**Effects of natal water concentration and temperature on the behaviour of up-river migrating sockeye salmon**

<table>
<thead>
<tr>
<th>Journal:</th>
<th>Canadian Journal of Fisheries and Aquatic Sciences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manuscript ID</td>
<td>cjfas-2017-0490.R1</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>22-Feb-2018</td>
</tr>
</tbody>
</table>
| Complete List of Authors:     | Middleton, Collin; University of British Columbia, Department of Forest and Conservation Sciences  
                                Hinch, Scott; University of British Columbia, Department of Forest and Conservation Sciences  
                                Martins, Eduardo; University of Northern British Columbia, Ecosystem Science and Management Program  
                                Braun, Douglas; Department of Fisheries and Oceans  
                                Patterson, David; Department of Fisheries and Oceans  
                                Burnett, Nicholas; University of British Columbia, Department of Forest and Conservation Sciences; Instream Fisheries Research  
                                Minke-Martin, Vanessa; University of British Columbia, Department of Forest and Conservation Sciences  
                                Casselman, Matthew; BC Hydro Burnaby Office |
| Is the invited manuscript for consideration in a Special Issue? | Oceans Tracking Network |
| Keyword:                      | Homing, Behaviour, Migration Delay, TELEMETRY < General, OLFACITION < General |
Effects of natal water concentration and temperature on the behaviour of up-river migrating sockeye salmon

Collin T Middelton1*, Scott G Hinch1, Eduardo G Martins2, Douglas C Braun3, David A Patterson3, Nicholas J Burnett4, Vanessa Minke-Martin1, Matthew T Casselman5

1Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, BC, Canada. collin.t.middleton@gmail.com & scott.hinch@ubc.ca

2Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC, V2N 4Z9, Canada. eduardo.martins@unbc.ca

3Fisheries and Oceans Canada and School of Resource and Environmental Management, Simon Fraser University, 643-A Science Road, Burnaby, British Columbia, V5A 1S6, Canada. david.patterson@dfo-mpo.gc.ca & douglas.braun@dfo-mpo.gc.ca

4InStream Fisheries Research Inc., 215 – 2323 Boundary Road, Vancouver, British Columbia, V5M 4V8, Canada. nich@instream.net

5BC Hydro, 6911 Southpoint Drive, 11th Floor, Burnaby, British Columbia, V3N 4X8, Canada. matt.casselman@bchydro.com

*correspondence author: Collin Middleton, 2424 Main Mall, Vancouver, BC, V6T 1Z4, 778-928-7094, collin.t.middleton@gmail.com
Abstract
Impoundments and diversions in freshwater corridors can alter the availability and concentration of natal water cues that migratory salmon rely on to guide homing during spawning migrations, although this has rarely been examined. By combining radio-telemetry and non-invasive biopsy, we provide the first detailed account of the effects of varying natal water concentrations, temperature, and individual physiology on the homing behaviour of wild adult Pacific salmon migrating through a regulated river. Most (89%) of the 346 sockeye salmon from the two distinct populations tracked in this study in southwestern British Columbia (Canada) delayed their migration in the outlet of a powerhouse that discharges strong concentrations of natal lake water, and subsequently wandered in the Fraser River before continuing upstream into the Seton River, where natal water cues can also vary. There were few associations between metabolic stress indices and reproductive hormone levels with this behaviour in either population, however, higher temperatures and elevated natal water concentrations in the Seton River were associated with shorter powerhouse delays and less wandering in late-run migrants.

Keywords:
Olfaction; homing; migration delay; behaviour; *Oncorhynchus nerka*; telemetry
Introduction

Anadromous fishes exhibit some of the most complex behaviours of any group of organisms (Dingle and Drake 2007), in large part because of the variable abiotic conditions encountered throughout their migrations and the inherent physiological changes associated with reproductive development (Alerstam et al. 2003; Donaldson et al. 2011). In the case of Pacific salmon (*Oncorhynchus* spp.), up-river migrating adults use olfactory cues to locate natal areas (Keefer and Caudill 2014) and do so while maturing and coping with environmental factors (e.g. high discharge and/or high temperature) that can lead to physiological stress, increased energy use (reviewed in Hinch et al. 2006), and slowed or delayed migration (e.g. Bugert et al. 1997; Keefer et al. 2008a). Because adults cease feeding prior to entering freshwater, individuals must complete migration, gonad development, and spawn using finite energy reserves (Brett 1971). Thus, any environmental factors that may delay migrations could influence migration or spawning success (Burnett et al. 2016).

Many freshwater corridors used by migratory salmon have been altered by impoundments or diversions (see reviews in Waples et al. 2008; Thorstad et al. 2008). While numerous studies have examined how changes in the amount of flow can affect migratory salmon (e.g. Quinn et al. 1997; Keefer et al. 2004b; Murchie et al. 2008), there have been few direct investigations of how changes in the specific natal water composition of flows affect migrations. For example, multiple impoundments of the Columbia River, U.S.A. have increased river channel cross-sections and led to substantial odour diffusion from natal tributaries (Quinn 2005; Keefer and Caudill 2014). Many adult salmon now exhibit wandering behaviour in this system which could be reflective of orientation challenges and active searching for natal water cues, though this is largely speculation (Keefer et al. 2008a). Adult salmon are known to be attracted to and delay their migrations in power station outlets which discharge natal water along...
migration routes (Andrew and Geen 1958; Thorstad et al. 2003b, 2008). Numerous forays in and out of these facilities into mainstem flows can result in substantial migration delays or failure to continue migrations upstream to pass dams (Fretwell 1989; Thorstad et al. 2003b). Adult Atlantic salmon (Salmo salar) have also been documented making ‘yo-yo’ movements or wandering back-and-forth between power station outlets and dam tailraces, ultimately causing migration delays and reduced dam passage success (Lundqvist et al. 2008). Many lab-based experiments have revealed that migration responses in adult salmonids can be triggered by even slight changes in natal water concentrations (reviewed in Bett and Hinch 2015), yet there has been comparatively little research examining how such changes to natal water along migration routes can influence the migration behaviour of free-swimming wild salmon.

In recent years, freshwater migration corridors have been warming (e.g. Patterson et al. 2007; Isaak et al. 2012) and many Pacific salmon now often encounter temperatures that can exceed population-specific thermal limits (Eliason et al. 2011). For adult sockeye salmon (O. nerka), exposure to high temperatures accelerates maturation (Hinch et al. 2006), depletes energy reserves (Hinch and Rand 1998; Burnett et al. 2014), increases physiological stress and disease development (Crossin et al. 2008; Bradford et al. 2010), and reduces aerobic scope (Eliason and Farrell 2015) – any or all of which can lead to en route mortality (e.g. Keefer et al. 2009; Hinch et al. 2012). Pacific salmon will seek cool-water refuges (e.g. hypolimnion of lakes, tributary outlets; Newell and Quinn 2005; Goniea et al. 2011) to reduce exposure to high temperatures and increase chances of migration survival (Mathes et al. 2010). However, the use of thermal refugia could also limit exposure to natal water cues if refuge is taken in non-natal tributaries or areas of substantial homestream odour diffusion, which could in turn lead to missed migration cues in the mainstem migration corridor, and potentially increase migration delays. Prolonged delay in
thermal refuges has also been shown to reduce the probability of surviving to natal sites by migrating adult salmon (e.g. Columbia River steelhead *O. mykiss*; Keefer et al. 2009).

The physiological state of salmon can have strong effects on migration behaviours (Hinch et al. 2006). For instance, elevated levels of acute metabolic stress and energy expenditure (as reflected by increased plasma glucose and lactate levels; Milligan 1996; Farrell et al. 2000) in ocean migrating adult Fraser River sockeye salmon are associated with delayed river entry and slowed migration rates (Cooke et al. 2006; Crossin et al. 2007). Whereas in contrast, advanced maturation (as reflected by high levels of plasma testosterone; Truscott et al. 1986; Leonard et al. 2002) is correlated with earlier river entry and fast migration rates (Sato et al. 1997; Crossin et al. 2009). The important role of physiology is further emphasized in how sexes can differ in migration behaviours. Females devote more energy to gonad development (Crossin et al. 2008) and typically have higher levels of reproductive hormones than males throughout freshwater migrations (Truscott et al. 1986). In the Fraser River, female sockeye salmon are energetically more efficient swimmers (Hinch and Rand 2000), but are often less successful at passing hydraulically challenging areas (Hinch and Bratty 2000; Burnett et al. 2013) compared to males. How an individual’s physiological condition or sex affects migration behaviour in regulated systems where natal water concentrations and flow composition can change during migration has not yet been examined.

