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Short-term Physiological Response Profiles of Tagged Migrating Adult Sockeye Salmon: A Comparison of Gastric Insertion and External Tagging Methods

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Abstract

A variety of electronic tag types are routinely applied to fish to better understand migration biology. However, tagging procedures have the potential to affect the postrelease behaviour and survival of tagged individuals. In this study, wild adult Sockeye Salmon *Oncorhynchus nerka* from the Harrison River, British Columbia, were radio-tagged by gastric insertion or external attachment techniques immediately after capture to understand the short-term physiological response to these two tagging methods. Plasma cortisol, glucose, lactate, sodium, and potassium levels, as well as white muscle lactate and glycogen concentrations, were measured in samples obtained from fish upon capture (0 h) as well as 1 or 4 h after the tagging treatment. The effects of key biological variables, such as sex and proximity to spawn, on the physiological response to the tagging events were also evaluated. Tagging occurred during two distinct time periods representing fish of different maturation states and durations of freshwater residency. Overall, the

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physiological response to the tagging scenarios was characteristic of the disturbance associated with exhaustive exercise. There were no significant differences detected in the response profiles following gastric or external tagging procedures. This was despite procedural differences such as stomach perforations observed in 68% of the gastric insertions in the late sampling period, and external attachments taking three times longer (43 s) than gastric insertion (15 s). Moreover, the tagged fish showed similar response profiles to control fish that were handled but not tagged. These results suggest that the capture and handling associated with a tagging event induced physiological disturbance, and that the addition of a quick tagging procedure appeared to be nonadditive over the 4-h assessment period. Sex and proximity to spawn had significant main and interaction effects on some of the physiological response variables, indicating that biological context is important for interpreting physiological assessments in experiments that manipulate exercise and stress responses in migrating adult Pacific salmon.

Advances in electronic tagging and tracking technology continue to provide researchers with unprecedented opportunities to study wild fish in their natural environment (Cooke et al. 2013a; Hussey et al. 2015). Telemetry techniques have provided remarkable insight into fish behavior and survival and are now a fundamental part of fisheries research, assessment, and management toolboxes (Cooke et al. 2016; Crossin et al. 2017). A common axiom of all tagging studies is that the tagged individuals are representative of the untagged individuals (Murray and Fuller 2000; Brown et al. 2011); however, adverse effects on behavior and survival caused by the tagging event and/or the presence of the tag can result in bias and limit the applicability of the study to the broader population (Mellas and Haynes 1985). As a result, those who manage fisheries and are affected by such management decisions (e.g., fisheries stakeholders) are sometimes wary when decisions are, in part, based on tagging studies (see Young et al. 2013; Cooke et al. 2013b). Therefore, understanding and minimizing adverse impacts of tags and tagging methods is important, not only for animal welfare (Wilson and McMahon 2006), but also to ensure that the data collected can be used to accurately reflect the behavior and survival of the population or species being studied (Brown et al. 2011).

Electronic tags have been used extensively to study the behavior and survival of Pacific salmon on their homeward spawning migration. More specifically, telemetry studies have explored the survival and behavior of Pacific salmon facing various migration pressures such as capture and release fisheries (e.g., Candy et al. 1996), pathogens (e.g., Miller et al. 2011), high water temperatures (e.g., Martins et al. 2011), and hydropower infrastructure (e.g., Trefethen 1956; Matter and Sandford 2003; Keefer et al. 2004a). There is the potential for the tagging procedure and/or the presence of the tag to have adverse effects on adult salmonids, such as altered migration rate (Chinook Salmon *Oncorhynchus tshawytscha*: Gray and Haynes 1979), decreased survival (Sockeye Salmon *O. nerka*: Ramstad and Woody 2003; Chinook Salmon: Corbett et al. 2012), and abnormal behavior (Rainbow Trout *O. mykiss*: Mellas and Haynes 1985; Atlantic Salmon *Salmo*

salar: Thorstad 2000; Hedger et al. 2017). However, studies designed to examine the physiological mechanisms underlying such negative consequences of tagging are lacking.

Two commonly used tagging techniques for adult migrating Pacific salmon are gastric insertion and external attachment (Cooke et al. 2013b). The former is possible for semelparous salmon because they cease feeding prior to freshwater entry. Gastric insertion is simple, rapid, and requires minimal fish handling (Bridger and Booth 2003), but there is potential for tag loss due to regurgitation (McCleave et al. 1978; Mellas and Haynes 1985; Smith et al. 1998; Keefer et al. 2004b) and stomach perforation due to presence of the tag in the gastrointestinal tract, which becomes more atrophied the longer a fish spends in freshwater (Dickhoff 1989; Corbett et al. 2012). An alternative to gastric insertion is external attachment (Bridger and Booth 2003). This method requires longer handling time and more skill from the tagger, but may be more appropriate if tagging takes place at an early stage in the migration when fish might still be feeding (e.g., Raby et al. 2015) or at a late stage when the degenerating gastrointestinal tissues could be damaged by gastric insertion. Both techniques have advantages and disadvantages under different tagging conditions and warrant an investigation of the possible adverse effects of tagging on the short-term physiological response of the fish.

