

Behaviour and thermal experience of adult sockeye salmon migrating through stratified lakes near spawning grounds: the roles of reproductive and energetic states

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Abstract – Little is known about physiological factors underlying thermal behaviour in Pacific salmon (*Oncorhynchus* spp.). We implanted acoustic transmitters and temperature loggers into migrating adult sockeye salmon (*Oncorhynchus nerka*) and nonlethally assessed their reproductive hormone levels and energetic states immediately prior to their passing through natal lakes *en route* to spawning grounds. We tested the hypothesis that energetic and reproductive status influence thermoregulatory and other in-lake behaviours. More reproductively advanced females with lower levels of energy transited through cooler temperatures compared to less mature females with high levels of energy, possibly to reduce metabolic energy expenditure and delay final maturation. Transit temperatures of males were not related to physiological variables. Salmon travelled on average 13.6 km·day⁻¹ through two lakes, and often circled or held for more than 1 day before moving upstream, but these behaviours were generally not related to physiological variables.

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Introduction

Across multiple taxa, reproductive migrations require that individuals travel long distances while coping with variable environmental conditions and preparing for reproduction (Dingle 1996). For Pacific salmon, such migrations are fuelled entirely by endogenous energy reserves as individuals cease feeding before leaving the ocean *en route* to freshwater spawning streams. Because Pacific salmon are semelparous, the successful completion of these migrations is paramount to lifetime reproductive success. Although there are a number of environmental factors that can influence the migration biology of fish (e.g., flows, suspended sediment, dissolved oxygen, temperature), water temperature is known to be particularly important. For example, water temperature regulates many aspects of Pacific salmon migrations including rates of

travel (Gonia et al. 2006; Crossin et al. 2008; Keefer et al. 2008), physiological condition (Hinch et al. 2006; Crossin et al. 2008) and *en route* mortality (Gilhousen 1990; Macdonald et al. 2000; Keefer et al. 2008). Given the importance of temperature, it is not surprising that migrating salmon are known to behaviourally thermoregulate. Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River Basin, USA, can mitigate negative effects of high water temperatures by utilising thermal refugia in cool-water tributaries (Berman & Quinn 1991; Gonia et al. 2006). In contrast, the Fraser River, British Columbia (BC), Canada, has many reaches that lack cool-water inputs and are therefore thermally homogenous (Patterson et al. 2007). Migrating salmon make only limited use of the few thermal refugia that are available in the lower Fraser River (Donaldson et al. 2009).

Unlike the river environment, many nursery lakes of sockeye salmon (*Oncorhynchus nerka*) in the Fraser Watershed – lakes near spawning grounds where juveniles rear – are thermally stratified during the spawning migration (Stockner & Shortreed 1983), providing a wide range of temperatures to migrants. Several studies have shown that sockeye salmon use cool water in the hypolimnion of lakes during spawning migrations. For instance, Hyatt et al. (2003) found that sockeye salmon in the Okanagan River ceased migration if river temperature exceeded 21 °C and moved downstream to a large lake where cooler water was available. Similarly, Weaver Creek sockeye (Fraser River, BC) that enter the Fraser River during peak summer temperatures are known to voluntarily move into a lake upstream of spawning grounds and hold in the hypolimnion prior to spawning (Mathes et al. 2009). Sockeye salmon return to Lake Washington, USA, in the early summer and reside there for several months, presumably to avoid high water temperatures in spawning streams in mid-summer (Hodgson & Quinn 2002). While residing in Lake Washington, sockeye spend the majority of their time in the hypolimnion at 9–11 °C, rarely occupying warmer or cooler areas (Newell & Quinn 2005). However, previous research has simply documented behavioural thermoregulation. No previous studies have examined how physiological factors may affect thermoregulatory behaviour in wild salmon.

In addition to behavioural thermoregulation, a few studies have reported on general patterns of movement and migration speeds of sockeye salmon in lakes. A study of Alaskan sockeye salmon showed that some fish milled in lakes for several weeks (Young & Woody 2007). Others described clockwise near-shore circling in lakes and wandering into non-natal tributaries (Burger et al. 1995). Thus, migration through nursery lakes by maturing sockeye salmon may not always be direct and rapid, as is usually the case for migration in-river (~17–40 km·day⁻¹; English et al. 2005) or ocean (30–55 km·day⁻¹, Neave 1964; 20–33 km·day⁻¹, Crossin et al. 2007).

Pacific salmon have been used as models to examine the physiological and energetic mechanisms underlying migration behaviour of fish (Hinch et al. 2006). For example, migratory behaviour is strongly influenced by reproductive physiology as high levels of reproductive hormones such as testosterone and estradiol are related to earlier river entry and faster migration rates (Sato et al. 1997; Crossin et al. 2007; Cooke et al. 2008). Energetic status also appears to be closely linked with migratory behaviour, as individuals with higher energy levels have slower rates of travel and greater survivorship during up-river migration (Young et al. 2006; Hanson et al. 2008).

Energy and reproductive physiology might also be expected to influence thermoregulatory behaviour, given the strong effects of temperature on energetics and maturation. For instance, metabolic rate increases with temperature (Brett 1971; Lee et al. 2003) and therefore fish experiencing higher temperature will more quickly deplete their finite energy reserves. In general, the rate of reproductive development is also positively related to water temperature, but very warm temperatures can also lead to over-ripening or damage of gametes (Flett et al. 1996; Pankhurst et al. 1996). For these reasons, Newell & Quinn (2005) proposed that the narrow range of temperatures occupied by sockeye salmon in Lake Washington (discussed above) represented a trade-off that balanced reproductive maturation and metabolic energy expenditure. However, the hypothesis that thermoregulatory or other in-lake behaviour is related to reproductive hormone levels and energy reserves has not yet been tested in migrating adult salmon.

