NRC Research Press

ARTICLE

Sex-specific differences in physiological recovery and short-term behaviour following fisheries capture in adult sockeye salmon (*Oncorhynchus nerka*)

Erika J. Eliason, Melissa Dick, David A. Patterson, Kendra A. Robinson, Jeremy Lotto, Scott G. Hinch, and Steven J. Cooke

Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

Abstract: Numerous laboratory and field studies have found that female Pacific salmon have higher mortality than males during their once-in-a-lifetime upriver spawning migration. However, the proximate cause(s) of this increased mortality are poorly understood. This study exposed sockeye salmon (*Oncorhynchus nerka*) to a mild capture and tagging stressor and evaluated physiological recovery and movement behaviour at 1 and 4 h postrelease. Female sockeye salmon did not expend more anaerobic energy in response to the stressor but did have higher plasma lactate levels 4 h after the stressor, indicating that females took longer to physiologically recover compared with males. In addition, female salmon had lower plasma glucose but higher plasma cortisol, plasma K^+, and cardiac lactate levels compared with males. Male and female salmon had markedly different postrelease behaviours within the first hour of release; males were more likely to hold position within the staging area. Two potential mechanisms leading to increased mortality in female salmon were identified in this study: (*a*) prolonged recovery duration (possibly mediated by elevated plasma cortisol levels) and (*b*) insufficient oxygen delivery to the heart.

Résumé : De nombreuses études en laboratoire et de terrain ont relevé que les saumons du Pacifique femelles présentent des taux de mortalité plus élevés que les mâles durant leur unique montaison de frai. Les causes immédiates de cette mortalité accrue demeurent toutefois mal comprises. Des saumons sockeyes (*Oncorhynchus nerka*) ont été exposés à un faible facteur de stress associé à la capture et au marquage, et leur rétablissement physiologique et leur comportement de déplacement ont été évalués 1 et 4 h après qu'ils aient été relâchés. Les sockeyes femelles ne dépensaient pas plus d'énergie anaérobie en réaction au facteur de stress, mais présentaient des concentrations de lactate plasmatique plus élevées après 4 h, indiquant que leur rétablissement physiologique était plus long que celui des mâles. En outre, les saumons femelles avaient de plus faibles teneurs en glucose plasmatique, mais de plus fortes teneurs en cortisol plasmatique, en K^+ plasmatique et en lactate cardiaque que les mâles. Les saumons mâles et femelles présentaient des comportements nettement différents durant la première heure après leur lâcher; les mâles étaient plus susceptibles de rester en place dans l'aire de repos. Deux mécanismes possibles menant à une plus importante mortalité des femelles ont été cernés dans l'étude, à savoir : (*a*) une durée prolongée du rétablissement (possiblement modulée par des concentrations élevées de cortisol plasmatique) et (*b*) un apport insuffisant d'oxygène au cœur. [Traduit par la Rédaction]

Introduction

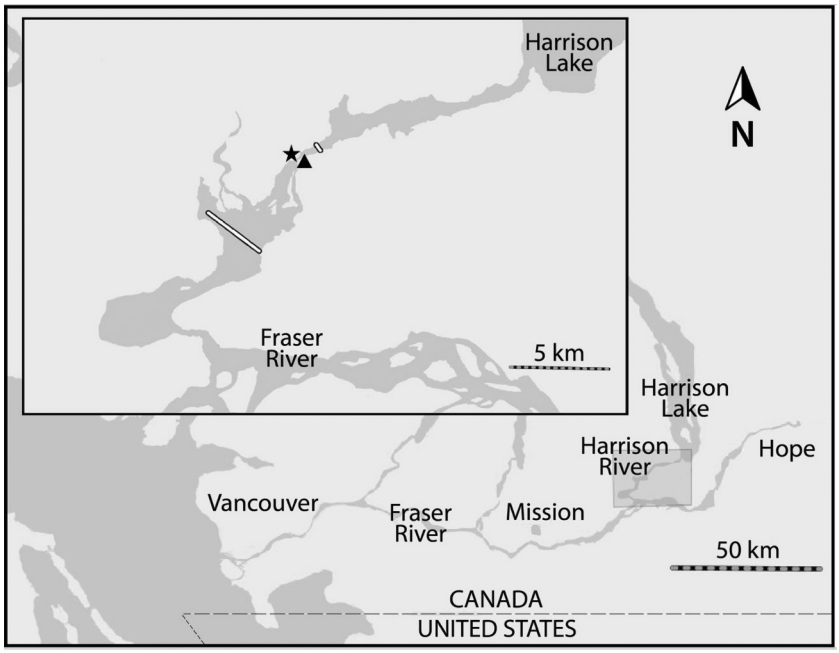
Sex-biased adult mortality can strongly influence population dynamics and extinction risk (Boukal et al. 2008; Melbourne and Hastings 2008), yet sex is often not considered as a factor in studies related to the biology of wild fish (Hanson et al. 2008). In recent years, several studies have discovered that sexually mature, adult female Pacific salmon (*Oncorhynchus* spp.) have higher mortality compared with males during their spawning migration (summarized in Patterson et al. 2016). This trend was revealed in tagging studies (e.g., Martins et al. 2012), dam passage studies (e.g., Burnett et al. 2014; Keefer et al. 2010; Roscoe et al. 2011), and lab-based holding studies (e.g., Gale et al. 2014; Jeffries et al. 2012; Nadeau et al. 2010; Patterson et al. 2004; Robinson et al. 2013; Teffer et al. 2017). Notably, differences in sex-biased mortality are more prevalent when fish are exposed to a secondary stressor (e.g., handling plus high temperature; Martins et al. 2012). Given that female salmon govern the reproductive capacity of a population, heightened female mortality raises grave conservation concerns. However, the proximate cause(s) underpinning the increased mortality in female salmon remain a mystery.

Pacific salmon exhibit sexual dimorphism in morphology, physiology, and behaviour during final maturation (Groot and Margolis 1991), which could play a role in the differential mortality patterns. Female salmon invest more energy stores into gonad development than males, resulting in gonads that represent 15% to 20% of the total body mass compared with just 3% in males (Crossin et al. 2004; Idler and Clemens 1959; Sopinka et al. 2016). Higher oxygen demand by the gonads could reduce the aerobic

Received 1 August 2019. Accepted 6 July 2020.

E.J. Eliason. Department of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93106-9620, USA; Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada.
M. Dick and S.J. Cooke. Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada.
D.A. Patterson and K.A. Robinson. Fisheries and Oceans Canada, Science Branch, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
J. Lotto and S.G. Hinch. Department of Forest and Conservation Sciences, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
Corresponding author: Erika J. Eliason (email: eliason@ucsb.edu).
Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

Fig. 1. Map of Harrison River in British Columbia, Canada (adapted from Dick et al. 2020). Map created using QGIS 2.21. Base map: Esri World Light Gray Base, data points collected by M. Dick, D. Patterson, and K. Robinson. Inset indicates the study location where salmon were tagged (star) and receiver location (triangle). The primary spawning area for Harrison sockeye salmon is located between the two white bars.



Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

scope available for other activities (e.g., swimming, recovery, behaviours) in females compared with males. Male pink salmon (*Oncorhynchus gorbuscha*) have a higher aerobic scope compared with females (Clark et al. 2011), and male sockeye salmon (*Oncorhynchus nerka*) have a lower resting heart rate compared with females (Sandblom et al. 2009). Mature male sockeye salmon have 12%–13% larger ventricles compared with female sockeye salmon of a similar size (Clark et al. 2009; Sandblom et al. 2009). Thus, male salmon may have enhanced cardiorespiratory capacity compared with females. Maturing female salmon are also well-known to have much higher plasma cortisol levels than males (e.g., Schmidt and Idler 1962). Cortisol has many functions (Mommsen et al. 1999), but elevated lactate levels are known to inhibit recovery from anaerobic exercise (Milligan 1996), which could have detrimental effects on migration progression for females. All told, any sex-specific differences affecting performance and energetics have the potential to influence overall survival in Pacific salmon.