The overall process of tagging a fish causes acute stress arising from the act of capture, handling, air exposure, and tagging (Donaldson et al. 2008), resulting in the activation of anaerobic metabolism. Following such exhaustive exercise, a variety of physiological disturbances occur. For example, plasma catecholamines increase (Wood et al. 1983; Cameron and Cech 1990; Pagnotta and Milligan 1991), tissue energy stores (e.g., ATP, creatine phosphate, muscle glycogen) are rapidly depleted, muscle and blood lactate levels increase, and ionic homeostasis is disturbed (Kieffer 2000; Barton et al. 2002). Excessive energy use during the capture and tagging event could compound the environmental and anthropogenic stressors already encountered during the spawning migration, and the mass (i.e., burden) of the tag itself may cause chronic stress and

contribute to additional anaerobiosis if routine swimming is affected. Further, biological factors, such as sex and proximity to spawn, influence short-term physiological response profiles of adult migrating Pacific salmon. Prolonged recovery from such physiological perturbation would presumably represent a primary mechanism underlying any whole-animal change associated with the overall tagging event (e.g., alterations in behavior or survival). Indeed, such an accumulation of stress responses could be detrimental to continued migration and reproductive success (Hinch et al. 2006). Thus, identifying the short-term physiological response profiles to tagging events, including different tag attachment techniques, may point to potential long-term causes of tagging-related alterations to behavior and survival.

The objective of this study was to evaluate the short-term physiological response of adult Sockeye Salmon to two common electronic tagging methods following capture and handling in a field environment. Comparisons focused on fish that were captured near their spawning grounds, tagged using either gastric or external attachment methods, and held for short-term sampling procedures. Tagging occurred during two distinct sampling periods (i.e., early and late with respect to their temporal proximity to spawning), providing the opportunity to investigate the potentially disparate physiological status and environmental conditions that characterize adult Pacific salmon spawning migrations. We hypothesized that tagged fish would display a higher magnitude response to stress and a prolonged recovery profile compared with untagged (i.e., control) fish due to the handling and procedures associated with tagging. Additionally, we predicted that externally tagged fish would elicit a greater and prolonged stress response than would gastrically tagged individuals due to the longer handling time necessitated by external attachment. We included multiple predictor variables (i.e., sex, sampling period, and holding time) in the experimental design to explore the potential for key interactions to influence tagging effects in the wild. In addition to blood plasma variables, we included muscle tissue variables that we hypothesized would provide a more direct and sensitive measure of the anaerobic response in fish (Pon et al. 2012). Overall, we expected these results to be useful in advancing the understanding of the physiological response profiles of fish that have undergone exhaustive exercise in the context of a realistic capture and tagging event in the wild.

METHODS

Study site.—This study took place on the Harrison River, British Columbia, which is a spawning tributary for Sockeye Salmon in the lower Fraser River watershed. The Harrison River is 16.5 km in length and approximately

100 km upriver from the mouth of the Fraser River. Since 1995, adult Harrison River Sockeye Salmon have exhibited river entry times that diverge from historical migration behavior (Hinch et al. 2012) despite the peak spawning period for this population consistently occurring in mid-November (Gilhausen 1990). Several tagging studies have occurred on adult Harrison River Sockeye Salmon since this elongation of their freshwater residency. These studies have employed a variety of tagging methods such as Petersen disc tagging (commonly used by the Fisheries and Oceans Canada Stock Assessment Program) and acoustic and radiotelemetry technology using both gastric (English et al. 2005; Mathes et al. 2010; Donaldson et al. 2012; Robinson et al. 2015) and external tagging techniques (Raby et al. 2015); however, no study has been specifically designed to determine the short-term physiological effects of different tagging techniques while taking into account multiple predictor variables such as sex and sampling period.