This study uses acoustic telemetry and temperature loggers to document the behaviour and thermal experience of adult sockeye salmon transiting through rearing lakes *en route* to nearby spawning areas. We nonlethally sampled levels of somatic energy and circulating reproductive hormones to investigate several inter-related hypotheses linking behaviour and temperature preference to levels of energy and reproductive maturation of sockeye salmon. We hypothesised that levels of energy and reproductive maturation would influence: (i) temperature preference, (ii) migration speed and (iii) directness of migration. We predicted that individuals with low levels of energy and an advanced reproductive status would: (i) select cooler temperatures, (ii) migrate faster and (iii) migrate more directly. Because males and females differ in terms of reproductive endocrinology and energy allocation, we hypothesised that relationships between behaviour and physiology would differ between the sexes.

Methods

Study site

The study was carried out in the Seton-Anderson watershed in the Southwestern interior of BC, Canada, on Gates Creek sockeye salmon (Fig. 1). As adults, this salmon stock migrates up the Fraser River 320 km from the Pacific Ocean before reaching the mouth of the Seton River, near Lillooet, BC. Migrants then travel 5 km up the Seton River where they must pass the Seton dam via a vertical-slot fishway. After passing the dam, migrants travel through Seton Lake (22 km), Portage Creek (3 km) and Anderson Lake (21.5 km), which serves as the nursery lake for Gates Creek

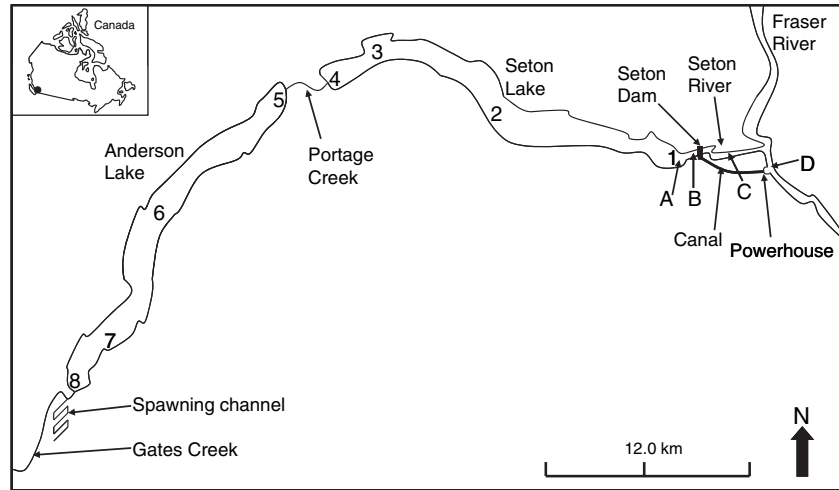


Fig. 1. Map of Seton-Anderson watershed showing locations of telemetry receivers (numbers), release sites of telemetered sockeye salmon (letters), the spawning channel and some hydroelectric facilities.

sockeye salmon. Spawning areas are immediately upstream of Anderson Lake in Gates Creek and in an artificial spawning channel ~800 m upstream of the creek mouth in the town of D'Arcy, BC. Seton Lake is a large lake along the migratory route, often known as a 'corridor' lake. Although the lake is natural, the outflow was impounded in 1956 about 760 m downstream of the lake, causing the water level to rise approximately 2 m. Only 16% of Seton Lake's inflow comes from the Seton-Anderson basin, whereas 78% comes from an inter-basin diversion from the adjacent Bridge River watershed. The remaining 6% of the lake's inflow comes from Cayoosh Creek, a tributary that naturally flows into the lower Seton River but that is diverted in part into Seton Lake ~300 m from the outflow (BCRP 2000).

Fish handling, tagging and biopsy

Fish were captured by dip-net from the top pool of the Seton dam fishway on August 16–24, 2007. To achieve various objectives of a parallel study concerning the impacts of hydro-facilities on spawning migration, we transported and released fish at different locations in the watershed. After capture by dip net, fish were transferred to a truck-mounted aluminium transport tank (1 m × 1 m × 1.5 m) filled with river water and continuously aerated with a 30-cm long air diffuser. Because transportation of salmonids can be stressful (Chandross et al. 2005), after transportation to the release site, fish were placed in a mesh net-pen for 5 h to recover before they were tagged, biopsied and released. Fish that were transported and held in net-pens before tagging were released at one of three locations (sites A, C and D, Fig. 1): (A) Seton Lake near the outflow (8 fish), (C) lower Seton River at Cayoosh Creek (27 fish) or (D) Fraser River, 1.2 km downstream of the Seton River at the powerhouse outflow (32 fish). In order to evaluate the effects of

transportation and net-pen holding, an additional 20 sockeye salmon were caught in the fishway, and transferred immediately (<10 s) to the sampling trough for biopsy sampling and tagging. After tagging, these fish were immediately released into the Seton River on the upstream side of the dam and fishway (site B, Fig. 1). We compared fish from different release sites and between net-pen held and immediately released fish to assess whether these different treatments affected subsequent migration behaviour.

Tagging and biopsy sampling followed procedures described in Cooke et al. (2005). Fish were placed in a foam-lined v-shaped trough with a continuous supply of fresh water directed towards the fish's head and gills. No anaesthetic was used and one researcher restrained the fish in the trough during the procedure. A 1.5-ml blood sample was taken from the caudal vasculature (Houston 1990) using a heparinised Vacutainer syringe (1.5 inches, 21 gauge, lithium heparin). Blood samples were centrifuged for 6 min to separate plasma from red blood cells and plasma was stored in liquid nitrogen then transferred to a -80 °C freezer for storage until analysis. Fork length was measured to the nearest 5 mm. A small tissue sample was removed from the adipose fin using a hole punch and stored in ethanol for subsequent DNA analysis to confirm population of origin (Beacham et al. 2004). Somatic lipid concentration was measured using a hand-held microwave energy metre (Fatmeter model 692; Distell Inc., West Lothian, Scotland, UK) and converted to estimates of gross somatic energy (GSE) using relationships described by Crossin & Hinch (2005). Fish were marked with an external tag (FT-4 Cinch up; Floy Tag Inc., Seattle, WA, USA) attached through the dorsal musculature immediately anterior to the dorsal fin using a hollow needle. The external tag permitted visual identification of study fish on spawning grounds or if they were caught by in-lake subsistence fisheries. An acoustic

telemetry transmitter (V16-1H-R64K coded transmitters; Vemco Inc., Shad Bay, NS, Canada) was inserted into the stomach using a plastic tag applicator (Ramstad & Woody 2003).

