish swam significantly faster in the fishway entrance area compared to all other areas of the dam (one-way ANOVA, $F = 70.94$, $\text{df} = 3$, $P < 2 \times 10^{-16}$; fig. 2). Fish swam faster within the fishway and in the dam forebay compared to when delaying in the radial gate spillway (one-way ANOVA; fig. 2). Four females swam at 80% U_{crit} while in the fishway entrance area, while 11 other females swam consistently above U_{crit} (fig. 2).

Migration Success to Spawning Grounds

Individuals that used more anaerobic effort near the fishway entrance were less likely to reach natal spawning streams compared to fish that swam more conservatively (fig. 3B). Anaerobic recruitment had an equal but opposite effect on fish reaching breeding grounds as capture location (fig. 5D). Anaerobic recruitment affected the ability of dam-successful migrants to reach natal sites, explaining 30% of the variation in the data after accounting for capture location (table 1). Fishway-naïve

Table 1: Model selection statistics for generalized linear models predicting dam passage (A), anaerobic recruitment in areas of high flow below Seton Dam (B), tailrace crossings (C), and the ability of Gates Creek sockeye salmon (*Oncorhynchus nerka*) to reach natal spawning streams (D)

Response variable and model	Log likelihood	AIC _c	ΔAIC _c	w _i	D
A. Dam passage:					
Sex + maximum temperature + anaerobic recruitment	−12.97	37.20	.00	.12	50
Sex + maximum temperature	−14.29	37.40	.21	.10	45
Sex + anaerobic recruitment	−14.30	37.40	.23	.10	45
B. Anaerobic recruitment:					
Sex + siphon 1 + tailrace crossings	−212.02	437.80	.00	.48	46
Sex + siphon 1 + tailrace crossings + maximum temperature	−212.01	440.50	2.63	.13	46
Sex + siphon 1 + tailrace crossings + tailrace delay	−212.02	440.50	2.64	.13	46
C. Tailrace crossings:					
Sex + anaerobic recruitment	−62.51	133.80	.00	.14	25
Sex + anaerobic recruitment + tailrace delay	−61.67	134.60	.77	.10	30
Sex + tailrace delay	−62.95	134.70	.89	.09	22
D. Reach natal sites:					
Anaerobic recruitment + siphon 1	−18.73	46.50	.00	.14	37
Anaerobic recruitment + siphon 1 + tailrace crossings	−17.65	46.90	.38	.11	41
Anaerobic recruitment + siphon 1 + sex	−18.07	47.70	1.23	.07	39

Note. ΔAIC_c represents the difference in AIC_c values between model *i* and the top-ranked candidate model. Models are ranked from lowest to highest ΔAIC_c (highest to lowest w_i); all top-ranked candidate models had a ΔAIC_c of 0. *D* represents the percentage of deviance explained by a generalized linear model. Capture location was included in all models as a fixed factor.

individuals were 154% ($e^{5.04}$; fig. 5D) more likely to complete their freshwater migration after passing Seton Dam compared to fishway-nonnaive individuals. Forty-four percent (8/18) of the fish that failed to reach natal spawning streams after passing the dam died in Seton Lake; all other individuals (56%; 10/18) migrated to within 4 km of Gates Creek but perished in Anderson Lake prior to spawning.

Discussion

Anaerobiosis significantly decreased the probability that migrants reached natal sites, explaining in part why Gates Creek sockeye salmon suffer exceptionally high mortality rates after passing Seton Dam (Roscoe et al. 2011). In a lab setting, Wood et al. (1983) found that 40% of rainbow trout (*Oncorhynchus mykiss*) perished within 12 h after 6 min of intensive exercise. Similarly, nearly half of the delayed mortality observed in this study occurred in Seton Lake within 1–3 d of dam passage, likely owing to the greater EPOC and long recovery times associated with prolonged periods of swimming at critical speeds (Lee et al. 2003a, 2003b). Using a swim tunnel respirometer at Seton Dam, Lee et al. (2003a, 2003b) showed that Gates Creek sockeye salmon exhibit significantly higher anaerobic contribution to swimming and are less efficient swimmers compared to other Fraser River sockeye salmon populations. Consistent with an electromyogram telemetry study on Gates Creek sockeye salmon (Pon et al. 2009), we found that burst swimming is required to negotiate the Seton Dam tailrace but is not needed to ascend the fishway. Gates Creek sockeye salmon are known to cross the dam tailrace multiple times toward the fishway entrance (Burnett et al. 2013a), perhaps as an attempt to be-

