

Limited behavioural thermoregulation by adult upriver-migrating sockeye salmon (*Oncorhynchus nerka*) in the Lower Fraser River, British Columbia

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Abstract: The objective of this study was to combine radio telemetry with individual thermal loggers to assess the extent to which adult migrating sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) behaviourally thermoregulate during their migration through the Fraser River mainstem, British Columbia. The Fraser mainstem represents a region of the migration route that contains some of the highest mean temperatures encountered by sockeye salmon during their life history. We found that throughout the study area, individual sockeye salmon body temperatures occasionally deviated from ambient temperatures (ΔT), yet individuals maintained a ΔT of -1°C or cooler for only 5% of their migration through the study region. There were moderate mean deviations of ΔT in two segments that are known to contain thermally stratified waters. In one of the study segments with the greatest ΔT , mean body temperatures decreased as river temperatures increased and ΔT became increasingly positive with higher river discharge rates, but these relationships were not observed in any of the other study segments. No relationship existed between ΔT and migration rate. While periodic associations with cool water were evident, mean body temperatures were not significantly different than mean river temperatures throughout the lower Fraser mainstem. This finding raises further conservation concerns for vulnerable Fraser River sockeye stocks that are predicted to encounter increasing peak summer river temperatures in the coming decades.

Résumé : L'objectif de notre recherche est de combiner l'utilisation de la radio-télémetrie et d'enregistreurs individuels de température afin d'évaluer dans quelle mesure les saumons rouges (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) adultes sont capables par leur comportement de faire de la thermorégulation durant leur migration le long du cours principal du Fraser, Colombie-Britannique. Le cours principal du Fraser est une portion de la route de migration qui contient quelques-unes des températures moyennes les plus élevées que connaît le saumon rouge durant son cycle biologique. Dans l'ensemble de la région d'étude, la température corporelle des saumons individuels diffère à l'occasion de la température ambiante (ΔT); néanmoins, les individus maintiennent un ΔT de -1°C ou davantage durant seulement 5% de leur migration à travers la région d'étude. Il y a des différences moyennes modérées de ΔT dans deux sections connues pour posséder des eaux à stratification thermique. Dans l'une des sections d'étude qui possède le ΔT le plus important, la température corporelle moyenne diminue à mesure que la température du fleuve augmente et ΔT devient de plus en plus positif en fonction de l'augmentation du débit de la rivière; ces relations ne s'observent cependant pas dans aucun autre segment étudié. Il n'existe pas de relation entre ΔT et le taux de migration. Tandis que les associations périodiques avec d'eau frais était évidentes, les températures corporelles moyennes ne diffèrent pas significativement des températures moyennes du fleuve dans l'ensemble du cours principal inférieur du Fraser. Cette observation soulève de nouvelles inquiétudes au sujet de la conversation des stocks vulnérables de saumons rouges du Fraser qu'on prédit devoir connaître des températures maximales plus élevées durant les prochaines décennies.

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Introduction

Migratory species have evolved some of the most complex behaviours of any group of organisms (Dingle 1996), owing in part to adaptations to variable environmental conditions. This is a particularly salient characteristic of adult anadromous Pacific salmonids (genus *Oncorhynchus* Suckley, 1861), which encounter highly variable water temperature and flow conditions during their spawning migrations as they return from the ocean to their natal freshwater spawning grounds (Hinch et al. 2006). Water temperature is known to influence migration timing (Hodgson and Quinn 2002; Cooke et al. 2004; Patterson et al. 2007), migratory behaviour (Berman and Quinn 1991; Newell and Quinn 2005; Goniea et al. 2006; Crossin et al. 2008; Farrell et al. 2008; Keefer et al. 2008a), swimming performance (Lee et al. 2003; MacNutt et al. 2006), migration speed (Hanson et al. 2008; Keefer et al. 2008b), physiology (Young et al. 2006; Crossin et al. 2008), energetics (Hinch and Rand 1998; Crossin et al. 2004; Rand et al. 2006), disease development (Wagner et al. 2005), and survival (Gilhausen 1990; Macdonald 2000; Crossin et al. 2008; Farrell et al. 2008; Keefer et al. 2008b). In fact, temperature has often been considered the abiotic “master” factor of fishes; this is particularly evident for salmonids during their spawning migrations (Brett 1971).

Stocks of sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) migrating through the mainstem Fraser River, British Columbia, Canada, could theoretically encounter river temperatures ranging between 12 and 22 °C (60-year mean minima and maxima daily temperatures during the summer migratory season; Patterson et al. 2007). Fraser River maximum summer water temperatures have increased by about 1.8 °C over the past 40 years (Patterson et al. 2007), and predictions suggest that this warming trend will continue over the next century (Morrison et al. 2002; Ferrari et al. 2007). Water temperatures exceeding 18 °C have been linked with a number of factors that contribute to mortality, including elevated incidence of disease, increases in energy expenditure, and physiological stress (Macdonald 2000; Crossin et al. 2008). A collapse of temperature-dependent aerobic scope has recently been proposed as one of the mechanisms of mortality at high temperatures (Farrell et al. 2008). For the Fraser River stocks measured to date, the optimal temperature for aerobic scope lies between 15 and 17 °C (Lee et al. 2003). At temperatures exceeding these optima, aerobic scope declines rapidly towards a stock-specific critical temperature. When the critical temperature for aerobic scope is reached (~20 °C for the stocks measured to date), sockeye salmon are unable to swim upstream in the Fraser River and high mortality rates are observed (Lee et al. 2003; Farrell et al. 2008; Mathes 2009). Servizi and Jensen (1977) found an exponential relationship between mortality and water temperature above 21 °C and the upper incipient lethal temperature has been reported at approximately 25 °C (Brett 1952; Servizi and Jensen 1977). Growing conservation concerns over the consequences of climate change on salmonid migration in the Pacific Northwest has prompted recent reviews on the subject (Carlson and Seamons 2008; Crozier et al. 2008). Such concerns are not unique to the Fraser River, as endangered Snake River sockeye salmon,

which are the most southerly distributed sockeye population, migrate over remarkably long durations to high elevations while coping with river temperatures that approach upper tolerance limits, often resulting in high mortality rates, particularly for late-timed migrants (Keefer et al. 2008b). Abnormally high mortality rates (>80%) have been observed for late-run Fraser River sockeye that now enter the Fraser River several weeks earlier than normal (Cooke et al. 2004, 2006a). The consequences of this abnormal behaviour is that late-run fish now encounter temperatures that are 4–5 °C higher than what would have been encountered historically (Patterson et al. 2007).

