


Physiological condition and migratory experience affect fitness-related outcomes in adult female sockeye salmon

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Abstract

Relating fish physiology, behaviour and experience to fitness-related outcomes at the individual scale is ecologically significant, but presents difficulties for free-ranging fishes in natural systems. Physiological state (e.g. level of stress or maturity) and experience (e.g. habitat use or exposure to stressors) may alter the probability of survival or reproduction. This study examined the relative influence of physiology and migratory experience on survival, migration duration, reproductive longevity, and egg retention in adult female sockeye salmon (*Oncorhynchus nerka*) from a Fraser River population. One hundred and thirty-five females were plasma sampled and tagged with radio transmitters and archival temperature loggers. Fish were tracked 55 km through two natal lakes to spawning grounds, following passage of a hydroelectric dam. For 39 females, we assessed the proportion of time within an optimal temperature (T_{optAS}) window (13.4–19.5°C), which provides $\geq 90\%$ of maximum aerobic scope. Females with lower plasma glucose concentrations were more likely to reach spawning grounds. Early migrants spent longer in natal lakes. More time in the T_{optAS} window was associated with greater reproductive longevity and lower probability of egg retention. Later arriving females had reduced longevity on spawning grounds, as did females that retained eggs. Exposure to higher dam discharge was associated with reduced reproductive longevity and greater probability of egg retention, but not lower survival, indicating a delayed effect of dam passage. Our results underscore the complexity of factors governing fitness-related outcomes for salmonids, particularly the importance of female experience in the days and weeks prior to spawning.

KEYWORDS

aerobic scope, dam passage, delayed effects, spawning success, thermoregulation

1 | INTRODUCTION

The success of a reproductive migration depends on interactions between the physiological state of an individual and the environmental conditions encountered (Nathan et al., 2008). Individuals that reach breeding grounds are possibly in better physiological condition, encounter more benign environments and (or) respond more effectively to migratory challenges than individuals that die *en route*. Adult

Pacific salmon (*Oncorhynchus* spp.) which return to natal sites with high fidelity have a single opportunity to reproduce before death, and unsuccessful migrants do not contribute genetically to the population. Thus, the energetic demands and historical environmental conditions of the adult migration have shaped the morphology, physiology and behaviour of Pacific salmon (Hinch, Cooke, Healey, & Farrell, 2006; Hodgson & Quinn, 2002). Despite these responses, some populations in some years exhibit high levels of mortality *en*

route and on spawning grounds (e.g. >90%; Keefer et al., 2010; Hinch et al., 2012).

Exposure to high water temperature underlies or exacerbates many causes of migration mortality in Pacific salmon. Spawning migrations are fuelled exclusively by stored energy, most of which is consumed by standard metabolism, swimming activity and gonad maturation in years of typical migration conditions (Brett, 1995). At high temperatures, energy reserves can become exhausted and fish perish *en route* (Rand & Hinch, 1998). Cardiorespiratory system function is also temperature-limited. Aerobic scope for activity—the difference between maximum and standard metabolic rates—is greatest at an optimal temperature (T_{optAS} ; Fry, 1947). Standard metabolism consumes an increasing proportion of available oxygen as temperature increases, limiting capacity for other activities, including swimming and maturation. At a critical temperature (T_{crit}), aerobic scope is zero, and swimming activity is fuelled by anaerobic metabolism (Pörtner, 2001). Although anaerobic swimming is essential to the adult migration (e.g. for passing rapids), it is costly and cannot be sustained for long periods of time (Martin, Nisbet, Pike, Michel, & Danner, 2015). In environments where high water temperatures and high flows coincide, such as some dam tailraces and fishways (Keefer & Caudill, 2015), reduced aerobic scope may impede migration. Indeed, the collapse of aerobic scope is thought to be responsible for poor survival in some recent sockeye salmon (*Oncorhynchus nerka*) spawning migrations (Farrell et al., 2008; Keefer, Peery, & Heinrich, 2008).

Thermal refuges along the migration route, including cool water tributaries and the hypolimnion of lakes and reservoirs, allow Pacific salmon to mitigate the negative effects of thermal stress and increase likelihood of survival to spawning grounds (Keefer & Caudill, 2015; Mathes et al., 2010; Newell & Quinn, 2005). Behavioural thermoregulation may be particularly important for females, which allocate considerable energy to gamete development in the final stages of maturation (Rand & Hinch, 1998); there is evidence that more mature females with lower levels of somatic energy occupy the coolest temperatures in natal lakes (Roscoe, Hinch, Cooke, & Patterson, 2010a). Water temperature affects maturation rate (Pankhurst & King, 2010), and it has been proposed that occupying temperatures near T_{optAS} allows migrating females to mature most efficiently (Eliason & Farrell, 2016); however, this has not been examined to date.

Females appear to be more vulnerable to migratory challenges than males—particularly exposure to high temperatures (Jeffries et al., 2012; Martins et al., 2012). Even females that overcome migratory challenges to reach spawning grounds may exhibit delayed effects on reproduction. High rates of egg retention—when females die prior to complete spawning—have been observed in populations of Pacific salmon exposed to high temperatures well below the lethal threshold (Quinn, Eggers, Clark, & Rich, 2007; West & Mason, 1987). Multiple behavioural and physiological mechanisms may contribute. First, recovery from stress may delay arrival, decreasing time on spawning grounds (“reproductive longevity”; Morbey & Ydenberg, 2003) required for reproductive behaviours (Hruska, Hinch, Patterson, & Healey, 2011). Second, energy may be diverted from maturation or reproductive behaviours to standard metabolism or recovery (Fenkes,

Shiels, Fitzpatrick, & Nudds, 2015). Third, thermal stress may inhibit synthesis of the sex steroid 17- β oestradiol and delay vitellogenesis (Jeffries et al., 2012; Pankhurst & King, 2010). Fourth, anaerobic swimming may also suppress reproductive hormones and oocyte development (Palstra, Crespo, van den Thillart, & Planas, 2010). The relationships between arrival date, reproductive longevity, competitive ability on spawning grounds, including morphological traits (e.g. fork length) and indicators of stress (e.g. plasma lactate), and spawning success have been studied in Pacific salmon (Hruska et al., 2011; McPhee & Quinn, 1998). However, research has not yet linked migratory experience to reproductive consequences on spawning grounds (Hruska et al., 2010).

The purpose of this study was to compare the relative importance of indices of physiological stress, maturity and migratory experience in the final stages of migration to fitness-related outcomes in female sockeye salmon. As physiological stress has a negative effect on survival and maturation, we predicted that female fish that exhibited lower indices of stress (lower plasma glucose and lactate concentrations) and higher maturation (lower plasma 17- β oestradiol concentration) and that experienced less stressful dam passage conditions (lower water temperature and discharge) would have higher survival, faster migration, greater reproductive longevity and lower egg retention. Additionally, we predicted that female fish that spent a greater proportion of migration through lakes at temperatures near T_{optAS} would have greater reproductive longevity and lower egg retention. Although reproductive longevity had a strong negative relationship with egg retention in two previous studies of female sockeye salmon (Burnett et al., 2016; Hruska et al., 2011), we treated them as separate outcomes to assess whether underlying mechanisms differ.

2 | METHODS

2.1 | Fish collection and tagging

We studied female fish from the population of wild sockeye salmon that spawns in Gates Creek, British Columbia. Adult Gates Creek sockeye salmon swim 350 km up the Fraser River to enter the Seton River, where migrants encounter the Seton Dam (Figure 1). After negotiating the vertical-slot fishway at Seton Dam, adult sockeye salmon swim 55 km through Seton Lake, Portage Creek and Anderson Lake to reach spawning areas in Gates Creek. A proportion of the Gates Creek population spawns on beaches adjacent to the mouth of Gates Creek in years of high returns, but this was not observed during this study. Approximately 800 metres upstream of the mouth of Gates Creek, a weir directs fish to a gate, which can be opened to guide fish into the natural creek upstream of the weir, or closed to load fish into a creek-fed artificial spawning channel (Figure 1).

