Effect of water temperature, timing, physiological condition, and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*)

M. Todd Mathes, Scott G. Hinch, Steven J. Cooke, Glenn T. Crossin, David A. Patterson, Andrew G. Lotto, and Anthony P. Farrell

Abstract: We coupled physiological biopsy and positional telemetry to examine survival to reach spawning grounds in relation to water temperature, timing, physiological condition, and holding location (river or lake) in adult migrating sockeye salmon (*Oncorhynchus nerka*). We tracked 83 fish across a large temperature range (13.5–21.5 °C), which included record highs. Only early-timed migrants that held in Harrison Lake survived to reach spawning grounds (16%, or $n = 4$). Normal-timed fish, those that migrated at historically observed times, survived at higher levels if they held in Harrison River (72%, or $n = 18$). Mortalities were identified on the bottoms of both the lake and river. Hypothetical degree-day (DD) accumulation revealed that early-timed river fish would have greatly surpassed (~800 °C DD) a critical disease threshold value (~500 °C DD). There was no difference in hypothetical DD accumulation between normal-timed river fish and early-timed lake fish. Early-timed sockeye had elevated physiological stress (e.g., plasma lactate, glucose, and hematocrit), which may have contributed to high levels of mortality. By using lakes as thermal refugia, early-timed fish likely reduce rates of disease development and may better recover from physiological stress associated with high encountered temperatures.

Résumé : Nous avons combiné des biopsies physiologiques et de la télémétrie de position afin d'étudier la survie jusqu'aux frayères en fonction de la température de l'eau, du calendrier, de la condition physiologique et du lieu de retenue (rivière ou lac) chez des saumons rouges (*Oncorhynchus nerka*) adultes en migration. Nous avons suivi 83 poissons sur une gamme étendue de températures (13,5–21,5 °C) qui comprenait des températures exceptionnellement élevées. Seuls les migrateurs à calendrier précoce qui se sont arrêtés dans le lac Harrison ont survécu jusqu'à leur arrivée sur les frayères (16 %, ou $n = 4$). Les poissons à calendrier normal, qui ont migré aux périodes observées dans le passé, ont eu un taux de survie plus élevé s'ils s'étaient arrêtés dans la rivière Harrison (72 %, ou $n = 18$). Des mortalités ont été observées sur le fond du lac et de la rivière. Une accumulation hypothétique de degrés-jours (DD) montre que les poissons de rivière à calendrier précoce auraient largement dépassé (~800 °C DD) le seuil critique de morbidité (~500 °C DD). Il n'y a pas de différence dans l'accumulation hypothétique de DD entre les poissons de rivière à calendrier normal et les poissons de lac à calendrier précoce. Les poissons à calendrier précoce ont un stress physiologique accru (par ex., le lactate plasmatique, le glucose et l'hématocrite), ce qui peut avoir contribué aux taux élevés de mortalité. En utilisant les lacs comme refuges thermiques, les poissons à calendrier précoce réduisent vraisemblablement leur taux de développement de maladies et peuvent récupérer plus facilement du stress physiologique associé aux températures élevées qu'ils rencontrent.

[Traduit par la Rédaction]

M.T. Mathes, G.T. Crossin, and A.G. Lotto. Centre for Applied Conservation Research and Department of Forest Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
S.G. Hinch.[1] Department of Forest Sciences and Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
S.J. Cooke. Fish Ecology and Conservation Physiology Laboratory, Ottawa–Carleton Institute for Biology, Carleton University, Ottawa, ON K1S 5B6, Canada.
D.A. Patterson. Fisheries and Oceans Canada, Science Branch, Pacific Region, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
A.P. Farrell. Department of Zoology and Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

[1]Corresponding author (e-mail: scott.hinch@ubc.ca).

Introduction

Migratory Pacific salmon (*Oncorhynchus* spp.) returning to their natal freshwater spawning grounds initiate freshwater entry when river discharge and temperature are most favourable, matching long-term average environmental conditions (Keefer et al. 2004; Hinch et al. 2006; Farrell et al. 2008). Temperature is the most important environmental factor governing fish because of its underlying effect on physiological, ecological, and behavioural aspects of life history (Fry 1971). To link fitness to changes in a fish's thermal environment has always proven difficult. However, for adult migrating Pacific salmon, which have only one lifetime opportunity to spawn, unsuccessful river migration ultimately represents zero lifetime fitness. Unsuccessful migration could be a result of many high-temperature-mediated factors (Quinn et al. 1997; Hodgson and Quinn 2002), such as the collapse of aerobic scope (Farrell 2002; Farrell et al. 2008), which refers to the reduction of oxygen available for activities between basal and maximal metabolic rates (Fry 1971). Other temperature-mediated factors include depletion of energy stores (Hinch and Rand 1998), poor recovery from stress and strenuous exercise (Macdonald et al. 2000), and increased susceptibility to disease and parasites (Gilhousen 1990).

Some of the best-documented effects of the mechanisms of how high temperatures influence salmon migrations come from laboratory and field studies on Fraser River sockeye salmon (*Oncorhynchus nerka*) (reviewed in Hinch et al. 2006). Biopsy telemetry (i.e., the coupling of physiological sampling with positional telemetry; approach reviewed in Cooke et al. (2008)) has revealed that Fraser River sockeye, which encounter higher than normal temperatures and perish during migrations, are characterized as having impaired ionoregulatory systems, advanced senescence, and symptoms of physiological stress (Cooke et al. 2006a; Young et al. 2006). Infection and disease have also been implicated has a major cause of migration mortality. For example, the bacterium *Flexibacter* spp. is more virulent at high temperature and can cause severe gill damage in migrating Fraser River sockeye (Gilhousen 1990). Also, a kidney parasite (*Parvicapsula minibicornis*) develops faster at warm temperature and its development in Fraser sockeye is associated with reduced laboratory swimming performance (Wagner et al. 2005) and migration mortality (Crossin et al. 2008) when degree-day (DD) accumulation is ~500 °C.

Most stocks of Pacific salmon now encounter warmer rivers during their spawning migration than in any time since records have been kept. Temperatures experienced by migratory salmon in summer have increased in recent years corresponding to decreases in river discharge (Quinn et al. 1997; Patterson et al. 2007). The Fraser River has experienced a >1.8 °C increase in average peak summer water temperature over the past 40 years with eight of the past 10 summers being the warmest on record (Patterson et al. 2007). Similarly, sockeye in the Columbia basin now migrate through waters that are ~2.5 °C above historical (Quinn and Adams 1996). Considering the negative effects of encountering high river temperatures, the timing of starting upriver migrations by adult salmon should be strongly influenced by the freshwater thermal environment. Indeed, many salmon populations may be attempting to avoid peak migration temperatures, which are now much warmer than ever before. This may be an explanation for why Columbia River sockeye (Quinn and Adams 1996; Quinn et al. 1997) and east coast Atlantic salmon (*Salmo salar*) (Juanes et al. 2004) are entering freshwater earlier than historically noted and why Columbia River summer steelhead (*Oncorhynchus mykiss*) are entering later (Robards and Quinn 2002).

The seeking of cool-water refugia after initiating upriver spawning migrations is another form of behavioural thermoregulation exhibited by Pacific salmon (Hyatt et al. 2003). Sockeye salmon, Chinook salmon (*Oncorhynchus tshawytscha*), and summer steelhead runs in the Columbia River system may be utilizing cold-water tributaries en route to spawning areas, thus slowing or temporarily stopping upriver migration (Hodgson and Quinn 2002; Goniea et al. 2006; High et al. 2006). But in some cases, Chinook entering the Columbia early migrate faster, presumably as an alternative means to minimize exposure to high temperatures (Chapman et al. 1995). Populations of sockeye that normally migrate through lakes en route to spawning streams do so through the hypolimnion presumably to take advantage of colder water (Newell and Quinn 2005; Pon et al. 2007).

The Late-run stock complex, which is composed of dozens of stocks, comprises the majority of adult sockeye in some years in the Fraser River. These fish, which normally begin their river migrations in early fall (and hence in "Late" summer), are initiating river migrations significantly earlier for reasons not fully understood although potentially related to changes in ocean conditions (Cooke et al. 2006a). Specifically, since 1994, large segments of the Late-runs have been entering the Fraser River 2–6 weeks ahead of historical average dates instead of milling in the adjacent estuary, which was their typical, "normal" behaviour (Lapointe et al. 2002). Historically, migration mortality rarely exceeded 20% but now generally exceeds 60% and in some years 90% (Cooke et al. 2004). These early-migrating Late-run fish are now encountering peak summer temperatures that are several degrees warmer than historically encountered, and because spawning times have not changed, they are spending considerably longer times in these environments. It is quite likely that these changes have a direct influence on physiological condition of fish and hence on their migration survival (e.g., Young et al. 2006), but there have been few investigations of how Late-runs may attempt to reduce the impacts of high temperatures through behavioural thermoregulation. Many Late-run stocks either transit through or can reside in deep portions of lakes that are adjacent to spawning areas, and it is possible that by utilizing thermal refugia, early migrants can slow deleterious physiological changes and increase the likelihood of reaching spawning grounds.