One leading possibility for female-biased mortality is that these sexual dimorphisms influence how fish respond to and recover from a stressor. Migrating adult salmon encounter numerous challenges (e.g., fast-flowing currents, fishways, fisheries encounters, predator events) and must use anaerobic metabolism to negotiate these challenges (Burnett et al. 2014; Donaldson et al. 2010, 2012; Hinch and Bratty 2000; Pon et al. 2012). During recovery from anaerobic activity, fish must restore glycogen, high-energy phosphates, and oxygen stores and must reverse homeostatic imbalances (Kieffer 2000; Scarabello et al. 1992). This takes both time and energy. It is unknown whether males and females differ in how they physiologically recover from anaerobic activity. However, one study found that female sockeye salmon tended to use more anaerobic burst swimming during dam passage compared with male salmon (Burnett et al. 2014). Thus, females tended to behave differently than males in response to a common stressor. Notably, that same study discovered that excessive anaerobic burst swimming during dam passage had a negative carryover effect on survival (Burnett et al. 2014). Repeated anaerobic activity and a prolonged rate of recovery are deleterious because they delay migration and impair predator-avoidance behaviours (Eliason and Farrell 2016). Thus, if females have impaired behavior and physiological recovery capacity, that could help elucidate the observed patterns of heighted female mortality.

The objective of this study was to determine whether differential recovery from an acute stressor underlies heightened female mortality. Specifically, we assessed whether male and female sockeye salmon differ in their physiological response to a mild capture and tagging stressor, their subsequent recovery, and their postrelease behaviour. We therefore ran two concurrent techniques: stream-side, physiological sampling and radiotelemetry tagging. We hypothesized that female sockeye salmon (*i*) exert a greater anaerobic effort in response to this stressor, (*ii*) have a prolonged physiological recovery duration, and (*iii*) consequently have impaired postrelease behaviour. For the physiological study, we sampled plasma as well as red muscle, white muscle, and ventricles. Plasma ions (Na^+, K^+), cortisol, glucose, lactate, and hematocrit were included, as they are all known to respond to catch and release stressors (e.g., Gale et al. 2011). Previous work has indicated that muscle is a more sensitive indicator of physiological recovery from exercise than plasma (Pon et al. 2012). Ventricles were included because of known sex differences in cardiovascular morphology and capacity (Clark et al 2011; Sandblom et al. 2009). Tissue ATP (energy currency of the cell), phosphocreatine (energy reserve that can rapidly donate a phosphate group to ADP during intense anaerobic exercise), glycogen (energy store of carbohydrate), and lactate (indicator of anaerobic glycolysis; pyruvate is converted into lactate) were measured.

Materials and methods

All research was conducted in accordance with Canadian Council of Animal Care guidelines and approved through Carleton University (Cooke protocols 2014 – B14). Sockeye salmon from the Harrison River population in the Fraser River watershed (British Columbia, Canada) were used for this study (Fig. 1). Adult Harrison River sockeye salmon enter the Fraser River between late July and early October and travel 121 km upstream to reach their spawning grounds in the Harrison River. Harrison River sockeye salmon are

Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

unusual because they display a protracted freshwater staging period during which they move upstream and downstream in the Harrison River or mill in Harrison Lake for several weeks before eventually spawning in the rapids section of the Harrison River (Fig. 1; Donaldson et al. 2012; Robinson et al. 2015). In contrast, most other Fraser River sockeye salmon populations display a directed migration to their spawning grounds with minimal staging time before spawning. Peak spawning for Harrison River sockeye salmon occurs in mid-November (Gilhousen 1990).

Capture, tagging, and holding

Adult Harrison River sockeye salmon were captured by beach seine on the Harrison River, ~9 km from the confluence of the Fraser and Harrison rivers, on 16 and 23 October 2014 (river temperature = 12.8–13.0 °C). Each day, four or more beach seine sets were performed to capture fish. Within each beach seine set, some fish were used for the telemetry study and some were used for the physiological study. Only a few fish were assigned to each treatment per set (see below for details of physiology treatments), and then a new set was performed. The beach seine capture method crowds the salmon together and elicits anaerobic burst swimming, crowding, and confinement stress.

For the telemetry study, individual fish were placed in the tagging trough and affixed with an external radiotelemetry tag (N = 10 females, N = 9 males) without using anesthetic (see established procedures in Cooke et al. 2005; Dick et al. 2018). The tags (model TX-PSC-E-45 from Sigma Eight Inc., Newmarket, Ontario; 32 mm in length, 10 mm in width, 9.8 mm in height, and 3.7 g in air) were attached to the musculature at the base of the dorsal fin and set to transmit a unique identifier code every 5 s. Metal pins at either end of the tag were pierced through the tissue and secured on the opposing side with a plastic buffer disc and a knot in each pin. Sex was determined from external secondary sexual characteristics, which can be done confidently at this stage of maturation. Capture and holding prior to tagging for the telemetry study took 33 min on average (range: 5–68 min), and the tagging procedure took 64 s on average (range: 46–98 s). Approximately equal numbers of males and females were tagged from each set, and there were no significant differences in holding or tagging duration between sexes (t test, $p > 0.05$). The fish were then immediately released into the Harrison River.

For the physiological study, fish were assigned to three different sampling times: Time 0 (N = 10 females, N = 10 males); Time 1 h (N = 10 females, N = 10 males); and Time 4 h (N = 11 females, N = 10 males). Approximately equal numbers of males and females were assigned to each treatment per beach seine set. Once the net was bagged (fish encircled and drawn close to shore), Time 0 fish were immediately removed and rapidly euthanized by cerebral concussion followed by severing the spinal cord. These fish did not undergo a tagging procedure and were immediately sampled to measure baseline physiological variables after the primary capture stressor. Individual fish for the 1 and 4 h sampling times were placed in a tagging trough and tagged with an external radiotelemetry tag (procedure described above). This procedure had a dual benefit of (*i*) allowing direct comparison of recovery with the telemetry fish (above) and (*ii*) imposing an additional secondary handling stressor to the fish. The fish were then transferred and assigned to one of four flow-through net pens (two at 1 h; two at 4 h) that were partially submerged in the river (dimensions: 2.4 m in length, 0.65 m wide, 1.3 m height with ~1 m in water depth). The four net pens were used for recovery to (*i*) keep time 1 h and time 4 h fish apart and (*ii*) decrease disturbance and entanglement to encourage recovery as much as possible. By performing this experiment over several sets and using multiple net pens, fish recovery times could be carefully controlled. The actual holding times for the 1 and 4 h time points were (mean ± SD) 64 ± 5 min and 4 h and 1 min ± 5.7 min and did not differ between males and females.

After a 1 or 4 h undisturbed recovery period, the fish were removed from the net pen and rapidly euthanized by cerebral concussion followed by severing the spinal cord. A blood sample was immediately collected from the caudal vein and stored in an ice slurry before being centrifuged at 7000*g* for 5 min. The plasma was frozen in liquid nitrogen and stored at −80 °C until analysis. A muscle sample (<0.5 cm thick) composed of both red and white muscle was removed from halfway between the dorsal and anal fin, and the ventricle was removed and bisected. The muscle and ventricle samples were blotted dry of blood, rapidly freeze-clamped in liquid nitrogen, and stored at −80 °C until analysis. Morphometric information was collected (body mass, length, organ masses), and population identification was confirmed via scale analysis.