Female sockeye salmon from the Gates Creek population were captured in the Seton River using a full-spanning picket fence and trap installed 200 metres downstream of Seton Dam (Figure 1). The fence was closed for fish collection up to 12 hr per day throughout the migration and left open each night. Between 16 August 2013–2

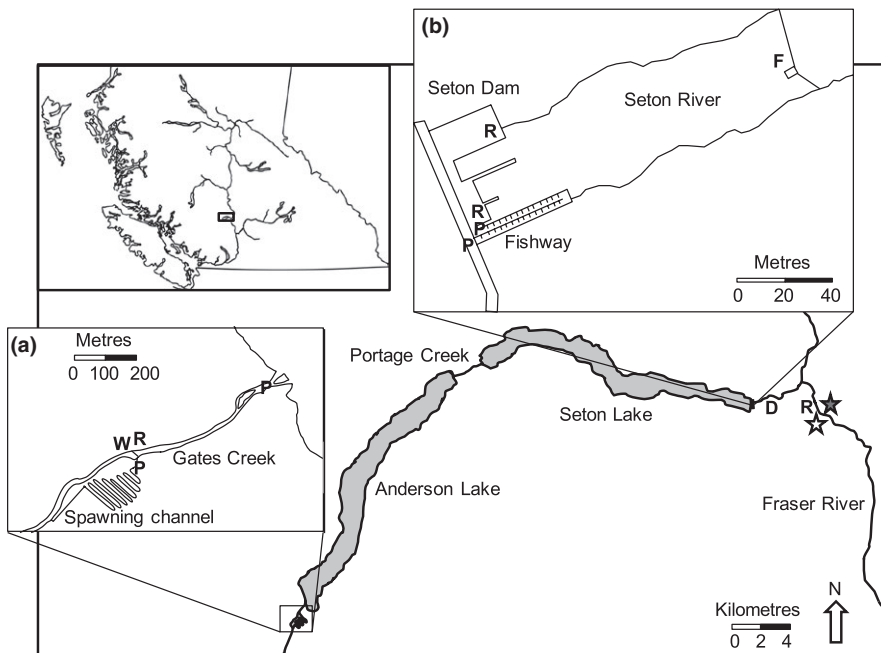


FIGURE 1 The Seton–Anderson watershed and its location in British Columbia, Canada (inset); Gates Creek and the artificial spawning channel (a); and the Seton Dam and fishway (b). R = radio receiver, P = pass-through PIT antenna, F = fish collection fence, D = Water Survey of Canada discharge gauge, W = spawning channel weir, white star = release site (2013+2014), filled star = release site (2013 only). Detections on telemetry receivers in A were grouped as “Gates Creek” and in B as “Seton Dam” for analysis

September 2013 and 5 August 2014–7 September 2014, 109 and 95 female sockeye salmon were collected respectively.

Fish were netted from the trap box and placed in a flow-through holding pen in the Seton River for up to two hours before tagging. Individual fish were held supine, unanesthetised, in a padded, V-shaped trough with water flowing continuously over the gills, following Cooke et al. (2006). Females were identified by secondary sexual characteristics (smaller kype and adipose fin, larger vent vs. male fish). Individuals were selected for tagging based on external condition and somatic energy density. Fish with deep wounds (skeletal system or organs visible) or extensive fungus cover were not tagged, as these individuals were unlikely to survive past Seton Dam. Sockeye salmon have very low stray rates (<5% of migrants; Keefer & Caudill, 2014), and Gates Creek was the only population migrating into the Seton River (and through Seton and Anderson lakes) during the tagging period. However, we used energy probe readings to distinguish Gates Creek sockeye salmon from other populations, with greater somatic energy density, travelling to spawning grounds hundreds of kilometres farther up the Fraser River. Individuals sampled at the fish fence with relatively high levels of lipids have been confirmed as strays from other populations using DNA population assignment (Casselman, Burnett, Bett, McCubbing, & Hinch, 2012). Somatic energy density was estimated using a handheld energy probe (FM 692 Fish Fatmeter, Distell Inc., West Lothian, Scotland, UK; see Crossin & Hinch, 2005), and presumed strays were released without tagging. Fork length (FL) was measured (to nearest 5 mm) and a 3-ml blood sample was taken from the caudal vein with a heparinised vacutainer (22 gauge syringe; BD Canada, Mississauga, ON, Canada). Blood samples were centrifuged for 6 min to isolate plasma, which was transferred to three 0.8-ml vials and stored in liquid nitrogen before transfer to a -80°C freezer prior to laboratory analysis. Fish were tagged with a half-duplex passive integrated transponder (PIT) tag (32 mm length \times

3.65 mm diameter; Texas Instruments, Dallas, TX, USA) in the dorsal musculature, a 12-inch spaghetti tag (Floy Manufacturing, Seattle, WA, USA) attached posterior to the dorsal fin (for visual identification on spawning grounds), and a uniquely coded radio transmitter (Pices5 model: 43 mm length \times 16 mm diameter, 15.2 g in air, 3 s burst rate; Sigma Eight Inc., Newmarket, ON, Canada) inserted gastrically with a plastic plunger. Archival temperature loggers (iButton Thermochron model DS1921Z or DS1922L; Maxim Integrated, San Jose, CA, USA) were glued to the nonantenna end of radio transmitters and waterproofed (Plasti Dip International, St. Louis Park, MN, USA), following Donaldson et al. (2009). Temperature loggers archived data at 15-minute intervals and had a resolution of $1/16^{\circ}\text{C}$ (manufacturer stated accuracy: $\pm 0.5^{\circ}\text{C}$, range: -10°C to $+65^{\circ}\text{C}$; model DS1922L) or $1/8^{\circ}\text{C}$ (manufacturer stated accuracy: $\pm 1^{\circ}\text{C}$, range: -5°C to $+26^{\circ}\text{C}$; model DS1921Z). An adipose tissue punch was taken and stored in ethanol (for DNA population identification), and the fish was photographed and returned to the holding pen for recovery. The time to tag each fish was not recorded in 2013, but was likely equivalent to 2014 (mean \pm SD: 4.7 ± 1.2 min, range: 2.7–9.1 min, $n = 95$), as the procedure did not differ between years. To achieve the objectives of a parallel study (Casselman et al., 2015), groups of ten to twelve fish were transferred to a 1,000-L aerated transport tank and driven for 20 min to release locations on the west ($50^{\circ}39'43''\text{N}$, $121^{\circ}55'06''\text{W}$) and east ($50^{\circ}39'40''\text{N}$, $121^{\circ}54'50''\text{W}$) bank of the Fraser River, 2.5 km downstream of the Seton River–Fraser River confluence (Figure 1). In 2014, fish were released from the west bank only, as survival to Seton Dam and dam passage did not differ by release location in 2013 (Casselman et al., 2013). All capture, tagging, sampling and transport procedures were approved by the University of British Columbia Animal Care Committee (animal use protocol A11-0125), following Canadian Council on Animal Care guidelines.

Stationary radio receivers (Orion, Sigma Eight Inc. or SRX-400, Lotek Wireless Inc., Newmarket, ON, Canada) with three-element Yagi antenna were placed at the release location on the west bank of the Fraser River, at Seton Dam (one directed at the tailrace, one directed at the fishway entrance), and at the entrance to the spawning channel in Gates Creek (Figure 1). During installation, a test tag was used to determine the detection area of each receiver and ensure complete coverage of the area of interest. Pass-through PIT antennas (Oregon RFID, Portland, OR, USA) were installed inside the entrance and exit basins of the Seton Dam fishway. Two PIT readers were installed on spawning grounds: a three-antenna array at the spawning channel entrance and a pass-through PIT antenna 120 m upstream of the mouth of Gates Creek in 2014 (Figure 1). All PIT antennas were tested at least once per week by placing a designated test tag in the water within 0.5 m of the antenna, at various locations along its length. If the read range was <0.5 m, the antenna was tuned. Data from all receivers were downloaded once or twice per week.