Pacific salmonids have evolved a number of complex behavioural adaptations to reduce migration costs in response to challenging thermal conditions. In fact, a key aspect to stock-specific timing of freshwater migration is believed to be the avoidance of deleterious environmental conditions (Hodgson and Quinn 2002; Keefer et al. 2004; Hinch et al. 2006). When cool-water refuges are available, behavioural thermoregulation is a strategy for mitigating exposure to stressful temperatures during Pacific salmonid spawning migrations (Berman and Quinn 1991; Tanaka et al. 2000; Newell and Quinn 2005; Clabough et al. 2006; Goniea et al. 2006; Keefer et al. 2008b). As a trade-off between reproductive development and energy savings, sockeye salmon will exploit colder depths of thermally stratified Lake Washington and can remain there for some time prior to resuming migration to spawning grounds farther upstream (Newell and Quinn 2005). The use of cool-water locations (e.g., deep-water lakes, tributary outflows) is thought to be especially important for adult salmon when river temperatures are high, and failing to seek thermal refugia has been linked with mortality. For example, Mathes (2009) provided evidence that during a period of abnormally warm water temperatures, a stock of Fraser River sockeye that milled in a cool, deep, oligotrophic lake had a higher survival rate relative to individuals from the same stock that milled in an adjacent river where temperatures were much higher.

The Fraser River mainstem contains segments with relatively little cool-water input, receiving cool water predominantly at locations of tributary outflows and areas of thermally stratified waters or subsurface flows (Lauzier et al. 1995; Patterson et al. 2007). As such, the Fraser mainstem has some of the highest mean temperatures encountered by sockeye salmon during their spawning migrations. The present study is the first of its kind to examine the extent to which adult migrating sockeye salmon engage in behavioural thermoregulation while actively migrating through the Fraser River mainstem. Specifically, differences between fish body temperatures and river temperatures were examined to identify the extent to which mean body temperatures deviate from measured river temperatures. The relationship between temperature deviation and a null relationship where no behavioural thermoregulation is assumed was explored to determine whether or not individuals behaviourally compensated for seasonal increases in water temperatures. Finally, migration speed, river discharge, and run-timing group and stock complex were also examined to test for a relationship between these factors and deviations between body and river temperatures.

Materials and methods

Sampling locations and tagging procedure

In total, 660 individuals were radio-tagged and equipped with thermal loggers in the marine environment and 378 in the freshwater environment in 2006. Detailed capture methods are described in Robichaud and English (2007). Briefly, marine tagging occurred in coastal British Columbia in Juan de Fuca Strait (6–10 August) and Johnstone Strait (sampling occurred over 10 days from 11 to 27 August; Fig. 1). Fish were captured by commercial purse seine. After each net set, individuals were selected from the purse seine and transferred by dip net to onboard holding totes (726 and 239 L) for tagging as described below. Freshwater tagging occurred in the lower Fraser River mainstem, 69 km of river from the mouth of the Fraser River (sampling occurred over 22 days from 9 July to 1 September). Fish were captured with an 8.9 cm mesh drift gill net, operated as a tangle net (i.e., the fine mesh of the net entangles the mouths and fins of individuals to minimize injury to the head, body, and gills). Captured individuals were immediately transferred aboard the vessel into onboard holding totes (190 L) that were aerated and constantly supplied with fresh river water, generally with <6 individuals per tote.

The marine and freshwater components of this study followed a previously established protocol for the tagging and release of Pacific salmonids in the Fraser River (see Cooke et al. 2005, 2006b). All protocols were approved by the University of British Columbia and Carleton University Animal Care Committees in accordance with the Canadian Council on Animal Care. Individuals were rapidly placed supine in a V-shaped tagging trough and a constant flow of clean water was passed through the individual's mouth and gills. The radio transmitter and thermal logger unit was inserted gastrically, through the mouth, with the trailing end of the antenna exiting the individual's mouth and positioned laterally to hang along the outside of the individual's body. DNA analyses were conducted to determine Fraser River sockeye salmon stock origin for all individuals (Beacham et al. 2004). Where possible, DNA results were confirmed using telemetry for individuals that reached spawning grounds.

Telemetry methods

iButton DS1921Z thermal loggers (factory-stated resolution = ± 0.1 °C, accuracy = ± 1 °C; Maxim Integrated Products, Inc., Sunnyvale, California), programmed to record temperatures at 1 h intervals (capable of continuous recording for ~180 days), were attached to each radio transmitter and waterproofed (Plasti Dip multipurpose rubber coating; Plasti Dip International, Blaine, Minnesota). Coded radio transmitters (MCFT-3A-3V; Lotek Wireless Inc., Newmarket, Ontario) were 16 mm in diameter, 46 mm long plus an additional 10 mm in length including the attached thermal logger, and had a 460 mm long antenna; the waterproofed transmitter and logger unit weighed ~17.0 g in air and 6.8 g in water. Tags transmitted on the 150 MHz bandwidth on one of six different frequencies (320, 360, 440, 460, 600, and 800 kHz) with one of three pulse intervals per frequency (4.5, 5.0, and 5.5 s). Individually coded transmitters enabled fish to be uniquely identified upon detection at each receiver. Transmitters were programmed to stop transmitting

after 154 days to minimize the chance of interference with other studies. Fixed receiver stations (Fig. 1; see Robichaud and English 2007) used SRX400, SRX400A, or SRX600 radio receivers (Lotek Wireless Inc.), and 3-element or 4-element Yagi antennas (Maxrad Inc., Hanover Park, Illinois, or Grant Systems Engineering Inc., King City, Ontario).