come accustomed to the entrance area (Laine 1995) or due to confusion in selecting the desired migration path (Hinch et al. 2002). At Seton Dam, individuals may have simply been forced away from the fishway entrance due to the supercritical flows from siphon 1. Nevertheless, we found that this behavior led to significant increases in anaerobic recruitment. A trade-off exists whereby multiple crossing events are associated with successful dam passage but contribute to the failure of migrants to reach breeding grounds (Burnett et al. 2013a). Releasing excess water from siphon 1 is part of the standard operational protocol at this facility, as it is believed to improve the attraction of fishes to the vertical-slot fishway (Andrew and Geen 1958). Fishways and their attraction flows should be designed to facilitate the upstream passage of aquatic species and minimize undue physiological stress (Clay 1995; Bunt 2001). Yet, our results indicate that small fluctuations ($<1 \text{ m}^3 \text{ s}^{-1}$) in fishway attraction flows can compromise the survival of sockeye salmon. Indeed, there is likely a trade-off between attraction efficiency and the high flows designed to attract fish to a passage structure. Future research is needed to investigate whether there are management strategies that would reduce attraction efficiency and the supercritical flows around a fishway in a way that might lead to optimal net survival to natal spawning streams.

Female Gates Creek sockeye salmon are less successful at passing Seton Dam and demonstrate significantly lower survival to reach natal sites compared to males (40% vs. 71%, Roscoe et al. 2011; 44% vs. 69%, fig. 5). A higher proportion of tagged females (two males vs. seven females) failed to reach the tailrace postrelease, further emphasizing the susceptibility of female

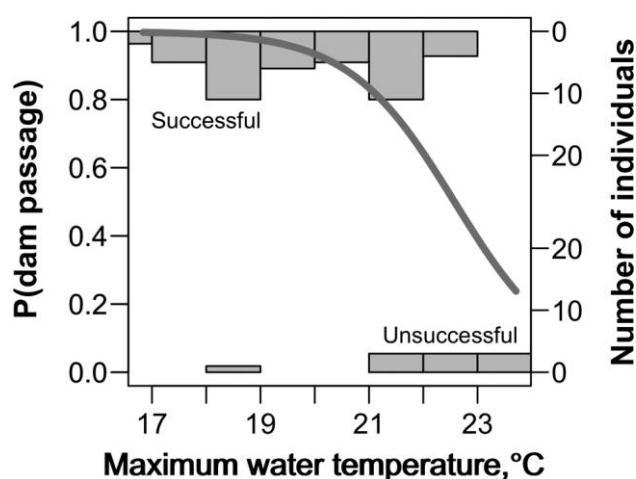


Figure 4. Predicted probability of Gates Creek sockeye salmon (*Onchorhynchus nerka*) passing Seton Dam, visualized by fitting a logistic regression to the maximum Seton River temperature successful and unsuccessful fish experienced while directly below the dam. A color version of this figure appears online.

sockeye salmon to stress. Nadeau et al. (2010) demonstrated this in a holding study whereby female sockeye salmon suffered higher mortality and exhibited elevated levels of physiological stress when exposed to high water velocities. Despite making fewer crossings, females swam with more anaerobic effort in areas of high flow, indicating that females swam faster and less efficiently in the Seton Dam tailrace compared to males (Burnett et al. 2013a; fig. 2). Overall, female sockeye salmon that relied heavily on glycolytic-fueled locomotion were more likely to succumb to mortality out of all individuals that passed the dam, providing a probable mechanism for the observed sex-specific differences in survival to spawning grounds in this watershed (Roscoe et al. 2011; fig. 5). A bimodal distribution in the swimming speeds of females near the fishway entrance (fig. 2) suggests individual variability in swimming strategies (Standen et al. 2002; Hasler et al. 2012). We highlight the need for future investigation into the swimming behaviors of anadromous fishes in areas of difficult passage, as it appears that some females (and most males) are capable of negotiating high flows with little to no anaerobic contribution to swimming effort. Several telemetry studies on Fraser River sockeye salmon have revealed that females often demonstrate higher temperature-induced mortality compared to males (e.g., Crossin et al. 2008; Martins et al. 2012). Certainly, the greater energetic investment into gonad development in females could limit their ability to negotiate hydraulically challenging reaches and cope with high water temperatures (Crossin et al. 2008). Taken together, our results suggest that female sockeye salmon are at greater risk of en route mortality following exhaustive exercise and metabolic stress, particularly when exposed to challenging migration conditions.