Radio telemetry data were filtered to remove false-positive detections using R (version 3.1.3; R Development Core Team 2015). Detections with radio frequency and tag code combinations not used in this study were removed. Next, detections that occurred prior to the release of a tagged fish or after the recovery of a tag in Gates Creek were removed; these detections typically occurred when the tag or tagged fish was driven past a receiver. Finally, we removed any detection that did not occur within two minutes of another detection from the same tag on the same receiver. The basis for the final filtering criterion is that a tag with a 3 s burst rate can be detected up to 40 times in two minutes, while multiple false-positive detections of the same radio frequency and tag code combination rarely occur on the same receiver within two minutes. First and last detections were then identified for each fish at each receiver from the filtered telemetry data. First and last detections at Seton Dam and Gates Creek were obtained by pooling radio and PIT telemetry data to account for possible missed detections at a single receiver (e.g. caused by turbulence in the dam tailrace and a power outage at the Gates Creek spawning channel in 2014).

Only females that successfully passed Seton Dam were included in the analyses. The 69 tagged females that did not pass Seton Dam (2013: 43, 2014: 26) were assessed in a parallel study (Casselman et al., 2015). The last detection at Seton Dam was considered the beginning of the in-lake migration. Survival to spawning grounds was determined by detection on any radio receiver or PIT antenna at Gates Creek. Migration duration, or the time spent in Seton and Anderson lakes, was calculated as the difference in days between the last detection at Seton Dam and the first detection at Gates Creek.

Although there was a well-advertised tag recovery programme in place during this study, wherein rewards were provided for returned tags, only four radio transmitters were returned from tagged fish captured in fisheries. We suspect that unreported harvest occurred between Seton Dam and Gates Creek but have no direct means of accounting for this mortality in the statistical models presented here. There is no reason to suspect that sockeye salmon captured in fisheries differed physiologically (see Cooke et al., 2009) or experienced

different migration conditions compared to survivors, as harvest occurred throughout the entire Gates Creek run. In 2015, mobile radio tracking in known fishing areas generated estimates of 5–10% of tagged fish being caught (Casselman et al., 2015). Although we cannot be certain whether this harvest rate is applicable to 2013 or 2014, it would reflect a relatively small component of total mortality.

2.2 | Dam passage conditions

A temperature data logger (manufacturer stated accuracy: $\pm 0.2^{\circ}\text{C}$, range: -20°C to $+50^{\circ}\text{C}$; TidBit v2, Onset Computer Corporation Inc., Bourne, MA, USA) in the top pool of the fishway recorded hourly Seton River water temperature throughout the study period. The highest hourly temperature recorded while each fish was in the tailrace and fishway at Seton Dam was used to characterise the temperature conditions experienced during dam passage.

We obtained hourly Seton Dam discharge data from a Water Survey of Canada gauge in the Seton River (Figure 1). Under standard operating procedure, Seton Dam spills water from a siphon directly adjacent to the fishway entrance (details in Burnett et al., 2014). Small fluctuations in discharge ($<1\text{ m}^3\text{s}^{-1}$) in the area around the fishway entrance can increase reliance on anaerobic swimming, which was found to be associated with high mortality of female fish following dam passage (Burnett et al., 2014). In 2014, the flow conditions in the Seton Dam tailrace were altered for a parallel study (Burnett et al., 2016). From 8 August 2014 to 19 August 2014, water was spilled from a siphon approximately 10 m from the fishway entrance, which increased mean Seton Dam discharge from 27.1 to 31.4 m^3s^{-1} (Figure 2). For this study, Seton Dam discharge was categorised as “low” (under standard flow conditions; throughout 2013, from 5 August 2014 to 7 August 2014 and 20 August 2014 to 9 September 2014) or “high” (under altered flow conditions; from 8 August 2014 to 19 August 2014), because the siphon change caused substantial differences in both discharge and tailrace flow dynamics (Burnett et al., 2016; Casselman et al., 2015). Individual fish were assigned to a discharge category (low or high) based on the date of first detection at Seton Dam.

2.3 | Plasma physiology

Plasma glucose and lactate concentrations were measured using YSI 2300 STAT Plus glucose and lactate analyser (YSI Inc., Yellow Springs, OH, USA). 17- β oestradiol and testosterone concentrations were measured from blood plasma samples, following procedures outlined in Roscoe et al. (2010a). Relative concentrations of plasma 17- β oestradiol and testosterone were used to verify visual sex assignments made at tagging for all 2013 fish. Visual sex assignments were 92% accurate in 2013 ($n = 214$ total fish tagged). Hormones were not used to verify sex in 2014, but visual sex assignments were 96% accurate, based on recovered carcasses ($n = 107$ carcasses recovered, $n = 103$ sex assignments correct). Across years, females were more likely to be misidentified as males (two fish incorrectly identified as females, 20 fish incorrectly identified as males). All confirmed females were included in analyses.

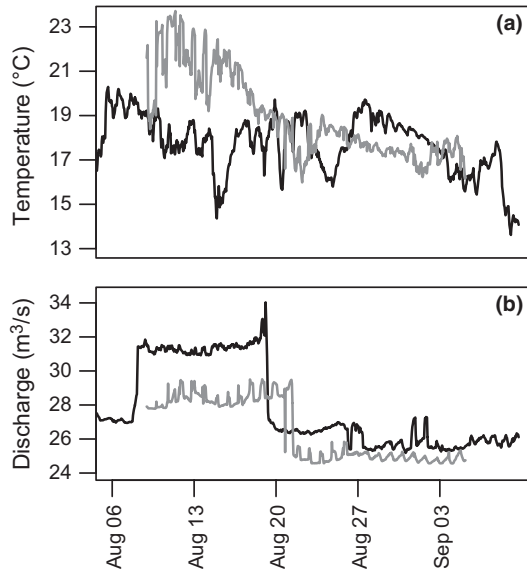


FIGURE 2 Fishway temperature (a) and Seton Dam discharge (b) during period when tagged females were detected in the dam tailrace, 9 August 2013–5 September 2013 (grey lines) and 6 August 2014–9 September 2014 (black lines). “High” discharge occurred 8 August 2014–19 August 2014 and “low” discharge occurred 5 August 2014–7 August and 20 August 2014–9 September 2014

2.4 | Reproductive longevity and spawning assessments

Each day, female carcasses containing radio transmitters were recovered from the spawning channel and off the weir in Gates Creek and assessed for egg retention. Reproductive longevity was calculated as the number of days between the first detection on the radio receiver or PIT reader at the spawning channel (arrival date) and the date each carcass was recovered. While it is not possible to assess male spawning success from carcasses (as males can retain approximately 50% of gonad size after spawning), spawning females typically expel most to all of their eggs (Brett, 1995). Females were categorised as “retained eggs” (unsuccessful spawner) if found with tight skeins or more than approximately 500 eggs in the body cavity. If all eggs were expelled, or <500 eggs remained in the body cavity, females were categorised as “did not retain eggs” (successful spawner). As few tagged females were recovered from the spawning channel or weir in 2013 ($n = 6$; all “retained eggs”), only data from 2014 females ($n = 39$) were used in analysis of reproductive longevity and egg retention.