Tagging and holding.—Capture, tagging, holding, and biopsy took place on the Harrison River approximately 9 km from the confluence of the Fraser and Harrison rivers. Fish were captured by beach seine, which was deployed by a powerboat to the middle of the river and pulled in by hand. A total of 135 females and 134 male Sockeye Salmon were included in the study (see Table 1). Female body mass and FL (mean \pm SD) were $2,351.7 \pm 293.3$ g and 59.0 ± 2.3 cm, respectively. Male body mass and FL were $2,960.4 \pm 462.5$ g and 64.8 ± 3.6 cm, respectively. Some captured individuals were removed immediately via dip net once the seine net was bagged and then rapidly sampled to assess baseline physiological status (termed baseline herein and representing the 0-h holding treatment). The time from when the seine net was deployed to when these individuals were sampled was 9 ± 4.4 min; therefore, the sample was taken following capture fatigue, which would include anaerobic exercise, crowding, and confinement stress (Wood 1991; Boutilier et al. 1993; Milligan 1996). In addition, there were three tagging-treatment groups that consisted of individuals that were (1) not tagged, termed control, (2) gastrically tagged, and (3) externally tagged. A flow-through riverside net-pen (dimensions: 2.4 m in length, 1.3 m in width, bisected to make two partitions 0.65 m wide and ~1 m deep) was used to hold fish for 1 or 4 h, which is consistent with other studies monitoring the responses of fish to exhaustion over time (e.g., Wood 1991). Control fish were dipnetted from the bagged beach seine and placed directly into the net-pen. Fish that were to be tagged were individually dipnetted and placed in a tagging trough affixed with a pump that allowed fresh river water to continuously flow over the mouth, gills, and body throughout the tagging procedure. Either a gastric or external radiotelemetry tag was affixed (procedures outlined in detail in Cooke

et al. 2012) using established protocols for tagging adult salmon without anesthetic (Cooke et al. 2005). External tags (model TX-PSC-E-45-M, Sigma Eight, Newmarket, Ontario; 32 mm in length, 10 mm in width, 9.8 mm in height, and 3.7 g weight in air) were affixed by inserting two metal pins through the dorsal musculature at the base of the dorsal fin and then securing the tag by adding plastic buffer discs on the opposing side and twisting the pin ends to create a knot. Gastric tags (model TX-PSC-I-1200-M, Sigma Eight; 43 mm in length, 16 mm in width, 16 mm in height, and 15.2 g weight in air) were secured by inserting the tag through the mouth into the stomach using a smooth plunger. Tagging took place over two periods in 2014, an early sampling period (September 18 and 25; water temperature range, 17.3–18.4°C) and a late sampling period (October 16 and 23; water temperature range, 12.8–13.0°C). This represented individuals that were 7 to 8 weeks and 3 to 4 weeks away from the peak spawning window, respectively. For female fish, the gonadosomatic index ($GSI = \text{gonad weight/body weight} \times 100$) was $11.5\% \pm 2.5\%$ (mean \pm SD) in the early sampling period and $18.6\% \pm 2.5\%$ in the late sampling period. The GSI for male fish in the early and late sampling periods was $3.9\% \pm 0.1\%$ and $3.4\% \pm 0.8\%$, respectively. We aimed to have groups of 10 fish for each sex, tagging treatment, holding time, and sampling period combination.

The tagging procedure was designed to mimic the tagging protocols of telemetry studies that release tagged individuals. A team of three people assisted with the tagging process; the first person held the fish in the trough and reported fish condition and estimated sex, the second individual applied the tag, and the third person recorded all relevant information. Each fish was assessed for capture vigor, maturity, injuries, and release vigor according to common stock assessment procedures. Vigor was assessed on a scale of 1 to 3, where 1 represents active behavior and fast response to stimuli, 2 represents slow movement and slow response, and 3 represents very slow movement and minimal response to any stimuli. Sex and maturity were estimated by observing secondary sexual characteristics, and the former was later confirmed during autopsy. Fish were confined (i.e., the bag was kept loose) in the seine net prior to tagging for 30 ± 18 min, which is consistent with other research tagging studies conducted on adult Fraser River Sockeye Salmon (e.g., Clark et al. 2010; Nguyen et al. 2014). Immediately following tagging, individuals were placed in net-pens alongside the control fish. Groups of 9–12 individuals were held in a net-pen during a single holding period, and it took approximately 10 min to load up a net-pen with fish from all three treatments. Throughout the study, one female control fish (4-h treatment group in the early sampling period) became

moribund while in the net-pen and was removed, euthanized, and omitted from the analysis.