Farrell et al. (2008) synthesized swim tunnel respirometry data and historical river temperature patterns to suggest that population-specific swimming performance in salmon is adaptive and that the collapse of population-specific metabolic scope is responsible for migration mortality under extremely high temperatures. They tested a conceptual model using some preliminary results from a tagging and telemetry study conducted on Weaver Creek sockeye, a lower Fraser River Late-run stock. Fish were tracked across a large tem-

perature range (13.5–21.6 °C) and across a broad range of river entry times (mid-August to the end of September). They also focused their analysis only on the "early-timed" segment of the migration (i.e., August migrants) and concluded that the high mortality (90%–100%) was caused by the collapse of aerobic scope. The few early-timed fish that survived to reach spawning grounds spent some time in a nearby lake after their high temperature exposure, leading the authors to conclude that thermal refugia were an important survival factor. However, the authors did not examine survival relationships for "normal-timed" migrants in terms of thermal refugia nor did they consider for any of the migrants mechanisms of mortality other than collapse of metabolic scope.

The present study reports on the complete telemetry data set preliminarily described in Farrell et al. (2008) for adult Weaver Creek sockeye. Moreover, we additionally use nondestructive biopsy and DD assessments to investigate linkages between survival, physiology, and thermal experience. We investigate three broad hypotheses. First is to assess how river migration timing and lake utilization influence migration success. Farrell et al. (2008) found that early-timed migrants that adopted a lake component to their migration had better survival than those that did not. We expect that normal-timed migrants (meaning those fish within the stock that migrate during the historical mean dates) will not receive the same survival benefits by residing in a lake because river temperatures are sufficiently cool for this group of fish. Second is to examine thermal indicators of disease development and relate these to survival. We predict that migrants that accumulate >500 °C DD, a known threshold for *P. minibicornis* expression, will be more likely to perish before reaching spawning grounds. Third is to examine the physiological state of migrants at time of capture and assess differences between timing and fate groups. We predict that early-timed migrants will have elevated stress levels and be more reproductively mature, characteristics that may put early fish at a greater risk of migration mortality.

Materials and methods

Study animals and area

This study was conducted in 2004 and focused on Weaver Creek sockeye, a large Fraser River stock that is part of the Late-run stock complex. Weaver Creek sockeye spawn naturally in Weaver Creek and in an artificial spawning channel. Fish arriving at Weaver Creek must pass through Morris Lake (8 ha, mean depth 4 m, maximum depth 12 m) after moving through Morris Slough, which feeds into the Harrison River 11 km upriver of the confluence with the Fraser River (Fig. 1). The Harrison River is relatively wide (2–3 km in some sections), shallow (much of the river is <2 m deep with a thalwag ~7 m maximum depth), and short (16.5 km total length). In 2004, ~126 000 Weaver Creek sockeye migrated past the hydroacoustic counting facility in the lower Fraser River near Mission, British Columbia (M. Lapointe, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada, personal communication (2006)) en route to spawning grounds (Fig. 1). Historically, river migrations began in late September, but in recent years, they have begun as early as mid-August (see

Cooke et al. 2004). Spawning usually begins in early October, but rarely before then owing to low water levels in Weaver Creek, Morris Lake, and Morris Slough. A limited water supply feeds the spawning channel, so it is not normally in operation until early October. Peak spawning occurs between 15 and 25 October (R. Stitt, Fisheries and Oceans Canada, 16250 Morris Valley Road, Agassiz, BC V0M 1A1, Canada, personal communication (2004)). Migrants that arrive at Harrison River prior to early October must therefore reside in either Harrison River or the nearby Harrison Lake (Fig. 1), which is large (surface area 220 km^2), deep (mean depth 150 m), and oligotrophic (Shortreed et al. 2001). As emergent fry, Weaver Creek sockeye migrate downstream into the Harrison River and then upstream into Harrison Lake where they rear for 1 year (Pon et al. 2007). Therefore, their early life history utilizes and likely imprints this lake.

Fish capture, biopsy, and tagging

Fishing occurred on 9 separate days between 18 August and 29 September 2004, a period that spanned a large range of freshwater entry times and temperatures (Table 1). Based on historical run-timing information (Cooke et al. 2004), we classified fish as "early-timed" if captured on or prior to 2 September and "normal-timed" if on or after 13 September. Immediately after capture, fish were held for <3 days at a local hatchery while stock identification occurred. Capture, biopsy, and release occurred at a site on the Harrison River located 10 km upstream of the confluence of the Fraser and Harrison rivers (Fig. 1) 1 km downstream of Weaver Creek. Details on sockeye capture, holding, release, and stock identification are provided in Farrell et al. (2008).

Details on our biopsy and tag insertion procedures have been reported in several recent papers (Cooke et al. 2005, 2006b, 2008). Briefly, a blood sample was taken via caudal puncture using a syringe (1.5 in., 21 gauge) and vacutainer (3 mL). Linesman pliers were used to remove 0.03 g of gill filament tips for enzyme assays. Fork length was measured. Sex was visually determined using external secondary sexual characteristics. A microwave energy meter was used to assess gross somatic energy (GSE) levels following the equations in Crossin and Hinch (2005). Blood samples were immediately processed to quantify hematocrit (Hct) and isolate plasma by centrifugation. Plasma and gill samples were stored on dry ice in the field and transferred to a –80 °C freezer upon return to the laboratory.

Transmitters were inserted through the mouth into the stomach using a plastic tag applicator (Cooke et al. 2005). Tagging and biopsy procedures were rapid (~2 min) and did not involve anesthesia. These approaches have been used extensively (reviewed in Cooke et al. 2008) and have been shown to have no detrimental effects on sockeye salmon migration rates or survival (Cooke et al. 2005, 2006a). Approaches were approved by the University of British Columbia Animal Care Committee. Biopsy samples were also obtained from additional fish that were collected on the same dates and net sets but that were sacrificed at time of capture (*n* = 84). These results will increase sample size and help in evaluating baseline physiology because they were sampled from holding pens before those to be tagged. Therefore, sacrificed fish had the shortest handling times.

Fig. 1. Map of the lower Fraser and Harrison rivers and Weaver Creek spawning area with an inset map of Canada showing the study area (box) within British Columbia (shaded). Locations of relevant cities, acoustic and radio receivers, and temperature data loggers are indicated. The capture and release site is indicated by a star.
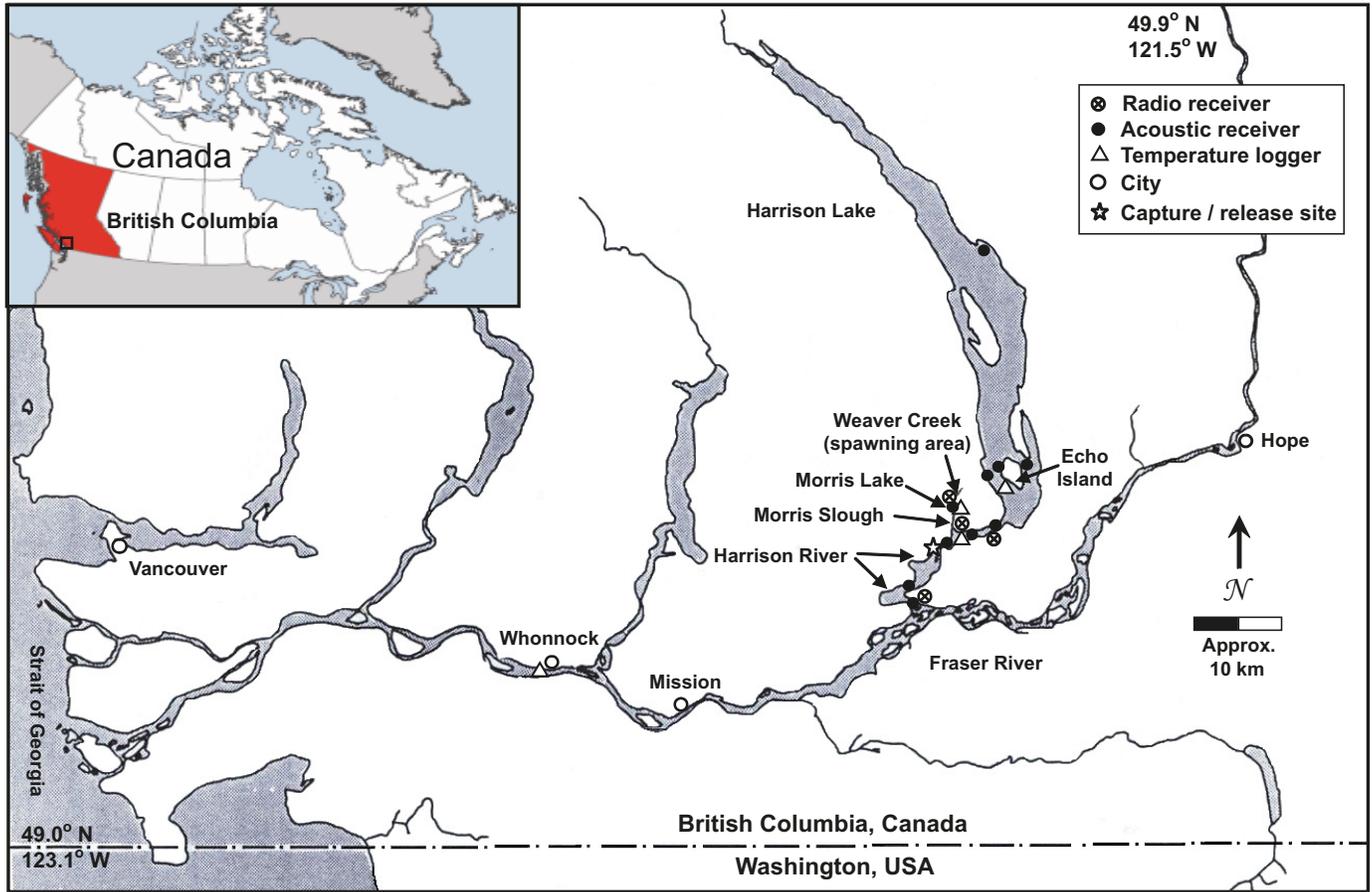
Table 1. Temperatures encountered (range and means) by Weaver Creek sockeye salmon (*Oncorhynchus nerka*) during their upriver migration in the Fraser River in relation to capture date at the tagging site on the Harrison River.