Laboratory analysis

Testosterone and 17- β estradiol concentrations were measured in duplicate using enzyme-linked immunosorbent assay (ELISA) kits (Neogen Co., Lexington, KY, USA). Plasma testosterone and 17- β estradiol were ether-extracted according to kit directions prior to completing the assays. Measurements were repeated if the coefficient of variation between replicates was >10%. To determine the sex of individual fish, 17- β estradiol was plotted versus testosterone resulting in two distinct clusters of points, which corresponded with males and females, a method validated previously on destructively sampled fish (D. Patterson, pers. comm.).

One assumption of our analysis was that the levels of hormones and GSE measured at the time of capture were representative of the fish's physiological and energetic state during subsequent migration through the lakes. All fish released downstream of the dam that we had temperature data for passed the dam and entered the lake relatively quickly (most in <3 days with a maximum of 6 days). All study fish had similar treatment and our handling did not cause undue physiological stress as indicated by plasma metabolite and ion analyses (Roscoe & Hinch 2007). Therefore, the assumption that hormones and energy levels measured at capture are representative of fish's condition in the lakes is likely sound.

Temperature logging

Archival temperature loggers (iButton Thermochrons, DS1921Z; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) were waterproofed and attached to all telemetry transmitters before transmitter insertion using a nontoxic adhesive. Loggers were the same diameter as transmitters and when attached increased the transmitter length by \sim 8 mm. Loggers were programmed to record temperature once every hour (manufacturer specified accuracy = 1 °C, resolution = 0.1 °C). Because temperature loggers do not transmit data, temperature profiles were only obtained from fish recovered on spawning grounds. A series of temperature loggers were suspended vertically in the water column to measure temperature at various depths at three locations in Seton Lake and two locations in Anderson Lake. These loggers were attached to the lines from moorings at telemetry receiver stations at various depths between 5 and 65 m. Temperatures from individual fish were also

used in conjunction with loggers at known depths in the water column to estimate approximate depths of fish and whether or not they made diurnal vertical migrations, as others have described for sockeye salmon (Mathes et al. 2009).

Acoustic telemetry and lake behaviours

A fixed array of eight telemetry receivers (VR2; Vemco Inc., Shad Bay, NS, Canada) was used to monitor fish movements (Fig. 1). In both Seton and Anderson lakes, there was one receiver at the inflow, one at the mouth and two along the migration route deployed at locations intended to maximise detection efficiency and coverage of the lake habitat. Receivers were either suspended in the water column using sandbags, rope and subsurface buoys (six receivers) or attached to a fixed structure (e.g., log or dock; two receivers). Data from telemetry receivers were downloaded and detection efficiency for each receiver was calculated using the method of Jolly (1982) as described by Welch (2007). As the receiver at the mouth of Seton Lake (Receiver 1, Fig. 1) was slightly downstream of the Seton Lake release site, fish released at this site were not included for detection efficiency for that receiver. As calculating a detection efficiency requires an upstream receiver, efficiency could not be calculated for the receiver at the inflow of Anderson Lake.

Fish that were detected at the inflow of Anderson Lake (receiver 8) were considered to be successful migrants as spawning areas are directly upstream in Gates Creek and spawning channel. Fish that were last detected in the lakes prior to reaching receiver 8, and were then either continuously detected on a receiver or disappeared between receivers, were considered to be in-lake mortalities. We calculated travel speeds through Seton (receiver 1–4) and Anderson (receiver 5–8) lakes, and for the total migration including migration through Seton Lake, Portage Creek and Anderson Lake (receiver 1–8; hereafter 'total migration'). Travel speeds were calculated by the distance of a segment divided by the difference in time between the first detections at the first and last receivers of a given segment. To describe differences among fish in the directness of migration, we classified individuals in terms of two additional lake behaviours, circling and holding, in each of the lakes. Circling was defined as any movement of one receiver station or more in a 'downstream' direction. Holding was defined as residing in the lake for longer than 24 h after having reached the inflow of the lake. Although some fish died in the lakes before reaching the inflow of Anderson Lake, we included all fish that were present in a given lake for analysis of travel speeds and behaviours, regardless of fate.

Statistical analysis

Analysis of variance (ANOVA) was used to compare travel speeds between sexes, release sites and between net-pen held and immediately released fish. The frequency of circling and holding behaviours was compared between sexes, release sites and net-pen holding groups using chi-squared analysis, or Fisher's exact test if expected cell sizes were less than five.

For each fish whose temperature logger was recovered, we calculated the mean temperature (T_{mean}), the 5th percentile (T_5) and the 95th percentile (T_{95}) while in Seton Lake, Anderson Lake and for the total migration through Seton Lake, Portage Creek and Anderson Lake. We chose these particular percentile temperature calculations to describe the coolest and warmest temperatures that fish experienced for an appreciable amount of time and which we believe are more likely to affect physiology rather than short-term exposure to minimum or maximum temperatures.