In this study, we used radio telemetry to track wild adult sockeye salmon from two populations as they migrated during the summer and fall from a large mainstem system (Fraser River) into a small, regulated, natal tributary (Seton River). Immediately prior to entering the Seton River, migrants must pass by a powerhouse tailrace, which is likely attractive because it discharges pure natal lake (Seton Lake) water directly into the migration route and is sometimes
cooler than the Fraser River, offering a potential thermal refuge. Natal water cues in the Seton River can vary daily because of inputs from a non-natal tributary (Cayoosh Creek), which in turn affects the availability and strength of natal Seton River water entering the Fraser River just upstream of (and passing by) the powerhouse. This locale provides an ideal system in which to examine the relative roles that flow composition (e.g. natal water cues), water temperature, and thermal refugia can have on individual adult salmon behaviour as they migrate towards spawning grounds.

We predicted that, if variation in natal water concentration does indeed affect migration behaviour, adult sockeye salmon would spend more time in the powerhouse tailrace when natal water concentration in the Seton River, entering the Fraser River just upstream, was low (see Fig. 1). We also predicted that if higher concentrations of natal water in the Seton River are expected to encourage upstream migration, fish would display signs of ‘migratory confusion’, such as enhanced wandering, when natal water concentration in the Seton River was reduced. Whereas, we predicted that migrants would make more direct migrations towards the Seton River when its natal water concentration was higher. We further hypothesized that if mainstem Fraser River temperatures were approaching physiologically critical levels, fish would spend more time delaying in the powerhouse tailrace, potentially using this area as a thermal refuge. Lastly, given the physiological condition and sex of migrants are known to differentially affect behaviour, we predicted that individuals that were more mature at tagging would migrate faster and more directly towards the Seton River, whereas those that showed signs of stress would delay their migration, likely in the powerhouse tailrace. We also expected that females would exhibit less wandering and less delay at the powerhouse given their more limited energy budget.

**Methods**

**Study system**
The Bridge-Seton hydrosystem is a complex network of reservoirs, inter-basin diversions, and power generating stations operated by BC Hydro near Lillooet, British Columbia, Canada (Fig. 1). Adult sockeye salmon first encounter the Seton Powerhouse (powerhouse) ~ 340 km from the Pacific Ocean on the western bank of the Fraser River near the confluence of the Seton River and Fraser River (Fig. 1). At the powerhouse, natal Seton Lake water diverted by the Seton Dam is discharged from an underwater outlet into a 5-meter deep tailrace directly adjacent to the Fraser River (Fig. 1). Notably, there is no fish passage facility at the powerhouse and migrants are prevented from entering the underwater outlet by steel grates. During adult sockeye salmon migrations, mean discharge from the powerhouse is ~ 84.5 m$^3$s$^{-1}$, or ~ 5% of the mean 1492.5 m$^3$s$^{-1}$ of the adjacent Fraser River. Discharge from the powerhouse creates a plume of natal Seton Lake water that visibly extends ~ 800 m downstream into the Fraser River (Fig. 1). The Seton River flows into the Fraser River 1.5 km upstream of the powerhouse (Fig. 1). The 5 km-long Seton River (22.7 m$^3$s$^{-1}$ mean annual discharge) is regulated by the Seton Dam, which is made passable to migratory fish by a 107 m long, 32-pool vertical slot fishway. Cayoosh Creek (13.9 m$^3$s$^{-1}$ mean annual discharge) is the only tributary of the Seton River; it drains a separate, non-natal watershed (Fig. 1). During times of increased discharge from Cayoosh Creek, which occurs due to operational changes at the Seton Dam or at Walden North (a small non-BC Hydro diversion dam on Cayoosh Creek), or during large precipitation events, flows from this tributary can ‘dilute the olfactory signature’ of the Seton River (Fretwell 1989) by reducing the concentration of natal water cues in the Seton River and its plume. It is the combination of pure natal Seton Lake water discharged at the powerhouse and reduction in natal water concentration in the Seton River that creates the variable olfactory conditions of interest in this study (Fig. 1).
Gates Creek (hereafter, GC) and Portage Creek (hereafter, PC) sockeye salmon are the two populations of Fraser River sockeye salmon that spawn and rear in this system, representing distinct ‘early-summer’ and ‘late-run’ populations, respectively. The GC population typically begins migrating into the hydrosystem in late July, travelling ~ 55 km past the Seton Dam through Seton and Anderson Lakes to reach terminal spawning grounds at Gates Creek. PC sockeye salmon begin migrating into the hydrosystem at the end of September, travelling ~ 20 km past the Seton Dam through Seton Lake to reach spawning grounds in Portage Creek.

Studies conducted throughout the 1970’s by the International Pacific Salmon Fisheries Commission indicated that the upstream migration of both populations could be delayed at the powerhouse, and that migrants often had difficulty navigating beyond this point (Fretwell 1989). Results of behavioural choice (Y-maze) experiments and limited radio-telemetry studies suggested that minimizing delay and encouraging upstream migration past the powerhouse was dependent on maintaining natal water levels in the Seton River and its plume at or above 80% and 90% during the GC and PC migrations, respectively (Fretwell 1989). BC Hydro currently operates the hydrosystem with measures in place to maintain these natal water dilution targets, though large fluctuations still occur. Migration delays at the powerhouse followed by wandering in the Fraser River are still observed in both populations (Casselman et al. 2015).

**Fish capture and tagging**

It was not possible to capture target or control populations of sockeye salmon in the Fraser River for this study; therefore, all fish were captured using a full-spanning fence and trap at a site 200 m downstream from the Seton Dam in the Seton River (Fig. 1). In total, we radio-tagged and monitored the movements of 517 sockeye salmon through the summer and fall of 2013 and 2014. Specifically, 138 GC sockeye salmon were tagged between 5 August and 2
September 2013, and 166 were tagged between 5 August and 7 September 2014. In 2013, PC sockeye salmon co-migrated with ~ 0.8 million pink salmon (*O. gorbuscha*) returning to the Seton River, making capture of PC sockeye salmon extremely difficult – only 24 individuals were tagged from 3 – 9 October 2013. However, pink salmon were not present in 2014 (pinks only return during odd years in the Seton River), enabling 189 PC sockeye to be captured and tagged from 27 September to 9 October.

Radio transmitters [(43 mm length × 16 mm diameter; 15.2 g in air); Sigma Eight, Newmarket, Ontario, Canada] were gastrically inserted into individual fish. Tags had a burst-rate of 3 s and a unique digital identification code. Individually labeled spaghetti tags (Floy Manufacturing, Seattle, WA, U.S.A.) were attached externally through the dorsum of each fish, with a tissue sample from the adipose fin and a 1.5 mL blood sample from the caudal vasculature taken for population identification and physiological assays. Average time to tag and biopsy sample each fish was < 4 minutes. Fish were not anesthetized to minimize handling and related stress (Cooke et al. 2005). All handling and intra-gastric tagging methods followed procedures used in many adult salmon tracking studies and are known not to affect behaviour or survival (e.g. Ramstad and Woody 2003; Cooke et al. 2005). All procedures followed the methods described in greater detail in (Roscoe et al. 2010b; Burnett et al. 2013, 2014), and were conducted in accordance with the guidelines of the Canadian Council of Animal Care administered by the University of British Columbia (A11-0125).

We selected fish for tagging based on visual inspection of injury, external pathogens and somatic lipid content (measured by a hand-held microwave energy meter – Fatmeter model 692; Distell Inc., West Lothian, Scotland, UK; see Crossin and Hinch 2005). Severely injured fish (e.g. lacerations exposing the coelomic cavity or skeletal system) or those with extensive fungus
cover on body or gills were not tagged, nor were those with high somatic lipid concentrations. An earlier study which compared DNA population identification to Fatmeter output from fish captured at the fish fence revealed that these high energy fish were strays which had entered the Seton River but whose spawning grounds were several 100 km’s further upstream in tributaries of the Fraser River (Casselman et al. 2015). Sex was assigned by analysis of 17-β estradiol and testosterone concentrations in blood plasma. Plasma concentrations of glucose and lactate were used as indices of metabolic stress (Cooke et al. 2008), and testosterone concentrations were used to infer maturity level (Crossin et al. 2007). All blood plasma analyses followed the methods described in (Roscoe et al. 2010b).