Temperature range (°C)	Mean thermal experience (°C)	Capture date	Survival (%)	n
21.2–21.3	21.3	19 August 2004	nap	0
20.0–21.6	20.8	24 August 2004	0	5
19.6–21.1	20.3	25 August 2004	0	3
18.1–18.2	18.1	30 August 2004	14.3	28
18.2–18.6	18.1	31 August 2004	0	2
18.0–18.6	18.4	2 September 2004	0	7
16.3–15.3	15.9	13 September 2004	28.6	7
13.9–14.2	14.0	20 September 2004	50	18
13.7–14.1	14.0	29 September 2004	77	13

Note: Survival percentage is based on fish successfully reaching the spawning area after release. Data were adapted from Farrell et al. (2008). We categorized fish into "early-timed" migrants if captured prior to 2 September and "normal-timed" migrants if captured after 13 September. nap, not applicable.

Telemetry

We examined the migrations of Weaver Creek sockeye throughout the Harrison River and in portions of Harrison Lake using both radio and acoustic telemetry systems. Some details are provided in Farrell et al. (2008) with extensive details in Mathes (2009). In brief, the radio transmitters were 16 mm in diameter, 46 mm long, and 16.1 g mass in air with a 460 mm long antenna (model MCFT-3A; Lotek Wireless Inc., Newmarket, Ontario). Four fixed-location radio receivers (SRX400 or SRX400A; Lotek Wireless Inc.) with up to three 3- or 4-element Yagi antennae (Max Inc., Hanover Park, Illinois; Grant Systems Engineering Inc.,

Fig. 2. Mean daily water temperatures (2004) for the Fraser and Harrison rivers and Harrison Lake at four different depths.
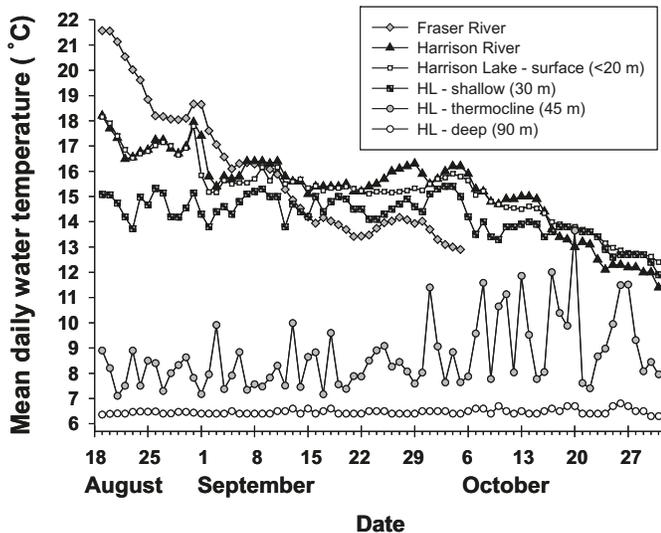
King City, Ontario) per receiver were deployed (Fig. 1). Acoustic transmitters were 16 mm in diameter, 70 mm long, and 25 g mass in air and transmitted depth information up to 340 m (model V-16P; Vemco, Shad Bay, Nova Scotia). Ten fixed-station acoustic receivers (model VR-2; Vemco) were deployed (Fig. 1).

Data were also collected by mobile tracking to confirm fish arrival at spawning grounds and to locate positions of fish that died within the lake or river. Fish that were detected at spawning grounds were classified as "successful", while those not detected were classified as "unsuccessful". Mobile tracking occurred weekly by foot and boat from 30 August to 10 November for fish with radio transmitters using an SRX-400 receiver (Lotek Wireless Inc.) and a handheld 3-element Yagi antenna (AF Antronics Inc., Urbana, Illinois) and from 29 September to 10 November for fish with acoustic transmitters using a VR-60 receiver (Vemco) and an omnidirectional hydrophone. For fish carrying acoustic transmitters, their locations were stored as waypoints using a Global Positioning System receiver and the coordinates were plotted on a navigational chart with depth. Due to the nature of the Harrison River bed, which is a tangle of logs, branches, and other woody debris, dead fish pile up in the snags and are not generally swept downriver until many days later when the fish have decayed, bloated, and floated upwards from the tangle. Individuals that were detected on three separate days at one location at the same depth on the bottom of the river or lake were thus considered to be "confirmed" mortalities. For all of these fish, these positions were often held for an additional 1–2 weeks after the initial assessment before finally being dislodged from their positions and swept away. These assessments could not be made for radio-tagged fish because they could not be accurately located while in the lake. There was no fishery in our area during our study and we have never observed tag expulsion with our tagging approach on adult sockeye.

Temperature data and DD calculations

Several temperature loggers were deployed within the

Harrison System, five in Harrison Lake, one in Harrison River, and one in Weaver Creek, each collecting data once per hour from 18 August to 10 November. The temperature loggers deployed in the river were fixed ~5 m depths. At each lake location, loggers were affixed to a moored float line and positioned at 20, 30, 45, and 90 m intervals. In the lower Fraser River, water temperatures were obtained from a Fisheries and Oceans Canada recording station located 60 km downstream at Whonnock, British Columbia (D.A. Patterson, unpublished data) (Fig. 1).

By summing the DDs experienced by an individual fish for its time spent migrating in the Fraser River, during holding, and after release, we calculated a variable termed "actual" DD accumulation. This could only be assessed for fish carrying acoustic transmitters as they obtained information on depth. Time spent in the Fraser River was estimated using historical migration rates for given river entry dates for Weaver sockeye from the river mouth to our capture location as assessed by acoustic telemetry in 2003 (Crossin et al. 2007). Thus, using 2003 travel rates and 2004 temperatures (Fig. 2), we were able to estimate the thermal experiences of sockeye prior to their capture. We also measured thermal experience during their brief holding period in captivity. After release, fish were tracked and temperatures of subsequent river or lake residency locations were assessed. Fish either remained within the river, termed "river" residents, or entered Harrison Lake, termed "lake" residents.

For lake residents, mean fish depths per hour were calculated as well as percent time at a particular depth stratum. Fish depths were then compared with temperature data collected from loggers deployed in the lake. The thermal experience of lake residents that migrated back to the river en route to spawning grounds was also included. We stopped accumulating actual DDs if a fish was a "confirmed" mortality and it died prior to reaching spawning grounds. We did not calculate actual DDs for fish that did not reach spawning grounds if they were classified as "unsuccessful" because we could not be certain of their thermal experience.

We estimated a "hypothetical" DD accumulation for all individuals regardless of transmitter type. This value was an estimate of the total DD exposure for the entire freshwater phase of a fish's migration from the Fraser River estuary to spawning grounds. To do this, we assumed a terminal date of 15 October for all fish except for those that had perished before this date. 15 October is near the historical peak spawning time for Weaver sockeye (Crossin et al. 2004). The calculation involved adding the DDs accumulated for each fish during its migration through the lower Fraser River (early timed fish = 4 day migration, normal timed fish = 6 day migration prior to capture on the Harrison River; see Crossin et al. 2007) to the DDs accrued after capture and release on the Harrison River (estimated from telemetry and associated river and lake temperatures). In a related analysis, Farrell et al. (2008) estimated that the lake-resident sockeye were spending on average ~80% of the time at depths below 50 m and 20% of their time at shallower depths. Therefore, based on thermal data from Harrison Lake (Fig. 2), we ascribed 80% of an individual's time at 6.5 °C and 20% of its time at 14.5 °C.

During August and early September, Fraser River water temperatures were ~2–4 °C above the 60-year average and

reached record high levels (i.e., exceeded 21.0 °C; Patterson et al. 2007) for the early-timed component of the migration (18.0–21.6 °C) (Fig. 2). Temperatures fell to more historically typical levels (Patterson et al. 2007) when the normal-timed migrants entered the Fraser River (15.0–16.3 °C) (Fig. 2). In late August, Harrison River water temperatures were also warm (16.5–18.0 °C) for the early component of the migration, whereas normal-timed fish experienced cooler temperatures that were similar to those that they had just experienced in the Fraser River (Fig. 2). Within Harrison Lake, surface temperatures closely resembled Harrison River temperatures at the start of our observations (~18 °C) and fell during September to 16 °C (Fig. 2). Water temperatures in the shallow regions of the lake (20–40 m) averaged 14.5 °C. Harrison Lake is stratified during the summer, and the thermocline was at ~45 m. The thermocline weakened in late October. In the deep regions of Harrison Lake (>50 m), the temperature throughout the study was 6.5 °C (Fig. 2).

Laboratory assays

Plasma osmolality, potassium (K^+), chloride (Cl^-), and sodium (Na^+) and concentrations of lactate and glucose were determined with protocols described by Farrell et al. (2001). These measures provide indexes of fish stress and ionoregulatory and osmoregulatory state. Gill tissue Na^+,K^+-ATPase activity, a measure of osmoregulatory preparedness, was determined with a kinetic assay and is expressed as micromoles of ADP per milligram of protein per hour (McCormick 1993). Plasma testosterone (T) and 17β-estradiol (E_2) levels were measured by radioimmunoassay (McMaster et al. 1992) and are used to assess gender as well as level of reproductive readiness.