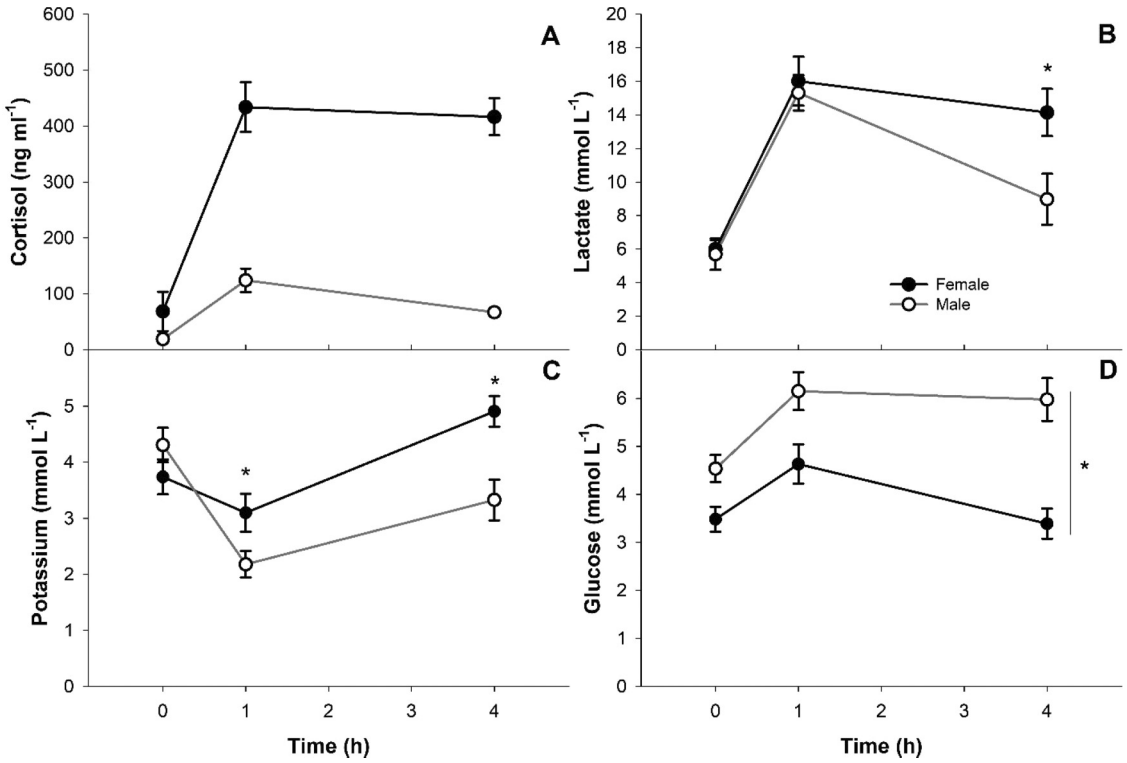
Blood and muscle metabolite analysis

Plasma variables and muscle metabolites were analyzed according to the methods described in Farrell et al. (2001) and Richards et al. (2002). Briefly, plasma potassium and plasma sodium were analyzed in duplicate using a Cole-Parmer Model 2655-00 Single-Channel Digital Flame Photometer. Plasma glucose and plasma lactate were measured in duplicate using a YSI 2300 STAT Plus Glucose/Lactate Analyzer. Plasma cortisol was analyzed in duplicate using an ELISA hormone kit (Neogen Corporation). Hematocrit (percentage of red blood cells in blood) was measured in duplicate via microhematocrit centrifuge tubes spun at 10 000*g*. Red muscle, white muscle, and heart [glycogen], [lactate], [adenosine triphosphate] (ATP), and [phosphocreatine] (CrP) were assayed spectrophotometrically in triplicate. Briefly, frozen red muscle, white muscle, and ventricle were ground under liquid nitrogen with a mortar and pestle. For each tissue, ~0.02 g was combined with ice-cold 8% $HClO_4$ and sonicated on ice with three bursts of 5 s. A 200 μL aliquot for [glycogen] and 70 μL aliquot for [glucose] were frozen at −80 until analysis (Bergmeyer 1983; Richards et al. 2002). The remaining homogenate was centrifuged at 10 000*g* for 10 min at 4 °C, and the supernatant (600 μL) was neutralized with 3 mol·L^{-1} K_2CO_3. The neutralized extracts were frozen at −80 °C until analysis for [ATP], [CrP], and [lactate] (Bergmeyer 1983; Richards et al. 2002). A subset of some of this data (a portion of the plasma data and the white muscle glycogen and white muscle lactate values for some of the female fish) were previously published in Dick et al. (2018).

Telemetry tracking and data processing

Tagged fish were tracked using a fixed radio receiver station located across from the capture and release site, which enabled immediate postrelease monitoring. The station was equipped with an Orion radio receiver (Sigma Eight Inc., Newmarket, Ontario) connected to a tree-mounted three-element Yagi antenna, and powered by deep cycle marine batteries. This location is a known holding and staging area for adult sockeye salmon, with spawning areas both upstream and downstream of the release site. We assumed that fish would return to this staging area upon release until they were ready to move onto the spawning grounds. The telemetry data from this site were processed to remove possible false detections using RStudio (version 1.0.143). Raw data was filtered to identify duplicates, to flag unusual data, and to remove potential false detections caused by electronic noise. A false detection was identified by assessing the surrounding detection patterns of a tag. A detection was considered "true" when it was a part of at least two other detections that occurred and when the time that elapsed between those detections was a multiple of the two burst rates (5 or 7 s) ± 1 s. The detections that met these criteria were then used to calculate the residency duration of individual tags at the site (Dick 2016). Once processed, single tag detections were transformed into site-specific residence events for each study fish. Event durations for individuals were calculated as periods in which at least three detections occurred within 60 s and

Fig. 2. Mean ± SE (A) plasma cortisol, (B) plasma lactate, (C) plasma potassium, and (D) plasma glucose for female (black circles) and male (white circles) adult sockeye salmon immediately after capture by beach seine (0 h) and 1 and 4 h after tagging (N = 10–11). Some of this data has been presented in Dick et al. (2018). Separate one-way ANOVAs were performed on cortisol for male and female fish (males: $p < 0.001$, $F = 41.209$; females: $p < 0.001$, $F = 29.628$). Two-way ANOVAs were performed on plasma lactate (Sex: $p = 0.021$, $F = 5.688$; Time: $p < 0.001$, $F = 38.303$; Sex × Time: $p = 0.049$, $F = 3.198$), plasma potassium (Sex: $p = 0.013$, $F = 6.560$; Time: $p < 0.001$, $F = 14.427$; Sex × Time: $p = 0.003$, $F = 6.421$), and plasma glucose (Sex: $p < 0.001$, $F = 36.439$; Time: $p = 0.003$, $F = 6.612$; Sex × Time: $p = 0.093$, $F = 2.480$). An asterisk indicates significant differences between sexes ($p < 0.05$).



Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

continued to occur without lapsing for longer than 60 s between single detections. The duration of these events was used to assess immediate postrelease behaviour, as in the longevity of the first residence event, as well as the cumulative proportion of time spent within range of the release station within the first hour, and within the first four hours after release. These time periods were set to cover the physiological sampling periods of the holding study.

Statistical analysis

Data are presented as mean ± SE unless otherwise indicated, and significance levels were set at 0.05. All statistical analyses were performed using Sigmaplot 11.0 (Systat Software, Inc.) or RStudio (version 1.0.143). Metrics were evaluated for homogeneity of variance using Levine's test, and normality was assessed using the Shapiro–Wilk test and quantile–quantile plots. When required, physiological data were log10- or square-root-transformed to meet normality assumptions. A Student's t test was used to compare body mass, fork length, gonadosomatic index (GSI), and residence time adjacent to tagging site between male and female fish. Two-way analysis of variance (ANOVA) was used to test for differences in sex and time for the physiological parameters with the exception of plasma cortisol. Male and female plasma cortisol values were analyzed separately using one-way ANOVA because equal variance assumptions could not be met even with data transformation, as reproductively mature females are well-known to have naturally higher cortisol levels than males (e.g., Kubokawa et al. 1999). Three covariates (time in seine net, time in trough during tagging, time in net pen) were not included in the final model because they were not significant. A post hoc Holm–Sidak test was used to test for differences.

Results

Physiological recovery holding study

Female sockeye salmon had a significantly smaller body mass and fork length (mean female body mass = 2.40 ± 0.04 kg; mean female fork length = 59.7 ± 0.3 cm; mean male body mass = 2.91 ± 0.07 kg; mean male fork length = 65.5 ± 0.6 cm) and a higher GSI compared with males (female GSI: 18.4% ± 0.4%, male GSI: 3.3% ± 0.1%). There were no differences in fish size within a treatment block ($p = 0.726$).

Female plasma cortisol levels were three- to sixfold higher than male levels (Fig. 2). Plasma glucose was significantly higher in male fish compared with female fish (Fig. 2). Plasma lactate did not differ between males and females at 0 or 1 h, but was significantly higher in females at 4 h (Fig. 2; significant sex × time interaction). Plasma K^+ did not differ between sexes at 0 h, but was significantly higher in females at 1 and 4 h (Fig. 2; significant sex × time interaction). Plasma Na^+ and hematocrit did not differ between sexes (Table 1).