Study segments

Six study segments were established within the Fraser River mainstem (segments A–F) based on radio telemetry receiver locations (Table 1, Fig. 1). Telemetry tracking occurred in the Fraser River watershed only, not in the marine environment. Sample sizes vary per study segment owing to occasional detection errors at certain fixed receiver stations, resulting in the inability to conclusively assign time of arrival and time of departure from certain study segments. Segment F had a reduced sample size because it excluded individuals that spawn within the tributaries of the Thompson River. Detection efficiencies (i.e., the number of fish passing each location relative to the number of fish detected at each receiver) for each receiver location is as follows: Mission (79.0%), Rosedale (85.7%), Hope (96.3%), Sawmill Creek (99.8%), Hell's Gate Canyon (97.7%), Thompson Confluence (97.6%), and Seton Confluence (100.0%; Robichaud and English 2007). Of the 1038 fish tagged with transmitters and thermal loggers, 452 individuals were detected at Mission, the first telemetry receiver location in the telemetry array. At subsequent receivers, 437, 444, 412, 386, 369, and 133 individuals were detected at Rosedale, Hope, Sawmill Creek, Hell's Gate Canyon, Thompson Confluence, and Seton Confluence, respectively (Robichaud and English 2007).

Recovery of transmitters and thermal loggers

This study focuses on 48 recovered thermal loggers that contained usable temperature data. If the recovered loggers were not detected at upstream telemetry receiver locations or the loggers contained insufficient data points (i.e., the fish was harvested before sufficient temperature data could be collected), they were excluded from analyses. For example, we recovered an additional 97 loggers.

To facilitate the recovery of thermal loggers, a public awareness campaign was launched to inform members of the commercial, recreational, and First Nations fisheries that operate in the coastal environment and lower Fraser River about the study. A small reward was offered, based on a lottery system, to encourage the return of transmitters and loggers. Information was collected on the date, time, and location of the captured fish. Extensive manual surveys were conducted in conjunction with Fisheries and Oceans Canada's (DFO) Stock Assessment Division to recover loggers from individuals at 21 spawning locations throughout the watershed. This approach meant that thermal data could only be obtained either from fisheries captures (37 that were included in the study), often resulting in a short duration of temperature data being logged, or from iButtons recovered on spawning grounds (11 that were included in the study), precluding the ability to compare temperature differences between individuals that died en route versus those that survived to reach spawning grounds.

Fig. 1. A map of the Fraser River watershed, British Columbia. Labels denote marine and freshwater release sites for adult sockeye salmon (*Oncorhynchus nerka*). Study segments in the Fraser River mainstem, based on fixed telemetry receiver locations, are denoted in the inset as A (Mission to Rosedale), B (Rosedale to Hope), C (Hope to Sawmill Creek), D (Sawmill Creek to Hell's Gate Canyon), E (Hell's Gate Canyon to Thompson Confluence), and F (Thompson Confluence to Seton Confluence). River temperature monitoring stations are labeled as Whonnock, Qualark, and Lillooet (inset).

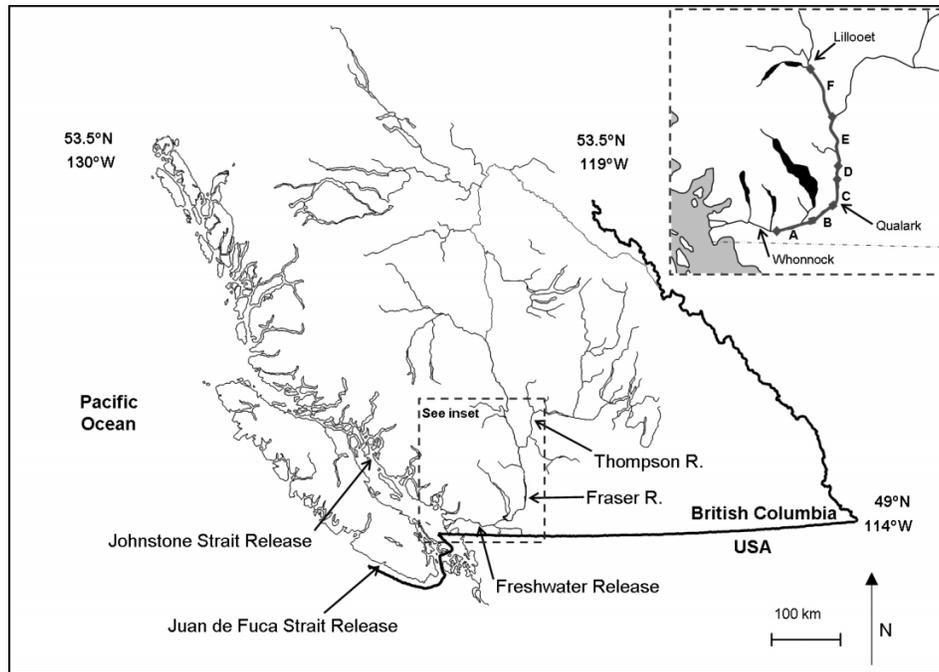


Table 1. Study segment names and corresponding river locations, segment distances, river temperature, and river discharge monitoring locations in the Fraser River, British Columbia, Canada.

