

**EFFECT OF WATER TEMPERATURE, TIMING, PHYSIOLOGICAL CONDITION
AND LAKE THERMAL REFUGIA ON SUCCESS OF MIGRATING ADULT
SOCKEYE SALMON**

by

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ABSTRACT

I related survival of adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*) to water temperature, migration timing, physiological condition, and lake residence in the lower Fraser River and Harrison System, British Columbia. Late-run sockeye were intercepted in the Harrison River after completing the Fraser River component of their spawning migration. Individual sockeye were tagged with radio or acoustic transmitters (equipped with depth sensor), biopsied for physiological assessment and released. Additional fish were sacrificed to increase sample size and to help evaluate baseline physiology. Fish were grouped by river entry timing (early or normal), migration residency (river or lake), and survival to spawning grounds. Of the early-timed fish, the majority (64%) resided in Harrison Lake and only those that resided in Harrison Lake survived to reach spawning grounds, ie none that resided in the Harrison River survived. In contrast, a majority of normal-timed fish (63%) resided in Harrison River and 72% of fish that survived to reach spawning grounds were river residents. Temperatures encountered by migrants during their Fraser River migration were strongly correlated with their subsequent fate to reach spawning grounds ($r = -0.9186$, $P = 0.0275$). Lake residents used the entire water column, but stayed in the cold, deep regions > 80% of the time. Estimates of ‘hypothetical’ degree-day (DD) accumulation revealed that early-river fish could have greatly surpassed (~ 800 °C DD) a critical disease threshold value of ~450 °C DD. There was no difference in hypothetical DD accumulation between normal-timed river fish, the most successful behaviour, and early-timed lake fish. According to calculations of ‘actual’ DD accumulation, based on knowing the precise fate and temperature exposure of a sub-sample ($n = 17$), all fish that survived accumulated ≤ 450 °C DD. Early-timed Weaver Creek sockeye had elevated levels of physiological stress (e.g. plasma lactate, glucose and

hematocrit), which was likely related to higher encountered temperatures and may have contributed to high levels of mortality in these fish. This thesis illustrates the influence of temperature on migratory success and the importance of thermal refugia for early migrants and provides insight into future challenges for a vulnerable species.

TABLE OF CONTENTS

Abstract.....	ii
Table of contents.....	iv
List of tables.....	v
List of figures.....	vi
Acknowledgements.....	iiiiv
Co-authorship statement.....	ix
Chapter 1: Introduction.....	1
References.....	5
Chapter 2: Effect of water temperature, timing, physiological condition and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (<i>Oncorhynchus nerka</i>).....	8
Introduction.....	8
Methods.....	12
Results.....	23
Discussion.....	29
References.....	51
Chapter 3: Management implications and future research.....	57
References.....	64

LIST OF TABLES

Table 2.1. Percentage of Weaver Creek sockeye classified by timing group and fate, timing group and residence location, and timing group and survival relative to residence location. Early-timed fish were captured prior to September 2nd; normal-timed fish were captured after September 13. Fish detected at Weaver Creek (radio) or Morris Lake (acoustic) were classified as successful migrants. Migrants which entered Harrison Lake were classified as lake residence; all others were classified as river residence. Sample sizes are in brackets. Early-timed unsuccessful migrants includes eight fish which were classified as ‘fall backs’; details in text.....37

Table 2.2. 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. 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 Hct). We indicate when variables were significant at the $\alpha = 0.05$ (bold) and at the specific Bonferroni-corrected value (bold*). Transformed variables are represented with (†).....38

Table 2.3. Mean (\pm SE; N = sample size) of physiological variables for sacrificed Weaver Creek sockeye by timing group, and by sex for some variables. P values from ANOVAs are presented for the effects of timing, and where effects were relevant for biopsied sockeye (see Table 2.2), 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 Hct). We indicate when variables were significant at $\alpha = 0.05$ (bold) and at the specific Bonferroni-corrected value (bold*). Transformed variables are represented with (†).....39

LIST OF FIGURES

- Figure 2.1.** 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.....40
- Figure 2.2.** Mean daily water temperature and corresponding discharge levels for the Fraser (A) and Harrison (B) Rivers during the study in 2004.....41
- Figure 2.3.** Mean daily Harrison Lake temperatures during the study period in 2004 at four different depths regions within the lake.....42
- Figure 2.4.** Relationships between mean daily water temperature and river discharge for the Fraser and Harrison Rivers during our study period in 2004.....43
- Figure 2.5.** Fraser River mean daily water temperature plotted with percent survival (spawning ground detection) for each capture day demonstrate the relationship between thermal experience and survival. Black diamonds represent the estimated range of thermal experiences by sockeye prior to their capture. Sockeye were captured in the Harrison River (see Figure 2.1) near the confluence with the Fraser River immediately after completing the Fraser River component of their migration. Capture dates are represented by triangles with numbers of tagged and released sockeye shown above. For the first two sampling periods, dates were collapsed to represent one capture day. The remaining three sampling periods were not collapsed. *capture date = 24 Aug {n=8} (combined dates; 24 Aug {n=5} and 25 Aug {n=3}); *capture date = 31 Aug {n=37} (combined dates; 30 Aug {n=28}, 31 Aug {n=2}, and 2 Sep {n=7}).....44
- Figure 2.6.** Depth recordings for four individual sockeye (Panels A-D) in Harrison Lake...45
- Figure 2.7.** Percent time six sockeye were present in a depth range, with associated Harrison Lake temperatures. Each column represents one of six individual fish. The data presented represent for each fish over 50% of the time they spent as lake residents. The inset is an example of an actual fish's depth history within the lake (mean depth per hour). This normal-timed, successful fish accumulated an estimated 200 DD while in the lake (white circles), with a total of ~370 DD by the time of detection at spawning grounds. The thermocline (45m) is represented by a dashed line.....46
- Figure 2.8.** Depth-time relationships for three individual acoustic transmitter sockeye (A–C) from time of release and travel in Harrison River (rectangles, 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). Degree-day estimates were based on individual recorded depth histories (time spent at depth) with the corresponding temperature data. The thermocline (45m) is represented by a dashed line. The map to the right indicates the location and number of confirmed sockeye mortalities within Harrison River and Lake.....47

Figure 2.9. Hypothetical mean degree-day accumulated (\pm SE) for all acoustic tagged sockeye from freshwater entry until 15 Oct, 2004 (peak spawning). Letters above the bars indicate significant differences at $\alpha = 0.05$, Scheffe's *post hoc* multiple comparison procedure. Sample sizes (n) are shown within each bar. The circles represent actual degree-day values estimated for successful fish detected on the spawning grounds (white circle) or that died in front of a stationary receiver (black circle).....48

Figure 2.10. Mean (\pm SE) energy and sex hormone concentrations based on sex and timing. Letters above the bars indicate statistically significant differences at $\alpha = 0.05$ using Scheffe's *post hoc* multiple comparison procedure. All male plasma 17 β -estradiol values were undetectable and are not shown; an asterisk (*) indicates a significant difference between female 17 β -estradiol values. Sample sizes (n) are shown within each bar. ANOVA P and F results presented in Table 2.2.....49

Figure 2.11. Physiological differences in ionoregulatory and stress measures (mean \pm SE) based on timing (sexes pooled). Asterisk (*) indicate statistical significance at $\alpha = 0.05$. Sample sizes (n) are shown within each bar. ANOVA P and F results presented in Table 2.2.....50

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Todd Mathes held primary responsibility for the fieldwork, data analysis, and writing of the thesis, and of the manuscript that comprises Chapter 2 - a version of which will be submitted for publication in the Canadian Journal of Fisheries and Aquatic Sciences. Use of the first person plural in Chapter 2 acknowledges the following co-authors, who will be named in the manuscript version of this chapter: Scott Hinch, Steven Cooke, David Patterson, Tony Farrell Glenn Crossin and Andrew Lotto. Some telemetry and survival data presented in Chapter 2 are published in a 'concept' paper (Farrell, A.P., S.G. Hinch, S.J. Cooke, D.A. Patterson, G.T. Crossin, M. Lapointe, and M.T. Mathes. 2008. Pacific salmon in hot water: applying metabolic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology*. 82: 697-708).

CHAPTER 1

INTRODUCTION

Background

Among the 35,000 species of fish, Pacific salmon (*Oncorhynchus* spp.) are relatively unique in that they are anadromous (representing < 0.4% of all fish species; Hinch et al. 2006). The ability to move from fresh to saltwater as juveniles and then back again as adults is characterized by several physiological changes (Hinch et al. 2006). Adults are faced with the particularly stressful challenge of moving from ocean environments, which are hypoosmotic, to freshwater ones, which are hyperosmotic, and also generally much warmer. Adult salmon cease feeding prior to freshwater entry, and rely exclusively on stored energy reserves to power their upriver migration, to complete reproductive development, and to engage in spawning activities (Brett 1995). Individuals which encounter unusually high river temperature or discharge may deplete their energy stores before completing migration (Rand and Hinch 1998). High temperatures in particular can make migrations very difficult by also increasing levels of physiological stress, decreasing aerobic scope, and increasing disease levels (Farrell et al. 2008; Crossin et al. 2007), factors which limit the migration (Macdonald 2000, Cooke et al. 2006, Young et al. 2006) and spawning success (Hruska et al. 2007).

Sockeye salmon (*O. nerka*) is the second most abundant Pacific salmon species and the best studied in terms of population-specific migration behaviour and physiology (see reviews in Hinch et al. 2006; Cooke et al. 2008). Their natural freshwater distribution ranges from southern Kotezabu Sound, Russia to the Sacramento River, California, USA, with populations that migrate inland as far as Idaho, USA (Burgner 1991). They generally spawn in the fall in streams though some use lakes. As juveniles, they have a unique life history

which involves lake rearing for at least one year before migrating to the ocean. After 2-3 years maturing at sea, sockeye return their natal streams to spawn and die. Fidelity to natal streams and lakes is relatively high in sockeye and serves to maintain separate populations or ‘stocks’, which are generally considered to be reproductively isolated (Varnavskaya et al. 1994; Wood 1995). Sockeye salmon spawning runs are generally highly predictable in space and time and though the timing of upstream migration varies considerably among sockeye stocks, the peak migration within a given stock typically occurs within the same week each year (Woodey 1987).

Research Rationale

The Fraser River in British Columbia is Canada’s largest producer of Pacific salmon and of sockeye salmon in particular. There are about 150 distinct stocks of sockeye which migrate into the Fraser system starting in June and ending in November. For the purposes of harvest management they have been grouped into four classes based on run-timing sequence: Early Stuart-run (mid-June to mid-July), Early summer-run (mid-July to mid-August), Summer-run (start August to end-August) and Late-run (September to November). Late-run sockeye are unique in that they historically have demonstrated a “holding” or delay behaviour for 4-6 weeks in the Strait of Georgia prior to river entry. Such a behaviour may be an adaptation to avoid high migration and spawning ground temperatures (Gilhousen 1990). Since 1995 segments of each stock within the Late-run group have been entering the Fraser River with little or no delay in the Strait of Georgia. This early freshwater entry timing is associated with very high freshwater migration mortality, generally over 50% each year, in some years exceeding 90% (Cooke et al. 2004). In contrast, prior to 1995, total freshwater mortality for Late-run stocks rarely exceeded 20% (Cooke et al. 2004). The

reasons for this aberrant behaviour are not fully understood though recent oceanographic assessments and biopsy telemetry suggest changes in both ocean conditions and physiological state of sockeye may be responsible (Hinch 2008). Factors such as energetics, osmoregulation, reproductive hormones and sexual maturation, oceanic environment, parasites and disease (Cooke et al. 2004), and con-specific abundance (English and Robichaud 2008) are likely to influence early migration. Factors such as photoreception, in-river environment, contaminants, and marine mammal predation are less likely to influence early migration.

Late-runs historically encountered relatively low Fraser River temperatures (~ 14-15 °C) but in recent years have encountered temperatures 5-6 °C warmer. This has occurred because the earlier migration brings salmon into the river in August instead of September (when the river is cooling), and because the Fraser River has experienced a >1.8 °C increase in average peak summer water temperature over the past 40 yrs with eight of the past 10 summers being the warmest on record (Patterson et al. 2007; Morrison et al. 2002).

Laboratory experiments have revealed that temperatures > 20 °C are lethal for adult Late-runs (Farrell et al. 2008). Moreover, by advancing their entry timing into freshwater, Late-runs are spending more time in freshwater because their spawning dates have not changed (Patterson et al. 2007). Therefore, they are exposed to freshwater disease and infection for longer periods at a time in their life when disease resistance ability is deteriorating (Miller et al. 2008). This phenomenon has also contributed to elevated mortality levels. For example, *Saprolegnia*, a fungus that can impair vision and reduce gill function, is commonly found in migrating adult salmon, particularly as temperatures increase and when fish approach spawning grounds (Van West 2006). In addition, an endemic parasite contracted in the

estuary by all migrating salmon, *Parvicapsula minibicornis*, affects the kidney of sockeye and is known to compromise their anaerobic capacity and recovery rates (Wagner et al. 2005). Histological examinations of kidneys reveals that the disease is full blown at ~ 450 °C accumulated freshwater degree days which corresponds with rapid increases in mortality of laboratory-held sockeye (Crossin et al. 2008).