Many of the ventricle, red muscle, and white muscle metabolites varied with time, and there were notable differences between males and females (Table 1). Specifically, female fish had significantly higher lactate levels in their ventricles and higher CrP levels in red muscle compared with male fish (Table 1). There was a significant sex × time interaction for white muscle ATP (Table 1); levels increased during the recovery period for females, while they remained constant for males.

Postrelease behaviour

Behaviour immediately after release and between 0 and 1 h was markedly different between sexes (Fig. 3; t test, $p = 0.039$). The

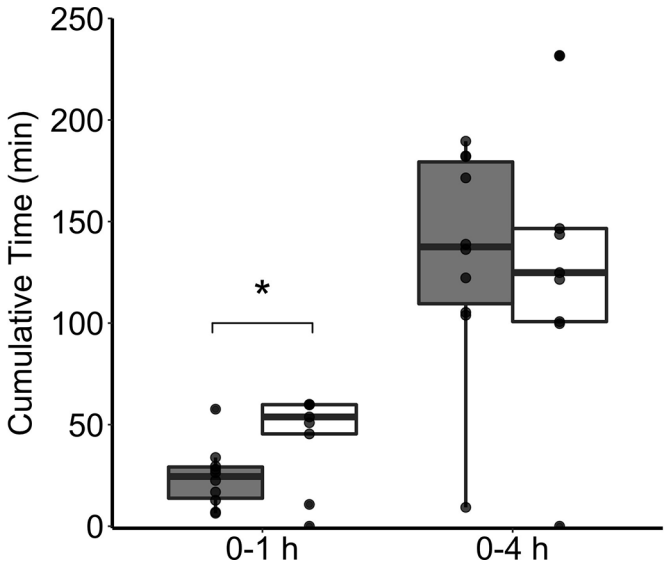
Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

Table 1. Mean ± SE for physiological variables of adult male and female sockeye salmon sampled immediately after capture (time 0 h) and 1 or 4 h after tagging (N = 10–11).

		0 h	1 h	4 h	Sex		Time		Interaction	
Physiological variable	Sex	(mean ± SE)	(mean ± SE)	(mean ± SE)	F	p	F	p	F	p
Plasma Na^+ ($mmol \cdot L^{-1}$)	Male	138.3±3.0a	148.4±2.1b	136.2±1.0a	0.103	0.749	19.017	**<0.001**	0.126	0.882
	Female	140.0±1.6	148.9±2.0	135.7±2.5						
Hematocrit (%)	Male	34.6±1.1a	41.6±1.7b	37.0±1.3b	1.411	0.240	7.085	**0.002**	0.923	0.404
	Female	35.6±2.3	41.4±2.2	41.3±1.3						
Ventricle										
Glycogen ($mmol \cdot kg^{-1}$)	Male	65.3±4.8	56.9±6.7	51.3±5.3	3.225	0.079	2.085	0.135	0.769	0.469
	Female	55.9±5.3	39.1±8.1	49.7±8.3						
Lactate ($mmol \cdot kg^{-1}$)	Male	17.5±2.2	21.5±1.6	15.3±1.7	5.399	**0.024**	2.655	0.079	1.552	0.221
	Female	18.6±1.6	24.5±3.5	23.6±2.2						
ATP ($mmol \cdot kg^{-1}$)	Male	3.9±0.5a	2.6±0.3b	3.5±0.4b	0.638	0.428	10.212	**<0.001**	2.240	0.116
	Female	4.8±0.3	2.9±0.3	3.0±0.3						
CrP ($mmol \cdot kg^{-1}$)	Male	2.3±0.2a	1.2±0.1b	1.2±0.1b	1.161	0.286	50.468	**<0.001**	0.242	0.786
	Female	2.4±0.2	1.1±0.1	1.1±0.1						
White muscle										
Glycogen ($mmol \cdot kg^{-1}$)	Male	13.6±1.3	10.3±1.6	12.5±2.0	0.024	0.878	3.245	**0.047**	1.194	0.312
	Female	16.4±3.8	10.1±1.4	9.2±1.1						
Lactate ($mmol \cdot kg^{-1}$)	Male	51.1±3.8a	43.8±2.2b	32.9±3.6c	0.018	0.895	25.088	**<0.001**	0.160	0.853
	Female	52.0±3.1	44.1±1.0	30.7±2.3						
ATP ($mmol \cdot kg^{-1}$)	Male	6.0±0.4	5.8±0.6	5.7±0.5*	1.876	0.177	3.211	**0.048**	5.077	**0.010**
	Female	4.8±0.5x	7.1±0.4y	7.2±0.3y						
CrP ($mmol \cdot kg^{-1}$)	Male	2.9±0.5a	3.2±0.6b	7.1±1.1c	0.130	0.720	24.752	**<0.001**	3.036	0.056
	Female	1.7±0.3	4.8±0.6	7.4±0.7						
Red muscle										
Glycogen ($mmol \cdot kg^{-1}$)	Male	9.1±0.9a	6.2±1.2b	6.5±1.5b	0.174	0.678	4.059	**0.023**	0.146	0.864
	Female	9.3±1.2	6.9±0.9	6.3±1.2						
Lactate ($mmol \cdot kg^{-1}$)	Male	4.8±0.8	5.6±0.8	4.9±1.0	0.777	0.382	0.005	0.995	0.641	0.531
	Female	5.9±0.7	5.9±1.5	6.1±0.7						
ATP ($mmol \cdot kg^{-1}$)	Male	2.3±0.2	2.7±0.3	2.7±0.4	0.037	0.848	1.702	0.192	0.312	0.733
	Female	2.2±0.3	2.8±0.2	2.4±0.4						
CrP ($mmol \cdot kg^{-1}$)	Male	0.5±0.1a	1.2±0.1b	0.7±0.1c	7.515	**0.008**	11.611	**<0.001**	0.750	0.477
	Female	0.7±0.1	1.6±0.3	1.2±0.2						

Note: Two-way ANOVA results are presented for each physiological variable, except cortisol where one-way ANOVA tests were run for each sex. Dissimilar lowercase letters denote significant differences ($p < 0.05$) between values, where a–c denotes significant differences with respect to the main effect of time, and q–s and x–z and an asterisk indicates differences with respect to significant Sex × Time interactions. The plasma Na^+ data and the white muscle glycogen and white muscle lactate data for only the female fish are from Dick et al. (2018). CrP = phosphocreatine.

Fig. 3. Box plots showing cumulative time spent in the holding area during the first hour (0–1 h) or the first 4 h (0–4 h) after release for males (N = 9; white boxes) and females (N = 10; grey boxes). An asterisk indicates statistically significant differences between sexes ($p < 0.05$).



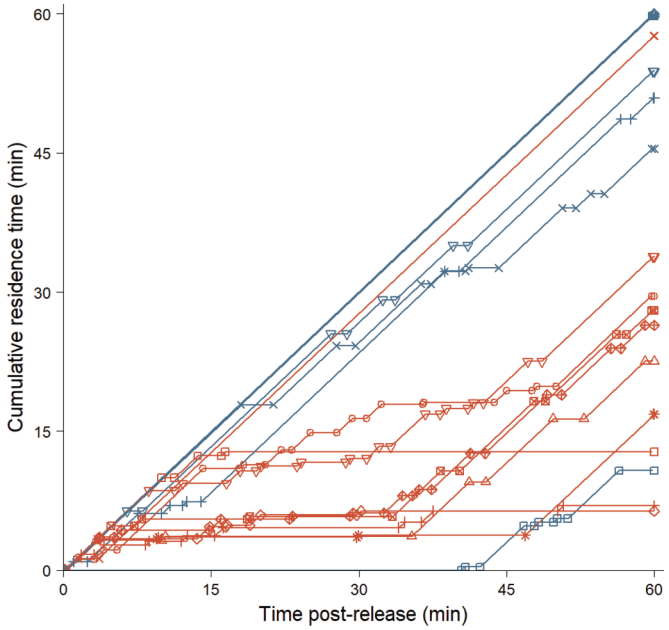
median duration of the first residence events calculated for females and males was 3.40 min (range: 1.18–9.95 min) and 17.85 min (range: 0.00–149.90 min), respectively. Detections from one male fish did not meet the criteria for a residence event within this window, suggesting this fish dispersed immediately after release (i.e., 0 min residence event). The cumulative time spent in range of the station in the first hour after release indicates that females spent less time (median: 24.47 min) than males (median: 53.80 min) in the staging area (Fig. 4). However, females did return to the area and spent similar cumulative time (median: 137.88 min) in the vicinity as males (median: 125.03 min) within the 4 h monitoring window (Fig. 3; t test, p value = 0.98).