Pearson's correlations were used to assess whether GSE or hormones were related to Julian date. Multiple linear regression was used to assess relationships between travel speed and measures of temperature exposure for the total migration (the response variable), and the predictor variables GSE, testosterone, estradiol and sex. The Julian date of entry into Seton Lake was also used as a predictor variable to assess the effect of timing within the migration season on speed and temperature selection. Because estradiol is female-specific, the variable representing male estradiol was removed from the regressions. To determine which of the variables were useful predictors of the response variable, stepwise regression model selection was used. The stepwise model selection process was forward-loading but also allowed variables that subsequently became nonsignificant to be removed (probability for entry or elimination = 0.1). Because of known sex differences in energy and reproductive hormones in sockeye salmon, the class variable sex was forced into the model. Travel speed in the lake was \log_{10} -transformed in order to meet model assumptions whereas all the other variables did not require transformation. To assess relationships between physiology and directness of migration, we used logistic regressions to predict the binary response variables circling and holding, in both Seton and Anderson lakes (i.e., four total logistic regressions). Stepwise model selection was used to select from the same combination of predictor variables used for linear regressions discussed above. All analyses were carried out in SAS v.9.1.3 (SAS Inc., Cary, NC, USA). Statistical significance was assessed at the 0.05 level. For analyses of the three temperature variables, Bonferroni correction for multiple comparisons resulted in a significance level of 0.017.

Results

We released 87 sockeye salmon at four different sites. Twenty-one fish never moved upstream of the fishway and therefore provided no information on in-lake behaviour. Detection efficiencies for all telemetry receivers in the array were 100% indicating an excellent ability to monitor fish movements in the lakes.

First, we compared behaviour among fish released at different locales and between fish held in net-pens and those that were not to evaluate potential differences among release groups (Table 1). Mean travel speed from the mouth of Seton Lake to the inflow of Anderson Lake was not different between net-pen held and immediately released fish or between fish released upstream (sites A and B pooled) and downstream of the dam (sites C and D pooled; Table 1). The frequency of circling and holding behaviours was independent of release site in Seton Lake. In Anderson Lake, circling was independent of release site but a greater percentage of fish released upstream of the dam displayed holding behaviour (88%) compared to fish released downstream (52%). More holding in the fish released upstream versus downstream of the dam may have been related to earlier tagging of the upstream released fish, as fish released upstream of the dam were caught and released primarily during the earlier portion of our tagging period. Because few fish were tagged and released downstream of the dam during the early part of our tagging period, we were not able to separate the effects of timing versus release site on holding behaviour in Anderson Lake. Because behaviour of fish from all release sites and net-pen holding treatments was generally not different (except for a greater frequency of holding in the fish tagged earliest in the season), we pooled these groups for subsequent analyses.

Travel speed (mean \pm SE) was $38.4 \pm 2.4 \text{ km}\cdot\text{day}^{-1}$ in Seton Lake (receiver 1–4; $n = 62$) and $17.0 \pm 2.2 \text{ km}\cdot\text{day}^{-1}$ in Anderson Lake (receiver 5–8; $n = 53$). Travel speed from the first detection at the mouth of Seton Lake to arrival at the inflow of Anderson Lake, including migration through Portage Creek and holding or circling before reaching the inflow of Anderson Lake, was $13.6 \pm 1.1 \text{ km}\cdot\text{day}^{-1}$ (receiver 1–8; $n = 51$). Travel speed did not differ by sex in Seton or Anderson lake ($P = 0.96$ and $P = 0.11$). Circling behaviour was displayed by 19 of 65 fish (29%) in Seton Lake and 22 of 58 of fish (38%) in Anderson Lake. Holding behaviour was displayed by 15 of 64 fish (23%) in Seton Lake and 37 of 53 fish (70%) in Anderson Lake. Neither circling nor holding were associated with sex in Seton Lake ($P = 0.7$ and $P = 0.13$, respectively) or Anderson

Table 1. Comparison of travel speed, behaviours (circling and holding), gross somatic energy (GSE), testosterone (T), estradiol (E2), and tagging dates of sockeye salmon tracked through Seton and Anderson lakes in British Columbia. Two-way analysis of variance (ANOVA) was used to compare GSE, T and E2 between fish that were held in net-pens and those that were not (control) and between sexes. Travel speed did not differ by sex and was compared between control and net-pen held fish, and between fish release upstream of the dam and those released downstream of the dam using one-way ANOVA. Proportion of fish that circled or held in lakes did not differ by sex and was compared between groups using chi-square tests. Differences significant at 0.05 are shown in bold text. Because there were few differences in behaviour between groupings of fish, control, net-pen held and upstream and downstream releases were pooled for other analyses of lake behaviour.

| | Control (site B) | | Net-pen held (site A,C,D) | | P-values | | |
|---------------|------------------|------------|---------------------------|------------|-------------------|-------------------|-------------|
| Travel speed | 11.6 ± 1.2 | | 14.8 ± 1.5 | | 0.17 | | |
| | Male | Female | Male | Female | Holding | Sex | Interaction |
| GSE | 5.6 ± 0.2 | 6.5 ± 0.2 | 6.0 ± 0.1 | 6.4 ± 0.1 | 0.33 | <0.0001 | 0.16 |
| T | 10.0 ± 3.1 | 22.9 ± 4.4 | 3.8 ± 2.1 | 10.4 ± 1.5 | <0.0001 | 0.0006 | 0.5 |
| E2 | n/a | 1.7 ± 0.3 | n/a | 1.5 ± 0.1 | 0.42 | n/a | n/a |
| Tagging dates | 15-16 August | | 17-24 August | | | | |

| | Upstream release (sites A,B) | Downstream release (sites C,D) | P-values |
|--------------------------|------------------------------|--------------------------------|--------------|
| Travel speed | 11.6 ± 1.0 | 15.4 ± 1.7 | 0.11 |
| % circled in Seton L. | 29 | 30 | 0.92 |
| % circled in Anderson L. | 26 | 48 | 0.079 |
| % held in Seton L. | 30 | 19 | 0.32 |
| % held in Anderson L. | 88 | 52 | 0.004 |
| Tagging dates | 15,16, 20 August | 17-19, 21-24 August | |

Lake ($P = 0.31$ and $P = 0.93$). Of 66 sockeye salmon detected in the lakes, 53 were successful migrants, 12 were in-lake mortalities and one was caught by recreational fisheries in Portage Creek.