The Canadian Department of Fisheries and Oceans has recognized for several years that chronic exposure to high temperatures can negatively effect migrating sockeye salmon and have suggested the following links between specific temperatures and their behavioural physiology (e.g. decreased swimming performance (18 °C), early signs of physiological stress and slow migration (19 °C), high en route mortality and disease (20 °C), and lead to severe stress and mortality with chronic exposure (21 °C) (DFO 2008). However, lacking is a thorough field evaluation of the effects of high temperatures on migration behaviour, physiology and survival in Late-run sockeye. Migrating sockeye can transit through or reside in lakes and thereby utilize cooler hypolimnetic waters to minimize their exposure to warm water temperatures (Newell and Quinn 2005; Pon et al. 2006). Little is known of the potential survival benefits that lake utilization may offer sockeye which are encountering high temperatures during their migration. This thesis reports on a large-scale field study conducted in 2004 which integrated the use of telemetry and physiological sampling on one Late-run population in order assess the effects of water temperature, timing, physiological condition and lake thermal refugia on success of migrating adult sockeye salmon (Chapter 2). It also overviews the management implications of the main research findings and briefly suggests future research that is needed which builds off of the results of my research (Chapter 3).

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CHAPTER 2

Effect of water temperature, timing, physiological condition and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*)¹

INTRODUCTION

Migratory Pacific salmon returning to their natal freshwater spawning grounds initiate freshwater entry when river discharge and temperature are most favorable, matching long-term average environmental conditions (Keefer et al. 2004; Hinch et al. 2006). 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, unsuccessful river migration ultimately represents zero lifetime fitness. Unsuccessful migration could be a result of many high temperature mediated factors (Hodgeson and Quinn 2002; Quinn et al. 1997), 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 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 (Gilhausen 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

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salmon (Hinch et al. 2006). Biopsy telemetry 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 (Young et al. 2006; Cooke et al. 2006a). Infection and disease has also been implicated as a major cause of migration mortality. For example, the bacterium *Flexibacter* spp. is more virulent at high temperature and can cause severe gill damage on 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 exceeds approximately 450 °C. Recently it has been suggested that the collapse of metabolic scope has been responsible for migration mortality under extremely high temperatures in some populations of Fraser sockeye (Farrell et al. 2008).

Most stocks of Pacific salmon now encounter warmer rivers during their spawning migration than in any time since records were kept. Temperatures experienced by migratory salmon in summer have increased in recent years corresponding with decreases in river discharge (Quinn et al. 1997; Patterson et al. 2007a). The Fraser River has experienced a >1.8 °C increase in average peak summer water temperature over the past 40 yrs with eight of the past 10 summers being the warmest on record (Patterson et al. 2007a). 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 it appears that many salmon

populations are attempting to avoid peak migration temperatures which are now much warmer than ever before, which may explain why Columbia River sockeye (Quinn and Adams 1996, Quinn et al. 1997) and east-coast Atlantic salmon (Juanes et al. 2004) are entering freshwater earlier than normal and Columbia River summer steelhead are entering later (Robards and Quinn 2002).

The seeking of cool water refugia after initiating upriver spawning migrations is another form of behavioral thermoregulation exhibited by Pacific salmon (Hyatt et al. 2003). Sockeye, Chinook and summer steelhead runs in the Columbia River system have been observed to delay and hold in cold water tributaries, slowing or temporarily stopping upriver migration (Gonia et al. 2006, Hodgson and Quinn 2002, High et al. 2006). Populations of sockeye that normally migrate through lakes do so through the hypolimnion presumably to take advantage of colder water (Newell and Quinn 2005; Pon et al. 2007). Some stocks of sockeye hold in deep portions of lakes adjacent to natal rivers for several days to weeks prior to spawning, while some that spend months holding at depth are thought to have evolved a strategy to avoid migration through surface waters at peak summer temperature (Newell and Quinn 2005).

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, normally beginning river migrations in early fall, are initiating river migrations significantly earlier for reasons not fully understood though potentially related to changes in ocean conditions (Cooke et al. 2006a). Specifically, since 1994, large segments of Late-runs are entering the Fraser River two to six weeks ahead of historical normal dates instead of migrating in the adjacent estuary which was their typical behaviour (Lapointe et al. 2002). Historically, migration mortality

rarely exceeded 20% but now typically exceeds 60% with mortality reported in some years > 90% (Cooke et al. 2004). These early migrating Late-run fish are now encountering peak summer temperatures which are several degrees warmer than normally encountered, and because spawning times have not changed, early migrants are spending considerably longer times in these environments. In addition to the effects of high temperatures, migrants are heading upriver under different levels of river discharge. High river discharge can increase metabolic or energetic costs and at low river discharge there is a potential increased influence of temperature. 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). However, there has been no investigation 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 which are adjacent to spawning areas and it is possible that by utilizing thermal refuges early migrants can slow deleterious physiological changes and increase the likelihood of reaching spawning grounds.

The present study uses non-destructive biopsy on individual telemetered adult sockeye to investigate the linkages between survival, physiology and thermal experience during freshwater migrations of a Late-run sockeye salmon stock. We investigate three broad hypotheses. The first one is to assess how river migration timing and lake utilization influence migration success. We predict that early-timed migrants, fish normally encountering the highest river temperatures, which adopt a lake-component to their migration, will survive better than those that do not. The second one is to examine thermal indicators of disease development and relate these to survival. We predict that migrants which accumulate > 450 °C DD, a known threshold for *P. minibicornis* expression, will be

more likely to perish before reaching spawning grounds. The third one is to examine the physiological state of migrants at time of capture and assess differences between timing and fate groups. We predict that early-time migrants will have elevated stress levels and be more reproductively mature – characteristics which may put early fish at a greater risk of migration mortality.

METHODS

Study Animals and Area

This study was conducted in 2004 and focused on Weaver Creek sockeye, a large Fraser River stock which 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, max. = 12 m lake) after moving through Morris Slough which feeds into the Harrison River 11 km upriver of the confluence with the Fraser River (Figure 2.1). In 2004, approximately 126,000 Weaver Creek sockeye migrated past the hydro-acoustic counting facility in the lower Fraser River near Mission, B.C. (M. Lapointe, Pacific Salmon Commission, Pers. Comm. 2004) en route to spawning grounds (Figure 2.1). 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 the 15th and 25th of October (R. Stitt, Fisheries and Oceans Canada. Pers. Comm. 2004). Migrants that arrive at Harrison River prior to early October must therefore reside in either Harrison

River or the nearby Harrison Lake (Figure 2.1). As emergent fry, Weaver Creek sockeye migrate downstream into the Harrison River and then upstream into Harrison Lake where they rear for one year (Pon et al. 2007). Therefore, their early life history utilizes and likely olfactory imprints this lake. Harrison Lake is a large (surface area 220 km²), deep (mean depth 150 m), oligotrophic coastal lake (Shortreed et al. 2001). Whereas its south end is shallow, depths north of Echo Island quickly reach > 250 m (Figure 2.1). Harrison Lake is unusual among the major lakes in British Columbia being only 10 m above sea level. At its outlet, the Harrison River flows almost 20 km before connecting to the Fraser River 120 km upriver from the Strait of Georgia.

Fish capture, biopsy and tagging

All tagged sockeye were captured, bio-sampled, and released from a site on the Harrison River located 10 km upstream of the confluence of the Fraser and Harrison Rivers (Figure 2.1), 1 km downstream of Weaver Creek. In addition to our biopsy tagging procedure, additional data were collected on the same physiological variables from fish which were sacrificed at time of capture ($n = 84$). These fish were captured on the same dates and net sets as the biopsy fish. Fish that were sacrificed serve to increase sample size in order to help in evaluating baseline physiology.

Fish were sampled on 9 separate days between 18 August and 29 September, 2004, a period which spanned a large range of freshwater entry times and temperatures, and included fish that were ‘abnormally’ early as well as those that were closer to the long-term median entry dates (Cooke et al. 2004; see chapter 1). Based on historical run-timing information (Cooke et al. 2004), we classified fish as ‘early-timed’ if captured on or prior to September 2nd and ‘normal-timed’ if on or after September 13th. Sockeye were captured by a 150 m

beach deployed from the stern of a jet boat to encircle and land groups of fish. Once landed, individual fish were netted out of the seine using dip nets and transferred to a holding pen (1.5 m x 1.5 m x 3 m) located along the river margin allowing fish to orient themselves into the current. No more than 40 fish were held in the pen at one time and none were held for more than 45 minutes. We did not record individual's specific information on time in net pen until biopsy and tagging, however fish that were sacrificed were always sampled before those to be tagged therefore sacrificed fish had the shortest handling times. At capture, all fish ($n = 140$) had silver colouration, loose scales, and poorly developed secondary sexual characteristics indicating they were not yet reproductively mature.

Individual fish were netted out of the holding pen and placed in a foam-lined, V-shaped trough which supplied flowing river water to the mouth of fish. The trough was slightly angled so that water was deep enough to submerge the entire head, while leaving the tail only partially submerged (Cooke et al 2006a; Cooke et al 2005). Fork lengths were recorded and sex was visually determined using external secondary sexual characteristics, and was confirmed using the hormone assay information (McMaster et al. 1992). Fish were placed ventral side up to collect a blood sample via caudal puncture (Houston 1990) using a syringe (1.5 ", 21 gauge) and vacutainer (3 ml). The sample was immediately stored in an ice-water slurry. To facilitate blood clotting, pressure was applied to the puncture site for remainder of the procedure. Linesman pliers were used to remove 0.03 g of gill filaments tips for enzyme assays. Fork length was measured with the fish ventral side down. To aid in immediate stock identification, scales were removed from the second row of scales above the lateral line just behind the dorsal fin (MacLellan 1987) and sent to the Pacific Salmon Commission in Vancouver BC for analysis of first year growth which can be used to classify

stock origin as Weaver fish have a distinctive first year annuli based on growth conditions in Harrison Lake (Gable and Cox-Rogers 1993). A 1 cm diameter portion of adipose fin was collected with a hole punch and stored in ethanol for later DNA analysis to confirm stock identification. Coloured, numeric cinch tags were inserted externally, anterior to the dorsal fin, to identify individuals. A micro-wave energy meter (Distell Fish Fatmeter model 692; Distell Inc., West Lothian, Scotland, UK) was used to assess gross somatic energy (GSE) levels following the methods in Crossin and Hinch (2005). Fish which took longer than two minutes to bio-sample or escaped from the trough during sampling were released immediately and data not used. Blood samples were immediately processed (Cooke et al. 2006) to quantify hematocrit (Hct) and isolate plasma by centrifugation of the remaining sample. Plasma and gill samples were stored on dry ice in the field and transferred to an -80 °C freezer upon return to the laboratory. Transmitters were inserted through the mouth into the stomach using a plastic tag applicator (Ramstad and Woody 2003; English et al. 2004), and immediately transferred to a 3 m³ insulated tank filled with 15 °C aerated water. The tagging and biopsy procedure was rapid (2-3 min) and did not require anesthesia. By avoiding anesthesia, fish recovered rapidly and we avoided affecting a potential First Nations food fishery if tagged fish were later captured and consumed. The bio-sampling process followed has been shown to have no detrimental effects to sockeye salmon migration rates or survival (Cooke et al. 2005; Cooke et al. 2006a) and was approved by the University of British Columbia Animal Care Committee.

Fish were transported 5 km from the capture site to the Fisheries and Oceans Canada Chehalis River Hatchery where they were held in concrete raceways (depth = 0.5 m) for 8 to 72 hours during which time the scale analyses were conducted. Using this information,

Weaver Creek sockeye ($n = 84$) were individually netted from raceways and placed into the transfer tank for release at their capture site. For all transfers, < 20 sockeye were moved at one time, and they were in the tank for no more than 45 minutes. All sockeye were released in vigorous condition. Radio tagged individuals from other stocks (Harrison River, Big Silver Creek, and Birkenhead River), which often co-migrate with Weaver Creek adults, were released after having the tag removed by gently pulling on the antenna. Acoustic tagged individuals from other stocks were sacrificed by cerebral concussion (there is no way to non-invasively retrieve these transmitters) and donated to First Nations elders. No acoustic or radio tags were ever regurgitated while fish were held in captivity.