Statistical analyses

All analyses were conducted using STATGRAPHICS Plus 5.1 (StatPoint, Inc., Herndon, Virginia) and assessed for significance at $\alpha = 0.05$. To meet statistical normality and homogeneity of variance requirements, several physiological variables were transformed, although nontransformed values are presented in the tables and figures. GSE and plasma K^+ were log_{10} transformed, Cl^- was squared, and the square root of lactate was used for analyses. Initially, one-way analyses of variance (ANOVAs) were used to determine if there were any physiological differences between fallbacks and fish that continued upstream. A series of two-way ANOVAs on transformed data were used to assess physiological differences in fish based on sex and timing group as well as sex and fate. Data from sockeye that were sacrificed in conjunction with the tagging process were analyzed by using two-way ANOVAs to examine differences in physiological, energetic, and sex hormone levels. To analyze data from sacrificed fish, several variables required transformation. Specifically, GSE and gill Na^+,K^+-ATPase values were log_{10} transformed and osmolality, Cl^-, and Na^+ were squared transformed. Bonferroni corrections were applied for the multiple comparisons involving the physiological variables. Two-way ANOVA was used to examine differences in estimates of hypothetical DD accumulation between fish fate and migration timing. A one-way ANOVA was used to test for differences in fish length between normal- and early-timed groups. Contingency table analyses (χ^2 or Fisher's exact

Table 2. Percentage of Weaver Creek sockeye salmon (*Oncorhynchus nerka*) classified by timing group and fate, timing group and residence location, and timing group and survival relative to residence location.

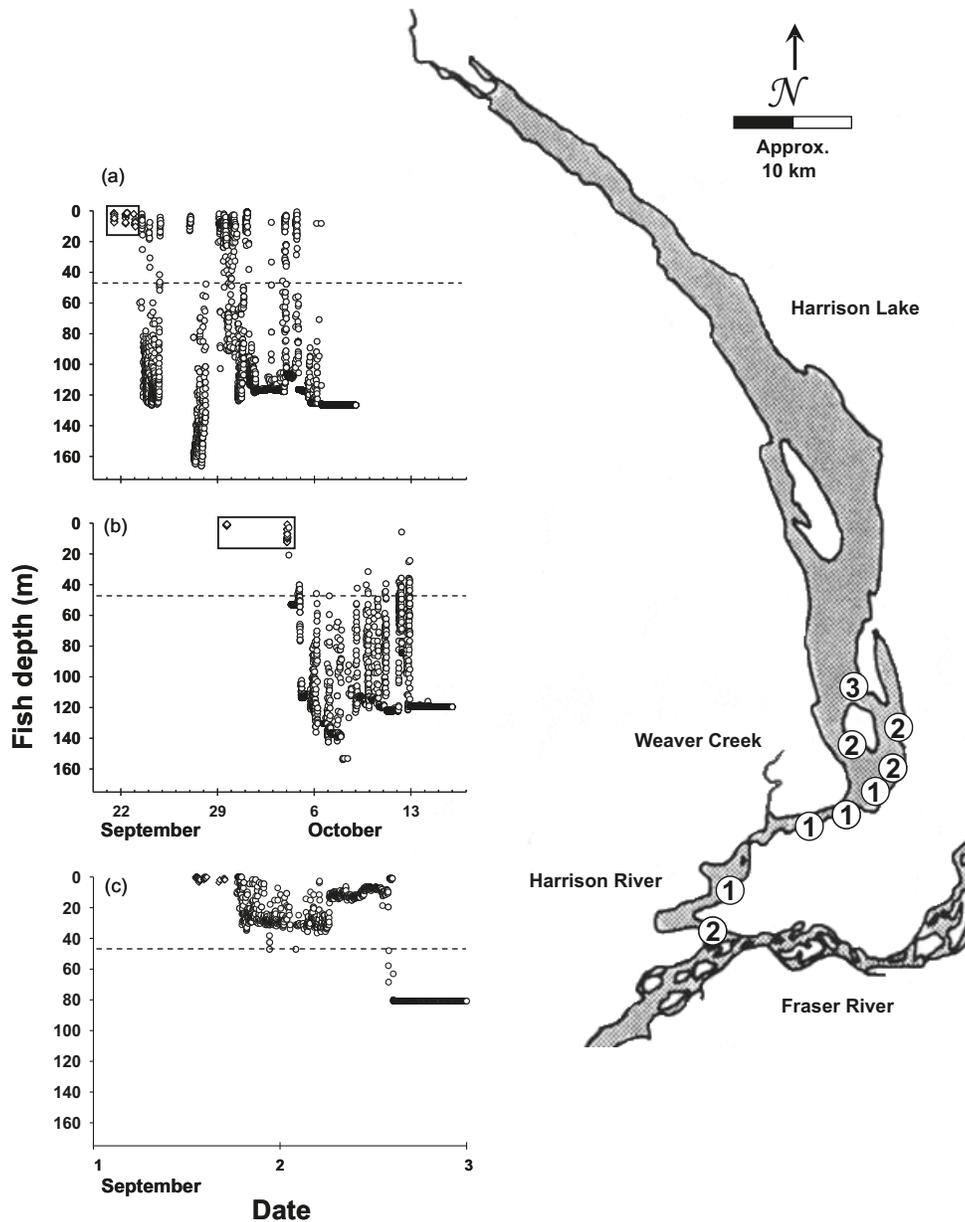|	Early	Normal
Fate (*n* = 83)		
Successful	5.3 (4)	25.3 (21)
Unsuccessful	49.4 (41)	20.5 (17)
Residence location (*n* = 83)		
River	19.3 (16)	28.9 (24)
Lake	34.9 (29)	16.9 (14)
Survival relative to residence (*n* = 25)		
River	0.0 (0)	72.0 (18)
Lake	16.0 (4)	12.0 (3)

Note: Fish detected at Weaver Creek (radio) or Morris Lake (acoustic) were classified as successful migrants. Migrants that entered Harrison Lake were classified as lake residence; all others were classified as river residence. Sample sizes are given in parentheses. Early-timed unsuccessful migrants includes eight fish that were classified as "fallbacks".

test) were conducted to determine if there were relationships between proportions of fish in particular timing and fate groups.

Results

Approximately 140 sockeye salmon were captured over nine sampling periods of which 84 were determined to be Weaver Creek sockeye (Table 1). No fish were captured on the first sample date. We released 40 sockeye with acoustic transmitters and 44 with radio transmitters. One acoustic transmitter failed and data for this fish were not used. Radio and acoustic transmitter carrying fish were pooled for all analyses unless otherwise stated. Of 83 fish, 53% (*n* = 45) were classified as early-timed and 47% (*n* = 38) as normal-timed. We found no differences in fish length between early-timed and normal-timed groups (*P* = 0.1775). There was a significant relationship between timing and fate (χ^2 statistic = 21.05, *P* < 0.0001). Approximately 5% of all fish were early-timed and successful at reaching spawning grounds, whereas success was five times higher when fish entered later and were normal-timed (Table 2). In contrast, ~49% of all fish were early-timed and unsuccessful at reaching spawning areas (Table 2), representing 91% of the early-timed migrants. Within the normal-timed fish category, the percentages of successful (55%, *n* = 21) and unsuccessful (45%, *n* = 17) fish were similar. There was also a significant relationship between timing and residence (χ^2 statistic = 6.287, *P* < 0.0122). Of the early-timed fish, the majority (64%, *n* = 29) resided in Harrison Lake following tagging, whereas a majority of normal-timed fish (63%, *n* = 24) resided in Harrison River. In terms of fish that survived to reach spawning areas, there was a relationship between residence strategy and timing group (Fisher's exact test, *P* = 0.0005). No early-timed fish survived to reach spawning grounds if they resided in Harrison River, whereas 16% of fish that survived (*n* = 4) were early-timed fish that resided in the lake. In contrast, 72% of the fish that survived (*n* = 18) were normal-timed and river residents, whereas only 12% of survivors (*n* = 3) were normal-timed and lake resi-

76

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

Fig. 3. (*a–c*) Depth–time relationships for three individual acoustic transmitter sockeye salmon (*Oncorhynchus nerka*) from time of release and travel in Harrison River (boxes, far left in each panel) until death occurred within range of a VR-2 receiver in Harrison Lake (solid lines, far right in each panel). The thermocline (45 m) is represented by a broken line. The map to the right indicates the location and number of confirmed sockeye mortalities within Harrison River and Harrison Lake.

dents. Within the normal-timed category, 86% of survivors were river residents.

The unsuccessful early-timed migrant category includes eight fish that did not proceed upstream after tagging and release. These "fallbacks" were all captured prior to 2 September and all resided for at least 3 days in the Harrison River prior to disappearing from the study area. We conducted a series of one-way ANOVAs comparing fallback fish (*n* = 8) with the other unsuccessful early-timed fish (*n* = 34) for each of the 11 physiological variables examined in this study and found no differences between groups on any variable (*P* > 0.05 with Bonferroni correction). As fallback fish did not differ in physiological state at capture, we pooled them with the other unsuccessful early migrants.