Temperature loggers suspended in the water column confirmed that Seton and Anderson lakes were both thermally stratified during the study period (Fig. 2). In Anderson Lake, the thermocline was situated between approximately 10 and 30 m depth and the hypolimnion started at approximately 30 m. In Seton Lake, the thermocline appeared to be deeper, between 25 and 45 m, although the epilimnion, thermocline and hypolimnion were less distinct compared to Anderson Lake.

Of 53 fish that reached spawning grounds, temperature loggers were recovered from 24 fish. Temperature exposure in the lakes varied among individuals (Fig. 3) and between the two lakes (Table 2). T_{95} ranged from 15 °C to 19 °C. The warmest temperatures were encountered mostly in Portage Creek, although some fish encountered temperatures as high as 18 °C in the epilimnion of Anderson Lake. The coolest temperatures experienced appeared to be much more variable, as indicated by the large range of T_5 (6–14 °C) among fish. Temperatures below 10 °C were typically encountered in Anderson Lake, whereas temperature experience was less variable in Seton Lake (11–16 °C; Table 2). Three examples of the varying thermal history among individual fish during migration through the lakes are shown in Fig. 4. None of the temperatures variables (T_5 , T_{mean} and T_{95}) differed between males and females (all $P > 0.5$).

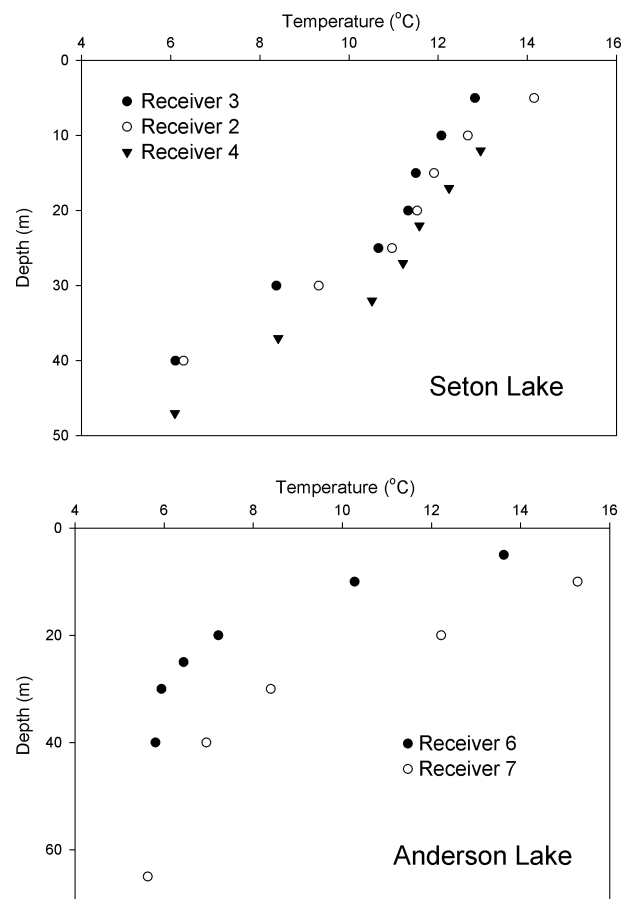


Fig. 2. Water temperature at various depths in Seton and Anderson lakes in 2007. Temperature was measured hourly at numbered receiver stations (see Figure 1) and values are means from August 16 – September 5.

Fig. 3. Box plots of temperature experience of 24 fish while migrating through Seton Lake, Portage Creek and Anderson Lake. For each individual, the mean, 25th and 75th percentile (boxes), 10th and 90th percentiles (whiskers), and 5th and 95th percentiles (black circles) are shown.

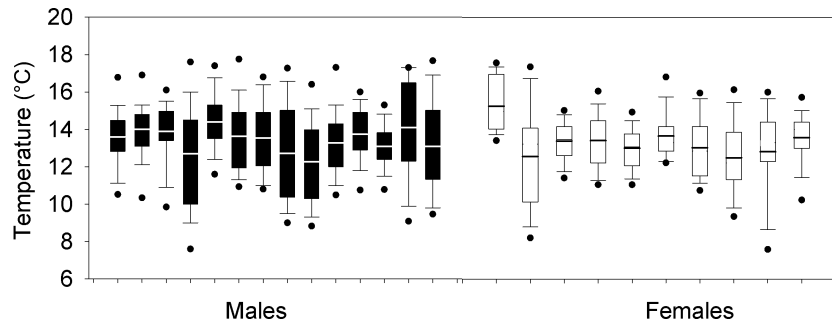


Table 2. Range of values of mean, 5th percentile (T_5) and 95th percentile (T_{95}) temperatures experienced by 24 sockeye salmon during migration through lakes to spawning areas. Values are shown for Seton Lake, Anderson Lake, and the total migration, which included migration through both lakes and Portage Creek. Values of the three temperature variables for the total migration were used in regressions using energy and reproductive hormones to predict temperature experience (see Table 3).

| Temperature variable | Range (min–max; °C) | | |
|----------------------|---------------------|---------------|-----------|
| | Seton Lake | Anderson Lake | Total |
| Mean | 12.9–15.0 | 9.6–14.5 | 12.3–15.9 |
| T_5 | 11.4–13.9 | 5.9–13.6 | 6.1–13.8 |
| T_{95} | 13.9–16.4 | 12.9–17.4 | 15.3–18.8 |

Some fish displayed diurnal vertical migrations, occupying cooler water in the hypolimnion during the day and moving into the epilimnion and near the surface during the night. An example of diurnal vertical migration is shown for one fish (Fig. 4a). However, many fish that did migrate to the surface at night did not do so every night, and some fish did not display this behaviour at all (e.g., Fig. 4c). Because diurnal vertical migration was displayed to varying degrees and therefore not a discrete behaviour, we did not evaluate associations with energy or hormones. This behaviour was observed only in Anderson Lake and not in Seton Lake.