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. Radio transmitters were 16 mm diameter and 46 mm length, weigh approximately 16.1 g in air, with a 460 mm long antenna (model MCFT-3A, Lotek Wireless, Inc., Newmarket, Ontario). Transmitters were started in the middle of August and were expected to stop transmitting by late December (programmed to stop transmitting after 150 days). They operated on six different frequencies in the 150 MHz band. Within each frequency, three different pulse intervals (4.5, 5.0, and 5.5) were used to reduce the incidence of signal collisions. Four fixed location radio receivers (SRX400 or SRX400A; Lotek Wireless, Inc. Newmarket Ontario) with up to three 3- or 4-element Yagi antennae (Max Inc., Hanover Park, Illinois; Grant Systems Engineering Inc., King City, Ontario) per receiver were deployed (Figure 2.1). One was located at the confluence of the Harrison and Fraser Rivers and served to monitor fish moving downstream out of the Harrison River. A second was placed at Morris Slough near

the confluence with the Harrison River to monitor fish approaching Weaver Creek. A third was located at junction of Weaver Creek and Morris Slough to determine arrival at the spawning grounds. A fourth was located near the outlet of Harrison Lake at the confluence with the Harrison River Lake to assess if sockeye entered or left Harrison Lake via its outlet.

Acoustic transmitters were 16 mm diameter and 70 mm long, weighed approximately 25.0 g in air, and transmitted depth information up to 340 meters (model V-16P, Vemco, Shad Bay, Nova Scotia). They operated on 69 kHz with an expected life of 80 days. These transmitters were started in late August and were expected to stop transmitting by December. Signals were sent on average once every 60 s, but randomly varied the timing (range of 30 to 60 s) to minimize signal collision. Ten fixed station acoustic receivers (model VR-2, Vemco, Shad Bay, Nova Scotia) were deployed (Figure 2.1) by boat using anchors, ropes and floats, at times with the assistance of a diver. Receivers were affixed to structures in the river such as large woody debris, docks, and pilings. A receiver was located at the confluence with the Fraser River and another 5 km upstream of the confluence - both served to monitor fish dropping back after tagging and moving downstream out of the Harrison River. A receiver was located across from the capture /release site to monitor the initial movements of tagged fish after release and to ascertain whether the sampling site was a transition or holding area for migratory sockeye. A receiver was positioned at the confluence of Morris Slough and Harrison River (near the radio receiver at that site) to monitor movement towards the spawning stream. A receiver was positioned at the outlet of Harrison Lake (near the radio receiver at this site) to assess movement into or out of the lake. A receiver was positioned in Morris Lake (at the outlet with Weaver Creek and above Morris Slough, near the radio receiver at this site) to assess arrival on spawning grounds. Four acoustic receivers were

deployed in Harrison Lake. Three were deployed 10 km north of the outlet which is the first ‘deep’ region that migrants would encounter as they move into Harrison Lake. These receivers provided information on how deep fish migrate when in the lake and what portion of their time they spend at particular depths. These three receivers also served as a “gate” to record movements out of the lower region of the lake. The fourth receiver was placed off the mouth of Big Silver Creek, approximately 40 km north of the outlet in order to gauge how far Weaver fish may travel up Harrison Lake. An additional receiver was deployed at the outlet of Harrison Lake, but was lost. In order to reduce the likelihood of anomalous detections and ensure that individual fish detections were real, we used the criterion that a receiver must record at least three detections within 30 minutes, which are at least one minute apart, for a given acoustic code. In order to be classified as a ‘confirmed’ mortality, an acoustic signal needed to be detected at one location at the same depth on the bottom for one week. Confirmed mortalities were only assessed using acoustic tagged fish. Nonetheless, we were able to assess with all data (radio and acoustic tagged fish combined) numbers that succeeded or failed to reach spawning grounds and from that infer ‘presumed’ mortality.

Data were collected by mobile tracking to confirm fish arrival at spawning grounds and to locate positions of fish that died within the lake or river. Mobile tracking occurred weekly by foot and boat from August 30th to November 10th for fish with radio transmitters using an SRX-400 receiver (LOTEK; Newmarket, Ontario) and a hand held 3-element Yagi antenna (AF Antronics Inc., Urbana, IL) and from September 29th to November 10th for fish with acoustic transmitters using a VR-60 receiver (Vemco, Shad Bay, NS) and an omni directional hydrophone. Acoustic tagged fish that were detected in the lake or river on three separate days over the tracking period at one location at the same depth on the bottom were

considered to be ‘confirmed’ mortalities. Fish locations were stored as waypoints using a GPS receiver and the coordinates were plotted on a navigational chart with depth.

Temperature data and degree-day 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 August 18 to November 10 (Figure 2.1). Within Harrison Lake, loggers were deployed with an acoustic receiver (to help in re-locating the loggers) anchored off the north western side of Echo Island at depths ranging from 10 to 90 m. The one logger for Harrison River temperature data was located mid-river (10 km upstream of the Fraser- Harrison confluence) at a depth of 5 m. In the lower Fraser River, water temperatures were obtained from a Fisheries and Oceans Canada recording station located 60 km downstream at Whonnock, B.C. (D. Patterson, Fisheries and Oceans Canada, Pers. Comm. 2006).

In order to estimate DD accumulation, two things were required. The first was temperature data for the study area (see Figures 2.2 and 2.3), and the second was to know where fish were positioned within a specific body of water in our study area at a given time. Calculations for DD accumulation began when a fish entered the lower Fraser River. Only acoustic tagged sockeye were used for this exercise. Degree-days for time spent while in the Fraser River were calculated based on known migration rates of Weaver sockeye in from the river mouth to our capture location as assessed by acoustic telemetry on early- and normal-timed migrants in 2003 (Crossin et al. 2007). Early-timed migrants (same date and temperature criterion as in the present study) traveled from Fraser-Pitt confluence to Misson, B.C. (~ 35 km) in approximately 1.1 days (32 km/day), whereas normal-timed fish took approximately 1.6 days (22 km/day). In 2003, early-timed migrants encountered lower

Fraser River temperatures, although still $>18^{\circ}\text{C}$, whereas normal-timed migrants encountered temperatures $<16^{\circ}\text{C}$. A one-way ANOVA revealed that travel rates in 2003 of early-timed fish ($n = 7$) from Crossin et al. (2007) were significantly faster than normal-timed fish ($n = 8$) ($F = 21.32$, $P = 0.0005$). Based on 2003 travel rates for Weaver Creek sockeye, we were able to estimate in 2004 the amount of time migrants spent in the Fraser River. In 2004, early-timed fish traveled from the mouth of the Fraser River to our capture site (~ 130 km) in approximately four days (32 km/day), whereas normal-timed fish took approximately six days (22 km/day). Using 2003 travel rates and 2004 temperatures, we estimated the thermal experiences by sockeye migrating in 2004 prior to their capture (Figure 2.5).

After capture, 2004 sockeye were held at the DFO Chehalis Hatchery. Water temperatures were recorded during captivity in order to assess thermal experience (early; mean = 16°C and normal; mean = 13°C). Once released back into the Harrison River, fish were tracked and temperatures of subsequent river or lake residency locations were assessed (Figures 2.2 and 2.3). 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 particular depth stratum. Fish depths were then compared to temperature data collected from loggers deployed in the lake.

We estimated ‘hypothetical’ DD accumulation for the entire migration for all individuals. We assumed that all fish successfully reached spawning grounds and that the end date for all migrations was October 15th. The calculation involved adding the thermal experience for each fish during its lower Fraser River migration, its captivity, and its subsequent residence in the Harrison River and Harrison Lake. Based on capture date, we

grouped fish as either early-timed (a 4 day Fraser River migration) or normal-timed (a 6 day Fraser River migration). It was assumed that river residents spent the remaining time until October 15th in Harrison River and lake residents spent their time in Harrison Lake. We did not adjust estimates in cases where we knew fish perished prior to October 15th. Fraser River and Harrison River temperature data that corresponded to estimated passage dates are provided in Figure 2.2. Preliminary results indicated that lake residents were spending approximately 80% of the time at depths below 50 m and 20% of their time at shallower depths (details provided below). Therefore, based on thermal data from Harrison Lake, we ascribed 80% of an individual's time to 6.5 °C and 20% of their time at 14.5 °C (Figure 2.3). We estimated 'actual' DD accumulation for each individual as above, but used actual time spent in either the river or lake environments. For fish that were confirmed mortalities, we stopped accumulating DD on the date of mortality.

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 are expressed as $\mu\text{mol ADP mg}^{-1}$ protein h^{-1} (McCormick 1993). Plasma testosterone (T) and 17 β -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, USA) and assessed for significance at $\alpha = 0.05$. In order to meet statistical normality and homogeneity of variance requirements, several measured physiological variables were transformed, although non-transformed 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 ANOVAs were used to determine if there were any physiological differences between fall backs and fish that continued upstream. Then, 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. Bonferoni corrections were applied for the 11 variables ($\alpha = 0.0045$). Two-way ANOVA was also used to examine differences in model predictions of theoretical estimates of DD accumulation between fish fate and migration timing. When analyzing for differences in travel rate, days were transformed using \log_{10} . A one-way ANOVA was used to test for differences in upriver travel rates between early and normal migrants. 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. In order to analyze data from sacrificed fish, several variables required transformation. Specifically, GSE and gill Na^+ , K^+ -ATPase values were \log_{10} -transformed; osmolality, Cl^- , and Na^+ were squared-transformed. Pearson's correlation was used to examine the relationship between river discharge and water temperature, as well as to explore the relationship between survival and water temperature, and survival and discharge. Chi-Square analysis was used to examine differences in survivorship between timing group and residence strategy.

RESULTS

Approximately 140 sockeye were captured over 9 sampling periods. No fish were captured on the first sample date. Of the 84 Weaver Creek sockeye that were released, 40 contained acoustic transmitters and 44 contained radio transmitters. One acoustic transmitter failed to function; data for this fish were not used in any analysis. Radio and acoustic transmitter carrying fish were pooled for all analyses. Of 83 fish, 53% ($n = 45$) were classified as early-timed and 47% ($n = 38$) as normal-timed (Table 2.1). There was no statistical difference in length measurements between early and normal-timed sockeye ($P = 0.1775$). While only 30% ($n = 25$ out of 83) of the telemetered fish successfully reached spawning areas, success was inversely related to the date the fish entered the Fraser River system. 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 2.1). About 49% of all fish were early-timed and unsuccessful at reaching spawning areas (Table 2.1), 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. A Chi-Square analysis revealed that there was a significant difference in survival between timing groups and residence strategy ($P = 0.0005$).

The unsuccessful early-timed migrant category includes eight fish that did not proceed upstream after tagging and release. These 'fall backs' were all captured prior to September 2 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 fall back fish ($n = 8$) to the other unsuccessful early-timed fish ($n = 34$) on 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 fall-back fish did not differ in physiological state at capture, we pooled them with the other unsuccessful early migrants.

All fish, except fall backs, continued their upriver migration after release, and we were able to determine mean travel rates for some early ($n = 31$) and normal ($n = 10$) timed fish. Early sockeye took less than half a day ($0.36 \text{ day} \pm 0.08 \text{ SE}$) to travel the 8 km upstream to the lake outlet, whereas normal timed migrants took almost five-times longer ($1.87 \text{ days} \pm .69 \text{ SE}$) to travel the same distance ($F = 13.63$, $P = 0.0007$, $n = 41$). All of these fish proceeded upstream immediately after release and all were detected on the uppermost receiver within Harrison River. Behaviour of our acoustic tagged sockeye suggests that captured fish were new arrivals to the area. The stationary receiver at the capture/release site indicated that tagged fish did not remain near the tagging site after release. Mobile tracking revealed that fish which remained within Harrison River and which were classified as 'river' residents were generally found in a few deep holding areas upriver of Morris Slough ($\sim 5 \text{ km}$ upriver of our tagging site).

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. 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 (Table 2.1). 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 residents. Within the normal-timed category, 86% of survivors were river residents. Chi-Square

analysis revealed that there was a significant difference in survival between timing groups and residence strategy ($P = 0.0005$).

In 2004, Fraser River water temperatures were well above the 60-year average reaching record highs ($> 21\text{ }^{\circ}\text{C}$) (Patterson et al. 2007a) for the early-timed component of the migration ($21.6 - 18.0\text{ }^{\circ}\text{C}$), but temperatures fell to more historically typical levels ($16.3 - 15.0\text{ }^{\circ}\text{C}$) when the normal-timed migrants entered the river (Figure 2.2). In late August, Harrison River water temperatures were also warm ($18.0 - 16.5\text{ }^{\circ}\text{C}$) for the early component of the migration, whereas normal-timed fish experienced cooler waters which were similar to those they just experienced in the Fraser River ($16.3 - 15.0\text{ }^{\circ}\text{C}$). Within Harrison Lake, surface temperatures closely resembled Harrison River temperatures at the start of our observations ($\sim 18\text{ }^{\circ}\text{C}$) and fell during September to $16\text{ }^{\circ}\text{C}$. The water temperature in the shallow regions of the lake ($20 - 40\text{ m}$) averaged $14.5\text{ }^{\circ}\text{C}$. Harrison Lake is stratified during the summer, and the thermocline was at approximately 45 m (Figure 2.3). The thermocline weakened in late October. In the deep regions of Harrison Lake ($>50\text{ m}$), the temperature throughout the study was $6.5\text{ }^{\circ}\text{C}$.