Discussion

This study evaluated potential mechanisms underlying elevated mortality in female Pacific salmon. In contrast with our first hypothesis, female sockeye salmon did not appear to exert a greater anaerobic effort in response to the capture and tagging stressor, given that plasma lactate levels were equivalent between males and females immediately after the stressor (Time 0) and after 1 h of recovery (Time 1 h). However, while plasma lactate levels were clearly declining back towards baseline levels in males after 4 h of recovery, plasma lactate remained elevated for females. Thus, our second hypothesis is supported; female sockeye salmon appear to have a prolonged physiological recovery duration compared with males. Furthermore, female fish had higher plasma cortisol, plasma K^+, and ventricle lactate and lower plasma

Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

Fig. 4. Cumulative time spent in the holding area for individual male (N = 9; blue lines) and female (N = 10; red lines) study fish within the first hour after release. The topmost blue line represents four males that all stayed on location for the entire hour. One male did not spend any time in the holding area within this period and therefore is not depicted here. [Colour online.]



glucose compared with male fish. There were also sex differences in the initial behavioural responses, as males were more likely to hold position in the staging area during the first hour postrelease. However, it is difficult to confirm whether this represents an "impaired" postrelease behaviour on the part of the females, as proposed by our third hypothesis, since this is one of the first attempts to examine sex differences in immediate postrelease behaviour for salmon. Below, we specifically focus on the physiological variables that differed between sexes and discuss how these variables may lead to heightened female mortality.

Fisheries interactions and exhaustive exercise induce a suite of physiological disturbances, including acid–base, osmotic, and metabolite imbalances (Farrell et al. 2000, 2001; Milligan 1996). Prolonged recovery can impede continued migration and can even have chronic effects that result in delayed mortality (Burnett et al. 2014; Wood et al. 1983). As expected, plasma lactate, plasma glucose, plasma Na^+, plasma cortisol, and hematocrit all increased following the tagging stressor in the present study in both male and female fish. However, none of the plasma values were as disrupted as those documented in some commercial fisheries (e.g., with coho salmon (*Oncorhynchus kisutch*); Farrell et al. 2000, 2001). Plasma lactate values peaked at 15–16 mmol·L^{-1} 1 h after tagging, which is well below maximum levels observed in other studies (e.g., mean values in adult coho salmon caught by gillnet reached 31.4 mmol·L^{-1} after 60 min of recovery; Farrell et al. 2000). Even so, these plasma lactate levels exceeded the proposed threshold of 10–13 mmol·L^{-1}, beyond which swim performance is typically impaired (Farrell et al. 1998; Jain and Farrell 2003; Stevens and Black 1966). Notably, 60% of male fish but only 18% of female fish had plasma lactate levels below this threshold at the 4 h recovery time point. Female salmon also had higher plasma K^+ levels, which is known to inhibit muscle contractility (Holk and Lykkeboe 1998). Thus, more than half the males were likely able to resume normal swimming behaviors within 4 h of the stressor while almost all the females were still recovering. So, even though the physiological disturbance in the present study was moderate and likely did not result in sex-specific effects on survival, clear differences in recovery profiles suggest that more arduous stressors could impose a deadly burden on female salmon.

The behavioural data corroborates the physiological data; both suggest there are sex-specific differences in recovery following the stressor. During the first hour after tagging, males and females exhibited markedly different behaviour. Males remained close to the staging area for the first hour, suggesting they were able to maintain position and recover swimming ability after the moderate stressor. In contrast, females were less likely to maintain position within the first hour, presumably moving downstream through possible exhaustion. These data do not provide conclusive evidence that female salmon had impaired behaviour following tagging, as it is possible females have a heightened escape response compared with males causing them to leave immediately postrelease. However, females did return to the staging area within the 4 h monitoring period postrelease. In fact, behavioural differences were no longer apparent over the full 4 h period, as both sexes spent similar cumulative time within the preferred staging area. The capture and handling stressor was mild (i.e., minimal handling, moderate water temperature) and thereby did not elicit a large physiological disturbance or prolonged recovery period (see above), which may explain why behavior differences between sexes were not obvious after 4 h postrelease. The capture event was sufficient to cause sex-specific differences in both physiological recovery and immediate postrelease behaviour, but are unlikely to result in conspicuous differences in survival. This underscores the idea that there may be some stressor threshold or combination of multiple stressors necessary to elicit sex-specific mortality differences (Patterson et al. 2016). Future work should continue to explore the relationship among physiology, behaviour, and long-term survival, coupling biotelemetry and physiology.

This study points to a few potential mechanisms leading to impaired female recovery from anaerobic activity. Pacific salmon have long been known to have high plasma cortisol levels during the final phase of their life cycle (Fagerlund 1967; Hane and Robertson 1959; Hinch et al. 2005; Schmidt and Idler 1962). Elevated cortisol levels in migrating adult salmonids have been postulated to be due to endogenous mechanisms associated with reproductive maturation or possibly to facilitate home-stream olfactory memory (Carruth et al. 2000, 2002; Kubokawa et al. 1999; McQuillan et al. 2003). Given the known role of cortisol in osmoregulation and metabolism (Mommsen et al. 1999), elevated cortisol levels may also be a response to osmotic and ionic disruption and immune function, particularly on the spawning grounds when cortisol levels increase in concert with senescence processes (Barry et al. 2001; Jeffries et al. 2011). In the present study, female salmon displayed augmented plasma cortisol levels in response to the same stressor relative to males. Further, these elevated levels of plasma cortisol showed no indication of recovery at the 4 h period in female salmon. This phenomenon of elevated cortisol levels in female salmon is consistent with the literature (Crossin et al. 2008; Donaldson et al. 2010, 2014; Hruska et al. 2010; Kubokawa et al. 1999; Robinson et al. 2013) and has been reported across the breadth of the return migration (i.e., in-river and on spawning grounds). However, the cause and consequences of the sexually dimorphic cortisol response have not been determined.

One possible consequence of the elevated and protracted cortisol levels found in female salmon is that it may preclude them from rapidly recovering from stressors. Indeed, elevated cortisol levels after exercise have been proposed to have a negative effect on metabolic recovery in rainbow trout (Milligan 1996). Pagnotta et al. (1994) found that postexercise metabolic recovery was greatly enhanced in fish that had pharmacologically blocked cortisol levels (via metyrapone and dexamethasone) compared with control fish. Specifically, cortisol-blocked fish had much lower plasma lactate levels compared with control fish and restored

Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

muscle glycogen, blood pH, and muscle intracellular pH to pre-exercise levels within 2 h (control fish required up to 8 h to recover; Pagnotta et al. 1994). Another study replaced cortisol in fish that had been administered metyrapone and found that they had equivalent recovery rates to control fish (Eros and Milligan 1996). These studies suggest that cortisol plays a role in regulating lactate metabolism. Prolonged recovery associated with elevated cortisol levels, such as the levels found in the present study, could have dire consequences to behaviour and long-term survival. Indeed, one study found that sockeye salmon with elevated cortisol responses during tagging were less likely to successfully migrate upstream (Cook et al. 2014). In addition, elevated cortisol levels are associated with immune suppression (Pickering and Pottinger 1989), which could be an additional mechanism contributing to delayed mortality in female salmon (Teffer et al. 2019). Future work should investigate the interaction between cortisol levels and sex in governing physiological recovery processes and immune function (e.g., via cortisol manipulations; see Sopinka et al. 2015).