2.5 | Temperature logging data and aerobic scope for activity

Analysis of survival rates across Fraser River sockeye populations led Eliason et al. (2011) to suggest that fish require 90% of maximum aerobic scope to complete migration. The maximum aerobic scope ($11.08 \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) and optimum temperature (T_{optAS} ; 16.4°C) for Gates Creek sockeye were previously derived from fish at rest and swum maximally in a swim tunnel respirometer at a range of

temperatures (Eliason et al., 2011; Lee et al., 2003). Ninety per cent of maximum aerobic scope is $9.98 \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$, which is associated with $13.4\text{--}19.5^\circ\text{C}$ (hereafter, the “ T_{optAS} window”). Salmon body temperatures logged after the last detection at Seton Dam and before the first detection at Gates Creek were selected, and the proportion of temperature readings within the T_{optAS} window was calculated for each fish.

2.6 | Statistical approach

Data were analysed using four statistical models, with one for each of the response variables: survival to spawning grounds, migration duration, reproductive longevity and egg retention. Model 1 had the response variable of survival (detected at Gates Creek [1], not detected [0]) and was fitted with a generalised linear model (GLM; family: binomial; link: logit). Model 2 had the response variable of migration duration (in days) and was fitted with a linear model. Both global models included the following explanatory variables: (i) year and (ii) tagging date, to account for inter- and intra-annual differences in fish condition and migration experience; (iii) FL (cm), to account for differences in fish size; (iv) plasma lactate ($\text{mmol} \cdot \text{L}^{-1}$) and (v) plasma glucose ($\text{mmol} \cdot \text{L}^{-1}$), to test the effects of indices of physiological stress; (vi) plasma $17\text{-}\beta$ oestradiol ($\text{ng} \cdot \text{mL}^{-1}$), to test the effect of maturity; and (vii) Seton Dam discharge (low [0] or high [1]) and (viii) Seton Dam water temperature (T_{dam} ; $^\circ\text{C}$), to test the effects of migratory stressors.

Model 3 had the response variable of reproductive longevity (in days) and was fitted with a linear model. Model 4 had the response variable of egg retention (retained eggs [1], did not retain eggs [0]) and was fitted with a GLM (family: binomial; link: logit). Both global models included the following explanatory variables: (i) FL; (ii) plasma lactate; (iii) plasma glucose; (iv) plasma oestradiol; (v) Seton Dam discharge; (vi) T_{dam} ; (vii) proportion of migration duration in T_{optAS} window, to test the effects of temperature experience in lakes; and (viii) arrival date on spawning grounds, to account for intra-annual differences in fish condition and migration experience. Variables included in each of the four models are summarised in Table 1.

All variables were assessed for correlation and multicollinearity and excluded if $r > |.7|$ (Zuur, Ieno, & Elphick, 2010) or variance inflation factor > 4 (O’Brien, 2007). Model residuals were visually assessed and met the assumptions of normality, independence and heteroscedasticity (Zuur et al., 2010). Seton Dam discharge was collinear with arrival date (VIF > 4) in Model 4, so inclusion of one of the two variables was determined based on the individual GLM (response: egg retention; explanatory variable: Seton Dam discharge or arrival date) with the lower AICc score (see Table S1). Reproductive longevity was not included in the egg retention model, as it does not provide a physiological explanation for spawning failure. Furthermore, inclusion in the egg retention model caused VIF > 6 .

All statistical analyses were conducted with R software. Candidate models were generated using the “MuMIn” package from all combinations of variables in the global model and compared using AICc for small sample sizes (Burnham & Anderson, 2002). The candidate sets for models 3 and 4 were limited to models with three or fewer

TABLE 1 Comparison of tagging date, fork length (FL), plasma lactate, glucose and oestradiol concentrations, maximum Seton Dam temperature (T_{dam}) and discharge (sample sizes shown for “low” and “high” categories), proportion of time in the T_{optAS} window (13.4–19.5°C), and arrival date at Gates Creek for female sockeye salmon tracked through Seton and Anderson lakes. The range (for tagging and arrival dates) or mean \pm SD (for other variables) is shown for the fish included in statistical models of (1) survival to spawning grounds, (2) migration duration, (3) reproductive longevity and (4) egg retention, along with the sample size (n). Models (1) and (2) have tagging date shown separately for 2013 and 2014, with years pooled for the remaining explanatory variables. Model 3 and Model 4 include data from 2014 only

Model response variable (n)	Tagging date	FL (cm)	Lactate (mmol·L ⁻¹)	Glucose (mmol·L ⁻¹)	Oestradiol (ng·ml ⁻¹)	T_{dam} (°C)	Discharge (n)		T_{optAS} window	Arrival date ^a
							Low	High		
							108	27		
1 Survival (135)	Aug 16–Sep 02, 2013 Aug 05–Sep 07, 2014	58.1 \pm 0.3	4.97 \pm 0.25	4.87 \pm 0.09	5.72 \pm 0.33	18.2 \pm 0.1				
2 Duration (83)	Aug 16–Sep 02, 2013 Aug 05–Sep 07, 2014	58.5 \pm 0.4	5.54 \pm 0.34	4.59 \pm 0.08	6.40 \pm 0.45	18.1 \pm 0.1	63	20		
3 Reproductive longevity (39 ^b)	Aug 11–Sep 06, 2014	59.3 \pm 0.6	5.60 \pm 0.40	4.51 \pm 0.10	8.13 \pm 0.65	18.0 \pm 0.2	25	14	0.33 \pm 0.03	Aug 22–Sep 12, 2014
4 Egg retention (38 ^b)	Aug 11–Sep 06, 2014	59.4 \pm 0.7	5.63 \pm 0.41	4.53 \pm 0.10	8.11 \pm 0.67	17.9 \pm 0.2	24	14	0.33 \pm 0.03	Aug 22–Sep 12, 2014

^aArrival date was omitted from Model 4 due to collinearity with discharge (see “Methods”).

^bSample sizes differ in models 3 and 4, as egg retention was not recorded for one female.

explanatory variables to maintain a 10:1 ratio of individuals to variables (Harrell, 2001). To account for uncertainty, because top model weights were small (e.g. 0.27 for Model 1; Table S2), a confidence set of models with cumulative weights summed to ≥ 0.95 was averaged using the “natural average” method to generate coefficient estimates and 95% confidence intervals for explanatory variables (Burnham & Anderson, 2002). To compare relative effect sizes within a model set, continuous variables were standardised with a mean of 0 and standard deviation of 2 (Gelman, 2008). Response variables were not transformed (Zuur et al., 2010). Fit of linear models was evaluated using adjusted- r^2 , and fit of GLMs was evaluated using pseudo- r^2 , following Hosmer and Lemeshow (1989). Two-sample t tests were used to compare the reproductive longevity of females that did and did not retain eggs at death and to compare plasma lactate, glucose and oestradiol concentrations between years. Statistical significance was assessed at $p < 0.05$. Untransformed data are presented as mean \pm SD, unless otherwise indicated.

3 | RESULTS

Females that passed Seton Dam were included in Model 1 (survival; $n = 135$: 52 in 2013, 83 in 2014). Successful migrants to Gates Creek were included in Model 2 (migration duration; $n = 83$: 23 in 2013, 60 in 2014). Females recovered in the spawning channel or from the Gates Creek weir in 2014 with thermal loggers ($n = 39$) and spawning assessments ($n = 38$) were included in Model 3 (reproductive longevity) and Model 4 (egg retention) respectively.

Plasma lactate, glucose and oestradiol concentrations, and FL did not show strong seasonal trends in either year or when years were pooled (all $r < 0.3$). Mean glucose concentration was higher in 2013 (5.36 ± 1.24 mmol·L⁻¹, range: 2.94–10.20 mmol·L⁻¹) than in 2014 (4.56 ± 0.84 mmol·L⁻¹, range: 3.03–9.34 mmol·L⁻¹; two-sample t test: $t_{80} = 4.09$, $p < 0.001$). Conversely, mean concentration of oestradiol was higher in 2014 (7.32 ± 3.54 ng·ml⁻¹, range: 0.13–8.11 ng·ml⁻¹) than in 2013 (3.16 ± 2.63 ng·ml⁻¹, range: 0.28–16.08 ng·ml⁻¹; two-sample t test: $t_{129} = -7.81$, $p < 0.0001$), but lactate did not differ significantly between years (two-sample t test: $t_{80} = -0.76$, $p = 0.45$).