River discharge and water temperature were correlated in both river systems (Pearson correlations, Fraser River: $r = -0.3774$, $P = 0.0082$, $n = 48$; Harrison River: $r = 0.3521$, $P = 0.0141$, $n = 48$) (Figure 2.4). River discharge was not correlated with migration success. Instead, the water temperature encountered by migrants during their upriver migration in the Fraser River was strongly and inversely correlated with their subsequent fate (Pearson correlation, $r = -0.9186$; $P = 0.0275$, $n = 5$). Specifically, all migrants that experienced temperatures in the Fraser River averaging $>20\text{ }^{\circ}\text{C}$ failed to reach spawning grounds; 89% failed at $18\text{ }^{\circ}\text{C}$; 71% at $16\text{ }^{\circ}\text{C}$; and 36% failed at $14\text{ }^{\circ}\text{C}$ (Figure 2.5). There was no

relationship between survival and Harrison River temperature (Pearson correlation, $r = -0.515$; $P = 0.3749$, $n = 5$). There was no relationship between either Fraser River discharge, or Harrison River discharge and survival (Pearson correlations, Fraser River: $r = 0.5580$, $P = 0.2969$, $n = 5$; Harrison River: $r = -0.8032$, $P = 0.1016$; $n = 5$).

Of the 39 fish that were tagged with acoustic transmitters, six provided detailed (at least one week of data) information on sockeye depth behaviour. All six fish displayed similar depth behaviours, but three of these fish subsequently died in the lake and three reached the spawning grounds. They used the entire water column (surface to 170 m), but stayed in the deep regions an average of 81% of the time. Sockeye seemed to transition quickly and in many cases diurnally between deep and shallow regions (Figure 2.6). These vertical migrations to the surface at night, along with entering and leaving the lake, make up the majority of time spent at the surface. Percent time at depth was calculated for each fish, and when matched with the corresponding temperature at depth, revealed that sockeye spent on average approximately 81% of the time at 6.5 °C. Most of the remaining time fish spent in shallow waters at 14.5 - 16 °C (Figure 2.7). An example is provided of an individual's pattern of movement within the lake (Inset - Figure 2.7). The depth-time series (mean depth/hour) reveals this fish spent about 21 days in the Harrison Lake with over 75% of the time in the deep regions. The last detection (upper right) occurs seven hours prior to river re-entry for this and several other successful sockeye.

Of the 39 acoustic-tagged sockeye, 15 were confirmed mortalities identified in both Harrison Lake ($n = 10$) and Harrison River ($n = 5$) (Figure 2.8). Some of the sockeye died within range of a stationary receiver ($n = 8$), others were identified by mobile tracking ($n = 7$). In Harrison Lake, mortalities were identified at depths ranging from 5 m 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. For a small sub-set ($n = 3$) of lake fish that remained within range of stationary receivers for long periods of time, death could be readily observed from the depth recordings (examples in Figure 2.8). Stationary receivers within the river were not located in holding areas, where most of the mortalities were identified by mobile tracking.

Estimates of hypothetical DD accumulation revealed that based on river entry timing (early or normal) and migration residency (river or lake) that early-river and normal-lake fish differed significantly from each other, as well as from early-lake and normal-river fish (all $P < 0.05$; Figure 2.9). However, early-lake and normal-river fish were the same ($P = 0.111$). 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 °C DD 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 near or under a known disease threshold level for the endemic parasite *Parvicapsula minibicornis* (~ 450 °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 (7 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 < 450 °C DD and contrary to expectations, mortalities were associated with relatively low DD accumulation compared to fish which reached spawning grounds (Figure 2.9).

We found few effects of sex on physiological state with the exception of reproductive hormones and GSE (Table 2.2). Females had higher GSE levels, and plasma T and E₂ concentrations than males (Figure 2.10). E₂ concentrations were non-detectable for males. In general, timing had a strong influence on physiological state. Early fish had higher GSE levels, lower reproductive hormone concentrations, higher osmolality, Na⁺, Cl⁻, lactate and glucose concentrations (Figures 2.10, 2.11). There were a few interactions between sex and physiology, specifically, normal timed females had the relatively highest plasma T and E₂, and gill Na⁺, K⁺-ATPase was highest in early males. Because fish fate and timing are correlated with each other (Table 2.1) it is not surprising that fate, like timing, also explained variation in the physiological variables (Table 2.2). However, generally the effect of fate was weaker than for timing (e.g. GSE, concentrations of E₂, glucose and Na⁺) or not significant (e.g. osmolality, gill Na⁺, K⁺-ATPase activity, Hct and concentrations of T, Cl⁻ and lactate). Only with plasma K⁺ was significant with fate but not timing (Table 2.2).

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 2.3). 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 2.3 and Figure 2.11). 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 hematocrit had means which were ~ 30% and 20% higher than biopsy mean values. Mean plasma lactate was approximately 70% lower in sacrificed early-timed fish but nearly identical to that in normal-timed biopsied fish.

DISCUSSION

Migrating sockeye which arrive in the Harrison River prior to early October must either reside in Harrison River or the nearby Harrison Lake because their spawning areas cannot be accessed due to low water. We predicted that early-timed migrants, fish normally encountering the highest river temperatures, which adopted a lake-component to their migration, would survive better than those that did not. Indeed, for the 45 early-timed sockeye, the only successful strategy was to make a directed migration past their spawning creek, and enter Harrison Lake. No early-timed fish that remained within Harrison River was ever detected on the spawning grounds. In fact, the majority of early-timed sockeye migrated into the lake after release. Once in the lake, we estimated that fish spent at least 80% of their time in the cool hypolimnion. Our results support those from other studies which have shown that Pacific salmon will behaviourally thermo-regulate during their upriver migration to increase their likelihood of reaching spawning grounds. Berman and Quinn (1991) found salmon capable of mitigating sub-lethal effects of high temperatures by residing within cool-water refugia and that they modified their homing behaviour to optimize energy conservation. Newell and Quinn (2005) found that sockeye will wait out the warm months in deep areas of Lake Washington at temperatures ideal for sexual maturation and energy conservation.

Early-timed Weaver Creek sockeye traveled significantly faster up the lower Fraser River (Crossin et al. 2008) and they traveled faster up the Harrison River (this study), than normal-timed sockeye. In our study, early fish traveled five-times as fast as their normal-timed counterparts. Differences in travel rates may be a behavioural response to avoid hot temperatures and access refugia as quickly as possible. The lower Fraser River is relatively thermally homogeneous (Patterson et al. 2007a) so rapid migration to the Harrison River provides some thermal refuge from high temperatures for early migrants; rapidly accessing Harrison Lake does the same for early migrants in the Harrison River. Our results are supported by findings in Young et al. (2006) for another Late-run Fraser sockeye stock (Adams River). Their early-timed component, which was exposed to temperatures approaching 20 °C, traveled significantly faster than their normal-timed component. As in our study system, Young et al. (2006) examined fish in a Fraser tributary (the Thompson River) which is thermally homogenous and with primary thermal refuges being lakes situated upstream. In the Columbia River, Goniea et al. (2006) found that salmon responded to high temperatures by delaying migration in areas that offered thermal refugia. Keefer et al. (2008) also found slowed migration rates for later-timed sockeye which experienced warm water and that late-season mortality was strongly associated with water temperatures near tolerance thresholds (21 - 24 °C).

Not all normal-timed river residents were successful; however, their strategy was more successful than becoming lake residents, in contrast to the early-timed component. 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, particularly as river temperatures

were < 16 °C by that time. Not using the lake also would have allowed normal-timed fish more time at the spawning grounds since accessing the lake involved migrating past their spawning area.

All migrants, regardless of timing group, exhibited diel behaviour in Harrison Lake. Forays into the epilimnion and to warmer surface waters seemed to occur predominantly at night. As juveniles, sockeye undertake a similar diel migration in lakes in response to feeding opportunities and predation risk (Clark and Levy 1988). Using data loggers that recorded temperature, Walker et al. (2000) found that several species of sub-adult Pacific salmon rearing in the north Pacific Ocean moved to the surface at night, possibly to feed, and descended to deeper, cooler water during the day. As our study animals are not feeding, surface forays at night may be used to aid in navigation and direction finding. Wada and Ueno (1999) suggested that vertical movements by Pacific salmon during migration in the open ocean may be associated with orientating and locating position. The olfactory cues needed for locating Weaver Creek will presumably be found in the epilimnion of Harrison Lake thus brief surface forays could be used to ensure location prior to leaving the lake while still receiving thermal refuge most of the time in the hypolimnion.

The ‘earliest’ of the early-timed migrants ($n = 8$; all 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 which 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 (Steinhausen et al. accepted). Thus fish either cannot migrate upriver, or must do so anaerobically but can do this only for a limited time before blood acidosis becomes lethal. Though we did not find lethally high

lactate concentrations (e.g. > 12 mmol/L; Jain and Farrell 2003) in these ‘earliest’ fish, early-timed fish had much higher levels than normal-timed fish supporting the hypothesis that cardiovascular collapse was a contributing cause of mortality in these very early-timed fish (Farrell et al. 2008).

A potential consequence of migrating early and at high temperatures is increased susceptibility to, and prolonged development of, freshwater diseases (Gillhausen 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 which had accumulated > 450 °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 has found little evidence that fish which accumulate such high DD levels 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 DD, and hence, disease levels. We confirmed with a sub-set of fish that actual DD accumulation for successful migrants was ≤ 450 °C DD. Very few fish died within range of an acoustic receiver so calculating actual DD accumulation for them was difficult. Those that did die in the detection radius of a receiver did so very early in

the migration with low DD accumulation. Unfortunately, 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. Patterson, Canadian Dept. Fisheries and Oceans, unpub. 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 hematocrit) than normal-timed migrants. High water temperatures, in some cases approaching or at lethal limits and the associated effects of reduced aerobic scope are likely responsible (Servizi et al. 1977; Lee et al. 2003; Farrell et al. 2008). 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. Dip-net sampling of adult sockeye, perhaps the quickest and least invasive sampling approach, during their Fraser River migration has recorded plasma lactate of 2 - 4.5 mmol·L⁻¹ (Pon et al. In press; Young et al. 2006). Our biopsy lactate values were about 2-3 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 into a net pen. Our destructive sampling lactate values should be more representative of ‘immediate capture’ because these fish were the first ones removed from the net pen to be sampled. Indeed, these lactate values overall were lower than biopsy values yet early-timed fish still were higher (averages: early = 6.6 mmol·L⁻¹; normal = 5.9 mmol·L⁻¹). Other physiological measures obtained from destructive sampling (e.g. osmolality, hematocrit) 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, all were $< 2 \text{ umol ADP} \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$, between early and normal-timed fish indicating that both groups were ionoregulatorily capable of functioning in freshwater and equally able to transport ions (Hinch et al. 2006), and these are levels expected for migrating sockeye salmon (Shrimpton et al. 2005). 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.

Relating our physiological measures at time of capture to ultimate migration fate can be a challenge particularly because many of the fish sought thermal refuge in the lake thus, high initial stress may not be indicative of stress levels at time of death. It is, however, possible that some of the early-timed fish may have succumbed to lactic acidosis early in their migration as some individuals had plasma lactate levels which exceeded laboratory-defined criterion of recovery (e.g. $12 \text{ mmol} \cdot \text{L}^{-1}$, Jain and Farrell 2003). However, one early fish that reached spawning grounds had an initial lactate level of $12.9 \text{ mmol} \cdot \text{L}^{-1}$ and one normal-timed fish that reached spawning grounds had initial lactate of $21.1 \text{ mmol} \cdot \text{L}^{-1}$. A recent biopsy telemetry study on marine-captured (with purse seine) and released sockeye found that several fish reached spawning areas with initial lactate values exceeding $11 \text{ mmol} \cdot \text{L}^{-1}$ and some as high as of $18 \text{ mmol} \cdot \text{L}^{-1}$ (Crossin et al. in press). It is clear that physiological stress, whether associated with warm temperatures and/or capture and handling can affect fish physiology, however, it is also apparent that sockeye are resilient and quite capable of completing successful spawning migrations even when metabolite or ion levels deviate significantly from 'homeostasis' levels at the start of their migration.