To examine how migrants behaved when they first encountered the powerhouse outflows and Seton River plume, tagged fish were transported by truck downstream of the powerhouse for release into the Fraser River. Groups of up to twelve individuals (approximate 50:50 sex ratio) were moved via a 1000 L insulated and oxygenated transport tank and released within 30 min (± 10 min) of tagging, 1.5 km downstream from the powerhouse on the western bank of the Fraser River (Fig. 1). We highlight that the use of passive capture methods followed by downstream transport have been used in other studies with little effect on behaviour or survival (Keefer et al. 2004a, 2009; Hubert et al. 2012). Moreover, methods of upstream capture and downstream release are common in studies of salmon migrating through regulated rivers (Thorstad et al. 2003b; Naughton et al. 2005; Caudill et al. 2007), and there is little evidence suggesting adult salmon have the ability to learn migration routes or consequently behave differently from non-study fish (Hansen and Jonsson 1994; Thorstad et al. 2003b).
Radio-telemetry monitoring of migration behaviour

We used a combination of fixed SRX (Lotek Wireless, Inc., Newmarket, Ontario, Canada) and Orion (Sigma Eight, Inc., Newmarket, Ontario, Canada) radio-receivers fitted with aerial Yagi antennas at different locations in the hydrosystem to monitor fish movement (Fig. 1). The powerhouse receiver was configured to detect tags only in the tailrace and not in the adjacent Fraser River. The receiver at the Seton-Fraser confluence was configured to only detect tags within a ~100 m radius of the Seton River mouth. A receiver at the Fraser River release site served as a ‘gate’ for detecting individuals exhibiting fallback in the Fraser River, whereas receivers upstream in the Seton River confirmed Seton River entry or arrival at the Seton Dam (Fig. 1). All receivers operated > 85% of the study duration, providing sufficient ability to monitor fish movements (e.g. Release Site: 92.4%; Seton Powerhouse: 98.3%; Lower Seton River: 94.8%; Seton-Fraser confluence: 91.2%; Seton-Cayoosh confluence: 91.2%; Seton Dam: 95.7%).

Raw telemetry data were filtered to remove false detections (e.g. likely false detections of study tag ID’s, non-study tag ID’s, detections recorded before release (Beeman & Perry 2012) and generate migration histories. Migration behaviour was quantified by (1) counting the number of entries individuals made into the powerhouse tailrace (hereafter ‘forays’) as a measure of attraction to the outflows at this facility; (2) determining the number of inter-receiver movements (hereafter ‘wandering’) in the Fraser River between radio receivers at the powerhouse and the Seton-Fraser confluence as an index of migration confusion; and (3) summing the duration of each foray into the powerhouse tailrace as an estimate of the total amount of migration delay incurred by individuals at this facility (hereafter ‘delay’). To ensure that the number of forays and thus delay at the powerhouse were representative of true migration behaviour, we calculated...
each metric based on detections that were part of ‘residence events’. Residence events for a
given fish were defined as a series of consecutive detections at an individual receiver separated
by no more than 30 minutes. The duration of a residence event continued indefinitely until being
terminated when either (1) the time elapsed between any two consecutive detections was > 30
minutes, or when (2) a detection was recorded on another receiver.

Individual migration histories were visually examined to count the number of wandering
events in the Fraser River. We classified every change in direction prior to final assignment of
care as a single wandering event. Fish with wandering values of zero exhibited directed
movements in the Fraser River, while fish with increasing wandering values exhibited the same
corresponding number of changes in direction prior to final assignment of care. Fate was
assigned to individuals as having (1) successfully entered the Seton River if their last known
detection occurred at any receiver upstream of the Seton-Fraser confluence or into the Seton-
Anderson watershed, (2) passed the Seton River and migrated further upstream in the Fraser
River if their last detection occurred at the Seton-Fraser confluence, (3) exhibited fallback
downstream in the mainstem Fraser River if their last detection occurred at the release site
receiver, or (4) be of unclassified care if detections did not conform any of the aforementioned
patterns. Of the 304 GC sockeye salmon originally released for this study, 90% (274 of 304)
successfully entered the Seton River, 4% (12 of 304) migrated upstream of the Seton-Fraser
confluence, 3% (9 of 304) fell back downstream in the Fraser River, and 3% (9 of 304) had
unclassified fates. Of the 213 PC fish released, 80% (170 of 213) successfully entered the Seton
River, 6% (13 of 213) migrated upstream of the Seton-Fraser confluence, 13% (28 of 213)
returned downstream, and 1% (2 of 213) had unclassified fates. Fish that fell back downstream
after release and did not re-ascend may have suffered from some form of experimenter-induced
stress. However, given that this occurred in a relatively small component of released fish, and 93% and 86% of GC and PC fish, respectively, reached the Seton River, we suspect our handling and transport approaches probably had minimal effects on fish behaviour and short-term survival.

**Environmental conditions**

We used hourly measurements from the Water Survey of Canada (www.wateroffice.ec.gc.ca) to monitor discharge in Cayoosh Creek (Station No. 08ME002) and the Seton River below the Seton Dam (Station No. 08ME003). Hourly discharge data from the powerhouse were provided by BC Hydro. We calculated hourly lower Seton River discharge by summing (1) the upper Seton River discharge, (2) Cayoosh Creek discharge, and (3) a constant 2.1 m$^3$s$^{-1}$ of Seton Lake water diverted to an artificial spawning channel that is returned into the lower Seton River before the Seton-Fraser confluence. We then calculated the concentration of natal water in the lower Seton River and its plume using discharges in the following equation:

$$\text{Natal water (\%) = } 100 - \left(100 \times \left(\frac{\text{Cayoosh Creek}}{\text{Upper Seton River} + \text{Cayoosh Creek} + \text{Spawning Channel}}\right)\right)$$

We confirmed differences in the water chemistry between natal Seton River and non-natal Cayoosh Creek water – which reflects differences in olfactory cues – by collecting daily conductivity measurements from Cayoosh Creek, the upper and lower Seton River, and the powerhouse using a hand held YSI Pro30 conductivity meter (YSI Inc., Yellow Springs, OH, USA). Conductivity has previously been used to distinguish between water sources used by other anadromous fishes that use olfaction to guide homing (e.g. Leduc et al. 2010; Vrieze et al. 2011). Hourly water temperatures were measured and collected using TidbiT v2 data loggers (Onset HOBO data loggers, Bourne, MA) at locations in the Fraser River, the powerhouse, and the lower Seton River (Fig. 1).
Data analysis

Statistical models

We used both generalized linear (GLM) and linear models (LM) to relate migration behaviour to characteristics of individual migrants and the environmental conditions they encountered. Our analyses included three specific models to examine: (1) the number of forays made into the powerhouse tailrace (Poisson or negative binomial GLM), (2) the number of wandering events between the powerhouse tailrace and Seton-Fraser confluence (Poisson or negative binomial GLM), and (3) the total amount of migration delay incurred at the powerhouse tailrace (LM). All analyses were conducted on the GC and PC populations independently given the different run-timing and environmental conditions experienced by the two populations.

Model construction

All global models included explanatory variables to account for effects of sex, physiological state (plasma glucose and lactate levels), and the maturity level (plasma testosterone level) of individuals at the time of tagging. Preliminary analyses included interactions between sex and testosterone to test for the differences in reproductive actions this hormone can have between males and females (Truscott et al. 1986; Ueda 2011). However, no significant effects were observed, so this interaction was removed from the models reported on below. Additionally, each model included variables to account for the effects of environmental conditions on different migrant behaviours, including: temperatures encountered in the Fraser River and in the powerhouse tailrace, the temperature differential between these two locations as a measure of thermal refuge potential, and the natal water concentration of the Seton River plume. Neither Fraser River nor Seton River discharge were included in any of the models because GC and PC sockeye migrate up-river when flows are lowest in the migration season and
at levels unlikely to affect behaviour (Rand et al. 2006; Macdonald et al. 2007). Moreover, water
temperature and discharge were highly correlated ($r = 0.89$). Powerhouse discharge was also not
included in any analyses because all fish included in the models experienced consistent discharge
of $\sim 87.3 \text{ m}^3\text{s}^{-1}$ in the tailrace.

Calculations of environmental variables were based on residence events and dependent
on each model response. Variables were calculated as means to ensure the best representation of
the overall conditions experienced by tagged individuals, and weighted-means to emphasize the
effect of conditions experienced over longer periods of time. For Model 1, measurements were
used from the time of an individual’s the first detection of every foray into the powerhouse to
represent what conditions were like at the moment of movement into the tailrace. In Model 2,
means of conditions were weighted based on the duration of residence events that occurred at the
moment individuals changed migration direction between the powerhouse tailrace and the Seton-
Fraser confluence. In Model 3, environmental variables were calculated as an overall average of
means were weighted by the duration of each foray into the powerhouse. Because each of the
models included explanatory variables that were measured on different scales (e.g. $^\circ\text{C}$, %), and to
facilitate comparisons of the relative effect size of each, all the data for these variables were
standardized by centering (subtracting the mean) and dividing by two standard deviations
(Gelman 2008; Schielzeth 2010).

Prior to analysis, the data exploration protocols described in Zuur et al. (2010) were
applied to each model separately. Examinations of Cleveland dotplots were used to identify
outliers and variables with inordinate values to the majority of observations were removed (1 – 4
observations per model). Pearson correlation coefficients > 0.7 and variance inflation factors
(VIF) > 3 were used as thresholds to identify collinear variables (Zuur et al. 2010). In Models 1
and 3 for PC sockeye salmon, the Fraser River temperature variable was highly collinear with the natal water concentration variable. To account for this, we substituted tagging date for Fraser River temperature because the two were related \( r = -0.68 \), but not to the extent that tagging date was collinear with the natal water concentration variable \( \text{VIF} < 3 \). All models were constructed based on a sample size of at least ten observations per explanatory variable.