Study segment	River location	River segment length (km)	River temperature monitoring location	River discharge monitoring location
A	Mission to Rosedale	44	Whonnock	Mission
B	Rosedale to Hope	36	Qualark	Hope
C	Hope to Sawmill Creek	34	Qualark	Hope
D	Sawmill Creek to Hell's Gate Canyon	12	Qualark	Hope
E	Hell's Gate Canyon to Thompson Confluence	55	Qualark	Hope
F	Thompson Confluence to Seton Confluence	57	Lillooet	Hope, excluding Thompson River discharge

Environmental variables

Locations of hourly Fraser River water temperatures and river discharge are summarized in Table 1. Hourly river discharge ($\text{m}^3\cdot\text{s}^{-1}$) was monitored by the Water Survey of Canada at Mission, Hope, and the Thompson River Confluence. These data were collated to estimate discharge at each study segment (Table 1).

River temperatures were collected by DFO's Fraser River Environmental Watch Program using Vemco data loggers (resolution = ± 0.1 °C and accuracy = ± 0.2 °C; Amirix Systems, Inc., Halifax, Nova Scotia) at Whonnock and Lillooet, and Unidata thermistor probes (resolution = ± 0.15 °C and accuracy = ± 0.2 °C; Unidata Pty, Ltd., Perth, Australia) at Qualark (Lauzier et al. 1995). These temperature monitoring stations were selected because they provide the most complete and accurate river temperatures that are encountered by migrating sockeye in the Fraser River mainstem, based on years of temperature collection data from many locations by DFO (Lauzier et al. 1995; Brown et al. 1998; Patterson et

al. 2007; Hague et al. 2008). Patterson et al. (2007) found that based on over 60 years of data, high-resolution Fraser river temperatures measured from the Qualark temperature station (Fig. 1, Table 1) were not different from temperatures measured at a series of locations throughout the lower Fraser River mainstem, while Brown et al. (1998) and Hague et al. (2008) found that river temperatures in the lower Fraser even correlate with temperature stations located upriver of Qualark and throughout much of the Fraser basin. These loggers are representative of temperatures encountered throughout the Fraser River mainstem owing to the thermal stability of this section of river, which has little input from tributaries and has a volume to surface area ratio that it is uniformly influenced by air temperature and solar radiation (Patterson et al. 2007). Fraser River temperature data collected from these monitoring stations have been used previously in numerous studies to assess the temperatures encountered by adult migrating salmon (e.g., Hanson et al. 2008).

Assessing thermal logger accuracy and precision

The accuracy and precision of the iButtons were tested under laboratory conditions. The sampling rate of the iButtons was set to 10 min intervals. iButtons were waterproofed with Plasti Dip and loosely placed in a fine-mesh net in a water bath. Water temperature was referenced to a YSI model 85 digital temperature probe (resolution = ± 0.1 °C and accuracy = ± 0.1 °C; YSI Inc., Yellow Springs, Ohio). The fine-mesh net allowed for water flow between the iButtons and the temperature probe. The water bath was incrementally adjusted across a range of temperatures between 15 and 21.5 °C, a range which was representative of the temperatures encountered by Fraser River sockeye salmon throughout the study. A total of 104 temperature observations were recorded per thermal logger. Linear regressions were used to assess the temperature deviation of individual iButton thermal loggers and the reference YSI temperature probe. Accuracy was calculated as the mean of the differences between iButton and YSI temperatures and precision was assessed based on their standard deviations (van Marken Lichtenbelt et al. 2006). For all of the 36 iButtons tested under laboratory conditions, the linear regressions between the thermal loggers and the YSI temperature probe were highly significant ($P < 0.001$, $R^2 > 0.973$). The mean iButton accuracy was 0.4 ± 0.3 °C and the mean precision was 0.2 ± 0.0 °C, which was more accurate than the values reported by the manufacturer. Because the calculated accuracy and precision was obtained from iButtons that had been waterproofed and placed in a water bath, we suggest that within the temperature range measured here, these ranges of values are representative of the resolution of the iButtons used in this study. Therefore, these values should be considered when assessing the accuracy and precision of the temperature deviation between body and river temperatures. Indeed, iButton thermal loggers have been used widely in studies of thermal biology on a range of animal taxa, including snakes (e.g., Row and Blouin-Demers 2006), turtles (e.g., Rollinson et al. 2008), and mammals (Warnecke et al. 2007).

Statistical analyses

Body temperature data were obtained from recovered thermal loggers ($N = 48$). Wilcoxon's sign-rank tests were used to test for differences between body temperature (T_B) and river temperature (T_R) at each study segment. Kruskal–Wallis tests followed by sequential Mann Whitney U post hoc tests (a Bonferroni correction of $\alpha = 0.003$ was applied to the post hoc tests) were performed to test for differences between body and river temperatures ($\Delta T = T_B - T_R$; °C) among the study segments. Because this approach is based on mean deviations, individual variation in thermal associations could be masked by averaging temperature values. We suggest that in this study, mean ΔT may actually be a more appropriate measure to test for broad identification of behavioural thermoregulation across a large spatial and temporal scale, as it measures the extent to which body temperatures differ from river temperatures during the entire migration through the lower Fraser River mainstem and indicates the temperature deviations most commonly encountered throughout this region across the migration period. Kruskal–Wallis tests were used to test for overall differences in ΔT with respect to date tagged. Wilcoxon's sign-rank tests were

used to test for differences between ΔT and tagging location (i.e., freshwater versus marine tagging sites). Wilcoxon's sign-rank tests were used to test for differences between ΔT at each study segment and sex. Linear regression analyses were used to test for differences in ΔT at each study segment with respect to body length (mean fork length = 60.9 cm, minimum fork length = 54.0 cm, maximum fork length = 70.0 cm).