Gross somatic energy (mean \pm SE) was $5.8 \text{ MJ}\cdot\text{kg}^{-1} \pm 0.09$ for males ($n = 26$) and $6.5 \text{ MJ}\cdot\text{kg}^{-1} \pm 0.07$ for females ($n = 36$). Testosterone concentration was $6.5 \text{ ng}\cdot\text{ml}^{-1} \pm 1.1$ for males ($n = 26$) and $10.7 \text{ ng}\cdot\text{ml}^{-1} \pm 1.5$ for females ($n = 31$). Estradiol concentration was $1.6 \text{ ng}\cdot\text{ml}^{-1} \pm 0.1$ for females and $<0.12 \text{ ng}\cdot\text{ml}^{-1}$ for all males. GSE was not correlated with the date of lake entry for males ($P = 0.6$) or females ($P = 0.7$). Testosterone was correlated with the date for males ($r = -0.48$; $P = 0.01$), but not for females ($P = 0.1$). Estradiol was not correlated with the date in females ($P = 0.4$). Because we did not have blood samples from three females, we had both temperature and physiological data for a total of 14 males and 7 females.

Stepwise regression model selection resulted in relatively simple models with only a few variables

used to predict a temperatures variable or migration speed (Table 3). A dummy variable representing sex was forced into all four models and was a significant variable in all cases. In the model predicting T_5 , female estradiol was positively related to T_5 and date was also a significant variable (Table 3). Female estradiol was a significant variable predicting T_{mean} . GSE was negatively related to T_{95} but only for females and not males. GSE was positively related to travel speed for males but not females and was the only significant predictor of travel speed. Stepwise selection for logistic regression models predicting circling or holding suggested that these behaviours were not related to physiological variables. Models predicting both circling and holding in Seton Lake, and holding in Anderson Lake included only the intercept and were not significant (all $P > 0.1$). The model predicting holding in Anderson Lake was significant ($P = 0.0001$) but only included the date of lake entry ($P = 0.003$) as a predictor variable.

Discussion

This study is the first to link individual variation in thermoregulatory behaviour to differences in physiological condition of Pacific salmon during spawning migration. We found evidence to support the hypothesis that thermal behaviour is related to energy levels and reproductive status of adult sockeye salmon. The warmest temperatures experienced (i.e., T_{95}) were positively related to energy levels, which was consistent with our prediction that fish with lower energy would select cooler temperatures. However, this relationship was only significant for females and not for males. As females allocate more energy to gonad development than males, there may be stronger selection for energy-saving tactics in females compared to males (Hinch et al. 2006). Indeed, studies of Fraser River sockeye salmon reported that females are more energetically efficient swimmers (Hinch & Rand 1998; Standen et al. 2002) and have more streamlined body shapes, which reduce energetic costs of swimming (Crossin et al. 2004). The present study provides further evidence of energy-saving patterns in migrat-

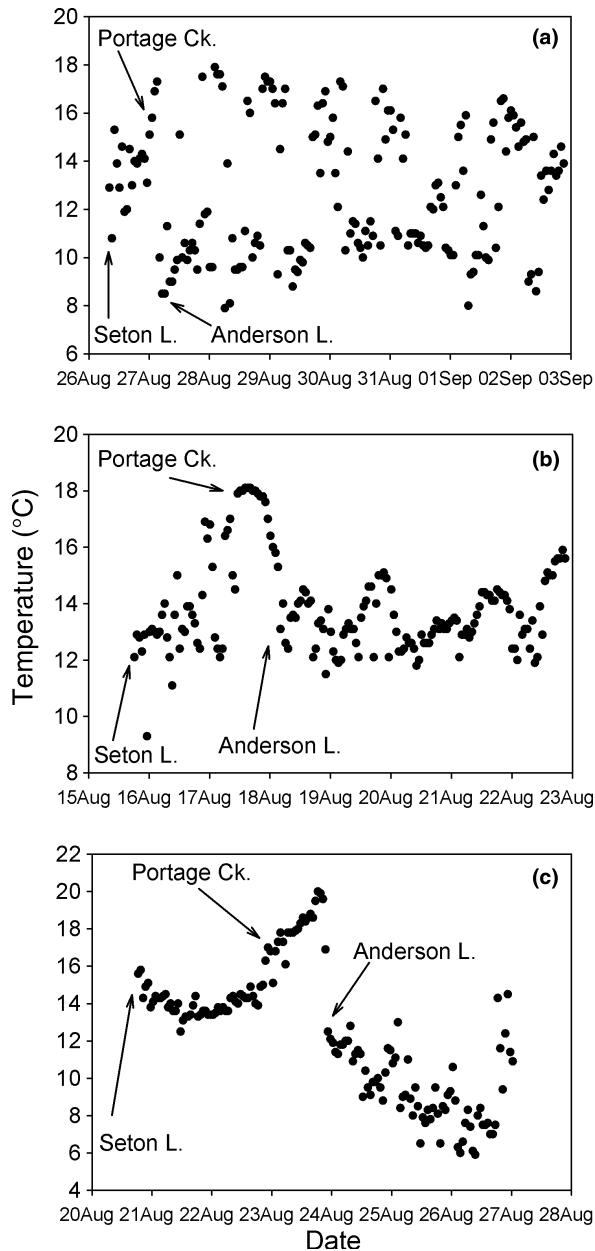


Fig. 4. Thermal history of 3 exemplar sockeye salmon during migration in the Seton-Anderson watershed in British Columbia, Canada. Temperature experience varied among individuals, particularly in Anderson Lake, with some fish displaying diurnal vertical migration (a), or experiencing relatively warm (b) or cool (c) temperatures. Temperatures were measured hourly by archival loggers attached to telemetry transmitter and inserted into stomach of each fish. Arrows show approximate time that fish entered different sections of the migration route.

ing adult female sockeye salmon. Females that had low energy did not select temperatures as high as those with relatively greater energy reserves and would have thus reduced their metabolic energy expenditure.