Models 1 and 2 were initially fit with a Poisson GLM and assessed for over-dispersion by summing the square of the Pearson residuals and dividing by the degrees of freedom (McCullagh and Nelder 1989). These models were deemed over-dispersed \( \text{dispersion parameter} > 1 \) and subsequently re-fit with a negative binomial GLM (O'Hara and Kotze 2010). All final GLMs fit the data adequately as assessed by a Chi-square test \( P > 0.05; \) Smyth 2003). In Model 3, the response variables were log-transformed to satisfy assumptions of linearity and homogeneity of residual variance (both assessed visually); linear model fits were evaluated using adjusted-\( R^2 \).

**Model selection and multimodel averaging**

In each analysis, models with all possible subsets of explanatory variables were fit to the data. Models were then ranked using the bias-corrected Akaike Information Criterion \( \text{AIC}_C \) and compared using \( \text{AIC}_C \) weights \( (w_i) \), which describes the probability of a model in a candidate set being the most parsimonious, given the data (Burnham and Anderson 2003). Uncertainty in model selection was accounted for by calculating model-averaged estimates of the coefficients using the ‘zero’ method (Grueber et al. 2011), where variables not included in the models were assigned coefficient values of 0 to indicate no effect. Only models included in the 95% confidence set were used for model averaging (Burnham and Anderson 2003), and only explanatory variables with 95% confidence intervals that did not include zero were considered to have an important effect on the response. Model selection statistics for all models with \( \Delta \text{AIC} \)
values < 2 are presented in Table 2. All statistical analyses were conducted in R using the
MuMIn package (R Development Core Team, 2008; version 3.1.2). All summary variables are
presented as means ±SD.

Results

Environmental conditions

The mean Fraser River temperature experienced by GC sockeye salmon in this study was
18.3°C (±1.3°C), although temperatures varied considerably over the entire 2013 and 2014
migrations, with some periods reaching near record summer highs (~ 22°C; Fig. 2a). On average,
GC fish encountered temperatures in the powerhouse tailrace of 17.9°C (±1.1°C); there were
opportunities for migrants to seek thermal refuge in this area as temperatures were between 0.5 –
4.0°C cooler than the adjacent Fraser River for 42% of the GC migration; although temperatures
in this area could also be warmer than the Fraser River as well (Fig. 2a). For more than 83% of
both study years, natal water concentration in the Seton River plume remained above the
recommended 80% target for the GC population (Fig. 2b), with tagged fish on average
experiencing concentrations of 90.3% (±4.6%) natal water.

PC sockeye salmon are a late-run population that migrates during the fall months, thus
they encountered Fraser River temperatures that were substantially cooler than during the GC
migration (Fig. 2a). For example, PC fish tracked in this study experienced mean Fraser River
temperatures of 11.8°C (±0.7°C) with no need for thermal refuge in the Powerhouse tailrace as
the average temperature in this area of 14.6°C (±0.5°C) was consistently warmer than the
adjacent Fraser River (Fig. 2a). Natal water concentration in the Seton River plume remained
above the 90% target for the PC population for over 87% of both 2013 and 2014 migrations,
while the mean concentration experienced by PC fish in this study was 91.4% (±1.2%) (Fig. 2b).
Physiological state and reproductive hormone levels

We compared mean levels of plasma glucose, lactate, and testosterone between sexes, populations, and years. There were no differences between years within each of the parameters measured for each population (Table 1). Glucose levels were very similar among males and females, both within and between the populations (Table 1). However, lactate was ~1.4 times higher in females compared to males in each population, and ~1.3 times higher among all GC fish relative to PC fish (Table 1). Testosterone was considerably higher in females compared to males for both populations (5.6 times higher in GC population; 4.9 times higher in PC population), and PC sockeye salmon had 2.2 times higher levels of this hormone than GC sockeye salmon (Table 1).

Powerhouse attraction and forays

Of all the tagged GC and PC sockeye salmon released into the Fraser River, 87% (265 of 304) and 91% (193 of 213), from each population respectively, made at least one foray into the powerhouse. However, we only included fish in models predicting forays that had complete physiological profiles (255 GC and 90 PC sockeye salmon) (fates are given by sex and population in Supplementary Table 1). Fifty-six percent (142 of 255) of these GC fish made only one foray into the powerhouse, while the remainder made up to 8 forays (Fig. 3a). In contrast, 43% of the modeled PC fish (39 of 90) made only one foray into the powerhouse, while the remainder made up to 17, with one PC female making 24 forays (Fig. 3b). On average, modeled PC sockeye salmon (3.6 forays ± 4.0) made nearly twice as many forays into the powerhouse as GC fish overall (1.9 forays ± 1.4) (Fig. 3a & b).

AIC model selection results indicated a large amount of uncertainty in foray models for GC fish, whereas there was less uncertainty in models for PC fish (Table 2; Supplementary Table 2). Nevertheless, there are trends among explanatory variables that are consistent between
populations. Sex was absent from the majority of models in the 95% confidence set for both populations because males and females made a similar number of forays (Table 2; Fig. 3 a & b). Model-averaged estimates for the effect of blood glucose on forays in both populations were negative and ~ 2 times larger than those of lactate, suggesting individuals with elevated levels of glucose may have made fewer forays into the powerhouse (Fig. 3 c & d). Testosterone effects were positive for both populations, implying that increasingly mature fish may have made more forays into this facility (Fig. 3 c & d). Blood glucose and testosterone, however, did not appear to influence forays in either population, as the 95% confidence intervals (hereafter ‘CIs’) included zero (Fig. 3 c & d).

Natal water concentration and powerhouse temperature had the largest effects on forays among PC fish and were included in the majority of models from the 95% confidence set (Table 2). Estimates for these effects were negative and had CIs that did not include zero, indicating that PC fish that encountered higher natal water concentrations or elevated powerhouse temperatures made fewer forays into this facility (Fig. 3d). Foray behaviour among GC sockeye salmon was largely unaffected by natal water concentration or powerhouse temperatures, as these effects were absent from most of the models in the 95% confidence set (Table 2; Fig.3c). We found little indication that foray behaviour in fish from either population was affected by the temperature differential between the powerhouse tailrace and Fraser River (Fig. 3 c & d).

**Wandering**

Models predicting wandering behaviour included 235 GC and 78 PC sockeye salmon with complete physiology and maturity profiles (fates are given by sex and population in Supplementary Table 1). Eighty-three percent (195 of 235) and 73% (57 of 78) of GC and PC sockeye salmon, respectively, migrated upstream in the Fraser River without exhibiting any inter-receiver movements (Fig. 4 a & b). Males and females within each population displayed
similar amounts of wandering (Fig. 4 a & b), although there was more variability in this
behaviour among PC fish. Twenty-seven percent of PC migrants wandered from 1 and 5 times,
while 17% of the GC migrants wandered from 1 to 4 times (Fig. 4 a & b).

There was a fair amount of uncertainty in the model selection results from models
predicting wandering (Table 2; Supplementary Table 2). Lactate was included in the majority of
the models from the 95% confidence set for both populations and had a negative effect that was
more than twice that of glucose, suggesting that wandering may have been reduced in fish with
higher levels of this stress metabolite (Table 2; Fig. 4 c & d). In each case, the CIs for these
effect estimates of lactate narrowly included zero (Fig. 4 c & d).

Fraser River temperature had little effect on wandering among GC fish but was included
in the majority of the models in the 95% confidence set for the PC population, suggesting this
behaviour may have been reduced in PC fish that encountered cooler Fraser River temperatures
(Table 2; Fig. 4 c & d). Temperatures in the powerhouse tailrace had similar size but opposite
effects on the two stocks, implying that warmer temperatures at this facility may have been
associated with increased wandering among GC sockeye salmon and less among PC sockeye
salmon (Fig. 4 c & d). We did not find evidence that the temperature differential between the
powerhouse tailrace and the Fraser River influenced wandering in either population (Table 2;
Fig. 4 c & d).

Natal water was included in the majority of the models from the 95% confidence set for
PC fish (Table 2) and had the largest effect of all predictors on wandering within this population
(Fig. 4d). Wandering was reduced among PC sockeye salmon that encountered higher
concentrations of natal water in the Seton River plume, while wandering among GC fish was
largely unaffected by changes in natal water (Fig. 4c).
**Powerhouse delay**

Models predicting the total amount of migration delay incurred by individuals in the powerhouse tailrace included 256 GC and 90 PC sockeye salmon with complete physiology and maturity profiles (fates are given by sex and population in Supplementary Table 1). We found no effect of sex on powerhouse delay in models for either population (Table 2; Fig. 5 b & c). Mean delay times of GC females (5.3 hours ± 6.4) were only slightly higher than GC males (3.4 hours ± 3.9), and only slightly lower among PC females (19.5 hours ± 18.5) compared to PC males (23.4 hours ± 27.1). Overall, PC sockeye salmon (21.1 hours ± 22.3) delayed ~ 5 times longer than GC fish (4.5 hours ± 5.6) (Fig. 5a).