Fish spent 8.3 ± 14.3 hr (range: 0.3–121.2 hr) in the tailrace and fishway at Seton Dam (i.e. between first and last detections), but times were not correlated with tagging date or the temperature or discharge experienced. Maximum fishway temperatures experienced ($18.2 \pm 1.1^\circ\text{C}$, range: 13.8–20.4°C; Figure 2a) were often above the optimal temperature for Gates Creek sockeye (16.4°C) and decreased with tagging date (2013: $r = 0.6$, 2014: $r = -0.3$). During “low” discharge periods, mean Seton Dam discharge was 26.5 ± 1.8 m³·s⁻¹ (in 2013; range: 24.6–29.5 m³·s⁻¹), 27.1 ± 0.1 m³·s⁻¹ (5 August 2014–7 August 2014; range: 26.9–27.2 m³·s⁻¹) and 26.1 ± 0.5 m³·s⁻¹ (8 August 2014–19 August 2014; range: 25.2–27.6 m³·s⁻¹). Mean “high” discharge was 31.4 ± 0.4 m³·s⁻¹ (20 August 2014–7 September 2014; range: 31.0–34.0 m³·s⁻¹). Discharge decreased with tagging date in both years (2013: $r = -0.5$, 2014: $r = -0.7$; Figure 2b).

3.1 | Receiver efficiency

Detection efficiency of the radio receiver at the release location on the west bank of the Fraser River was high (99%, $n = 135$). Detection efficiencies of individual receivers at Seton Dam were poor to high [radio receivers: tailrace (83%, $n = 135$) and fishway (2014 only: 47%, $n = 83$); PIT antennas: fishway entrance (93%, $n = 135$) and exit (92%, $n = 135$)], but all fish ($n = 135$) had multiple detections on at least one receiver when data were pooled. Receivers were also pooled at Gates Creek, as no single receiver detected all fish [radio: channel entrance (98% of survivors, $n = 83$); PIT antennas: lower Gates Creek (2014 only: 43%, $n = 60$) and channel entrance (64%, $n = 83$)]. Detection of a fish on any receiver at Gates Creek meant that the individual was considered a successful migrant in Model 1 and included in Model 2.

3.2 | Survival to spawning grounds (Model 1)

Plasma glucose and lactate concentrations, FL and year formed the most parsimonious survival model, which accounted for 15% of variation (Table S2). Lower plasma glucose concentrations at tagging were associated with higher survival to Gates Creek (Figures 3a and 4), and glucose was the most important explanatory variable, appearing in all models in the confidence set (Table S2). Plasma glucose concentrations were $4.59 \pm 0.75 \text{ mmol}\cdot\text{L}^{-1}$ (range: 2.94–7.15 $\text{mmol}\cdot\text{L}^{-1}$) in females that reached Gates Creek and $5.32 \pm 1.36 \text{ mmol}\cdot\text{L}^{-1}$ (range: 3.35–10.20 $\text{mmol}\cdot\text{L}^{-1}$) in females that died *en route*. Survival of tagged fish to spawning grounds was higher in 2014 (72% of fish, $n = 60$) than in 2013 (44%, $n = 23$; Figure 4), although the effect of year was uncertain, as the 95% CI crossed zero (Figure 3a). Fish tagged later had a higher probability of survival, as did larger fish and fish with higher plasma lactate or oestradiol concentrations. Contrary to predictions, fish that experienced high Seton Dam discharge had a higher

probability of survival, although the 95% CI was large and spanned zero. The effect of fishway temperature on survival was approximately zero.

3.3 | Migration duration (Model 2)

On average, females spent longer in Seton and Anderson lakes in 2014 (9.9 ± 5.1 days, range: 3.1–23.3 days; $n = 60$) than in 2013 (6.4 ± 4.2 days, range: 2.4–23.8 days; $n = 23$; Figure 5), and year was present in all models in the confidence set (Table S1). Females tagged earlier in the season took longer to reach spawning grounds ($r = -0.6$, years pooled; Figure 5). Tagging date was present in all models in the candidate set (Table S2), and the effect of tagging date was twice as strong as the effect of year (Figure 3b). All other explanatory variables had uncertain coefficient estimates, with 95% CI spanning zero (Figure 3b), and, when added to the top-ranked model in the candidate set (i.e. tagging date + year; $r^2 = 0.33$), did not describe any additional variation (Table S2). Exposure to high discharge was associated with longer migrations, but the effect was highly uncertain, as the 95% CI was wide and crossed zero. The effects of FL plasma glucose, lactate and oestradiol concentration, and fishway temperature were all approximately zero (Figure 3b).

3.4 | Temperature experience in natal lakes

In 2014, the females from which temperature loggers were recovered spent an average of 9.8 ± 5.3 days (range: 2.4–10.1 days; $n = 39$) in Seton and Anderson lakes. Mean lake temperatures experienced were between 9.2 and 14.8°C, and minimum and maximum temperatures were from 4.9 to 11.1°C and from 17.4 to 22.4°C respectively. On average, females spent 33% of the migration in the T_{optAS} window (13.4–19.5°C; Table 1). Time in the T_{optAS} window

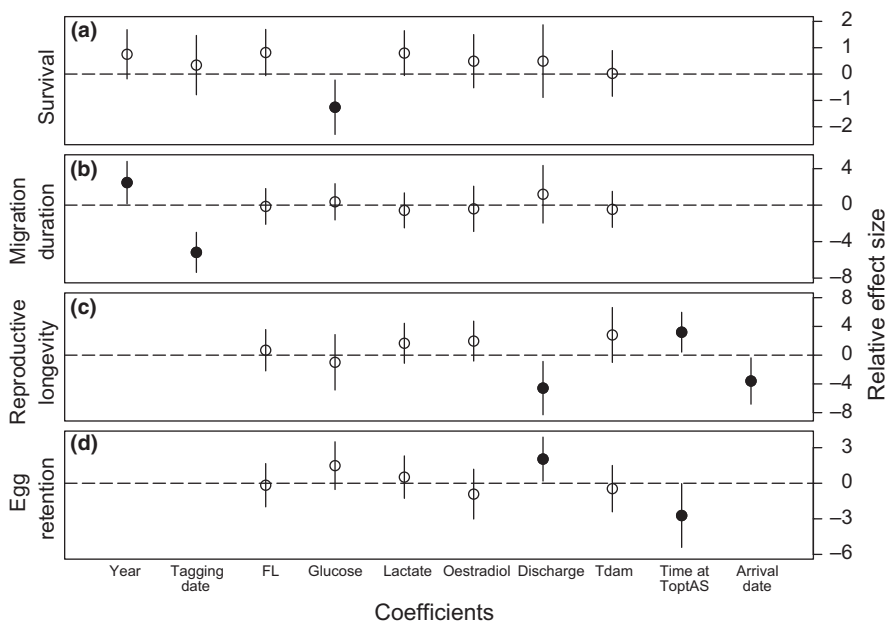


FIGURE 3 Model-averaged standardised coefficients (mean = 0, SD = 2) with 95% confidence intervals (CI) from models describing (a) survival, (b) migration duration, (c) reproductive longevity and (d) egg retention. Filled circles indicate coefficients with CI that do not cross zero