Data from the stationary receiver at the capture/release site indicated that tagged fish did not remain near the tagging site after release and aside from the fallbacks, the remaining fish all proceeded upstream immediately after release. All were detected on the uppermost receiver within Harrison River; some proceeded into the lake immediately following that. Mobile tracking revealed that fish that remained within Harrison River and that were classified as river residents were generally found in a few deep holding areas upriver of Morris Slough (~5 km upriver of our tagging site). These behaviours suggest that fish passing by the tagging site were new arrivals from the Fraser River and that captured fish had just arrived into the Harrison system.

Of the 39 acoustic-tagged sockeye, 14 were unsuccessful

Fig. 4. Hypothetical mean degree-days accumulated (±SE) for all tagged sockeye salmon (*Oncorhynchus nerka*) from freshwater entry until 15 October 2004 (peak spawning). Letters above the bars indicate significant differences at $\alpha = 0.05$ using Scheffé's post hoc multiple comparison procedure. Sample sizes (*n*): early/river (7), early/lake (12), normal/river (11), and normal/lake (9). The circles represent actual degree-day values estimated for successful fish detected on the spawning grounds (open circles) or that died in front of a stationary receiver (confirmed mortality, solid circles).

and a further 15 were confirmed mortalities (died in Harrison Lake, $n = 10$; died in Harrison River, $n = 5$) (Fig. 3). Some of the sockeye died within range of a stationary receiver ($n = 8$), while others were identified by mobile tracking ($n = 7$). Thus, only 10 acoustic-tagged fish successfully reached spawning grounds. In Harrison Lake, mortalities were identified at depths ranging from 5 to 120 m. Mortality depths in the lake and river were cross-referenced with a navigational chart with depth to verify that the fish were on the bottom.

Estimates of hypothetical DD accumulation revealed that based on river entry timing (early or normal) and migration residency (river or lake), early-river and normal-lake fish differed significantly from each other as well as from early-lake and normal-river fish (all $P < 0.05$) (Fig. 4). However, early-lake and normal-river fish did not differ ($P = 0.111$). Early-timed river residents averaged over 800 °C DD. Early-timed lake residents and normal-timed river residents had much lower estimates of theoretical DD accumulation (mean ~468 and ~425 °C DD, respectively). Normal-timed lake residents had the lowest mean theoretical DD accumulation at ~280 °C DD. Normal-timed and both lake residency strategies all fell under a known disease threshold level for the endemic parasite *P. minibicornis* (~500 °C DD: Wagner et al. 2005; Crossin et al. 2008).

We estimated actual DD accumulation for 17 individuals that had detailed information on fate and thermal experience (seven confirmed mortalities dieing within detection limits of a receiver; 10 reached spawning grounds). There appeared to be no relationship between DD accumulation and either migration timing or resident location. All successful fish accumulated <480 °C DD, and contrary to expectations, mortalities were associated with relatively low DD accumulation compared with fish that reached spawning grounds (Fig. 4).

We found few effects of sex on physiological state with the exception of reproductive hormones and GSE (Table 3). Females had higher GSE levels and plasma T and E_2 concentrations than males (Fig. 5). E_2 concentrations were nondetectable for males. In general, timing had a strong influence on physiological state. Early fish had higher GSE levels, lower reproductive hormone concentrations, and higher osmolality, Na^+, Cl^-, lactate, and glucose concentrations (Figs. 5 and 6). There were a few interactions between sex and physiology; specifically, normal-timed females had the relatively highest plasma T and E_2 and early males had the highest gill Na^+,K^+-ATPase. Because fish fate and timing are correlated with each other, it is not surprising that fate, like timing, also explained variation in the physiological variables (Table 3). However, generally the effect of fate was weaker than for timing (e.g., GSE and concentrations of E_2, glucose, and Na^+) or was not significant (e.g., osmolality, gill Na^+, K^+-ATPase activity, Hct, and concentrations of T, Cl^-, and lactate). Only plasma K^+ was significant with fate but not with timing (Table 3).

Normal-timed fish had lower concentrations of lactate, Cl^-, and osmolality, lower Hct and GSE, and higher sex hormone concentrations than early-timed fish. The primary purpose of these sacrificed fish was to help evaluate the potential added effects of biopsy handling stress on physiological measures because sacrificed fish were sampled with less handling. The differences in physiological measures between early- and normal-timed fish were similar for the sacrificed and the tagged fish (Table 4). Means (±SE) of the ionoregulatory variables from sacrificed fish all generally overlapped with means (±SE) of biopsied fish when timing groups were compared (see Table 4 and Fig. 6). However, plasma K^+ in sacrificed fish was ~50% higher than the biopsy mean. Means (±SE) of the stress measure variables from sacrificed fish generally did not overlap with means (±SE) of biopsied fish. Plasma glucose and Hct had means that were ~30% and 20% higher, respectively, than biopsy mean values. Mean plasma lactate was ~70% lower in sacrificed early-timed fish but nearly identical to that in normal-timed biopsied fish.

Discussion

Migrating Weaver Creek sockeye salmon that arrive in the Harrison River prior to early October must reside in either the Harrison River or nearby Harrison Lake because the managed spawning channels where they reproduce are not yet accessible due to low water. But because Harrison River temperatures in early to mid-September are generally much warmer that what they would encounter in migrating at normal (i.e., historical) times in early October, the only successful strategy for early-timed migrants was to seek thermal refuge in the cool waters of Harrison Lake where ~80% of their time was spent in the cool hypolimnion (Farrell et al. 2008). In contrast, of the early migrants choosing to remain in the much warmer Harrison River, none was ever detected on the spawning grounds. Although samples

Table 3. F and P value results from two-way ANOVAs assessing the effects of sex and timing, sex and fate, and interactions on physiological variables from biopsied sockeye salmon (*Oncorhynchus nerka*).

Physiological variable		Sex × timing			Sex × fate		
			F	*P*		*F*	*P*
Gross somatic energy (MJ·kg^{-1})^a	Sex		8.67	**0.0043**	Sex	4.16	**0.0047**
	Timing		23.69	**<0.0001**	Fate	6.21	**0.0148**
	Interaction		0.15	0.6966	Interaction	0.01	0.9038
Plasma testosterone (pg·mL^{-1})	Sex		135.8	**0.0005**	Sex	6.22	**0.0151**
	Timing		29.62	**<0.0001**	Fate	1.40	0.2406
	Interaction		7.79	**0.0069**	Interaction	0.14	0.7111
Plasma 17β-estradiol (pg·mL^{-1})	Sex		242.24	**<0.0001**	Sex	238.83	**<0.0001**
	Timing		7.08	**0.0097**	Fate	11.33	**0.0013**
	Interaction		6.84	**0.0110**	Interaction	10.97	**0.0015**
Gill Na$^+$,K$^+$-ATPase (µmol ADP·mg protein^{-1}·h^{-1})	Sex		1.03	0.3174	Sex	0.00	0.9961
	Timing		0.53	0.4730	Fate	0.00	0.9587
	Interaction		6.36	**0.0167**	Interaction	1.05	0.3130
Osmolality (mosmol·kg^{-1})	Sex		0.46	0.5004	Sex	0.52	0.4737
	Timing		18.54	**<0.0001***	Fate	1.00	0.3210
	Interaction		0.01	0.9539	Interaction	0.54	0.4638
Plasma Cl$^-$ (mmol·L^{-1})^a	Sex		0.44	0.5076	Sex	0.66	0.4201
	Timing		24.42	**<0.0001***	Fate	0.31	0.5764
	Interaction		3.13	0.0807	Interaction	1.34	0.2510
Plasma Na$^+$ (mmol·L^{-1})	Sex		1.42	0.2377	Sex	1.09	0.2997
	Timing		31.21	**<0.0001***	Fate	4.05	**0.0476**
	Interaction		0.05	0.8238	Interaction	0.13	0.7234
Plasma K$^+$ (mmol·L^{-1})^a	Sex		1.54	0.2176	Sex	4.77	**0.0319**
	Timing		3.75	0.0565	Fate	10.71	**0.0016**
	Interaction		0.53	0.4699	Interaction	2.38	0.1269
Plasma lactate (mmol·L^{-1})^a	Sex		3.23	0.0764	Sex	3.52	0.0644
	Timing		13.94	**0.0004***	Fate	0.01	0.9269
	Interaction		0.38	0.5391	Interaction	0.67	0.4164
Plasma glucose (mmol·L^{-1})	Sex		1.26	0.2651	Sex	2.51	0.1172
	Timing		26.47	**<0.0001***	Fate	4.30	**0.0414**
	Interaction		2.5	0.1179	Interaction	1.63	0.2059
Hematocrit (%)	Sex		2.61	0.1109	Sex	2.15	0.1472
	Timing		10.53	**0.0018***	Fate	3.20	0.0781
	Interaction		1.87	0.1761	Interaction	0.56	0.4550

Note: Statistical significance was assessed at Bonferroni-corrected $\alpha = 0.05$ for groupings of variables: for ionoregulatory, $\alpha = 0.01$ (gill Na$^+$,K$^+$-ATPase, osmolality, and ions), and for stress, $\alpha = 0.017$ (lactate, glucose, and hematocrit). We indicate when variables were significant at the $\alpha = 0.05$ (bold) and at the specific Bonferroni-corrected value (bold with an asterisk).