Glucose was included in the majority of models from the 95% confidence set and had the largest effect on delay among GC sockeye salmon (9 times greater than that of lactate), indicating that GC fish with elevated levels of this stress metabolite incurred less delay in the powerhouse tailrace (Table 2; Fig. 5b). Neither glucose nor lactate had any effect on delay among PC fish, and there was little support for testosterone effects on delay in either population (Table 2; Fig. 5 b & c).

Natal water concentration was included in the majority of models from the 95% confidence set for the PC population, with the largest relative effect size of all predictors (Table 2; Fig. 5c). Delay at the powerhouse decreased when PC fish encountered increasing concentrations of natal water emanating from the Seton River plume. Effects of temperatures in the powerhouse tailrace itself were also well-supported in models for the PC population, with a strong negative effect indicating that PC fish delayed less during periods of elevated temperatures at this facility (Table 2; Fig. 5c). Despite a similar trend among GC fish, CIs for the effect of powerhouse tailrace temperature included zero (Fig. 5b). Finally, there was no
indication that the temperature differential between the powerhouse tailrace and the Fraser River affected delay in either population (Fig. 5 b & c).

Discussion

We monitored the behaviour of two populations of Fraser River sockeye salmon in relation to metabolic stress, river temperature, and varying natal water concentration during migration past a powerhouse outlet and passage into their natal tributary, the Seton River. Contrary to our expectations, metabolic stress indices in fish from both populations had little influence on behaviour in this short section of the migration corridor. Fraser River temperature was also unrelated to behaviour in both populations, and there was little evidence that the ‘early-summer’ GC population utilized the powerhouse tailrace as an area of thermal refuge. However, encounters with higher concentrations of natal water led individuals from the ‘late-run’ PC population to make more direct migrations into the Seton River, in contrast to the GC population who’s behaviour was unaffected by changes in natal water concentration.

All radio-tagged sockeye salmon in this study entered the powerhouse tailrace as they migrated up the Fraser River enroute to the Seton River, spending varying amounts of time in this area before resuming their migration. Adult Atlantic salmon migrating up rivers in Norway and Sweden are known to be attracted to turbine outlets and can make several movements in and out of these tailrace areas (Thorstad et al. 2003a; Lundqvist et al. 2008). In these studies, tailrace discharges were usually far greater than bypass flows, and thus hypothesized to be the primary cause of tailrace attraction. However, in our study, discharge from the powerhouse was only ~5% of Fraser River discharge, suggesting that initial attraction to the powerhouse occurs either because of the strong olfactory cues coming directly from the natal Seton Lake water discharged at the powerhouse, and/or because the powerhouse provides some degree of thermal refuge during periods of the GC migration.
One of the most striking findings in this study were the population-specific differences in how migrants behaviourally responded to the environmental factors encountered in this short segment of their shared migration corridor. On average, PC sockeye salmon spent 4 to 5 times longer than GC sockeye in the powerhouse tailrace (mean ~ 25 hours vs. 5 hours, respectively). Late-run populations of Fraser River sockeye salmon (e.g. PC fish) are known to migrate slower up the Fraser River than summer run populations (e.g. GC fish; English et al. 2005). Unlike summer-runs, late-run fish usually mill in natal lakes prior to entering spawning grounds (Hinch et al. 2012), so this extended delay in the powerhouse tailrace was not unexpected considering that PC fish are only ~ 8 km from their natal lake. Consistent with our hypothesis, we found that changes in the concentration of natal water had a strong effect on migration behaviour, but only for the PC population. Specifically, lower natal water concentrations emanating from the Seton River into the Fraser River were associated with more forays into the powerhouse tailrace, more overall time in the tailrace, and more wandering in the Fraser River. It thus appeared that PC migrants became confused when natal water concentrations were reduced and migrated less directly along their correct migration path. Given the narrower natal water concentration range experienced by PC migrants during the study (~ 85 – 94% natal water) compared to that of GC migrants (~ 60 – 95% natal water), it is possible that PC migrants could be more sensitive to subtle changes in olfactory cues. PC fish were likely more mature than GC fish (based on higher testosterone concentrations and proximity to natal spawning sites) at the time of tagging, and thus may exhibit a degree of heightened olfactory sensitivity with increased maturity, similar to that observed in common carp (Cyprinus carpio) in the Mississippi River, U.S.A (Irvine and Sorensen 1993). If such a relationship does indeed exist, this may explain why PC fish could be more sensitive to even slight changes in natal homestream water concentration at this stage in
their migration. In addition, the densities of co-migrating conspecifics from other populations of Fraser River sockeye salmon are much higher during the GC migration than during the PC migration (English et al. 2005). Thus, the additional directional cues that adult salmon rely on for navigation (e.g. conspecific pheromones; Groot et al. 1986; Bett and Hinch 2015) may be less present during the PC migration and lead to more ‘confusion’ and delay within this later run population.

High migration temperatures are stressful for up-river migrating adult salmon and individuals will alter their migration times to avoid peak temperatures (e.g. Columbia River sockeye & steelhead; Quinn and Adams 1996; Robards and Quinn 2011), and seek cool water refugia in tributaries and lakes when possible (e.g. Columbia and Fraser River sockeye & Chinook; Hodgson and Quinn 2002; Goniea et al. 2011). However, the Fraser River provides very few areas of thermal refuge during summer migration periods (Donaldson et al. 2009), so we had hypothesized that the powerhouse tailrace could serve as a thermal refuge for migrants if mainstem temperatures were high. Indeed, many GC fish experienced Fraser River temperatures that were well above the population optimum (~ 17°C; Lee et al. 2003) and near their known thermal limit (~ 21°C; Eliason et al. 2011), where aerobic scope collapses and fish must rely on anaerobic metabolism risking acidosis and cardiorespiratory failure (Farrell et al. 2008). However, we found no evidence for GC fish that the number of forays into or delay in the powerhouse tailrace increased when tailrace water was cooler or when the temperature differential between the tailrace and the Fraser River was large. In fact, there were many periods in which tailrace temperatures were very similar to, or even greater than Fraser River temperatures, thus limiting opportunities for the powerhouse tailrace to act as a thermal refuge. Contrary to our hypothesis, GC fish spent relatively little time in the powerhouse tailrace, and
instead migrated quickly into the Seton River. It is worth noting, however, that the hypolimnion of Seton Lake is only ~ 6 km from the powerhouse tailrace; GC sockeye are known to occupy this cool lake water while *en route* to spawning grounds (Roscoe et al. 2010a) perhaps in part explaining the limited delays in the powerhouse tailrace and relatively fast passage through the lower hydrosystem. During the migration of PC fish, there was likely no need for individuals to seek thermal refuge in the powerhouse tailrace as the Fraser River was always 2 – 3°C cooler. Yet, temperature still appeared to play a role in behaviour in that warmer tailrace temperatures were associated with shorter delays and less forays into the tailrace of this facility. Caudill et al. (2013) found that adult Snake River Chinook salmon and steelhead would avoid high temperatures in fishways and remain in cooler dam tailraces. In a similar manner, PC fish may choose to avoid the powerhouse tailrace and spend more time in the cooler Fraser River where temperatures are closer to optimum for late-run sockeye at this time of year (Lee et al. 2003; Farrell et al. 2008; Eliason et al. 2011). High concentrations of natal Seton River water entering the Fraser River were associated with less delay and fewer forays into the tailrace, but the interactive roles of olfaction and thermal biology in altering behaviour of migrating PC fish could not be examined in these models because temperature and natal water variables were highly collinear.

We had anticipated that initial physiological state would play a role in population specific behaviours by predicting that sockeye salmon which were initially more mature would migrate more directly toward their natal tributary, while those with high levels of stress metabolites would delay their migration, likely in the powerhouse tailrace where they might be able to recover from stressful conditions away from the mainstem Fraser River. However, we found little evidence that the physiological state of individuals within a population influenced
behaviour. The only exception was GC fish, which spent less time delaying in the powerhouse tailrace when their plasma glucose concentrations were relatively high. Elevated glucose can be indicative of recovery from swimming fatigue and excessive handling or confinement (Nielsen et al. 1994; Farrell et al. 1998; Kubokawa et al. 1999). It is possible that GC fish were experiencing some modest physiological stress from migrating ~ 340 km up-river during peak summer temperatures. Plasma glucose levels at time of capture were well above baseline, although similar to levels found previously in GC fish captured at this locale (Roscoe et al. 2010b), but not as high as those recorded for summer run sockeye salmon captured in the lower Fraser River (Donaldson et al. 2010). Because we found there was only limited opportunity for thermal refuge in the powerhouse tailrace during the GC migration, exhausted or physiologically compromised individuals may have chosen to avoid this unfavorable area and move more quickly to the Seton River where flows and temperatures were lower and more conducive to physiological recovery. Indeed, it has been shown that sockeye salmon in the Columbia River migrate more rapidly toward natal tributaries as mainstem temperature increases (Naughton et al. 2005; Keefer et al. 2008b).