To test for evidence of increased behavioural thermoregulation with increasing temperatures, a Wilcoxon's sign-rank test was used to compare the mean differences between the regression coefficients of body versus river temperature with a hypothetical slope of 1 across each study segment. The hypothetical slope of 1 would indicate a 1:1 relationship between body and river temperatures, where significant differences would provide evidence for temperature-dependent selection among individuals. For each study segment, linear regression analyses were performed separately to assess the relationship between (i) ΔT and river discharge and (ii) ΔT and migration speed. Kruskal–Wallis tests were used to assess temperature deviations by run-timing group (i.e., Fraser sockeye salmon are grouped into four broad categories for management purposes, based on migration timing, called early Stuart, early summer, summer, and late; Beacham et al. 2004). Kruskal–Wallis tests were used to assess temperature deviations by stock complex across each study segment for three focal stock complexes, for which appropriate sample sizes enabled statistical comparisons: Chilko (summer-run stock), Stellako (summer-run stock), and Adams (late-run stock). Statistical analyses were conducted using JMP version 7.0.1 (SAS Institute Inc. 2007). The level of significance (α) for single comparison tests was assessed at 0.05 (Zar 1999). For statistical tests with multiple comparisons, a Bonferroni correction of $\alpha = 0.008$ was applied (see Tables 2, 3, 4). All values presented are means \pm SD, unless otherwise noted.

Results

Figure 2 shows four examples of individual body temperatures in relation to river temperatures and telemetry receiver detection locations throughout the study region. These examples show that individuals made periodic, short-term (i.e., generally 1 h or less) associations with cooler water temperatures throughout the study region. In total, we found that 435 of 8012 (5.4%) body temperature observations were cooler than river temperatures by at least 1 °C. The reach that contained the most frequent negative deviations of at least 1 °C was segment A (260 of 1719; 15.1%), followed by segment F (52 of 888; 5.9%), segment E (94 of 2001; 4.7%), segment D (22 of 848; 2.6%), segment B (5 of 1230; 0.4%), and segment C (2 of 1238; 0.2%). Overall trends revealed that mean body temperatures were 18.3 ± 0.8 °C in segment A, 18.1 ± 0.7 °C in segment B, 18.1 ± 0.7 °C in segment C, 18.0 ± 0.7 °C in segment D, 17.5 ± 1.6 °C in segment E, and 17.4 ± 1.1 °C in segment F. Within each study segment, mean T_B was not significantly different from mean T_R (Wilcoxon's sign-rank tests, all $P > 0.604$). However, mean ΔT varied among the study segments (Kruskal–Wallis test, $\chi^2_{[5]} = 35.594$, $P < 0.001$; Fig. 3). An important finding was that mean ΔT was always

Table 2. Results of a Wilcoxon’s sign-rank test between the regression slope of river versus body temperature and a hypothetical slope of 1 for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*).

Study segment	<i>n</i>	Difference (mean ± SD) from hypothetical slope of 1	Test statistic	df	<i>P</i>
A	48	-0.986±0.784	-536.000	47	<0.001
B	43	-0.445±1.343	178.500	42	0.9881
C	44	-0.125±0.562	-113.000	43	0.0876
D	46	-0.136±0.749	-86.500	45	0.175
E	42	-0.066±1.370	63.500	41	0.791
F	21	-0.262±0.792	-67.500	20	0.03

Note: The value in boldface type denotes significant differences following a Bonferroni correction ($\alpha = 0.008$).

Table 3. Regressions of the mean difference between river temperatures and body temperatures (ΔT ; °C) with log-transformed river discharge (logRDischarge; $m^3 \cdot s^{-1}$) for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*).

Study segment	Regression equation	<i>R</i> ²	df	Sum of squares	<i>P</i>
A	$\Delta T = -4.252 + 1.140 \cdot \log RDischarge$	0.202	48	10.677	0.001
B	$\Delta T = -1.073 + 0.308 \cdot \log RDischarge$	0.018	42	7.145	0.391
C	$\Delta T = -1.369 + 0.368 \cdot \log RDischarge$	0.029	43	5.655	0.271
D	$\Delta T = -1.839 + 0.491 \cdot \log RDischarge$	0.026	45	9.411	0.286
E	$\Delta T = -1.819 + 0.435 \cdot \log RDischarge$	0.038	41	4.862	0.214
F	$\Delta T = 1.531 - 0.587 \cdot \log RDischarge$	0.019	20	4.699	0.549

Note: The value in boldface type denotes significant differences following a Bonferroni correction ($\alpha = 0.008$).

Fig. 2. Example thermal profiles of four individual adult sockeye salmon (*Oncorhynchus nerka*) displaying body and river temperatures and corresponding telemetry receiver detection locations throughout the study region within the Fraser River mainstem, British Columbia.