We found that the maximum temperature fish experienced below Seton Dam had a significant effect on passage. During

the study period, Seton River water temperatures were often above the thermal optima for the study population (i.e., $>17.5^{\circ}\text{C}$; Lee et al. 2003b). Corroborating our findings, telemetry research on sockeye salmon elsewhere has found similar high-temperature-related mortality trends (Naughton et al. 2005; Keefer et al. 2008; Martins et al. 2012). Exposure to supraoptimal water temperatures while swimming at critical speeds can decrease aerobic and cardiac scopes, increase EPOC, and prolong recovery times in Fraser River sockeye salmon (Lee et al. 2003a, 2003b; Farrell et al. 2008; Eliason et al. 2013). In this study, Gates Creek sockeye salmon were exposed to near-lethal temperatures while performing exhaustive exercise, which could have resulted in cardiorespiratory collapse in the dam tailrace due to an insufficient scope for heart rate (Eliason et al. 2013). Indeed, 90% of the fish that failed to pass the dam experienced water temperatures near the species' lethal limit (24°C ; Servizi and Jensen 1977). Closures to the power canal during the study period prevented the release of hypolimnetic water from Seton Lake, resulting in 4°C increases in Seton River water temperatures. Managers should recognize the potential ecological consequences of such an operational change, especially considering female sockeye salmon are particularly sensitive to elevated water temperatures during their reproductive migration (Crossin et al. 2008; Martins et al. 2012).

Fish capture location had an effect on anaerobic recruitment in areas of high flow and the ability of migrants to reach natal sites. More specifically, fish that had previously passed Seton Dam (i.e., fishway-nonnaive individuals) were much less likely to pass a second time and reach spawning grounds. Past telemetry studies on Gates Creek sockeye salmon were logistically constrained to capture study subjects from the top pool of the fishway, selecting for individuals that had previously demonstrated the ability to locate, enter, and ascend the passage structure (Roscoe et al. 2011; Burnett et al. 2013a). Fishway efficiency estimates from these previous studies were consistent among years, whereby sockeye salmon appeared to have greater difficulty locating and entering the vertical-slot fishway compared to passing it (i.e., attraction efficiency $<$ passage efficiency). Telemetry data from this study suggest that fishway-nonnaive individuals were more inclined to delay in the low flows of the radial gate and siphon spillways. We attribute the apparent lack of motivation in fishway-nonnaive fish to traverse the high flows from siphon 1 to the EPOC required after their successful negotiation of the tailrace prior to capture. Indeed, the delayed mortality of fishway-nonnaive Gates Creek sockeye salmon in the lakes upstream of Seton Dam is likely due to the higher EPOC and long recovery times required following two successful dam passages (Roscoe et al. 2011; fig. 5D). Given the applicability and ecological significance of fishway efficiency estimates, we emphasize that researchers must consider a variety of biotic (e.g., study species motivation to migrate, timing of study) and abiotic (e.g., capture and tagging method, capture and release location) factors in their study design and analyses (Cooke and Hinch 2013). By tagging and releasing fishway-naive and fishway-nonnaive sockeye salmon under the same environmental conditions, our results highlight the importance