Early-timed fish were less reproductively advanced than normal timed fish, having higher GSE (likely because they had not diverted as much energy yet 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 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 entered the Fraser River but failed to show up on spawning grounds suggesting ~57% overall migration mortality (Williams 2005). Record high river temperatures were believed to be responsible for much of this mortality (e.g. Farrell et al. 2008). However, few carcasses were found along the migratory route which raised suspicions among several stakeholders that many missing fish did not perish naturally but rather were either illegally captured and not reported captured in legal fisheries, or in fact never existed, a result from errors in stock assessment (Williams 2005). Other high temperature years with reports of ‘missing adult salmon’ (e.g. 1993 and 1998) also commented on the lack of large numbers of carcasses along migratory routes (Fraser 2004). The phenomenon of ‘adult salmon going missing’ and being unaccounted for in the Fraser River system has generated over the past 20 years several federal and parliamentary inquiries or Fisheries and Oceans Canada investigations. Laboratory experiments that placed dead

mature adult sockeye into large tanks found that the fish sunk, and floated only after several days and once bacterial decay began (Patterson et al. 2007b). In turbid and muddy bottom migratory routes it is unlikely that carcasses would float up from the bottom as they would quickly get covered in sediments and rapidly scavenged. Alternatively, weakened fish could be eaten by predators prior to death. We witnessed no floating carcasses in the Weaver-Harrison system despite ~ 90,000 fish disappearing in freshwater en route to spawning grounds, representing ~ 80% migration mortality (M. Lapointe, Pacific Salmon Commission, Pers. Comm. 2004). In addition, we confirmed that over 50% of our acoustic-tagged sockeye ($n = 15$) sank to the bottom of Harrison Lake or Harrison River, where they remained until the end of our study and were presumed to have died. Our lower study mortality rate compared to that of the whole population is likely related to sampling predominantly from the second half of the run. In 2004, 50% of the run had passed Mission BC ~ August 22, about the time we started sampling (M. Lapointe, Pacific Salmon Commission, Pers. Comm. 2004). Therefore, we did not tag fish that were probably the most thermally stressed and most aberrantly early-timed individuals in the population – the ones which likely all perished prior to reaching our sampling locales.

Table 2.1. Percentage of Weaver Creek sockeye classified by timing group and fate, timing group and residence location, and timing group and survival relative to residence location. Early-timed fish were captured prior to September 2, normal-timed fish were captured after September 13. Fish detected at Weaver Creek (radio) or Morris Lake (acoustic) were classified as successful migrants. Migrants which entered Harrison Lake were classified as lake residence; all others were classified as river residence. Sample sizes are in brackets. Early-timed unsuccessful migrants includes eight fish which were classified as ‘fall backs’; details in text.

	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)

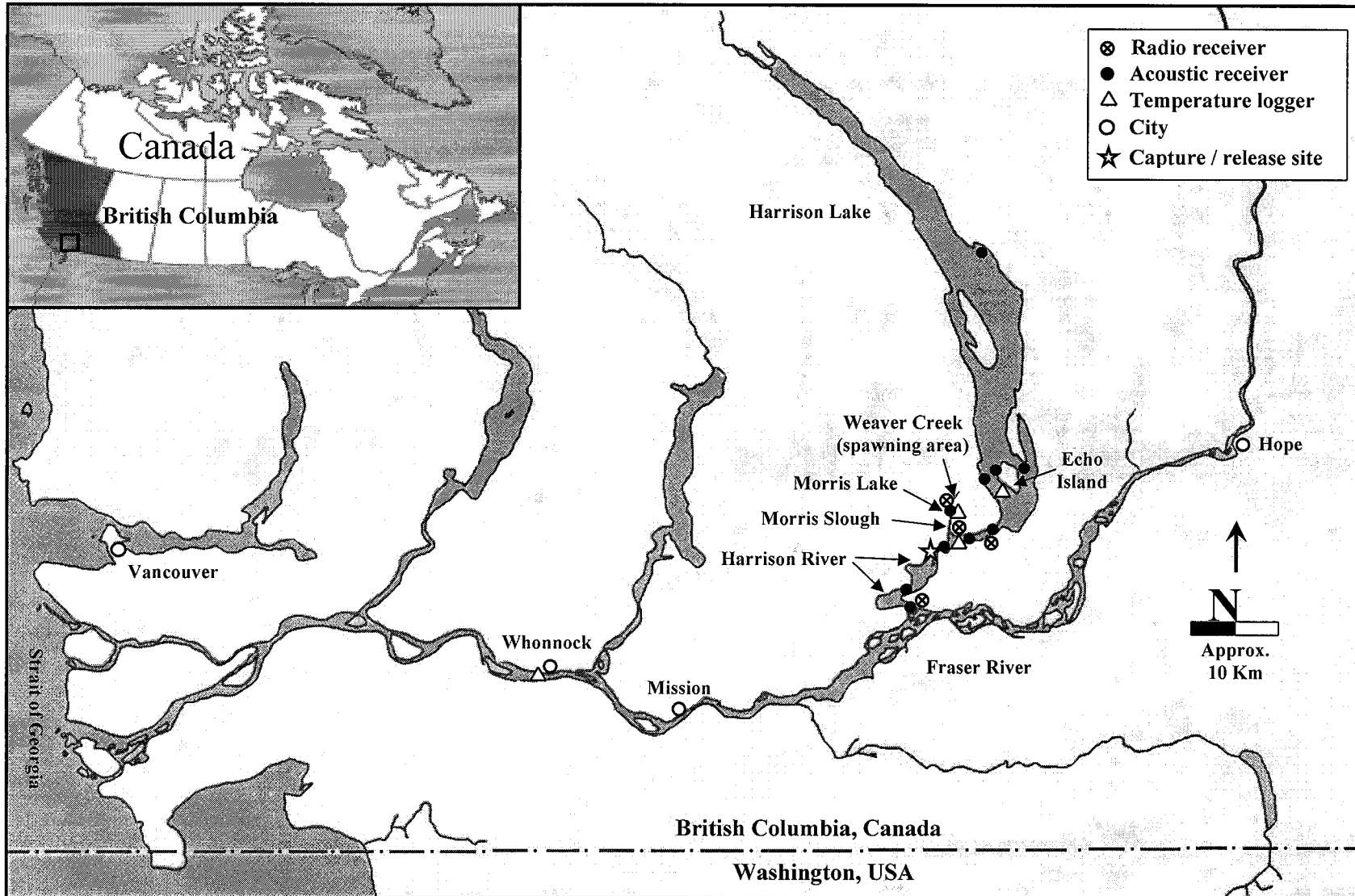
Table 2.2. F and P value results from two-way ANOVAs assessing the effects of sex and timing, sex and fate, and interactions on physiological variables from biopsied sockeye salmon. Statistical significance was assessed at Bonferroni corrected $\alpha = 0.05$ for groupings of variables: for ionoregulatory $\alpha = 0.01$ (gill Na^+, K^+ -ATPase, osmolality, and ions) and for stress $\alpha = 0.017$ (lactate, glucose, and Hct). We indicate when variables were significant at the $\alpha = 0.05$ (bold) and at the specific Bonferroni-corrected value (bold*). Transformed variables are represented with (\dagger).

Physiological variable	Sex x Timing			Sex x Fate		
		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>
Gross somatic energy (MJ·kg ⁻¹) \dagger	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	13.58	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 17 β -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 ($\mu\text{mol ADP} \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$)	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) \dagger	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) \dagger	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) \dagger	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

Table 2.3. Mean (\pm SE; N = sample size) of physiological variables for sacrificed Weaver Creek sockeye by timing group, and by sex for some variables. P values from ANOVAs are presented for the effects of timing, and where effects were relevant for biopsied sockeye (see Table 2.2), 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 Hct). We indicate when variables were significant at $\alpha = 0.05$ (bold) and at the specific Bonferroni-corrected value (bold*). Transformed variables are represented with (\dagger).

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

1



2

3 Figure 2.1. Map of the lower Fraser and Harrison Rivers and Weaver Creek spawning area with an inset map of Canada showing the
 4 study area (box) within British Columbia (shaded). Locations of relevant cities, acoustic and radio receivers, and temperature data
 5 loggers are indicated. The capture and release site is indicated by a star.

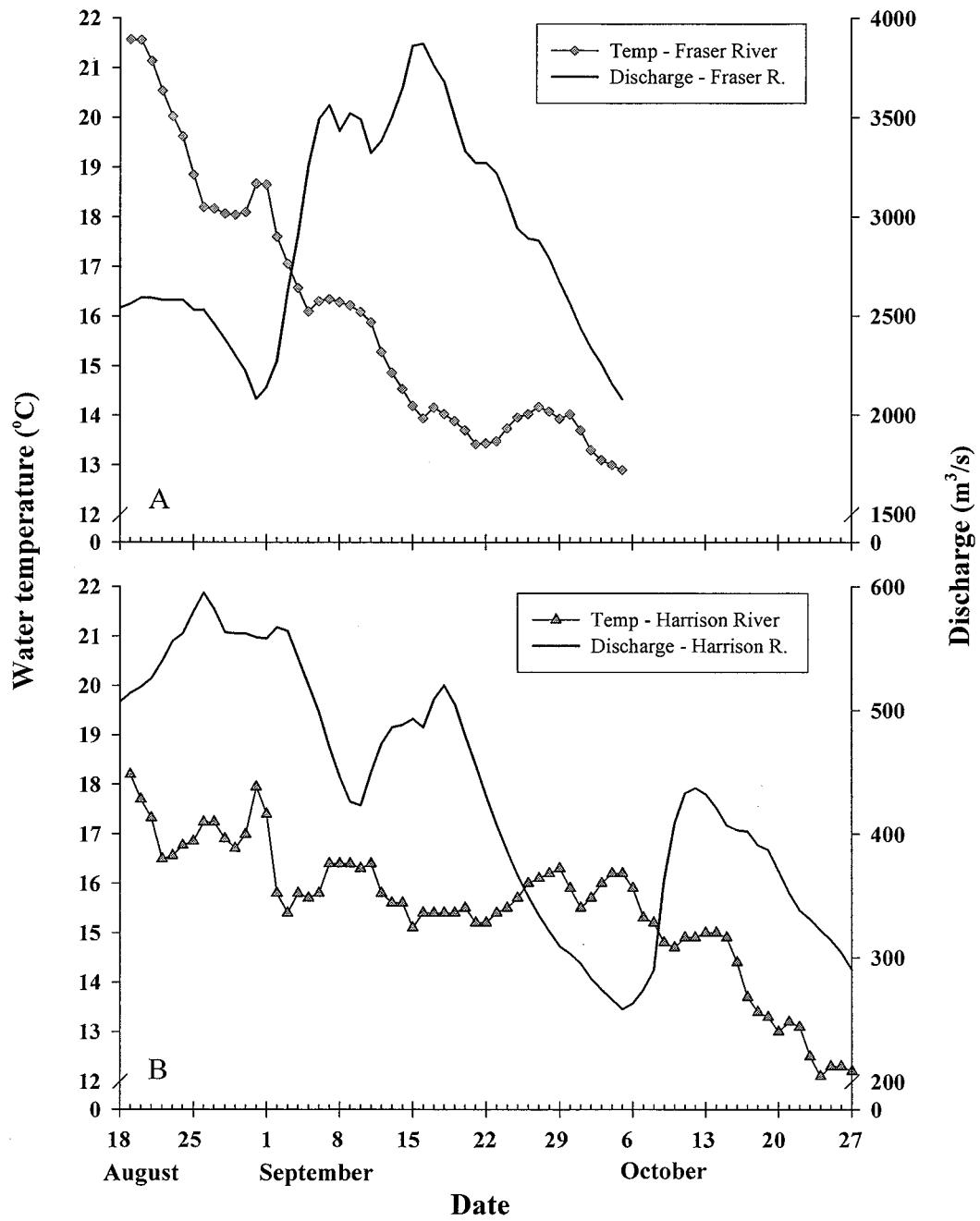


Figure 2.2. Mean daily water temperature and corresponding discharge levels for the Fraser (A) and Harrison (B) Rivers during the study in 2004.