Female fish that had lower levels of estradiol selected the coolest temperatures. Estradiol is a hormone that stimulates the synthesis of vitellogenin

Table 3. Results of multiple regressions predicting travel speed, and 5th percentile (T_5), mean (T_5), and 95th percentile (T_{95}) temperatures selected by sockeye salmon migrating through two lakes in British Columbia. Stepwise model selection was used to select predictor variables included but the class variable sex was forced into the models. Potential variables were testosterone, estradiol, gross somatic energy (GSE), and Julian date. P-values, coefficient of multiple determination (R^2) and parameter estimates (slope or intercept \pm SE) are shown.

| | P | R^2 | Parameter estimate |
|------------------|---------|-------|--------------------|
| T_5 | | | |
| Model | 0.0004 | 0.64 | |
| Intercept | <0.0001 | | 11.0 \pm 0.5 |
| Sex | 0.0002 | | -8.6 \pm 1.8 |
| Female estradiol | 0.0001 | | 2.6 \pm 0.6 |
| Male date | 0.04 | | -0.1 \pm 0.1 |
| T_{mean} | | | |
| Model | 0.001 | 0.64 | |
| Intercept | <0.0001 | | 13.4 \pm 0.2 |
| Sex | 0.0006 | | -4.0 \pm 1.0 |
| Female estradiol | 0.0003 | | 2.6 \pm 0.6 |
| T_{95} | | | |
| Model | 0.007 | 0.42 | |
| Intercept | <0.0001 | | 16.7 \pm 0.2 |
| Sex | 0.005 | | -18.1 \pm 5.7 |
| Female energy | 0.004 | | 2.8 \pm 0.8 |
| Travel speed | | | |
| Model | 0.003 | 0.26 | |
| Intercept | 0.3 | | |
| Sex | 0.004 | | |
| Male GSE | 0.001 | | |

(So et al. 1985), which is released into circulation and then taken up by oocytes in the ovary (Ng & Idler 1983). In migrating sockeye salmon, estradiol levels increase during coastal and early riverine migration, but decline quickly prior to reaching spawning grounds (Leonard et al. 2002) when vitellogenesis ends and final maturation of the oocytes begins (Truscott et al. 1986). Because fish in our study were <60 km from spawning areas and likely within 1–2 weeks of spawning, our interpretation is that female fish that had lower levels of estradiol were more reproductively advanced compared to fish with higher levels of estradiol. As predicted, the more reproductively advanced females had cooler temperature exposure with many individuals spending time at very cool temperatures (\sim 5–7 °C) by swimming into deep layers of the lake. Newell & Quinn (2005) suggested that the temperatures between 9 °C and 11 °C where sockeye salmon in Lake Washington, USA, spent the majority of their time were optimal for sexual maturation. Similarly, McCullough et al. (2001) concluded, based on their literature review, that temperatures of 10–12.5 °C are optimal for maturation of salmonids. The much cooler temperatures used by females in our study may have been selected to slow the rate of maturation, as over-ripening can lead to reduced fitness in salmon (Flett et al. 1996). Previous studies have shown that temperature preference of Atlantic stingrays (*Dasyatis sabina*) and

thermoregulatory behaviour of bluefin tuna (*Thunnus thynnus*) may vary depending on the stage of reproductive development (Wallman & Bennett 2006; Teo et al. 2007). Alternatively, cold temperatures could confer several other benefits to adult sockeye salmon including slowing the rate of disease development (Wagner et al. 2006) and reducing energetic costs of metabolism (Lee et al. 2003; Farrell et al. 2008).

Although we observed interesting patterns between temperature experience and estradiol, testosterone was not related to either in-lake behaviour or temperature experience. In both male and female sockeye salmon, levels of circulating testosterone increase during migration (Hinch et al. 2006) and then drop sharply after spawning (Truscott et al. 1986). We predicted that fish with higher levels of testosterone would select cooler water temperatures and travel faster and more directly than less mature fish but found no such relationships. However, testosterone has a number of roles in reproductive development, including acting as a substrate or precursor for other steroid hormones. It may be that other hormones, such as 11-ketotestosterone, the major androgen in sockeye salmon (Truscott et al. 1986), are more directly related to thermoregulation and other behaviours in males, whereas estradiol appears to be more closely linked with these behaviours than testosterone in females.

The lack of relationships between testosterone and behaviour might also be explained by small sample sizes and low statistical power. However, note that we detected relationships with estradiol despite having both temperature and physiological data for only seven females. Studies using temperature-sensing telemetry (e.g., Berman & Quinn 1991) can avoid the problem of recovering temperature loggers but the high cost of telemetry transmitters may also limit sample sizes and data are only collected when the transmitter is in the range of a receiver (Cooke et al. 2004).

In general, patterns of movement (i.e., holding and circling) and rates of travel of sockeye salmon in Seton and Anderson lakes were not related to levels of energy or the reproductive hormones measured. The only exception was that GSE was positively related to travel speed of males. This finding was contrary to our prediction that fish with lower energy reserves would travel faster and more directly in order to reach spawning areas and reproduce before exhausting their energy reserves. Crossin et al. (2004) estimated that the minimum energy density required to sustain life was $4 \text{ MJ}\cdot\text{kg}^{-1}$ whereas all but one of the individuals in our study had $\text{GSE} > 5 \text{ MJ}\cdot\text{kg}^{-1}$. Therefore, the positive relationship between energy and speed probably cannot be explained by critically low energy levels impairing and slowing migration in some fish. Alternatively, it could be that fish that had low energy swam at speeds that resulted in lower energy cost per

unit distance and slower overall travel speeds. However, because our travel speeds are minimum estimates averaged over relatively large distances, and fish likely do not swim in a straight line, we cannot comment on whether swim speeds of fish with lower energy were more energetically efficient.