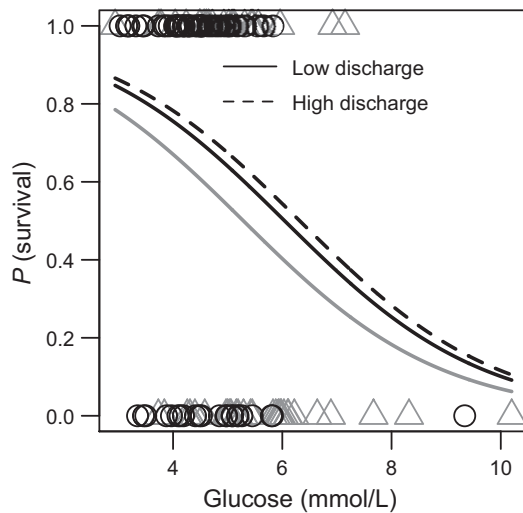


FIGURE 4 Scatterplot of plasma glucose concentration at tagging versus survival for females tagged in 2013 (grey triangles) and 2014 (black circles). Model 1 predictions shown for females that experienced low (solid line) and high (dashed line) discharge at the Seton Dam in 2013 (grey line) and 2014 (black line). High discharge (i.e. altered flow conditions) did not occur in 2013

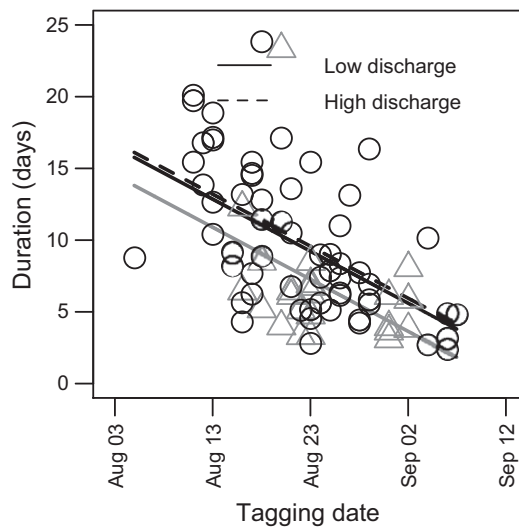


FIGURE 5 Scatterplot of tagging date versus migration duration for females tagged in 2013 (grey triangles) and 2014 (black circles). Model 2 predictions shown for females that experienced low (solid line) and high (dashed line) discharge at the Seton Dam in 2013 (grey line) and 2014 (black line). High discharge (i.e. altered flow conditions) did not occur in 2013

ranged from 8% to 80% of the total time individuals spent in the lakes (see Figure 6 for examples). Temperatures $>19.5^{\circ}\text{C}$ represented only 0.2% of records.

3.5 | Reproductive longevity (Model 3)

Radio-tagged females lived in the spawning channel for a mean of 10.8 ± 4.5 days (range: 4–22 days, $n = 39$) in 2014. Time in the

T_{optAS} window had a positive effect on longevity and appeared in all models in the confidence set (Table S2; Figure 3c). Females that experienced high Seton Dam discharge lived fewer days on spawning grounds than females that experienced low discharge (Figure 3c), and discharge also appeared in all top models (Table S2). Females that arrived on spawning grounds later lived fewer days than early arriving fish (Figure 3c). The top model, which included time in the T_{optAS} window, Seton Dam discharge and arrival date, accounted for 33% of variation in reproductive longevity (Table S2). According to model predictions, a female that arrived on 2 September (median arrival date) lived 12.1 days, following exposure to low Seton Dam discharge, and 8.5 days, following exposure to high discharge, given mean values of all other variables (Figure 7a). Females that spent 50% of time in the T_{optAS} window lived 13.2 days in the spawning channel, following exposure to low discharge, and 9.5 days, following exposure to high discharge, given mean values of all other variables (Figure 7b). Plasma glucose concentration was negatively associated with longevity, while plasma oestradiol and lactate concentrations, FL and fishway temperature were positively associated with longevity (Figure 3c); however, the directions of effect for these variables were uncertain, as the 95% CI spanned zero.

3.6 | Egg retention (Model 4)

Of the thirty-eight females assessed on spawning grounds in 2014, 32% ($n = 12$) retained eggs at death and 68% ($n = 26$) did not. Females that successfully spawned lived longer on spawning grounds (12.4 ± 3.9 days, range: 4–22 days, $n = 26$) than females that retained eggs at death (6.8 ± 2.6 days, range: 4–11 days, $n = 12$; two-sample t test: $t_{31} = -5.25$, $p < 0.0001$; see Figure 7d).

AICc scores from individual GLMs fitted to the egg retention data were compared for a model with Seton Dam discharge and a model with arrival date on spawning grounds as the only explanatory variable. The discharge model had more support from the data (AICc: 44) than the arrival date model (AICc: 51; Table S1), so Seton Dam discharge was included as a categorical variable in Model 4, and arrival date was excluded. Both the earliest and latest arriving females successfully deposited eggs on spawning grounds (Figure 7d).

Females that spent a greater proportion of time in Seton and Anderson lakes in the T_{optAS} window were less likely to retain eggs, as were females that experienced low Seton Dam discharge (Figure 3d); both variables appeared in all models in the confidence set (Table S2). The averaged model predicted that a female fish had a 50% probability of retaining eggs following exposure to high discharge and 30% of migration in the T_{optAS} window, or following exposure to low discharge and 6.8% of migration in the T_{optAS} window, given mean values of all other variables (Figure 7e). The top-ranked model, which explained 33% of the variation, also included plasma glucose concentration (Table S2). Females with higher plasma glucose at tagging were more likely to retain eggs, but the effect was uncertain, as the 95%

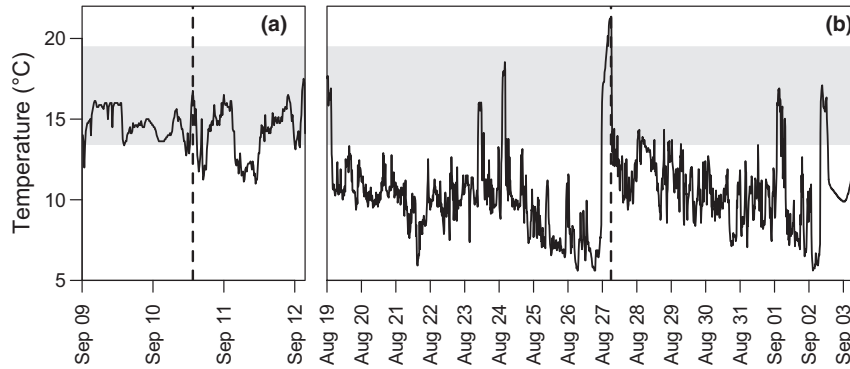


FIGURE 6 The thermal experience of two female sockeye salmon between Seton Dam and Gates Creek. These fish spent the highest (80%, left) and lowest (8%, right) proportion of time in the T_{optAS} window (13.4–19.5°C; indicated by shaded region), of the females with recovered archival temperature loggers ($n = 38$), during migration through Seton and Anderson lakes. Passage through Portage Creek is indicated by a dashed vertical line. The fish were tagged on 6 September 2014 (left) and 17 August 2014 (right), and one spawned successfully (left), while the other retained eggs at death (right)