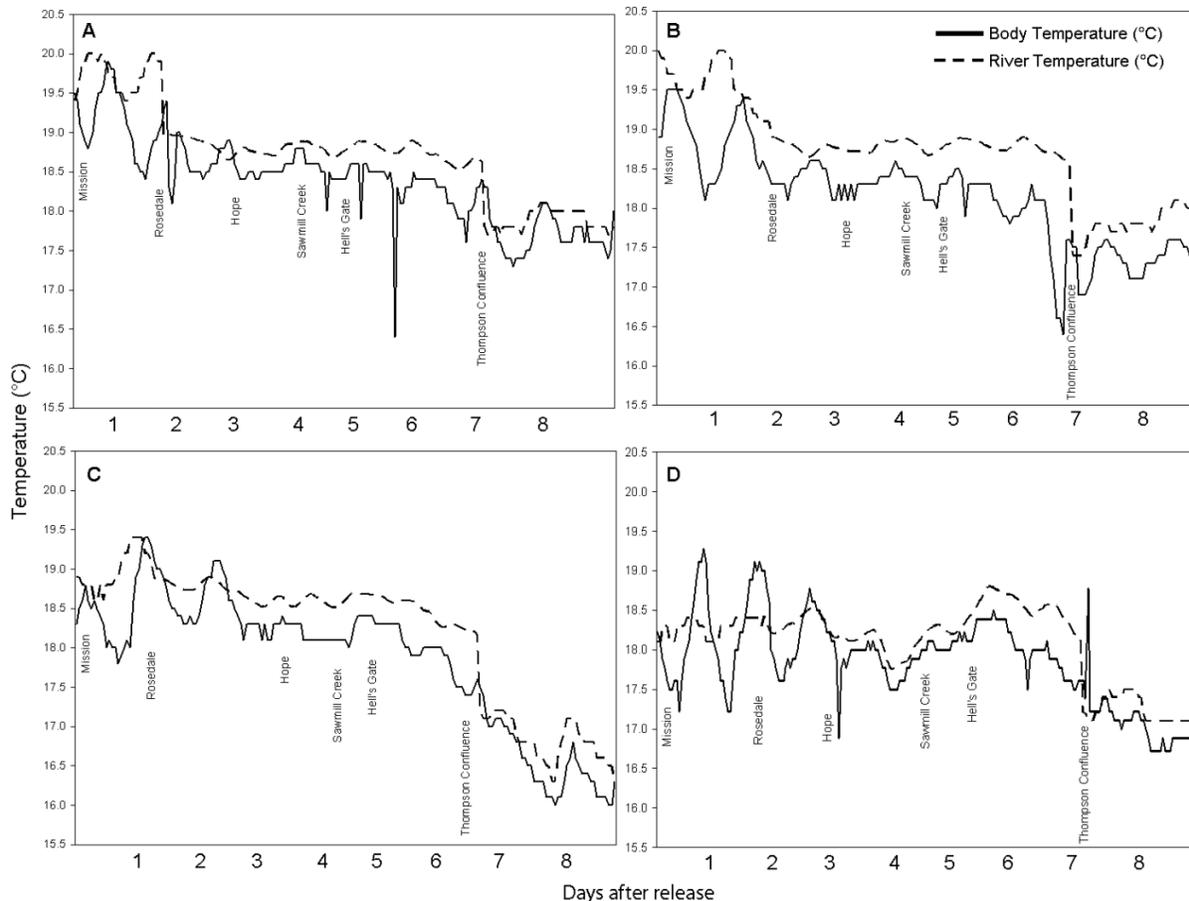


Fig. 3. Differences (mean \pm SD) between body temperatures and river temperatures ($^{\circ}\text{C}$) for adult Fraser River sockeye salmon (*Oncorhynchus nerka*) at each study segment in the Fraser River mainstem, British Columbia. Dissimilar letter groupings denote significant differences between segments (Kruskal–Wallis test followed by sequential Mann–Whitney U post hoc tests, where $\alpha = 0.003$).

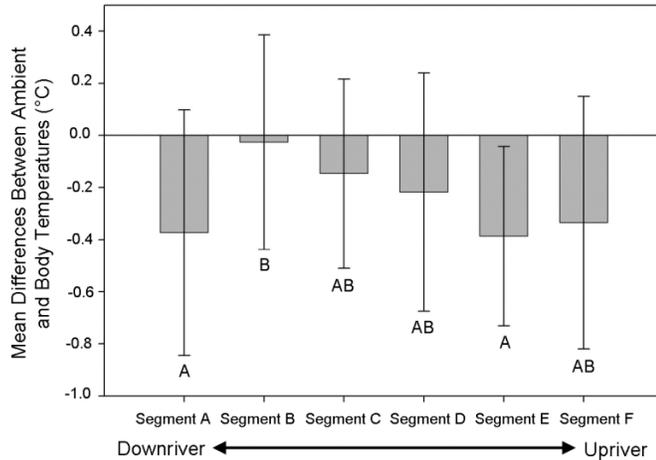


Fig. 4. Linear regression line of best fit between body and river temperatures (ΔT ; $^{\circ}\text{C}$) and river discharge ($\text{m}^3\cdot\text{s}^{-1}$) at segment A for adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in the Fraser River mainstem, British Columbia.

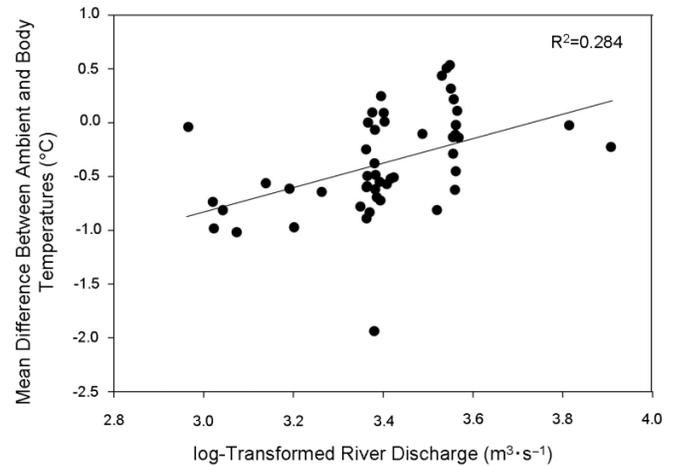


Table 4. Regressions of the mean difference (ΔT ; $^{\circ}\text{C}$) between river temperatures and body temperatures with migration speed (MSpeed; $\text{km}\cdot\text{day}^{-1}$) for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*).

Study segment	Regression equation	R^2	df	Sum of squares	P
A	$\Delta T = -0.120 - 0.194\cdot\text{MSpeed}$	0.014	48	10.677	0.427
B	$\Delta T = 0.277 - 0.225\cdot\text{MSpeed}$	0.015	42	7.145	0.431
C	$\Delta T = 0.094 - 0.201\cdot\text{MSpeed}$	0.022	43	5.587	0.346
D	$\Delta T = -0.199 - 0.025\cdot\text{MSpeed}$	0.001	45	9.410	0.935
E	$\Delta T = -0.691 + 0.245\cdot\text{MSpeed}$	0.088	41	4.862	0.056
F	$\Delta T = -1.083 + 0.519\cdot\text{MSpeed}$	0.080	20	4.699	0.215

negative, suggesting T_B remained consistently cooler than T_R , albeit by <0.5 $^{\circ}\text{C}$. The greatest mean difference in ΔT existed at segment E (Hell's Gate Canyon to Thompson Confluence; -0.39 ± 0.34 $^{\circ}\text{C}$). The least mean difference in ΔT occurred at segment B (Rosedale to Hope; -0.03 ± 0.41 $^{\circ}\text{C}$). Large standard deviations for mean ΔT were observed at each study segment (Fig. 3).