Although the spawning migrations of sockeye salmon have been studied extensively (reviewed in Burgner 1991 and in Hinch et al. 2006), most research has focused on the river or near-shore coastal environment and only a few previous studies have examined in-lake behaviour. We found that on average sockeye salmon travelled slower in the lakes ($13.6 \pm 1.1 \text{ km}\cdot\text{day}^{-1}$ through two lakes and 3 km-long creek) than has been reported during migration up-river ($17\text{--}40 \text{ km}\cdot\text{day}^{-1}$; English et al. 2005) or in the ocean ($30\text{--}55 \text{ km}\cdot\text{day}^{-1}$, Neave 1964; $20\text{--}33 \text{ km}\cdot\text{day}^{-1}$, Crossin et al. 2007). Sockeye salmon migrating through Lake Clark, Alaska, travelled even slower than fish in our study, averaging $4.7 \text{ km}\cdot\text{day}^{-1}$ for tributary spawning individuals and $1.6 \text{ km}\cdot\text{day}^{-1}$ for lake spawners (Young & Woody 2007). Interestingly, average travel speeds through Seton Lake ($38.4 \pm 2.4 \text{ km}\cdot\text{day}^{-1}$) were as fast or faster as in the river or ocean, although this rate did not include time spent milling at inlet of the lake before moving upstream into Portage Creek. These comparisons highlight the importance of considering the resolution of fixed telemetry arrays and the scale over which minimum travel speeds are calculated. For instance, Young & Woody (2007) calculated travel speeds from the time of release to when salmon reached spawning areas, thus, including all time spent on milling and potentially re-orientating after release and recovery. This difference in methods may explain the much slower travel speeds observed in that study compared to ours.

We observed many fish holding near lake inlets or circling, providing further evidence that lake migration is not necessarily linear and direct, which was reported previously in Lake Clark, Alaska (Young & Woody 2007). Interestingly, behaviour differed substantially between the two lakes studied, which were only a short distance apart and both near spawning areas. Although Seton and Anderson lakes are similar in size and were both thermally stratified, sockeye salmon travelled much faster through (38.4 ± 2.4 vs. $17.0 \pm 2.2 \text{ km}\cdot\text{day}^{-1}$) and were less likely to circle and hold in Seton Lake compared to Anderson Lake. This pattern may have arisen because Anderson Lake is adjacent to spawning areas and is not simply a migration corridor as is Seton Lake. We also found that more fish released upstream of the dam displayed holding behaviour in Anderson Lake compared to those released downstream of the dam. However, because behaviour was otherwise not different

between fish from different release sites, and date was a significant predictor of holding in Anderson Lake, we suspect that greater propensity to hold in Anderson Lake was related to the earlier timing of fish released upstream of the dam, and not because of their release location. Thus, it may be that earliest fish of the spawning run may hold longer in the lake adjacent to spawning areas to complete reproductive maturation (Hinch et al. 2006).

Temperature exposure also differed between Seton and Anderson lakes, with generally warmer and less-variable temperatures experienced by fish in Seton Lake compared to Anderson Lake. Sockeye salmon avoided very warm temperatures such as those in the epilimnion of the lake (approximately 16–18 °C) and spent little time in Portage Creek (~3 km migration distance), where temperatures were as high as 20 °C and cooler temperatures in deeper water are not available. Avoidance of high temperatures by Pacific salmon has been reported by others (Newell & Quinn 2005; Mathes et al. 2009) and is not surprising, given the high mortality associated with exposure to very high temperatures (Crossin et al. 2008; Farrell et al. 2008; Keefer et al. 2008). In Anderson Lake, the lowest temperatures experienced by fish (i.e., T_5) ranged from 6 °C to 13 °C. As water temperatures of 6 °C corresponded to depths of 30–50 m, some sockeye salmon were likely actively seeking out these cool temperatures by descending into the hypolimnion, whereas others continued to migrate closer to the surface. In contrast, Mathes et al. (2009) found that all tagged Weaver Creek sockeye salmon holding in Harrison Lake spent the majority of their time (>80%) in the hypolimnion at 6.5 °C. In addition, sockeye salmon in Harrison Lake had more consistent diel vertical migrations, travelling to the surface every night, whereas in our study only some fish displayed this behaviour, and not necessarily every day. It is unclear whether these differences in behaviour were related to previous migratory experience, natural differences between populations or differences between a lake within the migration corridor (Gates population) versus volitional movement into a nearby lake (Weaver population).

Our results suggest that thermoregulatory behaviour of migrating adult sockeye salmon is influenced by levels of energy and reproductive development. These findings further demonstrate the importance of thermal habitats in lakes and have implications for how forecasted warming temperatures associated with climate change (Ferrari et al. 2007) will affect sockeye salmon. That is, salmon exposed to higher than normal river temperatures may use thermal habitat in lakes to avoid energetic exhaustion or optimise reproductive development. One consequence of using archival temperature loggers is that data are typically only

recovered from successful migrants and not from fish that die before reaching spawning grounds. Interestingly, there was no single thermal behaviour pattern that was consistent with survival to spawning grounds, as successful migrants displayed a range of temperature preferences. However, we are unable to assess the effect of variable temperature exposure on fate and whether migrants that die before reaching spawning grounds may behave differently. Understanding the consequences of in-lake behaviour and thermoregulation are important future research priorities, as thermal refugia in lakes may be crucial to survival during warm temperature years (Mathes et al. 2009).

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