We had hypothesized that given their more limited energy budgets for swimming activity females would exhibit less wandering and less delay at the powerhouse compared to males. Testosterone levels were substantially higher among females from both populations, which is typical of sockeye salmon throughout their freshwater migration (Truscott et al. 1986; Crossin et al. 2007; Donaldson et al. 2010). Testosterone also increases steadily in both sexes with decreasing distance to natal sites as oocytes and testes prepare for final maturation (Truscott et al. 1986; Hinch et al. 2006), perhaps explaining why PC fish had nearly twice as high plasma testosterone as GC fish given the much shorter distance remaining to PC spawning grounds.
However, despite their higher testosterone level, females from both populations did not behave differently than males. We highlight that this was unexpected given that recent findings from physiological telemetry have found that females swim with more anaerobic effort (more burst swimming) when passing through the Seton Dam tailrace and through the adjoining fishway compared to males (Burnett et al. 2014). Female sockeye often suffer higher levels of mortality than males towards the end of freshwater migrations (Hodgson and Quinn 2002; Keefer et al. 2004a, Donaldson et al. 2010; Martins et al. 2012), in part due to exhaustion of energy reserves or cardiorespiratory collapse since they have a smaller ventricular mass (Sandblom et al. 2009). Perhaps we did not observe behavioural differences between sexes because our short study reach did not offer significant enough energetic challenges or obstacles (e.g. high discharge, temperatures frequently above optimal) necessitating females to either attempt to conserve energy by slowing or delaying migration, or, require a high degree of burst swimming.

**Management implications**

Although it is widely recognized that migrating adult salmon rely on the detection of natal water cues to successfully navigate toward natal spawning sites (reviewed in Bett and Hinch 2015), it is often overlooked how river regulation for hydropower production can affect flow composition and natal water concentration in migration corridors. Indeed, adult salmon have been documented exhibiting signs of migration confusion in rivers where natal water cues have become diffuse or re-directed through regulation (e.g. Columbia River Chinook salmon, Keefer et al. 2008; Atlantic salmon, Lundqvist et al. 2008). However, until now, there has been little research examining the relative effect of this factor on the behaviour of adult salmon migrating through regulated river corridors. In the current study, we present some of the first detailed analyses of how varying concentrations of natal water cues, in combination with
dynamic river temperatures, and the physiological condition of migrants can affect behaviour in wild adult salmon. We highlight the importance of accounting for dynamic natal water conditions in future studies aimed at improving adult salmon passage through regulated migration corridors.

In the Seton hydrosystem, it has long been recognized that the environmental conditions created by the Seton powerhouse and fluctuating natal water concentrations in the Seton River could cause significant delays for up-river migrating sockeye salmon (Fretwell 1989). Water preference experiments (‘Y-maze’ behaviour studies) conducted in the late 1970s and early 1980s demonstrated that adult sockeye salmon were capable of discriminating between Seton River and Cayoosh Creek water, and that olfaction was the primary sensory mechanism used by fish to select different water sources for homing through the hydrosystem (Fretwell 1989). These studies provided in-situ experimental evidence that suggested migration delay in the powerhouse tailrace could be mitigated by controlling Seton River discharge to maintain natal Seton River water concentrations equal to or greater than the threshold of sensitivity exhibited by the two populations (80% GC and 90% PC; Fretwell 1989). Based on these results, BC Hydro built a diversion dam on Cayoosh Creek in an attempt to maintain the Cayoosh Creek component of the Seton River discharge to 20% and 10% during the upstream migration period for GC and PC sockeye runs, respectively. Recent Y-maze experiments with both populations have re-confirmed these olfactory sensitivity thresholds (Casselman et al. 2015). In the present study, natal water concentrations generally exceeded threshold targets except for a one-week period during the 2013 GC migration (Fig. 2b). Despite a large range of natal water concentrations experienced by GC sockeye, we could not find any effects of this factor on delay or other behaviours, and these fish seemed to have little difficulty rapidly homing into the Seton River. On the other hand, even
though threshold natal water concentrations were exceeded for PC migrants, lower natal water concentration relative to the 90% threshold for this population increased tailrace delay and slowed migration into the Seton River. Given that tailrace temperature also affected delay at the powerhouse and the apparent olfactory sensitivity displayed by PC fish, the 10% Cayoosh Creek water threshold may need to be re-evaluated. Because of the difficulties associated with capturing control fish from non-natal populations of co-migrating sockeye salmon in the mainstem Fraser River, future experimental manipulation of natal water concentration in the Seton River and its plume should be explored to isolate the effect of the natal water factor from temperature and more thoroughly understand its effect on the migration behaviour of the PC population.

Fraser River water temperatures have a significant effect on sockeye salmon migration and spawning success and affect the condition of individuals upon arrival in the Seton-Anderson watershed. Peak summer water temperatures in the Fraser River have increased > 2°C in the past 60 years, with recent years exhibiting record high levels and climate models predicting even warmer peak temperatures in future years (Patterson et al. 2007; Ferrari et al. 2007). GC fish now typically encounter Fraser River temperatures exceeding 18 – 19 °C, with prolonged exposure to such stressful temperatures causing migration mortality (Eliason et al. 2011). Even though GC fish did not delay for long periods in the powerhouse tailrace enroute to the Seton River, the fact that fish are increasingly encountering thermally stressful migrations prior to reaching the Seton hydrosystem means that any small delay caused by the powerhouse or by varying olfactory cues from the Seton River could be devastating if delays expose fish to additional thermal stress. Thus, managers should continue to strive to achieve the natal water targets established for this population.
Acknowledgments

We thank W. Payne, R. Ledoux, J. Hopkins, A. Adolph, and C.F. White for their assistance in the field. We acknowledge D. McCubbing (InStream Fisheries Research), Lance and Leo O’Donaghey and C. Fletcher (N’Quatqua First Nation) for their support with the fish fence. C. Storey, T. Nettles, and J. Hills (Fisheries and Oceans Canada) provided logistical support and ran all physiological assays. Project funding was provided by B.C. Hydro, St’át’ímc Eco Resources, National Science and Engineering Research Council of Canada (NSERC) Discovery, Strategic and Network (Canada’s Ocean Tracking Network) grants to S.G.H. Some infrastructure was also supported by the Canada Foundation for Innovation. C.T.M. was supported by an NSERC CGS-M scholarship and a MITACS Accelerate internship.

References


doi:10.1371/journal.pone.0085586.


Society 135 (2): 408–419.


(Oncorhynchus nerka) and coho (O. kisutch) salmon stocks. Journal of Experimental Biology 206: 3239–3251.


Roscoe, D.W., Hinch, S.G., Cooke, S.J., and Patterson, D.A. 2010b. Fishway passage and post-


Thorstad, E.B., Okland, F., Aarestrup, K., and Heggberget, T.G. 2008. Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts.
Reviews in Fish Biology and Fisheries 18 (4): 345–371.


Table 1. Mean ± SD (range) of fork length (cm), glucose (mmol L$^{-1}$), lactate (mmol L$^{-1}$), and testosterone (ng ml$^{-1}$) for female (♀) and male (♂) Gates Creek and Portage Creek sockeye salmon. *Note, preliminary analyses of physiological variables from the three datasets used in behavioural Models 1, 2, and 3 yielded similar values; this table reports the data used in Model 3 as an example.

<table>
<thead>
<tr>
<th></th>
<th>Gates Creek</th>
<th>Portage Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2013 n = 63 (♀) n = 48 (♂)</td>
<td>2014 n = 83 (♀) n = 62 (♂)</td>
</tr>
<tr>
<td>Fork length (cm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>56.6 ± 3.0 (49 – 65.5)</td>
<td>57.4 ± 4.0 (51 – 63)</td>
</tr>
<tr>
<td>♂</td>
<td>60.0 ± 3.1 (52 – 67.5)</td>
<td>61.9 ± 4.0 (53 – 69)</td>
</tr>
<tr>
<td>Glucose (mmol L$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>5.5 ± 1.3 (2.9 – 10.2)</td>
<td>4.5 ± 0.8 (3.0 – 9.3)</td>
</tr>
<tr>
<td>♂</td>
<td>5.6 ± 1.5 (4.2 – 13.7)</td>
<td>5.4 ± 1.4 (2.5 – 10.1)</td>
</tr>
<tr>
<td>Lactate (mmol L$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>5.5 ± 3.7 (0.9 – 16.1)</td>
<td>5.0 ± 2.5 (1.4 – 11.0)</td>
</tr>
<tr>
<td>♂</td>
<td>3.6 ± 2.3 (0.8 – 10.2)</td>
<td>3.7 ± 1.9 (0.7 – 10.0)</td>
</tr>
<tr>
<td>Testosterone (ng ml$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>♀</td>
<td>82.0 ± 97.4 (1.1 – 398.1)</td>
<td>53.32 ± 56.5 (2.1 – 385.6)</td>
</tr>
<tr>
<td>♂</td>
<td>16.7 ± 17.7 (0.9 – 83.6)</td>
<td>8.0 ± 6.63 (1.2 – 31.1)</td>
</tr>
</tbody>
</table>
Table 2. AICc model selection statistics for generalized linear models and linear models predicting (1) the number of forays made into the powerhouse, (2) the amount of wandering in the Fraser River between the release site and the Seton-Fraser River confluence, and (3) the total amount of migration delay incurred by individuals in the powerhouse tailrace for Gates Creek (GC) and Portage Creek (PC) sockeye salmon.