^{a}Transformed variable.

sizes were not extremely large (19 early sockeye remained in Harrison River, whereas 29 early migrants entered Harrison Lake), the results are compelling and highlight the pervasive effect that temperature has on the behaviour and physiology of homing salmon (Brett 1971). This is corroborated by the results of other studies that show that Pacific salmon will behaviourally thermoregulate during their upriver migration to increase their likelihood of reaching spawning grounds and of spawning successfully. For example, Berman and Quinn (1991) found that salmon could mitigate the sublethal effects of high temperatures by modifying their homing behaviour towards cool-water refugia where energy conservation was optimized. Similarly, Newell and Quinn (2005) found that sockeye would wait out the warm summer months prior to spawning in deep areas of Lake Washington where temperatures were ideal for sexual maturation and energy conservation.

In contrast, the normal-timed fish in this study (meaning those that migrated into the Harrison River later, near historically observed times) were much more likely to reside in the river, which at that time was cooling in temperature. This strategy was more successful in terms of survival than normal-timed fish that entered the lake. It is possible that because normal-timed migrants entered the Harrison River closer to their peak spawning period, strong olfactory signals from Weaver Creek and the urge to spawn may have outweighed potential thermal benefits of using the lake. Not using the lake also would have allowed normal-timed fish more time at the spawning grounds, since accessing the lake involves migrating past their spawning area. Moreover, river temperatures at this time were close to the metabolic optima for Weaver sockeye (~14–16 °C; Lee et al. 2003) and physiological stress levels were relatively low, so there was likely little need for use of thermal refugia to save energy or recover from high levels of stress.

The "earliest" of our early-timed migrants ($n = 8$, all

Fig. 5. Mean (±SE) sockeye salmon (*Oncorhynchus nerka*) (*a*) energy and (*b* and *c*) sex hormone concentrations based on sex and timing. Letters above the bars indicate statistically significant differences at $\alpha = 0.05$ using Scheffé's post hoc multiple comparison procedure. All male plasma 17β-estradiol values were undetectable and are not shown; an asterisk indicates a significant difference between female 17β-estradiol values. Sample sizes (*n*) are shown within each bar. ANOVA *F* and *P* results are presented in Table 3.

limited time before blood acidosis becomes lethal. Although we did not find lethally high lactate concentrations (e.g., >12 mmol·L^{-1}; Jain and Farrell 2003) in these "earliest" fish, which might be expected if lactic acidosis caused by anaerobic metabolism was the mortality agent (e.g., Wood et al. 1983), early-timed fish had significantly higher levels than normal-timed fish.

A potential consequence of migrating early and at high temperatures is increased susceptibility to, and prolonged development of, freshwater diseases (Gilhousen 1990; Macdonald et al. 2000; Wagner et al. 2005). Weaver Creek sockeye that enter freshwater early do not spawn any earlier, resulting in a longer than typical freshwater residency. We predicted that migrants that had accumulated >500 °C DD, a known threshold for *P. minibicornis* expression and a correlate of elevated mortality rates in laboratory-based temperature experiments in adult Late-run Fraser River sockeye, would be likely to perish before reaching spawning grounds (Wagner et al. 2005; Crossin et al. 2008). We estimated that if early-timed fish that resided in the Harrison River survived to spawning grounds, then they would have accumulated ~800 °C DD. That none of these fish survived is consistent with other research on Late-run sockeye that has found little evidence that fish accumulating such high DD levels can survive (Wagner et al. 2005; Crossin et al. 2008) and supports the notion that disease could be responsible for some of the mortality of early-timed fish.

We also found no difference in hypothetical DD accumulation between early-timed lake-resident fish and normal-timed river-resident fish, supporting the notion that early-timed sockeye may be using the lake to reduce DDs and hence disease levels. We confirmed with a subset of fish that actual DD accumulation for successful migrants was <500 °C DD. Very few fish died within range of an acoustic receiver, which was required so that we could calculate actual DD accumulation, and those that did die in the detection radius of a receiver did so very early in the migration with low DD accumulation, likely for reasons unrelated to DD accumulation. The relatively low sample sizes of early-timed fish for which we could calculate actual DDs and in particular those that resided in the river limit our ability to conclusively demonstrate how DDs influence mechanisms of mortality. We were unable to recover the carcasses of any of the mortalities to assess disease status. Histological assessments of kidney tissue from our sacrificed fish did not find evidence of *P. minibicornis* (D.A. Patterson, unpublished data). However, DD accumulation would have been too low at that early stage of migration to expect expression in the kidney (Wagner et al. 2005).

As predicted, early-timed migrants were more physiologically stressed (e.g., higher plasma lactate, glucose, and Hct) than normal-timed migrants. High water temperatures, in some cases approaching or at lethal limits, were likely responsible. However, the role of our sampling approaches should be considered, as early-timed fish, perhaps because of the high temperature, may have been more susceptible to handling-induced stress. Dipnet sampling of adult sockeye, perhaps the quickest and least invasive sampling approach, during their Fraser River migration yields plasma lactate of 2–4.5 mmol·L^{-1} (Young et al. 2006; Pon et al. 2009). Our

Migration timing and sex

perished) were exposed to Fraser River temperatures of 19–21 °C for at least 4 days. This temperature level is near or at the critical thermal limit where aerobic scope collapses and that was empirically established for Weaver Creek sockeye (Lee et al. 2003; Farrell et al. 2008). At these temperatures, oxygen availability to tissues becomes a limiting factor (A.P. Farrell, unpublished data) and fish either cannot migrate upriver or must do so anaerobically, but for only a

Fig. 6. Physiological differences in sockeye salmon (*Oncorhynchus nerka*) ionoregulatory and stress measures (mean ± SE) based on timing (sexes pooled): (*a*) plasma osmolality, (*b*) gill Na⁺,K⁺-ATPase, (*c*) sodium, (*d*) chloride, (*e*) lactate, (*f*) potassium, (*g*) glucose, and (*h*) hematocrit. Asterisks indicate statistical significance at $\alpha = 0.05$ using Scheffé's post hoc multiple comparison procedure. Sample sizes (*n*) are shown within each bar. ANOVA *F* and *P* results are presented in Table 3.
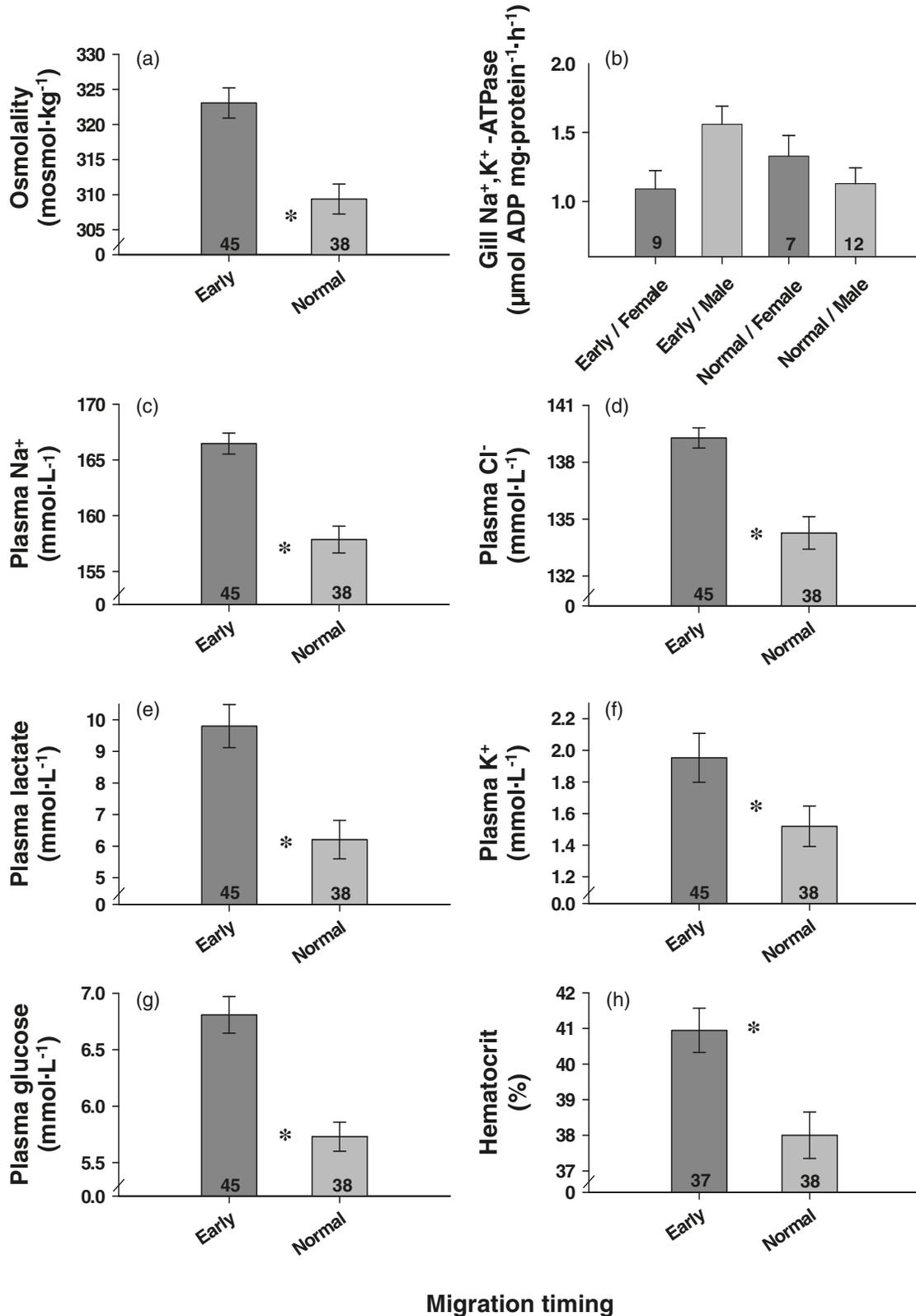
Table 4. Mean (±SE) (n = sample size) of physiological variables for sacrificed Weaver Creek sockeye salmon (*Oncorhynchus nerka*) by timing group and by sex for some variables.