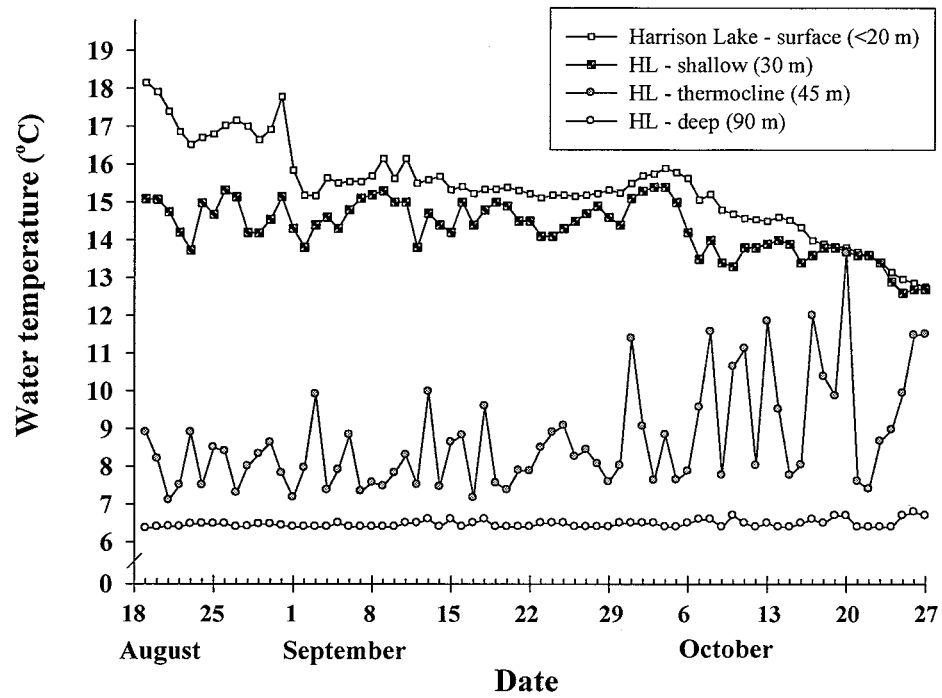


Figure 2.3. Mean daily Harrison Lake temperatures during the study period in 2004 at four different depths regions within the lake.

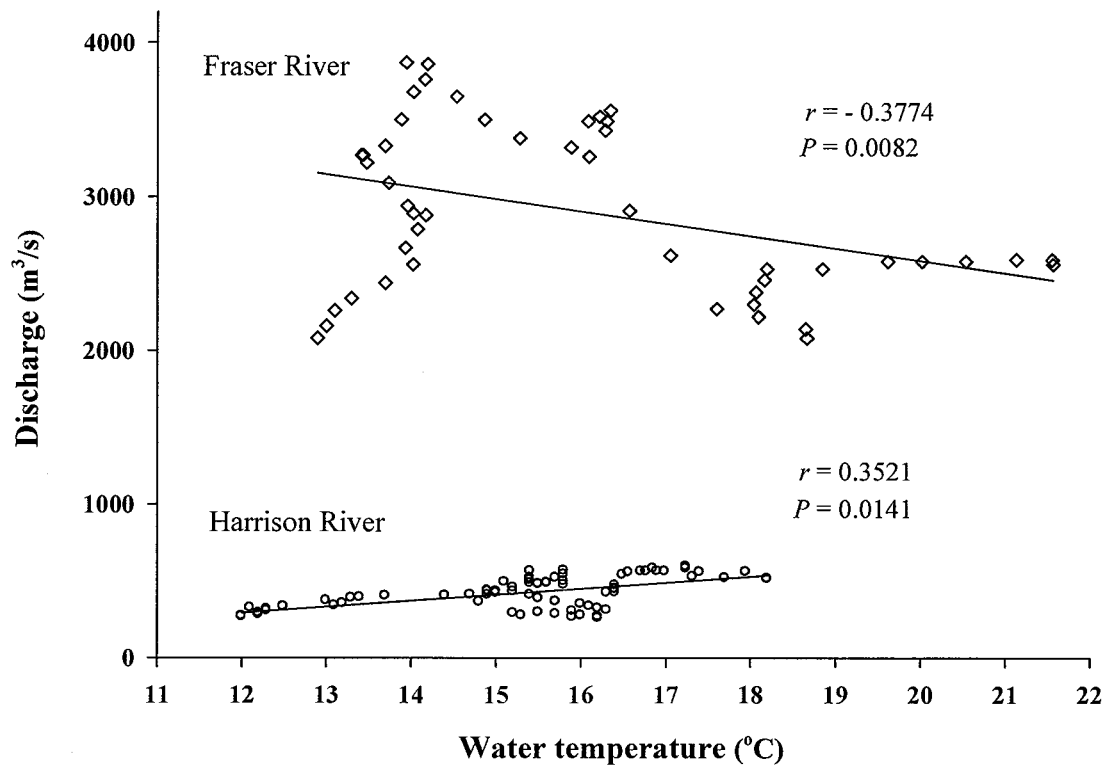


Figure 2.4. Relationships between mean daily water temperature and river discharge for the Fraser and Harrison Rivers during our study period in 2004.

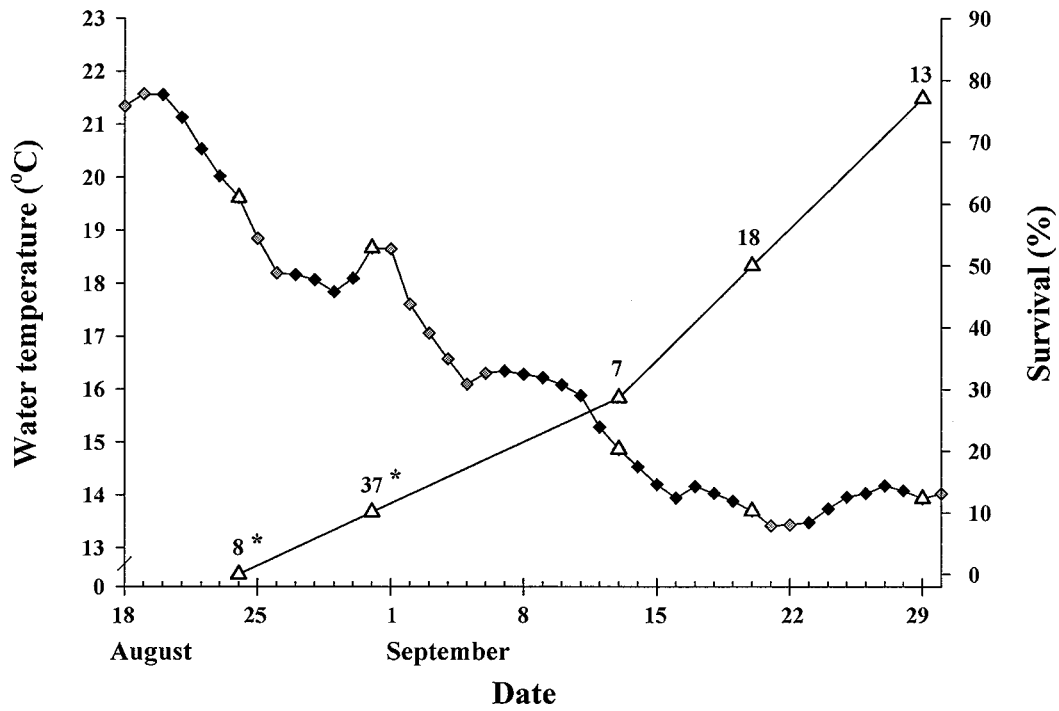


Figure 2.5. Fraser River mean daily water temperature plotted with percent survival (spawning ground detection) for each capture day demonstrate the relationship between thermal experience and survival. Black diamonds represent the estimated range of thermal experiences by sockeye prior to their capture. Sockeye were captured in the Harrison River (see Figure 2.1) near the confluence with the Fraser River immediately after completing the Fraser River component of their migration. Capture dates are represented by triangles with numbers of tagged and released sockeye shown above. For the first two sampling periods, dates were collapsed to represent one capture day. The remaining three sampling periods were not collapsed. *capture date = 24 Aug {n=8} (combined dates; 24 Aug {n=5} and 25 Aug {n=3}); *capture date = 31 Aug {n=37} (combined dates; 30 Aug {n=28}, 31 Aug {n=2}, and 2 Sep {n=7}).

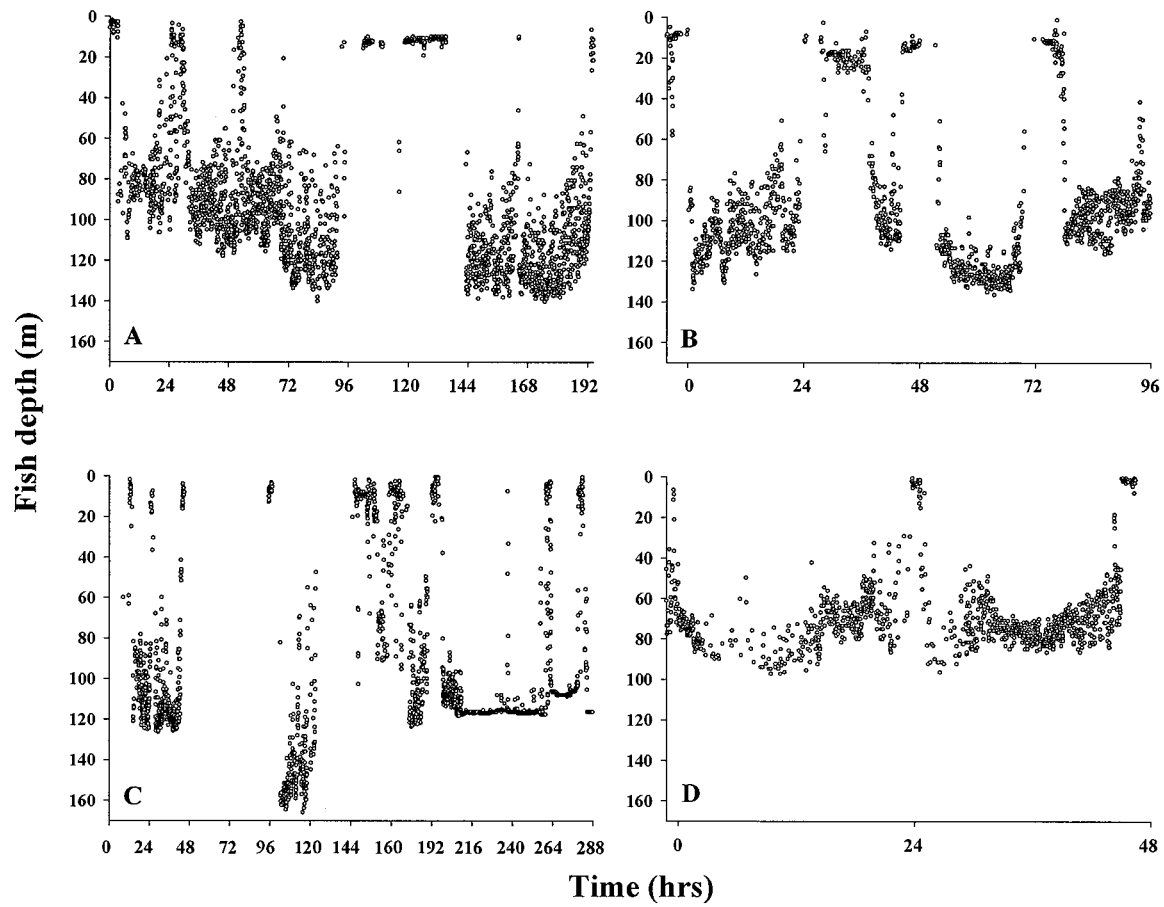


Figure 2.6. Depth recordings for four individual sockeye (Panels A-D) in Harrison Lake.

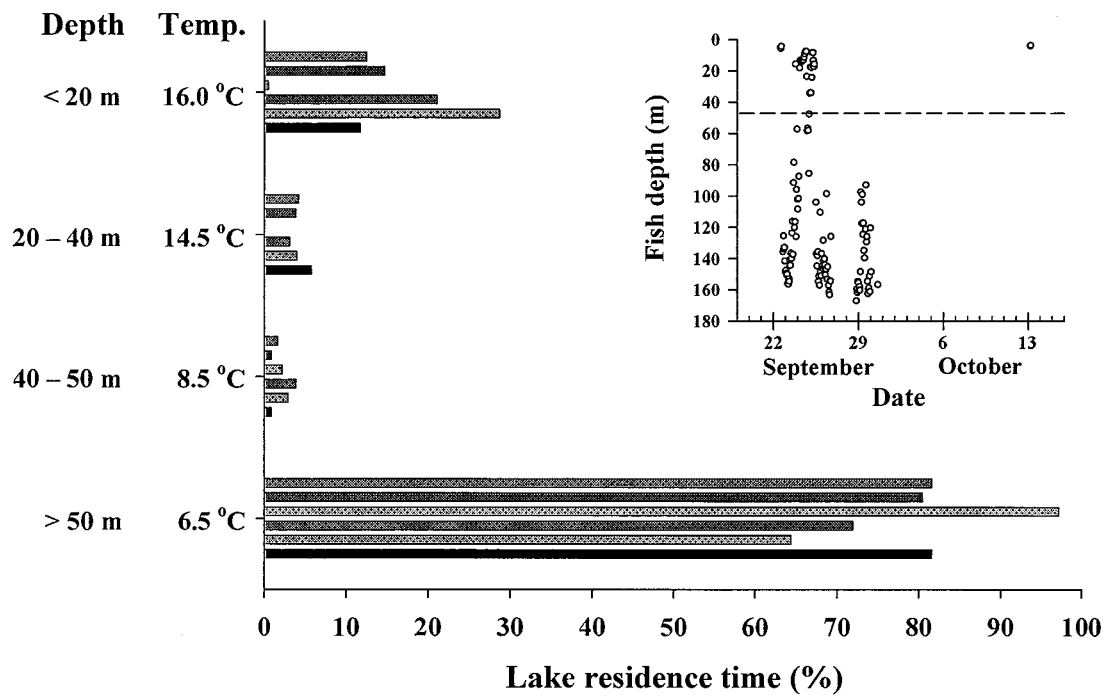


Figure 2.7. Percent time six sockeye were present in a depth range, with associated Harrison Lake temperatures. Each column represents one of six individual fish. The data presented represent for each fish over 50% of the time they spent as lake residents. The inset is an example of an actual fish's depth history within the lake (mean depth per hour). This normal-timed, successful fish accumulated an estimated 200 DD while in the lake (white circles), with a total of ~370 DD by the time of detection at spawning grounds. The thermocline (45m) is represented by a dashed line.