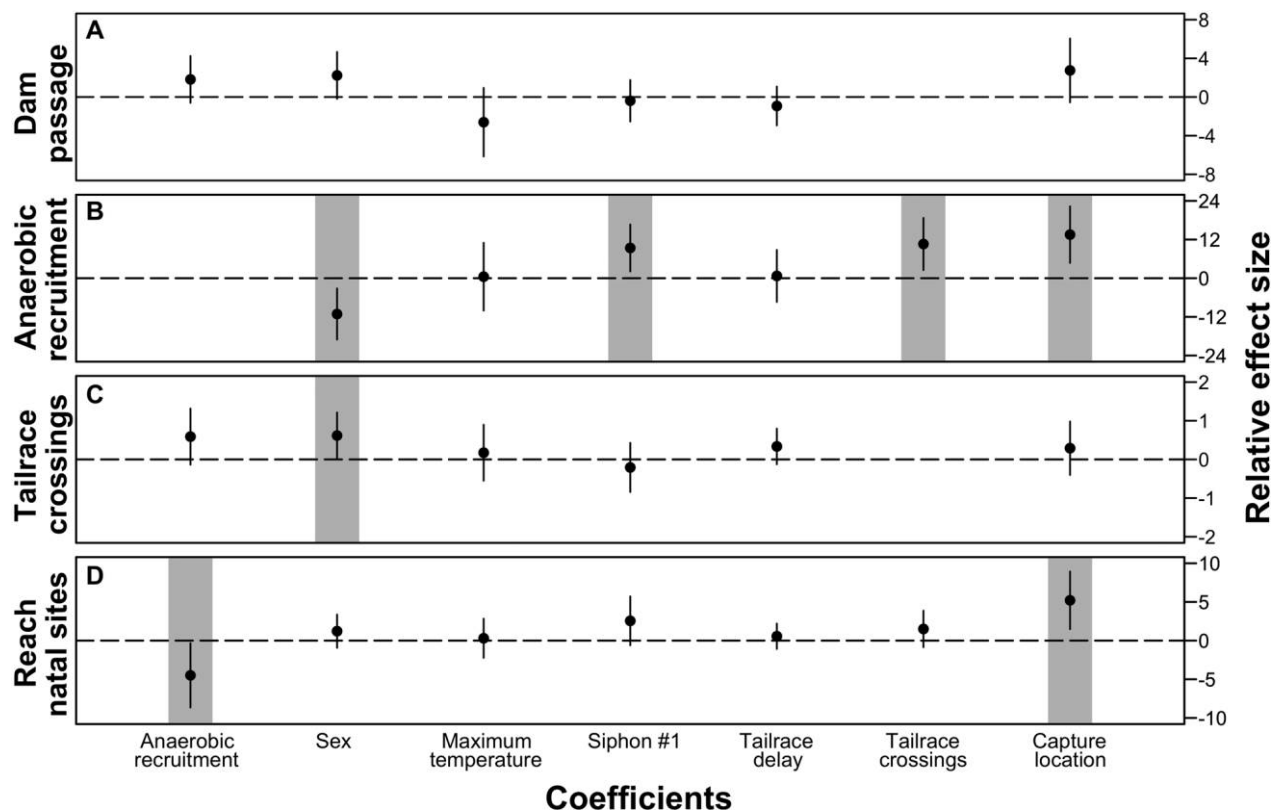


Figure 5. Model-averaged standardized coefficients for models describing dam passage (A), anaerobic recruitment in areas of high flow below Seton Dam (B), tailrace crossings (C), and the ability of Gates Creek sockeye salmon (*Oncorhynchus nerka*) to reach natal spawning streams (D). Coefficients have been highlighted in gray if the error bars (representing 95% confidence intervals) do not cross 0. Capture location was included in all models as a fixed factor and has been included to show its relative effect on the response variables. Note the different secondary Y-axes scales.

of considering capture location when conducting fish passage research to avoid costly management decisions and biological consequences.

We do not rule out a probable infectious disease component to the inability of sockeye salmon to traverse the Seton Dam tailrace and complete their freshwater migration. Pacific salmon exposed to high water temperatures can become immunocompromised and more susceptible to parasites that exhibit accelerated rates of development in warm conditions (Miller et al. 2014). Further, ill health has been shown to impair the swimming performance of sockeye salmon (Tierney and Farrell 2004) and lead to eventual mortality (Crossin et al. 2008). We monitored the health of dead and moribund Gates Creek sockeye salmon (e.g., internal and external macroscopic injuries, presence of internal parasites) that failed to pass the dam and subsequently collected on the upstream side of the fish fence. Abundant parasitic nematodes (*Anisakis* spp.) were present in the coelomic cavity of 60% (34/57) of the fish sampled, including a single acoustic-tagged female that was found moribund <24 h postrelease. We are unaware of any study to date that has investigated whether infectious disease plays a role in fish passage. Our anecdotal findings emphasize the need for future research to advance our understanding of the contrib-

uting factors influencing migration success in anadromous fishes.

Our models used to predict swimming speed and Mo_2 from RMS acceleration were not as effective at high water velocities. Further, the sampling frequency of the acoustic accelerometer transmitter (10 Hz) may not have been high enough to capture the rapid successive tail beats often exhibited in burst swimming (Wilson et al. 2013). To account for this, we used the model to predict Mo_2 for swimming speeds $<U_{crit}$ and assumed that maximum oxygen consumption (i.e., $Mo_{2\ max}$) occurred at swimming speeds $\geq U_{crit}$. Thus, the swimming speeds, Mo_2 , and EPOC values presented herein may be underestimated. Regardless, our study clearly shows that dam passage success and postpassage survival are correlated with anaerobic muscle recruitment.

Pacific salmon must recruit white muscle fibers to successfully navigate areas of difficult passage (Hinch and Bratty 2000; Brown et al. 2006; Burnett et al. 2013a). Until now, there has been limited research examining the potential consequences of exhaustive exercise on the spawning migrations of wild adult Pacific salmon. Human-made alterations to the Seton River's flow and thermal regime had a direct impact on the ability of sockeye salmon to pass a diversion dam and complete their

reproductive migration. Consistent with our predictions, we found that anaerobic swimming in high flows contributed to the inability of Gates Creek sockeye salmon to reach spawning grounds. This finding provides insight to the potential carry-over effects of velocity barriers on other fish species. Moreover, it points to opportunities to refine the design and operation of fishway attraction flows. Future studies should focus on elucidating the specific physiological mechanisms by which anaerobiosis can lead to mortality, as well as the compounding effects of disease on survival. Our findings also show the need for research that investigates whether dams can impose other carryover effects on wild aquatic animals (Caudill et al. 2007; O'Connor et al. 2014). We present the first field-based evidence that burst swimming by anadromous adult salmonids can result in delayed mortality, providing a foundation for future studies investigating the costs of swimming in wild aquatic animals.

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