Physiological variable	Sex	Timing group Early	n	Normal	n	P Timing	Sex	Interaction
Gross somatic energy (MJ·kg⁻¹)[a]	Female	6.67±0.19	16	5.77±0.12	29	**<0.0001**	**0.0010**	0.8193
	Male	6.65±0.27	10	5.27±0.07	24			
Plasma testosterone (pg·mL⁻¹)	Female	20725±1845	16	33529±2333	29	**<0.0001**	**<0.0001**	0.2613
	Male	8512±1087	10	16388±1056	24			
Plasma 17β-estradiol (pg·mL⁻¹)[a]	Female	8298±684	16	9446±508	29	**<0.0001**	0.4055	0.4457
	Male	190±967	8	240±627	19			
Gill Na⁺,K⁺-ATPase (μmol ADP·mg⁻¹ protein·h⁻¹)[a]	na	1.08±0.12	23	1.18±0.16	33	0.9085	na	na
Osmolality (mosmol·kg⁻¹)[a]	na	322±4.2	26	313±2.7	53	**0.0481**	na	na
Plasma Cl⁻ (mmol·L⁻¹)[a]	na	137±2.0	26	133±1.1	53	**0.0446**	na	na
Plasma Na⁺ (mmol·L⁻¹)[a]	na	162±2.6	26	159±1.3	53	0.2242	na	na
Plasma K⁺ (mmol·L⁻¹)	na	1.64±0.21	26	2.32±0.21	53	**0.0449**	na	na
Plasma lactate (mmol·L⁻¹)	na	6.67±0.21	26	5.88±0.16	53	**0.0043***	na	na
Plasma glucose (mmol·L⁻¹)	na	8.90±0.66	26	7.35±0.54	53	0.0895	na	na
Hematocrit (%)	na	50.0±2.17	26	44.5±1.32	37	**0.0258**	na	na

Note: *P* values from ANOVAs are presented for the effects of timing, and where effects were relevant for biopsied sockeye (see Table 2), timing, sex, and the interaction are explored. Statistical significance was assessed at Bonferroni-corrected $\alpha = 0.05$ for groupings of variables: for ionoregulatory, $\alpha = 0.01$ (gill Na⁺,K⁺-ATPase, osmolality, and ions), and for stress, $\alpha = 0.017$ (lactate, glucose, and hematocrit). We indicate when variables were significant at $\alpha = 0.05$ (bold) and at the specific Bonferroni-corrected value (bold with asterisk). na, not available.

[a]Transformed variable.

biopsy lactate values were about two to three times higher, which is not surprising given the fact that beach seining causes fish to thrash about while being landed and our biopsy sampling did not occur until after fish were placed in a net pen. Lactate levels in the destructively sampled fish should be more representative of "immediate capture" because these fish were the first ones removed from the net pen for sampling. Indeed, these lactate values were lower than in the telemetry fish, but early-timed fish still had higher values (averages: early = 6.6 mmol·L⁻¹ and normal = 5.9 mmol·L⁻¹). Other physiological measures obtained from destructive sampling (e.g., osmolality and Hct) also suggested that early-timed fish were more stressed than normal-timed fish. There was no difference in mean gill Na⁺,K⁺-ATPase activity levels between groups. All were <2 μmol ADP·mg protein⁻¹·h⁻¹, which are levels expected for river-migrating sockeye (Shrimpton et al. 2005) and indicative of full ionoregulatory functionality in freshwater (Hinch et al. 2006). Thus, our capture and biopsy approach may have exacerbated a stress response in early-timed fish; however, it is clear that early-timed fish were more stressed at time of capture than normal-timed fish.

Early-timed fish were less reproductively advanced than normal-timed fish, having higher GSE (likely because they had not yet diverted as much energy to gonads) and generally lower reproductive hormone levels. Contributing to low reproductive hormone levels in early-timed fish could also be their relatively higher stress levels, which can suppress reproductive development (Hinch et al. 2006). There was no relationship between fish that died versus those that survived to spawning grounds in GSE or reproductive hormone levels. Fraser sockeye that migrate long distances upriver against fast currents are limited in some years by energy reserves (Rand and Hinch 1998; Rand et al. 2006). However, Weaver Creek sockeye migrate a relatively short distance from the ocean to spawning grounds and experience relatively low river discharge levels. Therefore, GSE would not be expected to be a limiting factor for this stock (Crossin et al. 2004).

In 2004, ~1.34 million adult sockeye from all run-timing groups entered the Fraser River but failed to show up on spawning grounds, suggesting ~57% overall migration mortality (Williams 2005). Record high river temperatures were a significant factor in this large-scale mortality. Early-migrating Late-run stocks were particularly hard hit. Based on numbers of fish passing Mission, British Columbia, in relation to spawning ground arrival numbers, ~80% of the total Weaver Creek run perished during the freshwater migration (~90 000 fish; M. Lapointe, Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada, personal communication (2004)). Our telemetry study estimated ~70% mortality. Individuals from all run-timing groups encountered temperatures that were often 2 °C higher than normal but our early-timed migrants encountered Fraser River temperatures at least 4 °C above their historic norms. Climate models predict a 2–4 °C warming of the Fraser River over the next several decades (Morrison et al. 2002), suggesting that the mortality levels displayed by Weaver Creek sockeye in 2004 may be indicative of future survival trends for Fraser River sockeye. It is clear that thermal refu-

82

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

gia will be key in the survivorship of stocks as temperatures continue to warm.

Acknowledgements

References

Berman, C.H., and Quinn, T.P. 1991. Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. J. Fish Biol. **39**(3): 301–312. doi:10.1111/j.1095-8649.1991.tb04364.x.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. **11**: 99–113.

Chapman, D., Peven, C., Giorgi, A., Hillman, T., Utter, F., Hill, M., Stevenson, J., and Miller, M. 1995. Status of sockeye salmon in the mid-Columbia region. Don Chapman Consultants, Inc., Boise, Idaho.

Cooke, S.J., Hinch, S.G., Farrell, A.P., Lapointe, M.F., Jones, S.R.M., Macdonald, J.S., Patterson, D.A., Healey, M.C., and Van Der Kraak, G. 2004. Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. Fisheries, **29**(2): 22–33. doi:10.1577/1548-8446(2004)29[22:AMTAHE]2.0.CO;2.

Cooke, S.J., Crossin, G.T., Patterson, D.A., English, K.K., Hinch, S.G., Young, J.L., Alexander, R.F., Healey, M.C., Van Der Kraak, G., and Farrell, A.P. 2005. Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. J. Fish Biol. **67**(5): 1342–1358. doi:10.1111/j.1095-8649.2005.00830.x.

Cooke, S.J., Hinch, S.G., Crossin, G.T., Patterson, D.A., English, K.K., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2006*a*. Physiology of individual late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) sampled in the ocean correlates with fate during spawning migration. Can. J. Fish. Aquat. Sci. **63**(7): 1469–1480. doi:10.1139/F06-042.

Cooke, S.J., Hinch, S.G., Crossin, G.T., Patterson, D.A., English, K.K., Healey, M.C., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2006*b*. Mechanistic basis of individual mortality in Pacific salmon during spawning migrations. Ecology, **87**(6): 1575–1586. doi:10.1890/0012-9658(2006)87[1575:MBOIMI]2.0.CO;2. PMID:16869433.

Cooke, S.J., Hinch, S.G., Farrell, A.P., Patterson, D.A., Miller-Saunders, K., Welch, D.W., Donaldson, M.R., Hanson, K.C.,

Crossin, G.T., Mathes, M.T., Lotto, A.G., Hruska, K.A., Olsson, I.C., Wagner, G.N., Thomson, R., Hourston, R., English, K.K., Larsson, S., Shrimpton, J.M., and Van Der Kraak, G. 2008. Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics, and experimental biology: an interdisciplinary case study on adult Fraser River sockeye salmon. Fisheries, **37**(7): 321–338.

Crossin, G.T., and Hinch, S.G. 2005. A non-lethal method for assessing the somatic energy content of freely migrating adult Pacific salmon. Trans. Am. Fish. Soc. **134**(1): 184–191. doi:10.1577/FT04-076.1.

Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., and Healey, M.C. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J. Fish Biol. **65**(3): 788–810. doi:10.1111/j.0022-1112.2004.00486.x.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Batten, S.D., Patterson, D.A., Van Der Kraak, G., Shrimpton, J.M., and Farrell, A.P. 2007. Behaviour and physiology of sockeye salmon homing through coastal waters to natal rivers. Mar. Biol. (Berl.), **152**(4): 905–918. doi:10.1007/s00227-007-0741-x.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Can. J. Zool. **86**(2): 127–140. doi:10.1139/Z07-122.

Farrell, A.P. 2002. Cardiorespiratory performance in salmonids during exercise at high temperature: insights into cardiovascular design limitations in fishes. Comp. Biochem. Physiol. Part A, **132**: 797–810.