This study also found evidence of a cardiac oxygen limitation in female salmon. Specifically, ventricle lactate levels were 6% (Time 0), 14% (Time 1 h), and 54% (Time 4 h) higher in females compared with males. The heart is a highly aerobic organ and is essential for oxygen delivery to the tissues (e.g., to sustain aerobic swimming performance and gonadal development). Elevated lactate levels in ventricles of female fish indicate a mismatch between oxygen supply and demand. A cardiac oxygen limitation could develop if there was insufficient oxygen in the venous blood supplying the avascular spongy myocardium (i.e., the inner part of the ventricle) or reduced coronary flow to the compact myocardium (i.e., the outer part of the ventricle). One possibility is that the much-larger female ovaries (18% GSI for study females) could have increased oxygen demands compared with male testes (3% GSI for study males), thereby reducing oxygen in the venous blood. Final GSI in female Harrison sockeye salmon is ~21% (Sopinka et al. 2016), so the female fish in our study were likely still undergoing vitellogenesis. Given that sockeye salmon are semelparous (single opportunity to spawn), blood flow to the gonads is likely to be maintained even under stressful conditions (e.g., high temperature, during exercise) to ensure reproductive success (Braun et al. 2013; Patterson et al. 2004). These ideas remain to be tested since, to our knowledge, no one has directly measured gonadal oxygen uptake or gonadal blood flow. Regardless of the mechanism, insufficient cardiac oxygen supply coupled with elevated K^+ levels may indicate impaired cardiac contractility and compromised swimming performance and could ultimately lead to death in female salmon (Eliason et al. 2013; Farrell et al. 2009; Hanson et al. 2006).

Muscle tissue is proposed to be more sensitive to exercise-related physiological changes than blood (Pon et al. 2012); thus, we expected it to play important role in this study. We predicted that both males and females would rapidly deplete their muscle energy stores (ATP, CrP, glycogen) and accumulate lactate (Scarabello et al. 1992; Wood et al. 1983) but that females would take longer to recover those stores and clear lactate. Instead, few differences in red and white muscle metabolites were found between sexes. Anaerobic exercise is primarily supported by white muscle, so it was surprising to observe no difference in lactate recovery dynamics between the sexes in white muscle. Females did recover white muscle ATP more quickly than males, which was unexpected. Red muscle primarily relies on aerobic metabolism through oxidative phosphorylation to generate ATP. Interestingly, females had significantly higher CrP than males in their red muscle, but no difference in ATP. All told, red and white muscle metabolites did not reveal a potential mechanism to explain differential recovery or mortality between sexes.

In summary, the present study found clear sex-specific differences in physiological and behavioural responses to a mild capture, handling, and tagging stressor in wild adult sockeye salmon en route to their spawning grounds. The stressor elicited a similar magnitude of anaerobic effort for both sexes but females took longer to recover, as evidenced by elevated plasma lactate and plasma K^+ levels after 4 h of recovery. Accordingly, we suggest that the phenomenon of heightened female mortality during the spawning migration may be, in part, mechanistically attributed to prolonged physiological recovery from stressors. Furthermore, we suggest that the prolonged recovery may be mediated by the elevated and prolonged cortisol response that has been routinely documented in female salmon. We also identified potential cardiac oxygen limitation as a second possible mechanism contributing to elevated female mortality. Specifically, female ventricles had higher lactate levels, indicating insufficient oxygen delivery to the myocardium. Given the key role of the heart in supporting aerobic metabolism and swim performance, impaired cardiac performance in female salmon could contribute to failed migration. However, we caution that more work is needed to connect the differences in postrelease behaviour between the sexes to both physiological condition and survival. There are several other potential mechanisms that could contribute to sex-specific differences in mortality that were not explored here, including impaired immune function and energy exhaustion (particularly for salmon populations with long migrations). Mechanisms may differ across Pacific salmon species and even populations, given the variation in environmental selection pressures across the species range (e.g., migration distance, river flow, temperature, elevation) and corresponding morphological and physiological differences across populations (Crossin et al. 2004; Eliason et al. 2011). In conclusion, sexually dimorphic traits and mortality have been clearly identified in Pacific salmon, and more research should address whether this is a general phenomenon found across other species and systems. We echo Hanson et al.'s (2008) call for researchers, especially those working on wild fish, to consider sex as a factor in analyses and to explore the fundamental basis for sex-specific differences in survival, which have become increasingly well-documented.

Acknowledgements

The authors thank the Sts'ailes Community, especially K. Charlie, A. Charlie, and the Sts'ailes fishing crew members. Field assistance was provided by J. Hills, A. Lotto, K. Dionne, T. Nettles, C. Storey, L. Gardner, L. de Mestral Bezanson, P. Szekeres, G. Neely, J. Chapman, and A. Luscombe. Lab support and advice was provided by K. Cook, A. Farrell, M. Regan, and J. Richards. Telemetry data analysis code was provided by E. Martins. This project was financially supported by the Southern Endowment Fund (Pacific Salmon Commission) and the Ocean Tracking Network Canada. Additional support was provided by NSERC Discovery and Strategic grants (Cooke and Hinch), Canada Research Chairs Program (Cooke), and an NSERC postdoctoral fellowship (Eliason).

References

Barry, T.P., Unwin, M., Malison, J., and Quinn, T. 2001. Free and total cortisol levels in semelparous and iteroparous chinook salmon. J. Fish Biol. **59**(6): 1673–1676. doi:10.1111/j.1095-8649.2001.tb00230.x.

Bergmeyer, H.U. 1983. Methods of enzymatic analysis. Academic Press, New York.

Boukal, D.S., Berec, L., and Køivan, V. 2008. Does sex-selective predation stabilize or destabilize predator–prey dynamics? PLoS ONE, **3**(7): e2687. doi:10.1371/journal.pone.0002687. PMID:18628951.

Braun, D.C., Patterson, D.A., and Reynolds, J.D. 2013. Maternal and environmental influences on egg size and juvenile life-history traits in Pacific salmon. Ecol. Evol. **3**(6): 1727–1740. doi:10.1002/ece3.555. PMID:23789081.

Burnett, N.J., Hinch, S.G., Braun, D.C., Casselman, M.T., Middleton, C.T., Wilson, S.M., and Cooke, S.J. 2014. Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. Physiol. Biochem. Zool. **87**(5): 587–598. doi:10.1086/677219. PMID:25244372.

Carruth, L.L., Dores, R.M., Maldonado, T.A., Norris, D.O., Ruth, T., and Jones, R.E. 2000. Elevation of plasma cortisol during the spawning migration of landlocked kokanee salmon (*Oncorhynchus nerka kennerlyi*). Comp. Biochem.

Physiol. Part C Toxicol. Pharmacol. **127**(2): 123–131. doi:10.1016/S0742-8413(00)00140-7. PMID:11083023.

Carruth, L.L., Jones, R.E., and Norris, D.O. 2002. Cortisol and Pacific salmon: a new look at the role of stress hormones in olfaction and home-stream migration. Integr. Comp. Biol. **42**(3): 574–581. doi:10.1093/icb/42.3.574. PMID:21708753.

Clark, T.D., Hinch, S.G., Taylor, B.D., Frappell, P.B., and Farrell, A.P. 2009. Sex differences in circulatory oxygen transport parameters of sockeye salmon (*Oncorhynchus nerka*) on the spawning ground. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. **179**(5): 663–671. doi:10.1007/s00360-009-0349-1. PMID:19252914.

Clark, T.D., Jeffries, K.M., Hinch, S.G., and Farrell, A.P. 2011. Exceptional aerobic scope and cardiovascular performance of pink salmon (*Oncorhynchus gorbuscha*) may underlie resilience in a warming climate. J. Exp. Biol. **214**(18): 3074–3081. doi:10.1242/jeb.060517. PMID:21865520.

Cook, K.V., Crossin, G.T., Patterson, D.A., Hinch, S.G., Gilmour, K.M., and Cooke, S.J. 2014. The stress response predicts migration failure but not migration rate in a semelparous fish. Gen. Comp. Endocrinol. **202**: 44–49. doi:10.1016/j.ygcen.2014.04.008. PMID:24769043.

Cooke, S.J., Crossin, G.T., Patterson, D.A., English, K.K., Hinch, S.G., Young, J.L., et al. 2005. Coupling noninvasive physiological assessments with telemetry to understand inter individual variation in behavior and survivorship of sockeye salmon: development and validation of a technique. J. Fish Biol. **67**(5): 1342–1358. doi:10.1111/j.1095-8649.2005.00830.x.