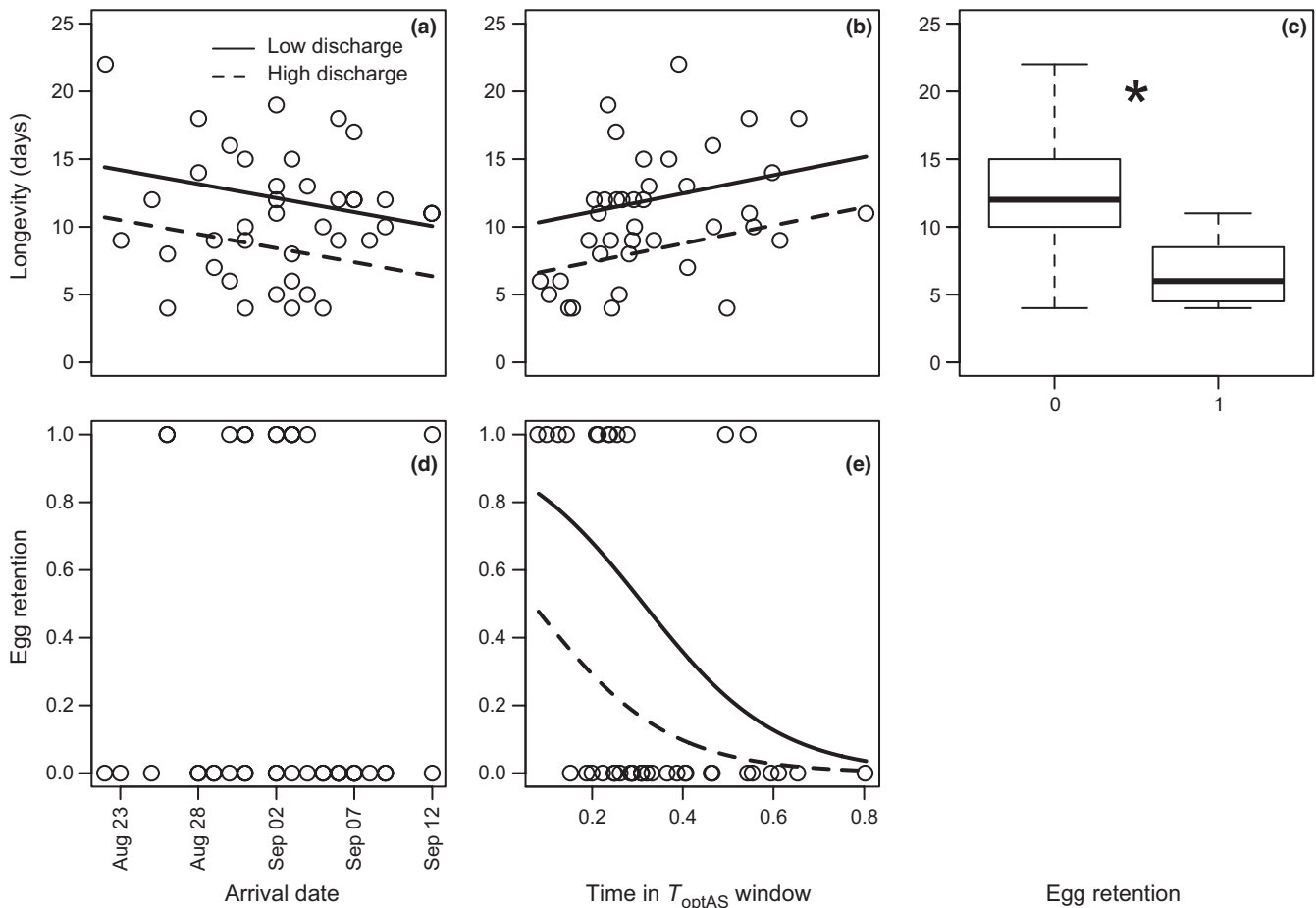


FIGURE 7 Scatterplots of reproductive longevity versus (a) arrival date and (b) proportion of time in T_{optAS} window ($n = 39$) and egg retention versus (d) arrival date and (e) proportion of time in T_{optAS} window ($n = 38$) for female sockeye salmon tagged in 2014. Predictions from the averaged model are shown for low (solid line) and high (dashed line) discharge at the Seton Dam in (a), (b) and (e), but not (d), as the relationship between arrival date and egg retention was not modelled. Boxplots (c) show reproductive longevity differed significantly for females that did ($n = 12$) and did not ($n = 26$) retain eggs (two-sample t test: $t_{31} = -5.25$, $p < 0.0001$), with the mean and range (whiskers) shown.

CI crossed zero (Figure 3d). The other explanatory variables also had uncertain effects on egg retention, although Model 4 predicted that females with higher plasma oestradiol concentration

were less likely to retain eggs. The effects of FL, plasma lactate concentration and fishway temperature were approximately zero (Figure 3d).

4 | DISCUSSION

We examined the relative importance of physiological condition and migratory experience in the final stages of reproductive migration to female sockeye salmon fitness-related outcomes. Physiological factors and migration timing were most important to the duration and success of migration, while migratory experience strongly affected reproductive longevity and egg retention.

Plasma glucose concentration was the only measure of fish physiological condition that affected fitness-related outcomes. Females with lower plasma glucose concentrations at tagging had a greater probability of survival to spawning grounds, which has been previously observed in migrating sockeye salmon (Roscoe, Hinch, Cooke, & Patterson, 2010b; Young et al., 2006). Fish mobilise glucose as an energy substrate for swimming, and high levels have been used as indicators of exhaustive exercise (Farrell, Gallagher, & Routledge, 2001; Wood, 1991). The highest concentrations measured in this study were similar to peak concentrations following maximal swimming (Eliason, Clark, Hinch, & Farrell, 2013), indicating that some fish arrive in the Seton River in a state of physiological stress and may be unable to recover from dam passage. Sockeye salmon exposed to high Fraser River temperatures had similar plasma glucose concentrations ($4.68 \pm 0.24 \text{ mmol}\cdot\text{L}^{-1}$; Young et al., 2006) to those observed here, and high river temperatures may have contributed to relatively high plasma glucose concentrations in the females we tagged. Indeed, glucose levels were higher and survival was lower in 2013, when Fraser River temperatures surpassed 21.0°C (D.A. Patterson, Fisheries and Oceans Canada, unpublished data).

Plasma $17\text{-}\beta$ oestradiol concentration was not important to any fitness-related outcome, but we observed higher plasma oestradiol in females in 2014 than in 2013. During female reproductive maturation, plasma oestradiol stimulates liver vitellogenin synthesis, which is taken up by oocytes in the ovary (Ng & Idler, 1983). During the upstream migration, female sockeye salmon are undergoing vitellogenesis and plasma oestradiol concentration is high, but levels decrease immediately before reaching spawning grounds (Truscott, Idler, So, & Walse, 1986). Roscoe et al. (2010a) inferred that female Gates Creek sockeye salmon with relatively lower plasma oestradiol at capture in the Seton River were more mature than females with higher concentrations, as migrants are 55 km from spawning grounds and within 1–2 weeks of spawning. In the current study, lower plasma oestradiol may indicate that females were more mature in 2013 than in 2014. However, levels of circulating sex hormones can also be depressed by physiological stress processes (reviewed by Schreck, Contreras-Sanchez, & Fitzpatrick, 2001), and $19\text{--}22^\circ\text{C}$ temperatures, like migrants experienced in the Fraser River in 2013, suppress synthesis of plasma oestradiol in female salmonids (Jeffries et al., 2012; Pankhurst & King, 2010).

Females tagged early in the migration spent up to 20 days longer in Seton and Anderson lakes than females tagged later. Roscoe et al. (2010a) observed that early migrants hold and circle in Anderson Lake, while in the current study, late migrants swam through the lakes in approximately two days. The negative relationship between tagging

date and migration duration synchronises arrival on spawning grounds; in sockeye salmon populations, most fish arrive within a one- to two-week window (Killick, 1955). In 2013, females reached spawning grounds more quickly than females in 2014, which may be attributed to several factors. First, fish may have migrated more quickly when exposed to high Fraser River temperatures (Keefer et al., 2008; Naughton et al., 2005). Second, the near-lethal temperatures in 2013 likely contributed to the very low survival of fish tagged early in the run, which we might expect to migrate more slowly. Furthermore, a later mean tagging date in 2013 may have biased the data, as fewer of the early migrants were sampled. Ultimately, only one tagged female with a migration duration >15 days survived to Gates Creek in 2013.