<table>
<thead>
<tr>
<th>Response variable and model</th>
<th>log Lik</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>wi</th>
<th>adj-R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Powerhouse forays</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose</td>
<td>-421.42</td>
<td>848.94</td>
<td>0.00</td>
<td>0.03</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + PHT</td>
<td>-420.67</td>
<td>849.50</td>
<td>0.56</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + Tdiff</td>
<td>-420.68</td>
<td>849.52</td>
<td>0.57</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Intercept</td>
<td>-422.82</td>
<td>849.69</td>
<td>0.74</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Tdiff</td>
<td>-421.80</td>
<td>849.70</td>
<td>0.75</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Testosterone + PHT</td>
<td>-420.84</td>
<td>849.84</td>
<td>0.89</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Testosterone</td>
<td>-421.90</td>
<td>849.90</td>
<td>0.96</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + testosterone</td>
<td>-420.87</td>
<td>849.91</td>
<td>0.97</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + testosterone + PHT</td>
<td>-419.84</td>
<td>849.91</td>
<td>0.97</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + NW</td>
<td>-420.89</td>
<td>849.94</td>
<td>1.00</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>PHT</td>
<td>-422.12</td>
<td>850.33</td>
<td>1.39</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Testosterone + Tdiff</td>
<td>-421.18</td>
<td>850.52</td>
<td>1.57</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + Tdiff + NW</td>
<td>-420.22</td>
<td>850.68</td>
<td>1.73</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + Testosterone + Tdiff</td>
<td>-420.30</td>
<td>850.85</td>
<td>1.91</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + FRT + Tdiff</td>
<td>-420.35</td>
<td>850.94</td>
<td>1.99</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + FRT + Tdiff</td>
<td>-420.35</td>
<td>850.94</td>
<td>1.99</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + FRT + PHT</td>
<td>-420.35</td>
<td>850.94</td>
<td>1.99</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Glucose + PHT + Tdiff</td>
<td>-420.35</td>
<td>850.94</td>
<td>1.99</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>PC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TD + PHT + Tdiff + NW</td>
<td>-204.36</td>
<td>421.73</td>
<td>0.00</td>
<td>0.06</td>
<td>-</td>
</tr>
<tr>
<td>(N=90)</td>
<td>Combos</td>
<td>M</td>
<td>E</td>
<td>G</td>
<td>H</td>
</tr>
<tr>
<td>--------------</td>
<td>------------------------------------------------------------------------</td>
<td>---</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>PHT + NW</td>
<td>-206.68 421.84 0.11 0.06 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + Tdiff + NW</td>
<td>-205.56 421.84 0.11 0.06 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testosterone + PHT + NW</td>
<td>-205.65 422.02 0.29 0.06 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex + PHT + NW</td>
<td>-206.00 422.72 0.99 0.04 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + PHT + NW</td>
<td>-206.02 422.75 1.02 0.04 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testosterone + T + PHT + Tdiff + NW</td>
<td>-203.78 422.93 1.20 0.04 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testosterone + PHT + Tdiff + NW</td>
<td>-204.99 422.99 1.26 0.03 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + PHT + Tdiff + NW</td>
<td>-205.14 423.29 1.56 0.03 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex + PHT + Tdiff + NW</td>
<td>-205.20 423.40 1.67 0.03 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + T + PHT + Tdiff + NW</td>
<td>-204.08 423.52 1.79 0.03 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + Testosterone + PHT + NW</td>
<td>-205.27 423.55 1.82 0.03 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex + T + PHT + Tdiff + NW</td>
<td>-204.17 423.70 1.97 0.02 -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(2) Wandering  

| GC (N=235) |
|-------------|-----------------|---|-----|-----|-----|  
| Sex + Lactate + PHT | -142.09 294.44 0.00 0.05 - |   |     |     |     |  
| Sex + Lactate + Testosterone + PHT | -141.95 296.27 1.83 0.02 - |   |     |     |     |  
| Lactate + PHT | -144.06 296.29 1.84 0.02 - |   |     |     |     |  
| Sex + Lactate + FRT + PHT | -142.01 296.40 1.95 0.02 - |   |     |     |     |  
| Sex + Lactate + PHT + Tdiff | -142.01 296.40 1.95 0.02 - |   |     |     |     |  
| Sex + Lactate + FRT + Tdiff | -142.01 296.40 1.95 0.02 - |   |     |     |     |  
| Sex + Lactate + FRT + Tdiff | -142.01 296.40 1.95 0.02 - |   |     |     |     |  

(3) Wandering  

| PC (N=78) |
|-----------|-----------------|---|-----|-----|-----|  
| Sex + Lactate + FRT + NW | -73.44 160.07 0.00 0.03 - |   |     |     |     |  
| Lactate + FRT + NW | -74.72 160.28 0.21 0.03 - |   |     |     |     |  
| FRT + NW | -75.96 160.47 0.40 0.03 - |   |     |     |     |  
| Lactate + Testosterone + FRT + NW | -73.94 161.07 1.00 0.02 - |   |     |     |     |  

---

https://mc06.manuscriptcentral.com/cjfas-pubs
<table>
<thead>
<tr>
<th>Combination</th>
<th>B</th>
<th>SE</th>
<th>t</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lactate + FRT</td>
<td>-76.34</td>
<td>161.22</td>
<td>1.15</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Lactate</td>
<td>-77.52</td>
<td>161.36</td>
<td>1.29</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Sex + Lactate + FRT + Tdiff + NW</td>
<td>-72.91</td>
<td>161.42</td>
<td>1.35</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Sex + Lactate + FRT + Tdiff + NW</td>
<td>-72.91</td>
<td>161.42</td>
<td>1.35</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Sex + Lactate + FRT + PHT + NW</td>
<td>-72.91</td>
<td>161.42</td>
<td>1.35</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Sex + Lactate + PHT + Tdiff + NW</td>
<td>-72.91</td>
<td>161.42</td>
<td>1.35</td>
<td>0.02</td>
<td>-</td>
</tr>
<tr>
<td>Lactate + FRT + Tdiff + NW</td>
<td>-74.31</td>
<td>161.81</td>
<td>1.74</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Lactate + FRT + Tdiff + NW</td>
<td>-74.31</td>
<td>161.81</td>
<td>1.74</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Lactate + FRT + PHT + NW</td>
<td>-74.31</td>
<td>161.81</td>
<td>1.74</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Lactate + PHT + Tdiff + NW</td>
<td>-74.31</td>
<td>161.81</td>
<td>1.74</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Sex + Lactate + PHT + NW</td>
<td>-74.32</td>
<td>161.83</td>
<td>1.77</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Sex + Lactate</td>
<td>-76.65</td>
<td>161.85</td>
<td>1.78</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Sex + FRT + NW</td>
<td>-75.52</td>
<td>161.86</td>
<td>1.80</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>FRT + Tdiff + NW</td>
<td>-75.59</td>
<td>162.02</td>
<td>1.95</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>FRT + Tdiff + NW</td>
<td>-75.59</td>
<td>162.02</td>
<td>1.95</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>FRT + PHT + NW</td>
<td>-75.59</td>
<td>162.02</td>
<td>1.95</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>PHT + Tdiff + NW</td>
<td>-75.59</td>
<td>162.02</td>
<td>1.95</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td>Lactate + PHT</td>
<td>-76.75</td>
<td>162.04</td>
<td>1.98</td>
<td>0.01</td>
<td>-</td>
</tr>
</tbody>
</table>

(3) Powerhouse delay

<table>
<thead>
<tr>
<th>Combination</th>
<th>B</th>
<th>SE</th>
<th>t</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glucose + Tdiff + NW</td>
<td>-481.06</td>
<td>972.35</td>
<td>0.00</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>Glucose + Testosterone + Tdiff + NW</td>
<td>-480.02</td>
<td>972.38</td>
<td>0.03</td>
<td>0.03</td>
<td>0.06</td>
</tr>
<tr>
<td>Glucose + Tdiff</td>
<td>-482.40</td>
<td>972.97</td>
<td>0.61</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Glucose + NW</td>
<td>-482.49</td>
<td>973.13</td>
<td>0.78</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Glucose + PHT</td>
<td>-482.49</td>
<td>973.14</td>
<td>0.79</td>
<td>0.02</td>
<td>0.04</td>
</tr>
<tr>
<td>Glucose + PHT + NW</td>
<td>-481.68</td>
<td>973.60</td>
<td>1.24</td>
<td>0.02</td>
<td>0.04</td>
</tr>
</tbody>
</table>