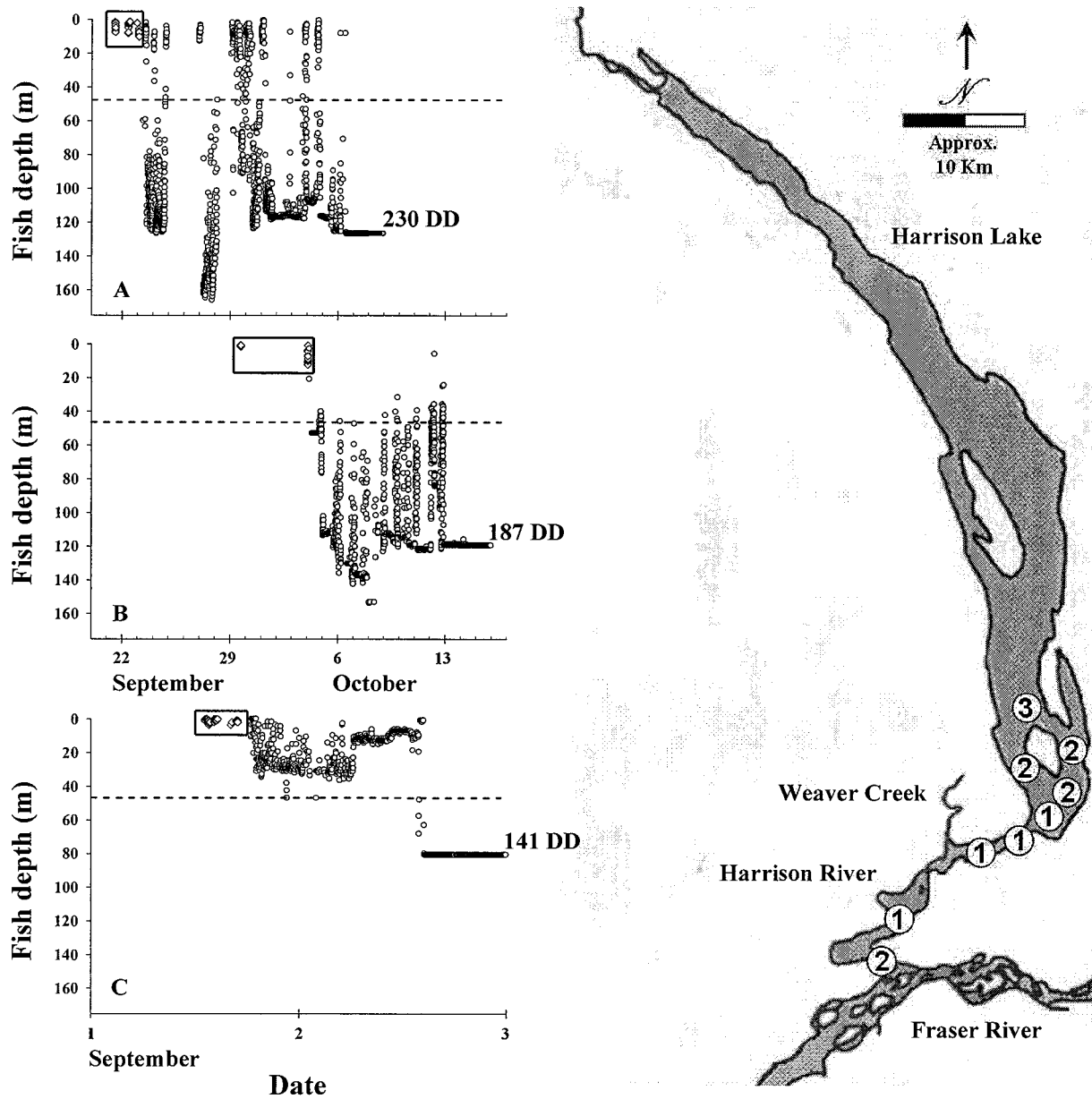


Figure 2.8. Depth-time relationships for three individual acoustic transmitter sockeye (A–C) from time of release and travel in Harrison River (rectangles, far left in each panel) until death occurred within range of a VR-2 receiver in Harrison Lake (solid lines far right in each panel). Degree-day estimates were based on individual recorded depth histories (time spent at depth) with the corresponding temperature data. The thermocline (45m) is represented by a dashed line. The map to the right indicates the location and number of confirmed sockeye mortalities within Harrison River and Lake.

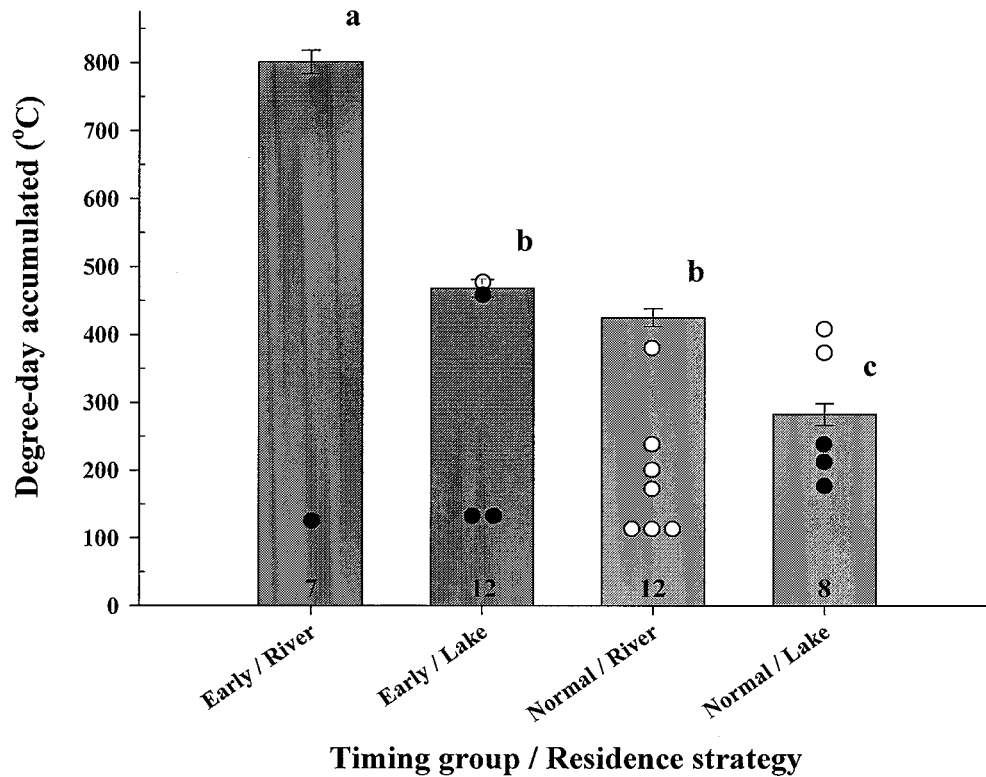


Figure 2.9. Hypothetical mean degree-day accumulated (\pm SE) for all acoustic tagged sockeye from freshwater entry until 15 Oct, 2004 (peak spawning). Letters above the bars indicate significant differences at $\alpha = 0.05$, Scheffe's *post hoc* multiple comparison procedure. Sample sizes (n) are shown within each bar. The circles represent actual degree-day values estimated for successful fish detected on the spawning grounds (white circle) or that died in front of a stationary receiver (black circle).

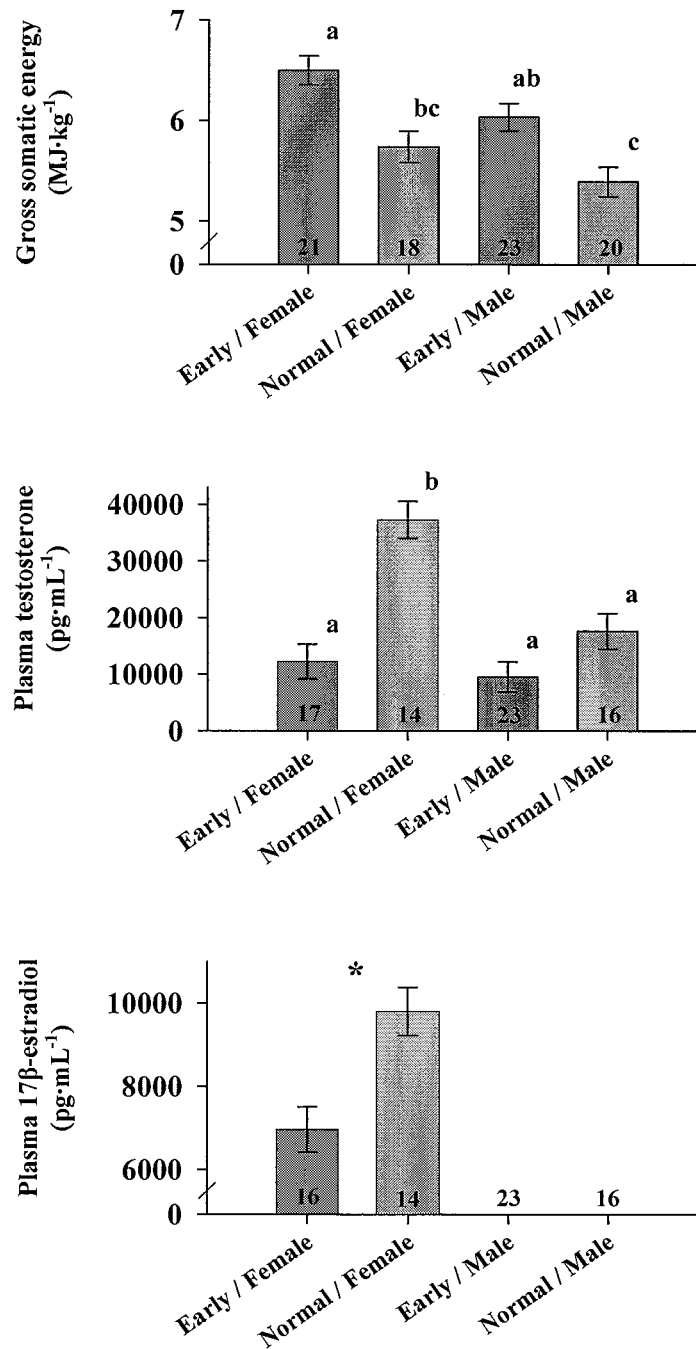


Figure 2.10. Mean (\pm SE) energy and sex hormone concentrations based on sex and timing. Letters above the bars indicate statistically significant differences at $\alpha = 0.05$ using Scheffe's *post hoc* multiple comparison procedure. All male plasma 17 β -estradiol values were undetectable and are not shown; an asterisk (*) indicates a significant difference between female 17 β -estradiol values. Sample sizes (n) are shown within each bar. ANOVA P and F results presented in Table 2.2.