Mean travel time was 1.5 days through segment A, 1.2 days through segment B, 1.3 days through segment C, 0.8 days through segment D, 1.9 days through segment E, and 1.8 days through segment F. Although body and river temperatures were variable throughout the study period, we did not detect differences between tagging date and mean ΔT for segments B through F (Kruskal–Wallis tests, all $P > 0.05$). However, a significant relationship between tagging date and ΔT was observed at segment A (Mission to Rosedale; Kruskal–Wallis test, $\chi^2_{[8]} = 18.042$, $P = 0.006$), where ΔT was found to be increasingly negative throughout the tagging period, corresponding with increasing river temperatures. This result was corroborated by the finding that the mean differences between the slopes of body versus river temperature regressions and hypothetical slopes of 1 were significantly different for only segment A following a Bonferroni correction (Table 2). Similarly, for segment A only,

linear regression analysis yielded a significant positive relationship between ΔT ($^{\circ}\text{C}$) and river discharge ($\text{m}^3\cdot\text{s}^{-1}$; Table 3, Fig. 4). Linear regression analyses did not yield significant relationships between ΔT and migration speed for any of the study segments (Table 4).

The location where the individual was tagged (i.e., marine versus freshwater environment) did not have an effect on mean ΔT within each study segment of the river mainstem (Wilcoxon's sign-rank tests, $P > 0.05$). Mean ΔT within each study segment did not differ based on sex (22 males, 26 females; Wilcoxon's sign-rank tests, $P > 0.05$). We did not detect relationships between ΔT and body length within each study segment (linear regressions, $P > 0.05$). The four run-timing groups (i.e., early Stuart, early summer, summer, and late) did not differ in ΔT for any of the segments (Kruskal–Wallis tests, all $P > 0.05$). Similarly, there were no significant differences in study segment-specific temperature associations among three major stocks for which reasonable sample sizes were available (Chilko, Stellako, and Adams; Table 5).

Discussion

Mean T_B exceeded 18 $^{\circ}\text{C}$ in the lower study segments,

Table 5. Results of Kruskal–Wallis tests comparing the temperature deviation (ΔT ; °C) between the Chilko, Stellako, and Adams stock complexes for each study segment for adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*).

Study segment	Stock	<i>n</i>	Mean \pm SD	χ^2	df	<i>P</i>
A	Chilko	9	-0.6 \pm 0.6	5.947	24	0.797
	Stellako	7	-0.4 \pm 0.5			
	Adams	9	-0.4 \pm 0.5			
B	Chilko	7	0.0 \pm 0.3	3.487	21	0.789
	Stellako	7	0.0 \pm 0.5			
	Adams	8	-0.1 \pm 0.4			
C	Chilko	9	-0.2 \pm 0.3	2.849	23	0.797
	Stellako	7	-0.1 \pm 0.4			
	Adams	8	-0.2 \pm 0.4			
D	Chilko	11	-0.3 \pm 0.3	6.738	26	0.818
	Stellako	7	-0.4 \pm 0.8			
	Adams	9	-0.2 \pm 0.5			
E	Chilko	11	-0.5 \pm 0.1	1.829	25	0.196
	Stellako	7	-0.3 \pm 0.4			
	Adams	8	-0.6 \pm 0.2			
F	Chilko	9	-1.0 \pm 0.4	2.19	13	0.156
	Stellako	5	-1.2 \pm 1.0			

and body temperatures greater than 19 °C were commonly encountered, particularly in the lower Fraser (e.g., Fig. 2A). These temperatures exceed thermal optima for aerobic scope of known Fraser River sockeye stocks and approach the critical threshold of ~20 °C (Lee et al. 2003; Farrell et al. 2008). Our finding that ΔT was negative throughout the study area and that individuals displayed occasional, periodic temperature deviations (~5% of all detections) of at least -1 °C between body and river temperatures provide some evidence for the occurrence of limited behavioural thermoregulation throughout the study area. Previous studies, both in the Fraser watershed and other river systems, have found that salmonids will select for cool-water locations including tributaries and lakes en route to spawning grounds (Hodgson and Quinn 2002; Cooke and Hinch 2005; Newell and Quinn 2005; Clabough et al. 2006; Goniea et al. 2006; Pon et al. 2006). However, the extent of behavioural thermoregulation observed in the lower Fraser River mainstem is minimal relative to findings from salmon thermoregulation studies in other river systems, potentially linked with limited access to thermal refuge throughout the study area. In contrast, Yakima River Chinook salmon maintained a mean internal temperature that was 2.5 °C lower than river temperatures during their spawning migrations (Berman and Quinn 1991).

We found that while mean T_B was not significantly different from mean T_R within each study segment, ΔT differed significantly between study segments. In a similar study, Clabough et al. (2006) found that Snake River Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum in Ardeidi, 1792)) and steelhead (*Oncorhynchus mykiss* (Walbaum, 1792)) selected for lower than mean river temperatures during summer coldwater releases from the Dworshak reservoir. Yet, similar to the present study, the extent of behavioural thermoregulation varied considerably depending on location, which Clabough et al. 2006 speculated was linked with the availability of cool-water refuge. In the present study, within both segments A and E, mean ΔT were larger and more

negative relative to all other study segments (i.e., approximately -0.4 °C for both segments A and E). Segment A and segment E are the two locations within the study area that are known to contain vertically stratified waters, owing to depth and flow conditions (Lauzier et al. 1995). We found that segment A contained the most frequent occurrences of ΔT being cooler than or equal to -1.0 °C, where body temperatures were at least three times more commonly detected (~15% of detections) at these cooler deviations in segment A than in any other location in the study region. Also at segment A, our finding that the regression slope of the difference between T_B and T_R differed from a hypothetical 1:1 relationship suggests that individuals behaviourally compensated for higher temperatures in this segment, linked with increasing seasonal temperatures. Figure 2 exemplifies this trend, as Figs. 2A and 2B show that between Mission and Rosedale body temperatures are at their coolest when river temperatures peak. Taken together, these findings suggest that segment A offers a greater opportunity for behavioural thermoregulation than the other locations throughout the study area.