Early arrival on spawning grounds was associated with greater reproductive longevity, which has been attributed to strong selective pressure for early spawning females to live long enough to defend redds from disturbance by later arrivals (Dickerson, Quinn, & Willson, 2002; Morbey & Ydenberg, 2003). We also observed a close association between reproductive longevity and spawning success, whereby longer-lived females were more likely to deposit all eggs before death (Burnett et al., 2016; Hruska et al., 2011). However, egg retention was not strongly related to arrival date, as both the earliest and latest arriving females spawned successfully. The absence of a strong effect of arrival date is unusual for patterns of egg retention, because prespawning mortality is thought to be more prevalent among early arriving female fish (Gilhousen, 1990; Fukushima, Quinn, & Smoker, 1998; but see Hruska et al., 2011). Our observations may be related to unusual migration timing in 2014, when the first fish arrived at Gates Creek nine days later than in 2013 (S. Lingard, InStream Fisheries Research Inc., pers. comm.). It is possible that early migrants arrived on spawning grounds with greater reproductive preparedness, as final maturation is driven by environmental cues, such as photoperiod and temperatures (Davies & Bromage, 2002).

We found new evidence to support the hypothesis that exposure to a migratory stressor can have a delayed negative effect on fitness-related outcomes in Pacific salmon (see also Caudill et al., 2007; Fenkes et al., 2015). From 8 August 2014 to 19 August 2014, water was released from a siphon approximately 10 m from the Seton Dam fishway entrance, rather than directly adjacent, as is standard operating procedure. The operational change increased water velocities below the dam, the area of the tailrace covered by turbulent flows, and Seton Dam discharge by up to 25%. A parallel study examined Gates Creek sockeye salmon swimming behaviour during each of the flow conditions and found that although fish delayed longer in the dam tailrace under high discharge, survival to spawning grounds was higher (Burnett et al., 2016). In the current study, Model 1 predicted a slightly higher, but uncertain, probability of survival for females that experienced high discharge in 2014. Yet, dam passage appeared to affect reproduction in a subset of the females we tagged. Female fish that experienced high discharge at Seton Dam had lower reproductive longevity and were more likely to retain eggs at death. According to model predictions, a female that experienced high Seton Dam discharge would have had to arrive on spawning grounds 10–15 days earlier

or spend a greater proportion of the migration at T_{optAS} to achieve the same longevity as a female that experienced low discharge. Cumulative stress, suppression of maturation processes and energy depletion caused by swimming against high flows are possible explanations for the reduced reproductive longevity and spawning success that we observed (Fenkes et al., 2015; Nadeau, Hinch, Hruska, Pon, & Patterson, 2010; Palstra et al., 2010).

This is the first study to relate spawning success to use of a physiologically relevant temperature range ($\approx T_{\text{optAS}} \pm 3^\circ\text{C}$) by Pacific salmon in the natural environment. Gates Creek is one of only a few populations of Pacific salmon with a known aerobic scope curve (Eliason et al., 2011; Lee et al., 2003), which can be used to infer cardiac capacity and scope for activity from the thermal experience of individual fish. Consistent with predictions, females that spent a greater proportion of the migration through Seton and Anderson lakes in the T_{optAS} window (13.4–19.5°C) lived longer on spawning grounds and had lower egg retention at death. Temperature-dependent maturation processes may be driving these differences in fitness-related outcomes. The optimum and upper threshold temperatures for vitellogenesis have not been defined for species of Pacific salmon, but female salmonids held at temperatures $>18^\circ\text{C}$ exhibit suppressed plasma oestradiol and vitellogenin synthesis and lower egg survival, relative to fish held at temperatures $<15^\circ\text{C}$ (sockeye salmon, Macdonald et al., 2000; Atlantic salmon (*Salmo salar*), King, Pankhurst, Watts, & Pankhurst, 2003), and the quality of ovulated eggs declines quickly above 13°C (coho salmon (*Oncorhynchus kisutch*), Flett, Munkittrick, Van Der Kraak, & Leatherland, 1996). In the current study, few females occupied temperatures in the upper half of the T_{optAS} window (16.5–19.5°C) for prolonged periods, indicating that fish were avoiding these warmer temperatures. Exposure to temperatures above 19.5°C was rare; the warmest temperatures were experienced in Portage Creek ($>20^\circ\text{C}$), where there is no opportunity for thermal refuge. Tagged fish were observed at temperatures below the T_{optAS} window, with many females exhibiting a preference for temperatures near $10\text{--}12^\circ\text{C}$, consistent with behavioural thermoregulation by sockeye salmon in other lakes (e.g. Armstrong, Ward, Schindler, & Lisi, 2016; Newell & Quinn, 2005). It is important to note that a variety of thermal experiences (15–80% of time in the T_{optAS} window, at different instances in the migration) were associated with successful spawning in the current study. Unfortunately, we could not assess the effect of lake thermal experience on survival, because archival temperature loggers were not recovered for fish that died *en route* to spawning grounds. This is an important gap in current research, as unsuccessful migrants may experience warmer temperatures than survivors when adult salmon are migrating near the limits of thermal tolerance (Keefer et al., 2008, 2015).

It remains unclear whether insufficient time on spawning grounds is a direct cause of spawning failure—because females are unable to complete necessary reproductive behaviours before death—or whether both decreased longevity and spawning failure are caused by poor physiological condition. It is possible that disease processes in some tagged females led to both cool thermal preference ($<13.4^\circ\text{C}$) and poor fitness-related outcomes. Use of cool temperatures may prevent pathogen-associated mortality (Mathes et al., 2010), as

water temperature increases virulence and replication rates in some pathogens (Holt, Sanders, Zinn, Fryer, & Pilcher, 1975; Udey, Fryer, & Pilcher, 1975). It is yet to be examined whether Pacific salmon with higher pathogen loads or in more advanced stages of disease select cooler lake temperatures and whether these fish also die prematurely on spawning grounds with retained eggs.

Thermal behaviour of sockeye salmon in lakes reflects trade-offs between multiple physiological processes, including energy conservation, swimming activity, stress recovery, olfactory homing, maturation and disease responses (Bradford et al., 2010; Newell & Quinn, 2005; Roscoe et al., 2010a). For example, use of cool temperatures conserves limited somatic energy. Roscoe et al. (2010a) observed that females with low energy levels avoided high temperatures, and sockeye salmon populations with longer freshwater holding exhibit cooler average temperatures (e.g. Katinic, Patterson, & Ydenberg, 2014; Newell & Quinn, 2005). Yet, our observation that tagged females did not use the coolest temperatures available was consistent with previous studies that have shown fish to select intermediate temperatures in lakes (Armstrong et al., 2016; Eckmann, Dunham, Connor, & Welch, 2016). At low temperatures, sockeye salmon have reduced aerobic scope for oxygen-dependent processes, such as swimming. Eliason et al. (2011) proposed that Fraser River sockeye salmon require at least 90% of aerobic scope to complete upstream migration, and our results demonstrate that females can swim through natal lakes with a lower proportion of maximum aerobic scope (at temperatures $<13.4^\circ\text{C}$). Preference for $10\text{--}12^\circ\text{C}$ by tagged females in this study suggests a temperature window that balances aerobic scope for migration with somatic energy conservation and suitable temperatures for vitellogenesis.

In summary, the explanatory variables we investigated differed in importance across four fitness-related outcomes, demonstrating the complexity of factors governing the final stages of migration and spawning. Our work indicates that researchers should measure multiple fitness-related outcomes at the individual scale if we are to broaden our understanding of how different factors—including lethal and sublethal stressors—affect adult Pacific salmon in the final stages of migration.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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