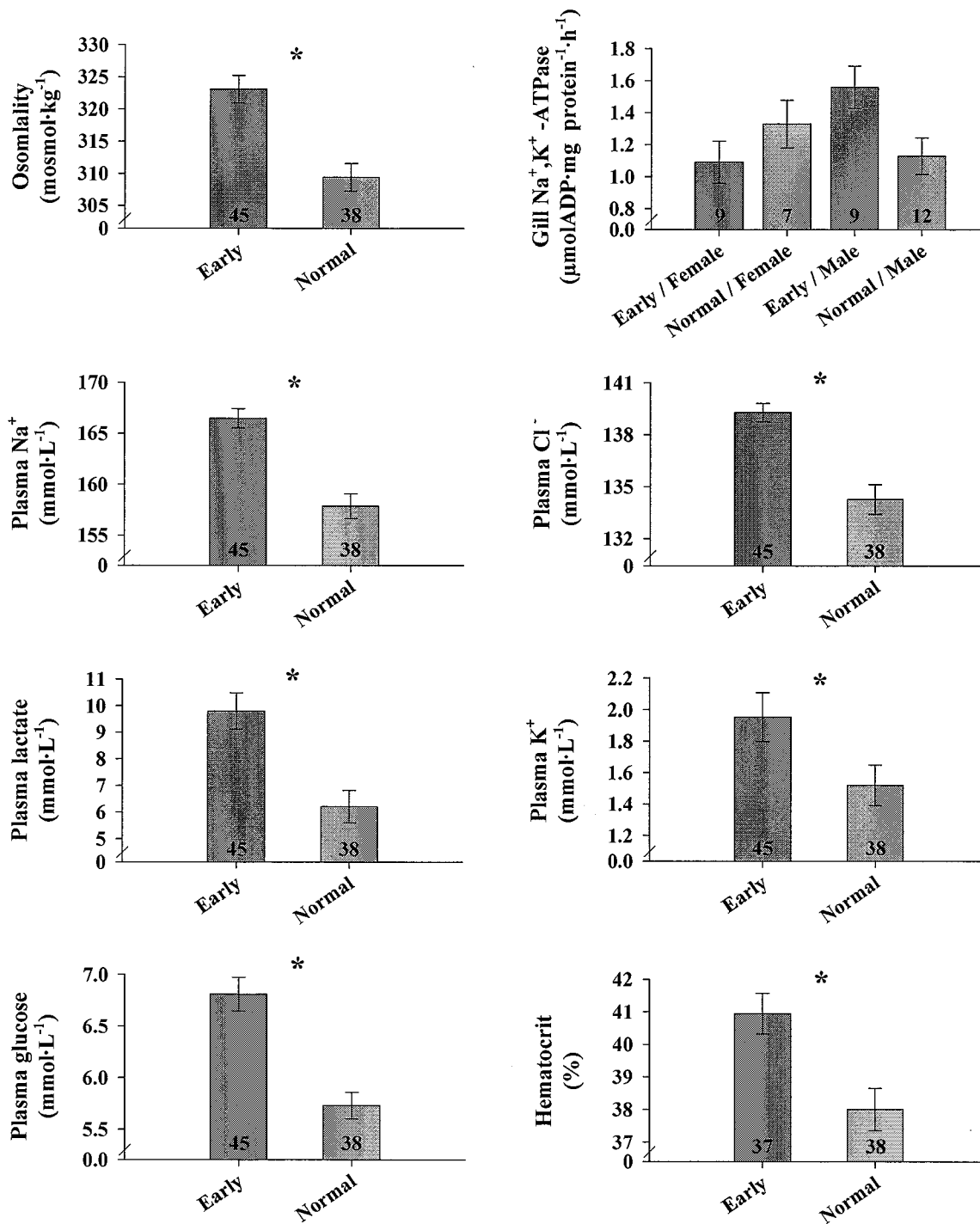


Figure 2.11. Physiological differences in ionoregulatory and stress measures (mean \pm SE) based on timing (sexes pooled). Asterisk (*) indicate statistical significance at $\alpha = 0.05$. Sample sizes (n) are shown within each bar. ANOVA P and F results presented in Table 2.2

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CHAPTER 3

Management Implications and Future Research

Management implications

Each year, several months prior to their freshwater migration, managers estimate the expected number of adult sockeye salmon returning to the Fraser River and meet with stakeholders to discuss potential fisheries and allocation of fish to various stakeholder groups (Williams 2005). Shortly after adults make landfall from the open ocean, coastal test fisheries are conducted to refine stock assessments and to modify fishing plans accordingly. Fishing plans are further adjusted based on test fisheries and hydroacoustic sampling of migrants as they enter the lower Fraser River (Williams 2005). Fraser River sockeye salmon are currently managed with an exploitation rate approach, which allows managers to balance conservation risks to Late-run stocks, while allowing harvest on healthier co-migrating stocks (Lapointe 2008). During Weaver-dominant years, a 15% target exploitation rate is used (Lapointe 2008). The harvest rate and season openings are set to protect endangered stocks from over-exploitation and, first and foremost, to ensure adequate spawning ground escapement as well as First Nations allotments.

Since the late 1970s, the Pacific Salmon Commission has been estimating the number of sockeye entering the Fraser River using a hydroacoustic approach at Mission, BC. Managers estimate the number of fish by run timing group and stock where possible and compare these values to spawning ground escapement estimates. The differences between these two estimates, after correcting for in-river harvest, are termed 'discrepancies' which could arise from unreported catch, measurement errors, en route mortality, or some elements of all three (Williams 2005). Discrepancies tend to be large when environmental conditions

are difficult for migration (e.g. high temperatures or discharge), suggesting that natural mortality is a significant component of these discrepancies (Hague and Patterson 2008; Williams 2005). Empirical models using several years of data for each run-timing group have been developed, enabling managers to predict ‘discrepancies’ based on temperature and discharge levels (Hague and Patterson 2008). These ‘Environmental Management’ models are now used, along with predictions from a Fraser River hydrological model which uses daily discharge and temperature information collected throughout the Fraser River watershed, to forecast thermal and flow conditions approximately 10 days into the future (DFO Environmental Watch Program 2008) and predict potential en route mortality. If mortality is expected, adjustments to harvest can be made (termed ‘Environmental Management Adjustments’, or EMA), which normally entail some level of reduced harvest in order to ensure that escapement goals can be met.

My research is beneficial to fisheries managers as it confirms that ‘discrepancies’ can indeed be largely associated with actual mortality, and by providing potential mechanisms to explain the mortality (e.g. accumulated DD, disease, and stress) (see chapter 2; Wagner et al. 2005; Young et al. 2006; Crossin et al. 2008; Farrell et al. 2008). By identifying mechanistic links between warm temperatures, stress and mortality, my research findings also can provide guidance to fisheries managers as they begin to deal with how climate warming affects fisheries. Specifically, sockeye migrating in warm rivers are physiologically stressed and may be further stressed by handling during recreational catch and release fisheries. Research on the impacts of recreational fisheries clearly demonstrates that warm water is an important determinant of sub-lethal disturbance and mortality for many fish species (Cooke and Suski 2005). For example, mortality of Atlantic salmon which were captured and released during

spawning migration increased exponentially when fish are caught in water temperatures above 18 °C (Thorstad et al. 2003). Although less studied, commercial fishing may also play an influential role in migration success of salmon in warm years. Capture gears (e.g. gill nets) are not 100% efficient; some fish are briefly captured, but will struggle and escape. In a pilot study with Fraser sockeye, post-release mortality after artificial entanglement was significant at extreme temperatures (H. Kriebert, DFO, unpub. data). In warm years, if fish are caught/released or escape commercial fishing gear in the lower Fraser, an area offering little thermal refugia, some fish may be too stressed to recover and complete their spawning migration.

The early-entry behaviour of Late-run stocks has caused a major conservation crisis resulting in severe limitations on harvest (Lapointe 2008). Since large segments of Late-run fish that enter the Fraser River early will die before reaching the spawning grounds (see Chapter 2), it has been suggested that the 15% harvest rate should be applied in-river rather than in the marine environment (Lapointe 2008). By shifting harvest towards fish that have entered the river early, there would be a large escapement of fish entering when conditions were more favourable, thus increasing the probability of each fish completing a successful spawning migration. Mortality rates in my research were consistent with previous studies for early-timed migrants in the Fraser River (> 90%) and strengthen the argument to harvest early-timed fish. From a commercial fisherman's point of view, the vast majority of these fish will die prematurely and they should not be wasted.

However, from a population genetics point of view, protecting the few early-timed sockeye that are able to spawn is potentially the only hope for the perpetuation of a given stock particularly as this segment of the stock experiences the highest temperatures thus they

may reflect individuals with the highest temperature tolerance or best behavioural adaptations to survive in a future warming climate. Moreover, thermal tolerance can evolve in wild fish given the right conditions (Crozier et al. 2008). Also, from an ecologist's perspective, these fish are an important input of nutrients into the food chain; protecting these fish mitigates potential ecosystem disruptions in upriver habitats.

In addition to considering the implications of early migration and increasing water temperatures for harvest management, habitat management issues must also be considered. Not all sockeye incorporate a lake component into their life history, however, for the majority that do, natal lakes are a critical habitat providing thermal refuge. Recent research into lake behaviour of adult sockeye has revealed that sockeye are found at depths which correspond to preferred thermal ranges (Pon et al. 2006; Newell and Quinn 2005). My research demonstrates that, in a very warm year, lakes provide critical habitat for thermally stressed sockeye. To mitigate the negative effects of high temperatures for vulnerable stocks, managers need to provide heightened habitat protection for areas that offer thermal refuge (e.g. lakes and cold water tributaries). Future habitat management decisions involving water use (e.g. water diversions) should take into consideration the role that lakes can play in the survival of sensitive stocks.

In addition to the protection of natal lakes, managers may consider other options. Habitat manipulations such as cool water diversions have been attempted within the Fraser River system. Especially in snow dominated watersheds, cold water storage facilities can be used as a source of cold water. While cold water releases have been considered successful in California, those attempted in British Columbia (e.g. Horsefly) have had questionable results (Nelitz 2007) and have incurred huge capital costs. My research demonstrates that cold

water diversions may offer little help for adult sockeye that enter the lower Fraser early. While water temperatures were high, fish that migrated through areas offering little to no thermal refuge (e.g. the lower Fraser River) experienced high mortality. The amount of cool water needed to artificially create a thermal refuge would require unrealistically large diversions. In addition, once fish migrate into smaller systems such as the Harrison River, diversions would offer limited added benefits considering the close proximity and accessibility of the lake.

The results from Chapter 2 provide a looking glass into the future for all Fraser River sockeye stocks that will feel the increasing pressures of rising water temperatures and shifting flow patterns associated with climate change (Ferrari et al. 2007; Morrison et al. 2002). According to Morrison (2002), future peak flows may occur as many as 24 days earlier, possibly influencing migration entry timing. All Fraser River sockeye stocks now encounter temperatures 1-2 °C higher than average (Natural Resources Canada 2008; Patterson et al. 2007), but this increase is still within stock-specific historical ranges and probably within stock-specific aerobic scope of activity. Extreme temperature years like 2004 reveals what the future may hold for non-Late run stock groups. The thermal experience by Late run sockeye in 2004 of 4-6 °C above their long-term average, and the associated high levels of mortality, is what all stocks will likely experience in the next 60-80 years (Morrison et al. 2002; Rand et al. 2006). It is possible that some stock groups may be able to adapt to warmer temperatures, or some may alter their migration timing and routes to avoid these future high temperatures if thermal refuges are available. Regardless, managers will be forced to further limit fisheries in the future to ensure that adequate numbers of fish from all stocks reach spawning grounds.

Future research

Further research is needed to better understand the function natal lakes play in migration success and to further explore the thermal benefits offered by them. Many sockeye stocks transit through lakes in order to reach spawning grounds. However, for a few stocks like Weaver Creek sockeye, the spawning grounds can be reached without entering their natal lake. The choice to enter the lake is not clearly understood. It is evident that early-timed migrants must enter the lake to survive; however, it is unclear if normal-timed sockeye gain the same benefits. The reason that normal-timed migrants enter the lake may be a part of their normal behaviour, retracing their out-migration path as juveniles, or it may be for the thermal benefits, or for some other reason.

Intergenerational aspects of early migration are also poorly understood. Experimental energy depletion studies have shown that the most energy depleted fish had poor spawning success (K. Hruska, UBC PhD student, unpub. data) and that embryo and fry survival were affected (P. Nadeau, UBC MSc student, unpub. data). However, further studies are needed to gain a better understanding of how thermal migration challenges affect fitness. Do successful migrants which experience warm river temperatures pass along physiological or behavioural traits to their offspring which makes them better at surviving warm migrations? Considering the implications of climate change, Crozier et al. (2008) suggests the importance of understanding how (and if) populations differ genetically in their tendency and ability to adopt such traits.

Finally, research is also needed that not only examines stock-specific temperature thresholds (e.g. Lee et al. 2003) but does so using realistic thermal experiences. Laboratory research has been able to provide valuable insights into thermal mortality patterns (e.g.

Crossin et al. 2008; Farrell et al. 2008), yet it has not examined how hourly or daily variation in thermal exposure which occurs in the wild affects migration survival, nor how thermal refugia of differing intervals affects survival.

In conclusion, my thesis research provides insight into future challenges for an important ecological, economic, and socio-cultural resource in British Columbia. However, further research is needed to better understand stock-specific temperature thresholds, intergenerational effects, and the role of natal lakes in migration success. If water temperatures continue to rise as predicted, sockeye salmon populations will face ever-increasing challenges, especially in the Fraser River as they are at the southern limits of the species distribution.

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