A deviation from the hypothetical 1:1 relationship was not apparent in any of the segments upriver from segment A (i.e., B through F). Segments B through F receive relatively low volumes of tributary input and have a sufficient volume to surface area ratio to resist the influence of local atmospheric parameters that would create large diurnal variation and vertical thermal stratification within the water column (Patterson et al. 2007). In segment E, behavioural compensation for increasing temperatures was not recorded, but mean ΔT was quite cool in this segment, consistent with evidence for thermal stratification in the upriver portion of this region (Lauzier et al. 1995). Interestingly, an area of difficult migration passage, known as Hell's Gate, is also included within this region (between segments D and E). Hell's Gate is a river constriction that is characterized by areas of increased water velocity and turbulent conditions, resulting in mostly homogeneous thermal conditions and a greater chal-

lenge for individuals to swim against the strong river flow to seek out any thermal refuge that might be available (Hinch et al. 2006). Previous Fraser River sockeye salmon studies have identified that relative to other segments of the Fraser River mainstem, Hell's Gate is energetically costly to navigate and, similar to the findings of this study, results in slower migration speeds (Hinch and Rand 1998; Hinch and Bratty 2000; Hanson et al. 2008).

River discharge had a positive linear relationship with increasingly positive ΔT in segment A only (Fig. 4). Higher river discharge causes more thermal mixing in the water column and less thermal stratification (Patterson et al. 2007). Increasing river discharge in segment A may have promoted greater amounts of mixing and reduced the amount of thermally stratified water that was available to migrants under lower flow conditions, resulting in ΔT becoming increasingly positive as flow increased. The finding that this relationship was not observed throughout the majority of the study area may be explained by the fact that segments B, C, and F are not known to be thermally stratified (Lauzier et al. 1995).

Although travel times varied considerably among many of the study segments, no relationship between body temperature and travel times was observed. This result indicates that individuals did not delay for prolonged periods of time in cool-water regions to incur a thermal benefit. Delayed migration associated with holding in cool-water locations has been observed in the Columbia River, where cool-water tributary use has been found to increase exponentially with increasing water temperatures (Hyatt et al. 2003; Goniea et al. 2006). Although our telemetry receiver layout provided excellent spatial coverage, we were unable to determine the extent to which individuals used cool-water locations within a given reach. Instead we infer from individual temperature records and the minimal deviation between river and body temperatures in most study segments that there is occasional, short-term (i.e., ~1 h), periodic holding behaviours (e.g., Fig. 2); however, these transient associations did not influence migration rates. Further study is required to determine if migration behaviour within the Fraser mainstem changes during abnormally high temperature years so that individuals spend more time using cool-water locations (i.e., tributary outflows) for either longer durations or more frequent associations. In an abnormally high temperature year, there was evidence for selection of cool-water refuge conferring a survival benefit for Fraser River sockeye that reside in thermally stratified Harrison Lake, relative to those that hold in the warmer Harrison River, which is a tributary of the Fraser River (Mathes 2009).

With the growing body of evidence that high temperature exposure during the freshwater component of the sockeye salmon spawning migration contributes to mortality, it is necessary to understand how individuals respond to elevated water temperatures (Hinch et al. 2006; Crossin et al. 2008). This is particularly warranted because Fraser sockeye are expected to encounter peak summer river temperatures that exceed current mean values by up to 4 °C in the coming decades (Morrison et al. 2002; Rand et al. 2006). While mean ΔT in certain segments were only approximately -0.5 °C, and 5% of the deviations between body and ambient temperatures were less than or equal to -1 °C, these

slight mean deviations between body and ambient temperatures are given greater importance because mean temperatures observed in this study (~18 °C) are likely above the optimal temperature (T_{opt}) for the aerobic scope of these fish and the narrow thermal window between the T_{opt} and the critical temperature (T_{crit} equals an aerobic scope of zero) is typically 5–6 °C (Lee et al. 2003; Farrell et al. 2008). This means that even a 1 °C behavioural shift in body temperature represents a large relative shift away from T_{crit} . This narrow thermal window for sockeye salmon will become increasingly concerning with warming temperatures (Pörtner and Farrell 2008) and warrants further study.

The results of this study indicate that behavioural thermoregulation in the lower Fraser River mainstem by adult upriver-migrating sockeye is relatively limited, although our results demonstrate that important periodic exposures to cool temperatures do occur. Combining these results with the evidence that prolonged high temperature exposure leads to magnified mortality, under both experimental (Crossin et al. 2008) and field (Farrell et al. 2008) conditions, suggests that high mortality rates can be expected for Fraser sockeye unless they are able to behaviourally adapt during high temperature years by using the cool-water refuges that occur in the Fraser River system (e.g., deep, thermally stratified lakes; Mathes 2009). Future research must examine not only how individuals associate with river temperatures in a high temperature year, but also how individuals use available thermal refugia in tributaries and lakes (e.g., Harrison Lake) in the upper Fraser watershed to understand the extent to which individuals compensate for prolonged exposure to the high temperatures that they encounter in the Fraser mainstem. Improved knowledge of the interactions between environmental conditions and migration success is of paramount importance to improving our understanding of the basic migration biology of Pacific salmonids and can be used to further enhance robust management initiatives for the commercial, recreational, and First Nations fisheries that operate in the Fraser River watershed.

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