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

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

Dick, M.L. 2016. The physiological, behavioural, and survival consequences of two radio transmitter attachment techniques on migrating adult sockeye salmon. M.Sc. thesis, Department of Biology, Carleton University, Ottawa, Ont.

Dick, M., Patterson, D.A., Robinson, K.A., Eliason, E.J., Hinch, S.G., and Cooke, S.J. 2020. Adult sockeye salmon gastrically tagged near spawning grounds exhibit lower survival rates throughout the spawning period than externally tagged conspecifics. N. Am. J. Fish. Manage. **40**(4): 939–951. doi:10.1002/nafm.10455.

Dick, M., Eliason, E., Patterson, D., Robinson, K., Hinch, S., and Cooke, S. 2018. Short-term physiological response profiles of tagged migrating adult Sockeye salmon: A comparison of gastric insertion and external tagging methods. Trans. Am. Fish. Soc. **147**(2): 300–315. doi:10.1002/tafs.10027.

Donaldson, M.R., Clark, T.D., Hinch, S.G., Cooke, S.J., Patterson, D.A., Gale, M.K., et al. 2010. Physiological responses of free-swimming adult coho salmon to simulated predator and fisheries encounters. Physiol. Biochem. Zool. **83**(6): 973–983. doi:10.1086/656336. PMID:20961224.

Donaldson, M.R., Hinch, S.G., Raby, G.D., Patterson, D.A., Farrell, A.P., and Cooke, S.J. 2012. Population-specific consequences of fisheries-related stressors on adult sockeye salmon. Physiol. Biochem. Zool. **85**(6): 729–739. doi:10.1086/664931. PMID:23099469.

Donaldson, M.R., Hinch, S.G., Jeffries, K.M., Patterson, D.A., Cooke, S.J., Farrell, A.P., and Miller, K.M. 2014. Species-and sex-specific responses and recovery of wild, mature pacific salmon to an exhaustive exercise and air exposure stressor. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. **173**: 7–16. doi:10.1016/j.cbpa.2014.02.019.

Eliason, E.J., and Farrell, A.P. 2016. Oxygen uptake in Pacific salmon *Oncorhynchus* spp.: when ecology and physiology meet. J. Fish Biol. **88**: 359–388.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., et al. 2011. Differences in thermal tolerance among sockeye salmon populations. Science, **332**(6025): 109–112. doi:10.1126/science.1199158. PMID:21454790.

Eliason, E.J., Clark, T.D., Hinch, S.G., and Farrell, A.P. 2013. Cardiorespiratory collapse at high temperature in swimming adult sockeye salmon. Conserv. Physiol. **1**: cot008. doi:10.1093/conphys/cot008. PMID:27293592.

Eros, S.K., and Milligan, C.L. 1996. The effect of cortisol on recovery from exhaustive exercise in rainbow trout (*Oncorhynchus mykiss*): potential mechanisms of action. Physiol. Zool. **69**(5): 1196–1214. doi:10.1086/physzool.69.5.30164253.

Fagerlund, U. 1967. Plasma cortisol concentration in relation to stress in adult sockeye salmon during the freshwater stage of their life cycle. Gen. Comp. Endocrinol. **8**(2): 197–207. doi:10.1016/0016-6480(67)90066-4. PMID:6040052.

Farrell, A.P., Gamperl, A.K., and Birtwell, I.K. 1998. Prolonged swimming, recovery and repeat swimming performance of mature sockeye salmon *Oncorhynchus nerka* exposed to moderate hypoxia and pentachlorophenol. J. Exp. Biol. **201**: 2183–2193. PMID:9639592.

Farrell, A.P., Gallaugher, P., Clarke, C., DeLury, N., Kreiberg, H., Parkhouse, W., and Routledge, R. 2000. Physiological status of coho salmon (*Oncorhynchus kisutch*) captured in commercial nonretention fisheries. Can. J. Fish. Aquat. Sci. **57**(8): 1668–1678. doi:10.1139/f00-116.

Farrell, A.P., Gallaugher, P.E., Fraser, J., Pike, D., Bowering, P., Hadwin, A.K.M., et al. 2001. Successful recovery of the physiological status of Coho salmon on board a commercial gillnet vessel by means of a newly designed revival box. Can. J. Fish. Aquat. Sci. **58**(10): 1932–1946. doi:10.1139/f01-136.

Farrell, A.P., Eliason, E.J., Sandblom, E., and Clark, T.D. 2009. Fish cardiorespiratory physiology in an era of climate change. Can. J. Zool. **87**(10): 835–851. doi:10.1139/Z09-092.

Gale, M.K., Hinch, S.G., Eliason, E.J., Cooke, S.J., and Patterson, D.A. 2011. Physiological impairment of adult sockeye salmon in fresh water after simulated capture-and-release across a range of temperatures. Fish. Res. **112**(1–2): 85–95. doi:10.1016/j.fishres.2011.08.014.

Gale, M.K., Hinch, S.G., Cooke, S.J., Donaldson, M.R., Eliason, E.J., Jeffries, K.M., et al. 2014. Observable impairments predict mortality of captured and released sockeye salmon at various temperatures. Conserv. Physiol. **2**(1): cou029. doi:10.1093/conphys/cou029. PMID:27293650.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. International Pacific Salmon Fisheries Commission 26.

Groot, C., and Margolis, L. 1991. Pacific salmon life histories. UBC Press, Vancouver, B.C.

Hane, S., and Robertson, O.H. 1959. Changes in plasma 17-hydroxycorticosteroids accompanying sexual maturation and spawning of the Pacific salmon (*Oncorhynchus tschawytscha*) and rainbow trout (*Salmo gairdnerii*). Proc. Natl. Acad. Sci. U.S.A. **45**(6): 886–893. doi:10.1073/pnas.45.6.886. PMID:16590465.

Hanson, K.C., Gravel, M.A., Graham, A., Shoji, A., and Cooke, S.J. 2008. Sexual variation in fisheries research and management: When does sex matter? Rev. Fish. Sci. **16**(4): 421–436. doi:10.1080/10641260802013866.

Hanson, L.M., Obradovich, S., Mouniargi, J., and Farrell, A.P. 2006. The role of adrenergic stimulation in maintaining maximum cardiac performance in rainbow trout (*Oncorhynchus mykiss*) during hypoxia, hyperkalemia and acidosis at 10°C. J. Exp. Biol. **209**(13): 2442–2451. doi:10.1242/jeb.02237. PMID:16788027.

Hinch, S.G., and Bratty, J. 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. Trans. Am. Fish. Soc. **129**: 598–606.

Hinch, S.G., Cooke, S.J., Healey, M.C., and Farrell, A.P. 2005. Behavioural physiology of fish migrations: salmon as a model approach. Fish Physiol. **24**: 239–295. doi:10.1016/S1546-5098(05)24007-4.

Holk, K., and Lykkeboe, G. 1998. The impact of endurance training on arterial plasma K^+ levels and swimming performance of rainbow trout. J. Exp. Biol. **201**(9): 1373–1380. PMID:9547318.

Hruska, K.A., Hinch, S.G., Healey, M.C., Patterson, D.A., Larsson, S., and Farrell, A.P. 2010. Influences of sex and activity level on physiological changes in individual adult sockeye salmon during rapid senescence. Physiol. Biochem. Zool. **83**(4): 663–676. doi:10.1086/652411. PMID:20482369.

Idler, D.R., and Clemens, W.A. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart lakes. International Pacific Salmon Fisheries Commission Progress Report, pp. 1–80.

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

Jeffries, K.M., Hinch, S.G., Donaldson, M.R., Gale, M.K., Burt, J.M., Thompson, L.A., et al. 2011. Temporal changes in blood variables during final maturation and senescence in male sockeye salmon *Oncorhynchus nerka*: reduced osmoregulatory ability can predict mortality. J. Fish Biol. **79**(2): 449–465. doi:10.1111/j.1095-8649.2011.03042.x. PMID:21781102.