Farrell, A.P., Gallaugher, P.E., Fraser, J., Pike, D., Bowering, P., Hadwin, A.K.M., Parkhouse, W., and Routledge, R. 2001. Successful recovery of the physiological status of coho salmon on-board a commercial gillnet vessel by means of a newly designed revival box. Can. J. Fish. Aquat. Sci. **58**(10): 1932–1946. doi:10.1139/cjfas-58-10-1932.

Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M., and Mathes, M.T. 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. Physiol. Biochem. Zool. **81**(6): 697–708. doi:10.1086/592057.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. *In* Fish physiology. Vol. 6. Environmental relations and behavior. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 1–98.

Gilhousen, P. 1990. Prespawning mortality of sockeye salmon in the Fraser River system and possible casual factors. Int. Pac. Salmon Fish. Comm. Bull. **26**: 1–58.

Goniea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H., and Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Trans. Am. Fish. Soc. **135**(2): 408–419. doi:10.1577/T04-113.1.

High, B., Peery, C.A., and Bennett, D.H. 2006. Temporary staging of Columbia River summer steelhead in coolwater areas and its effect on migration. Trans. Am. Fish. Soc. **135**(2): 519–528. doi:10.1577/T04-224.1.

Hinch, S.G., and Rand, P.S. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. Can. J. Fish. Aquat. Sci. **55**(8): 1821–1831. doi:10.1139/cjfas-55-8-1821.

Hinch, S.G., Cooke, S.J., Healey, M.C., and Farrell, A.P. 2006. Behavioural physiology of fish migrations: salmon as a model ap-

proach. *In* Behaviour and physiology of fish. Fish physiology series. Vol. 24. *Edited by* K. Sloman, S. Balshine, and R. Wilson. Academic Press, London, U.K. pp. 240–285.

Hodgson, S., and Quinn, T.P. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Can. J. Zool. **80**(3): 542–555. doi:10.1139/z02-030.

Hyatt, K.D., Stockwell, M.M., and Rankin, D.P. 2003. Impact and adaptation responses of Okanagan River sockeye salmon (*Oncorhynchus nerka*) to climate variation and climate change effects during freshwater migration: stock restoration and fisheries management implications. Can. Water Resour. J. **28**(4): 689–713.

Jain, K.E., and Farrell, A.P. 2003. Influence of seasonal temperature on the repeat swimming performance of rainbow trout *Oncorhynchus mykiss*. J. Exp. Biol. **206**(20): 3569–3579. doi:10.1242/jeb.00588. PMID:12966048.

Juanes, F., Gephard, S., and Beland, K.F. 2004. Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. Can. J. Fish. Aquat. Sci. **61**(12): 2392–2400. doi:10.1139/f04-207.

Keefer, M.L., Peery, C.A., Jepson, M.A., Tolotti, K.R., Bjornn, T.C., and Stuehrenberg, L.C. 2004. Stock-specific migration timing of adult spring–summer Chinook salmon in the Columbia River basin. N. Am. J. Fish. Manag. **24**(4): 1145–1162. doi:10.1577/M03-170.1.

Lapointe, M., Cooke, S.J., Hinch, S.G., Farrell, A.P., Jones, S., Healey, M., Patterson, D., Macdonald, S., Jones, S., and Van Der Kraak, G. 2002. Late-run sockeye salmon in the Fraser River, British Columbia, are experiencing early upstream migration and unusually high rates of mortality — What's going on? Georgia Basin/Puget Sound Research Conference Proceedings. Available from www.psat.wa.gov/Publications/03_proceedings/PAPERS/ORAL/5c_lapoi.pdf [accessed 20 June 2006].

Lee, C.G., Farrell, A.P., Lotto, A.G., MacNutt, M.J., Hinch, S.G., and Healey, M.C. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. J. Exp. Biol. **206**(18): 3239–3251. doi:10.1242/jeb.00547. PMID:12909705.

Macdonald, J.S., Foreman, M.G.G., Farrell, T., Williams, I.V., Grout, J., Cass, A., Woodey, J.C., Enzenhofer, H., Clarke, W.C., Houtman, R., Donaldson, E.M., and Barnes, D. 2000. The influence of extreme water temperatures on migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) during the 1998 spawning season. Can. Tech. Rep. Fish. Aquat. Sci. 2326.

Mathes, M.T. 2009. Effect of water temperature, timing, physiological condition and lake thermal refugia on success of migrating adult sockeye salmon (*Oncorhynchus nerka*). M.Sc. thesis, Department of Forestry, The University of British Columbia, Vancouver, B.C.

McCormick, S.D. 1993. Methods for nonlethal gill biopsy and measurement of Na$^+$,K$^+$-ATPase activity. Can. J. Fish. Aquat. Sci. **50**(3): 656–658. doi:10.1139/f93-075.

McMaster, M.E., Munkittrick, K.R., and Van Der Kraak, G.J. 1992. Protocol for measuring circulating levels of gonadal sex steroids in fish. Can. Tech. Rep. Fish. Aquat. Sci. 1836.

Morrison, J., Quick, M., and Foreman, M.G.G. 2002. Climate change in the Fraser River watershed: flow and temperature projections. J. Hydrol. (Amst.), **263**(1-4): 230–244. doi:10.1016/S0022-1694(02)00065-3.

Newell, J.C., and Quinn, T.P. 2005. Behavioral thermoregulation by maturing adult sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. Can. J. Zool. **83**(9): 1232–1239. doi:10.1139/z05-113.

Patterson, D.A., Macdonald, J.S., Skibo, K.M., Barnes, D.P., Guthrie, L., and Hills, J.A. 2007. Reconstructing the summer thermal history for the lower Fraser River, 1941 to 2006, and implications for adult sockeye salmon (*Oncorhynchus nerka*) spawning migration. Can. Tech. Rep. Fish. Aquat. Sci. 2724.

Pon, L.B., Hinch, S.G., Wagner, G.N., Lotto, A.G., and Cooke, S.J. 2007. Swimming performance and morphology of juvenile sockeye salmon, *Oncorhynchus nerka*: a comparison of an inlet and outlet fry population. Environ. Biol. Fishes, **78**(3): 257–269. doi:10.1007/s10641-006-9094-4.

Pon, L.B., Hinch, S.G., Cooke, S.J., Patterson, D.A., and Farrell, A.P. 2009. Physiological, energetic, and behavioural correlates of successful fishway passage of adult sockeye salmon (*Oncorhynchus nerka*) in the Seton River, British Columbia. J. Fish Biol. **74**(6): 1323–1336. doi:10.1111/j.1095-8649.2009.02213.x.

Quinn, T.P., and Adams, D.J. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology, **77**(4): 1151–1162. doi:10.2307/2265584.

Quinn, T.P., Hodgson, S., and Peven, C. 1997. Temperature, flow and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Can. J. Fish. Aquat. Sci. **54**(6): 1349–1360. doi:10.1139/cjfas-54-6-1349.

Rand, P.S., and Hinch, S.G. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. Can. J. Fish. Aquat. Sci. **55**: 1832–1841. doi:10.1139/cjfas-55-8-1832.

Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P., and Higgs, D.A. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. Trans. Am. Fish. Soc. **135**(3): 655–667. doi:10.1577/T05-023.1.

Robards, M.D., and Quinn, T.P. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. Trans. Am. Fish. Soc. **131**(3): 523–536. doi:10.1577/1548-8659(2002)131<0523:TMTOAS>2.0.CO;2.

Shortreed, K.S., Morton, K.F., Malange, K., and Hume, J.M.B. 2001. Factors limiting juvenile sockeye production and enhancement potential for selected nursery lakes. Fisheries and Oceans Canada, Marine Environment and Habitat Science Division, Cultus Lake Laboratory. ISSN 1480-4883. Available from www.dfo-mpo.gc.ca/csas/Csas/publications/ResDocs-DocRech/2001/2001_098_e.htm

Shrimpton, J.M., Patterson, D.A., Richards, J.G., Cooke, S.J., Schulte, P.M., Hinch, S.G., and Farrell, A.P. 2005. Ionoregulatory changes in different populations of maturing sockeye salmon *Oncorhynchus nerka* during ocean and river migration. J. Exp. Biol. **208**(21): 4069–4078. doi:10.1242/jeb.01871. PMID:16244166.

Wagner, G.N., Hinch, S.G., Kuchel, L., Lotto, A.G., Jones, S.R.M., Patterson, D.A., Macdonald, J.S., Van Der Kraak, G., Shrimpton, M., English, K.K., Larson, S., Cooke, S.J., Healy, M., and Farrell, A.P. 2005. Metabolic rates and swimming performance of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) after controlled infection with *Parvicapsula minibicornis*. Can. J. Fish. Aquat. Sci. **62**(9): 2124–2133. doi:10.1139/f05-126.

Williams, B. 2005. 2004 southern salmon fishery post-season re-

view. Part one. Fraser River sockeye report. Available from www.dfo-mpo.gc.ca/Library/314601.pdf.

Wood, C.M., Turner, J.D., and Graham, M.S. 1983. Why do fish die after severe exercise? J. Fish Biol. **22**(2): 189–201. doi:10. 1111/j.1095-8649.1983.tb04739.x.

Young, J.L., Hinch, S.G., Cooke, S.J., Crossin, G.T., Patterson, D.A., Farrell, A.P., Van Der Kraak, G., Lotto, A.G., Lister, A., Healey, M.C., and English, K.K. 2006. Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River, British Columbia. Can. J. Fish. Aquat. Sci. **63**(5): 1067–1077. doi:10.1139/F06-014.