GC

(N=256)

https://mc06.manuscriptcentral.com/cjfas-pubs
<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>adj-R&lt;sup&gt;2&lt;/sup&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>adj-R&lt;sup&gt;2&lt;/sup&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glucose + Testosterone + Tdiff</td>
<td>-481.69</td>
<td>973.62</td>
<td>1.27</td>
<td>0.02</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + Testosterone + NW</td>
<td>-481.77</td>
<td>973.79</td>
<td>1.44</td>
<td>0.02</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + FRT + Tdiff</td>
<td>-481.79</td>
<td>973.82</td>
<td>1.46</td>
<td>0.02</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + FRT + PHT</td>
<td>-481.79</td>
<td>973.82</td>
<td>1.46</td>
<td>0.02</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + PHT + Tdiff</td>
<td>-481.79</td>
<td>973.82</td>
<td>1.46</td>
<td>0.02</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + Tdiff + NW</td>
<td>-480.86</td>
<td>974.05</td>
<td>1.70</td>
<td>0.01</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + FRT + PHT + NW</td>
<td>-480.86</td>
<td>974.05</td>
<td>1.70</td>
<td>0.01</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + PHT + Tdiff + NW</td>
<td>-480.86</td>
<td>974.05</td>
<td>1.70</td>
<td>0.01</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + FRT + Tdiff + NW</td>
<td>-480.86</td>
<td>974.05</td>
<td>1.70</td>
<td>0.01</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + Lactate + Tdiff + NW</td>
<td>-480.87</td>
<td>974.07</td>
<td>1.72</td>
<td>0.01</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + Tdiff + NW</td>
<td>-480.95</td>
<td>974.24</td>
<td>1.88</td>
<td>0.01</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glucose + Lactate + NW</td>
<td>-482.02</td>
<td>974.28</td>
<td>1.92</td>
<td>0.01</td>
<td>0.04</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW</td>
<td>-163.15</td>
<td>334.76</td>
<td>0.00</td>
<td>0.07</td>
<td>0.23</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + Glucose</td>
<td>-162.08</td>
<td>334.88</td>
<td>0.12</td>
<td>0.06</td>
<td>0.24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + TD + Tdiff</td>
<td>-161.20</td>
<td>335.41</td>
<td>0.65</td>
<td>0.05</td>
<td>0.26</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + TD</td>
<td>-162.56</td>
<td>335.83</td>
<td>1.07</td>
<td>0.04</td>
<td>0.24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + Glucose + TD</td>
<td>-161.53</td>
<td>336.07</td>
<td>1.30</td>
<td>0.04</td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + Glucose + TD + Tdiff</td>
<td>-160.46</td>
<td>336.29</td>
<td>1.53</td>
<td>0.03</td>
<td>0.27</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + Glucose + Testosterone</td>
<td>-161.83</td>
<td>336.67</td>
<td>1.90</td>
<td>0.03</td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PHT + NW + Glucose + Lactate</td>
<td>-161.87</td>
<td>336.75</td>
<td>1.98</td>
<td>0.03</td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

ΔAIC<sub>c</sub> is the difference in AIC<sub>c</sub> values between model <i>i</i> and the top model in the candidate set. Models are ranked from lowest to highest ΔAIC<sub>c</sub>, and by w<sub>i</sub> – the probability that a given model is the best in the 95% confidence set. adj-R<sup>2</sup> is an estimate of the proportion of variance explained by each model, adjusted by the number of explanatory variables; this is only shown for linear models as generalized linear model fits were evaluated by Chi-square tests (see Methods). Abbreviations
used for model variables include: Fraser River temperature (FRT), powerhouse temperature (PHT), temperature differential between the Fraser River and powerhouse (Tdiff), natal water concentration (NW), and tagging date (TD). In Model 3 for the PC, TD is shown with FRT in parentheses to indicate that tagging date was substituted for Fraser River temperature.
Fig. 1. Study area in the Seton-Anderson watershed in southwestern British Columbia, Canada (inset). Capture, release and fixed radio-telemetry stations, along with temperature monitoring locations, are indicated by the legend and map. The location of the Seton powerhouse tailrace and the visible extent of the powerhouse discharge plume of natal Seton Lake water is shown extending into the Fraser River, as is the extent of the Seton River plume that fluctuates in its concentration of natal water given relative flow contributions of Cayoosh Creek.

Fig. 2. Mean daily Fraser River (solid lines) and powerhouse tailrace (dashed lines) temperatures (panel a), and natal water concentration of the Seton River and its plume (panel b) in 2013 (grey) and 2014 (black). Shaded grey boxes represent the periods in which fish from each population were tagged. Dashed red lines represent the current natal water concentration targets for Gates Creek (80%) and Portage Creek (90%) sockeye salmon, and are approximately proportional to the migration timing of each population through the hydrosystem.

Fig. 3. Panels a & b – Histograms of the number of forays female (grey bars) and male (black bars) Gates Creek (a) and Portage Creek (b) sockeye salmon made into the powerhouse as a proportion of all the individuals included in models predicting this behaviour. In panel b, 1 female that made 24 forays was removed from the histogram for clarity. Panels c & d – Model-averaged standardized coefficient estimates for models predicting the number of forays Gates Creek (c) and Portage Creek (d) sockeye salmon made into the Seton powerhouse. Coefficient estimates with 95% confidence intervals that do not cross zero are highlighted by solid black circles. Vertical dashed line indicates the coefficient value of zero. Abbreviations for predictor variables include: Fraser River
temperature (FRT), powerhouse temperature (PHT), temperature differential between the Fraser River and powerhouse (Tdiffer), and natal water concentration (NW). FRT is shown with TD in parentheses to indicate that tagging date was substituted for Fraser River temperature in the Portage Creek foray model (panel d only). Note the difference in x-axis scales between panels.

Fig. 4. Panels a & b – Histograms of wandering (the number of back-and-forth movements) in the Fraser River between the release site and the Seton-Fraser River confluence for female (grey bars) and male (black bars) Gates Creek (a) and Portage Creek (b) sockeye salmon shown as a proportion of all individuals included in the models predicting this behaviour for each population. In panel a, 1 female that wandered 9 times was removed from the histogram for clarity. Panels c & d – Model-averaged standardized coefficient estimates for models predicting wandering for Gates Creek (c) and Portage Creek (d) sockeye salmon. Coefficient estimates with 95% confidence intervals that do not include zero are highlighted by solid black circles. Vertical dashed line indicates the coefficient value of zero. Abbreviations for predictor variables include: Fraser River temperature (FRT), powerhouse temperature (PHT), temperature differential between the Fraser River and powerhouse (Tdiffer), and natal water concentration (NW). Note the difference in x-axis scales between panels.

Fig. 5. Panel a – Beanplots of total migration delay in the powerhouse tailrace for female (black beans) and male (grey beans) Gates Creek and Portage Creek sockeye salmon used in models predicting this behaviour. Shaded polygons represent the distribution of individual delay times (small horizontal lines) and bold horizontal lines represent means. Panel b & c – Model-averaged standardized coefficient estimates from models predicting the total amount of migration delay incurred by Gates Creek (b) and Portage Creek (c)
sockeye salmon in the powerhouse tailrace. Coefficient estimates with 95% confidence intervals that do not include zero are highlighted by solid black circles. Vertical dashed line indicates the coefficient value of zero. Abbreviations for model variables include: Fraser River temperature (FRT), powerhouse temperature (PHT), temperature differential between the Fraser River and powerhouse (Tdiff), and natal water concentration (NW). FRT is shown with TD in parentheses to indicate that tagging date was substituted for Fraser River Temperature in the Portage Creek delay model (panel c only). Note the difference in x-axis scales between panels.
Figure 1

[Diagram of the Seton River system with labels for Seton Dam, Water Diversion Canal, and various capture and release locations.]
Figure 2

(a) Temperature (°C) over time with different lines representing different conditions or groups.

(b) Natal Water (%) over time with GC tagging and PC tagging indicated.

Date range from Aug 01 to Oct 31.
Figure 3
Figure 4

(a) and (b) show the proportion of wandering events over different time periods. (a) indicates a peak at around the 2nd event, while (b) shows a slight increase at around the 1st event.

(c) and (d) display the standardized coefficients for various factors influencing wandering events. Sex, Glucose, Lactate, Testosterone, FRT, PHT, Tdiff, and NW are the factors considered. The coefficients range from -2.2 to 0.8, indicating varying degrees of influence on wandering events.
Figure 5

(a) Gates Creek Portage Creek

(b) Sex
   - Glucose
   - Lactate
   - Testosterone
   - FRT (TD)
   - PHT
   - Tdiff
   - NW

(c) Standardized coefficients

https://mc06.manuscriptcentral.com/cjfas-pubs