Jeffries, K.M., Hinch, S.G., Martins, E.G., Clark, T.D., Lotto, A.G., Patterson, D.A., et al. 2012. Sex and proximity to reproductive maturity influence the survival, final maturation, and blood physiology of Pacific salmon when exposed to high temperature during a simulated migration. Physiol. Biochem. Zool. **85**(1): 62–73. doi:10.1086/663770. PMID:22237290.

Keefer, M., Taylor, G., Garletts, D., Gauthier, G., Pierce, T., and Caudill, C. 2010. Prespawn mortality in adult spring Chinook salmon outplanted above barrier dams. Ecol. Freshw. Fish, **19**(3): 361–372. doi:10.1111/j.1600-0633.2010.00418.x.

Kieffer, J.D. 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. **126**(2): 161–179. doi:10.1016/S1095-6433(00)00202-6.

Kubokawa, K., Watanabe, T., Yoshioka, M., and Iwata, M. 1999. Effects of acute stress on plasma cortisol, sex steroid hormone and glucose levels in male and female sockeye salmon during the breeding season. Aquaculture, **172**: 335–349. doi:10.1016/S0044-8486(98)00504-3.

Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., et al. 2012. High river temperature reduces survival of sockeye salmon (*Oncorhynchus nerka*) approaching spawning grounds and exacerbates female mortality. Can. J. Fish. Aquat. Sci. **69**(2): 330–342. doi:10.1139/f2011-154.

McQuillan, H.J., Lokman, P.M., and Young, G. 2003. Effects of sex steroids, sex, and sexual maturity on cortisol production: an in vitro comparison of chinook salmon and rainbow trout interrenals. Gen. Comp. Endocrinol. **133**(1): 154–163. doi:10.1016/S0016-6480(03)00163-1. PMID:12899856.

Melbourne, B.A., and Hastings, A. 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature, **454**: 100–103. doi:10.1038/nature06922. PMID:18596809.

Milligan, C.L. 1996. Metabolic recovery from exhaustive exercise in rainbow trout. Comp. Biochem. Physiol. Part A Physiol. **113**(1): 51–60. doi:10.1016/0300-9629(95)02060-8.

Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.

Mommsen, T.P., Vijayan, M.M., and Moon, T.W. 1999. Cortisol in teleosts: dynamics, mechanisms of action, and metabolic regulation. Rev. Fish Biol. Fish. **9**(3): 211–268. doi:10.1023/A:1008924418720.

Nadeau, P., Hinch, S., Hruska, K., Pon, L., and Patterson, D. 2010. The effects of experimental energy depletion on the physiological condition and survival of adult sockeye salmon (*Oncorhynchus nerka*) during spawning migration. Environ. Biol. Fishes, **88**(3): 241–251. doi:10.1007/s10641-010-9635-8.

Pagnotta, A., Brooks, L., and Milligan, L. 1994. The potential regulatory roles of cortisol in recovery from exhaustive exercise in rainbow trout. Can. J. Zool. **72**(12): 2136–2146. doi:10.1139/z94-286.

Patterson, D.A., Macdonald, J.S., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2004. The effect of exercise and captivity on energy partitioning, reproductive maturation and fertilization success in adult sockeye salmon. J. Fish Biol. **64**(4): 1039–1059. doi:10.1111/j.1095-8649.2004.0370.x.

Patterson, D.A., Cooke, S.J., Hinch, S.G., Robinson, K.A., Young, N., Farrell, A.P., and Miller, K.M. 2016. A perspective on physiological studies supporting the provision of scientific advice for the management of Fraser River sockeye salmon (*Oncorhynchus nerka*). Conserv. Physiol. **4**(1): cow026. doi:10.1093/conphys/cow026. PMID:27928508.

Pickering, A.D., and Pottinger, T.G. 1989. Stress responses and disease resistance in salmonid fish: effects of chronic elevation of plasma cortisol. Fish Physiol. Biochem. **7**(1–6): 253–258. doi:10.1007/BF00004714. PMID:24221779.

Pon, L., Hinch, S., Suski, C.D., Patterson, D., and Cooke, S. 2012. The effectiveness of tissue biopsy as a means of assessing the physiological consequences of fishway passage. River Res. Appl. **28**(8): 1266–1274. doi:10.1002/rra.1508.

Richards, J.G., Heigenhauser, G.J.F., and Wood, C.M. 2002. Lipid oxidation fuels recovery from exhaustive exercise in white muscle of rainbow trout. Am. J. Physiol. Regul. Integr. Comp. Physiol. **282**(1): R89–99. doi:10.1152/ajpregu.00238.2001. PMID:11742827.

Robinson, K.A., Hinch, S.G., Gale, M.K., Clark, T.D., Wilson, S.M., Donaldson, M.R., et al. 2013. Effects of post-capture ventilation assistance and elevated water temperature on sockeye salmon in a simulated capture-and-release experiment. Conserv. Physiol. **1**(1): cot015. doi:10.1093/conphys/cot015. PMID:27293599.

Robinson, K.A., Hinch, S.G., Raby, G.D., Donaldson, M.R., Robichaud, D., Patterson, D.A., and Cooke, S.J. 2015. Influence of postcapture ventilation assistance on migration success of adult sockeye salmon following capture and release. Trans. Am. Fish. Soc. **144**(4): 693–704. doi:10.1080/00028487.2015.1031282.

Roscoe, D.W., Hinch, S.G., Cooke, S.J., and Patterson, D.A. 2011. Fishway passage and post-passage mortality of up-river migrating sockeye salmon in the Seton River. British Columbia. River Res. Appl. **27**(6): 693–705. doi:10.1002/rra.1384. doi:, 10.1002/rra.1384.

Sandblom, E., Clark, T.D., Hinch, S.G., and Farrell, A.P. 2009. Sex-specific differences in cardiac control and hematology of sockeye salmon (*Oncorhynchus nerka*) approaching their spawning grounds. Am. J. Physiol. Regul. Integr. Comp. Physiol. **297**(4): R1136–R1143. doi:10.1152/ajpregu.00363.2009. PMID:19675278.

Scarabello, M., Heigenhauser, G.J., and Wood, C.M. 1992. Gas exchange, metabolite status and excess post-exercise oxygen consumption after repetitive bouts of exhaustive exercise in juvenile rainbow trout. J. Exp. Biol. **167**(1): 155–169. PMID:1634861.

Schmidt, P.J., and Idler, D.R. 1962. Steroid hormones in the plasma of salmon at various states of maturation. Gen. Comp. Endocrinol. **2**(2): 204–214. doi:10.1016/0016-6480(62)90005-9. PMID:13908787.

Sopinka, N.M., Patterson, L.D., Redfern, J.C., Pleizier, N.K., Belanger, C.B., Midwood, J.D., et al. 2015. Manipulating glucocorticoids in wild animals: basic and applied perspectives. Conserv. Physiol. **3**(1): cov031. doi:10.1093/conphys/cov031. PMID:27293716.

Sopinka, N.M., Middleton, C.T., Patterson, D.A., and Hinch, S.G. 2016. Does maternal captivity of wild, migratory sockeye salmon influence offspring performance? Hydrobiologia, **779**(1): 1–10. doi:10.1007/s10750-016-2763-1.

Stevens, E.D., and Black, E.C. 1966. The effect of intermittent exercise on carbohydrate metabolism in rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. **23**(4): 471–485. doi:10.1139/f66-039.

Teffer, A.K., Hinch, S.G., Miller, K.M., Patterson, D.A., Farrell, A.P., Cooke, S.J., et al. 2017. Capture severity, infectious disease processes and sex influence post-release mortality of sockeye salmon bycatch. Conserv. Physiol. **5**(1): cox017. doi:10.1093/conphys/cox017. PMID:28852514.

Teffer, A.K., Hinch, S., Miller, K., Jeffries, K., Patterson, D., Cooke, S., et al. 2019. Cumulative effects of thermal and fisheries stressors reveal sex-specific effects on infection development and early mortality of adult coho salmon (*Oncorhynchus kisutch*). Physiol. Biochem. Zool. **92**: 505–529. doi:10.1086/705125. PMID:31397628.

Wood, C.M., Turner, J.D., and Graham, M.S. 1983. Why do fish die after severe exercise? J. Fish Biol. **22**: 189–201. doi:10.1111/j.1095-8649.1983.tb04739.x.

Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by CARLETON UNIV on 05/05/21
For personal use only.