Blood and tissue collection.—After a treatment group was held for the allotted time (1 or 4 h), fish were individually removed from the pen by dip net and quickly euthanized by cerebral concussion. Removal and euthanization of all fish in a treatment group took less than 3 min, which is a time period typically regarded as suitable for not altering some of the key blood variables such as glucose, cortisol, and lactate (Romero and Reed 2005; M. J. Lawrence, Carleton University, unpublished data). A blood sample was taken immediately from the caudal vasculature using a 21-gauge needle and a 3-mL vacutainer syringe containing lithium heparin (BD Vacutainer, Franklin Lakes, New Jersey). The blood sample was temporarily stored in an ice–water slurry and then centrifuged at $7,000 \times g$ for 5 min (Clay Adams Compact II Centrifuge). Plasma was flash-frozen in liquid nitrogen (N_2) and stored at -80°C until processing. Immediately following extraction of the blood sample, a thin muscle sample (<0.5 cm thick) was excised halfway between the dorsal and anal fin and across the lateral line using a scalpel. The tissue sample was blotted to remove excess blood, freeze-clamped in liquid N_2 and stored in a freezer at -80°C until processing. A sample of tissue from the adipose fin and a scale were removed, consistent with other tagging studies that use this information for stock assignment and age information, respectively. Morphometric information (e.g., body mass, organ masses, length) and notes on stomach quality (i.e., stomach perforations) were recorded.

Plasma sodium and plasma potassium were analyzed to assess possible osmoregulatory dysfunction (Barton et al. 2002) using a Cole Parmer model 2655-00 single-channel digital flame photometer. Plasma glucose and plasma lactate were measured to assess the metabolic response to stress (Barton et al. 2002) using a YSI 2300 STAT Plus glucose/lactate analyzer. Plasma cortisol was analyzed to evaluate the primary endocrine response (Barton et al. 2002) using an ELISA hormone kit (Neogen Corporation). Methods are described in Farrell et al. (2001). Muscle samples were ground to a fine powder under liquid N_2 using a precooled mortar and pestle. Muscle glycogen and lactate were isolated and assayed spectrophotometrically as described by Richards et al. (2002). Cost limitations at the time of analysis limited our ability to run muscle metabolites for both sexes. We anticipated that female salmon would demonstrate a stress response of greater magnitude in muscle metabolites than would males, as seen in other blood plasma stress indicators; therefore, we measured these metabolites in females only.

Data analysis and statistics.—All analyses were conducted in RStudio (version 0.99.467, RStudio, Boston,

TABLE 1. Mean and SE values (n = sample size) of the physiological response variables and sample sizes amongst the treatment groups: control (C), gastrically tagged (G), and externally tagged (X) female (♀) and male (♂) Harrison River Sockeye Salmon sampled immediately (i.e., 0-h baseline [B]), or 1 or 4 h after the tagging treatment in both the early (September 18 and 25) and late (October 16 and 23) sampling periods. Muscle metabolite variables were analyzed for female fish only. Differences in sample sizes are caused by constraints in laboratory analyses (e.g., limited sample volume, repeat failures).

Statistic	Early						Late								
	0 h		1 h		4 h		0 h		1 h		4 h				
	B	C	G	X	C	G	X	B	C	G	X	C	G	X	
♀	Mean	136.9	141.6	147.8	145.2	130.4	130.7	130.2	140.0	151.6	148.1	148.9	134.5	131.0	135.7
	SE	1.4	4.4	2.2	2.4	1.7	2.1	1.7	1.6	1.9	3.4	2.0	3.0	2.8	2.5
	n	8	9	10	10	10	10	8	10	8	11	10	10	9	11
♂	Mean	145.0	140.1	144.6	148.8	133.6	134.6	133.8	138.3	152.2	149.6	148.4	134.4	137.7	136.2
	SE	3.7	2.0	2.1	1.8	1.4	1.6	1.5	2.9	3.3	2.6	2.1	2.4	1.4	0.9
	n	9	9	9	7	10	10	12	10	9	9	10	10	11	10
♀	Mean	1.5	2.3	2.1	1.9	3.1	5.7	4.7	3.7	2.5	2.8	3.1	4.5	4.9	4.9
	SE	0.42	0.6	0.5	0.45	0.49	1.38	0.67	0.31	0.37	0.39	0.34	0.60	0.58	0.28
	n	8	9	10	10	10	10	8	10	8	11	10	10	9	11
♂	Mean	1.5	2.5	2.4	2.4	4.1	4.3	4.1	4.3	2.2	2.5	2.2	4.5	3.7	3.3
	SE	0.2	0.7	0.8	0.3	0.6	0.5	0.7	0.3	0.4	0.4	0.2	0.2	0.4	0.4
	n	9	9	8	7	10	10	12	10	9	9	10	10	11	11
♀	Mean	122.5	416.9	418.4	445.8	446.8	456.9	420.5	68.6	395.4	424.6	433.6	348.4	339.9	416.4
	SE	72.4	32.8	32.2	54.9	45.6	48.8	37.5	35.1	50.5	20.2	44.4	56.2	25.3	33.1
	n	8	9	10	10	10	10	8	10	7	11	10	10	10	10
♂	Mean	36.6	224.6	221.7	164.7	140.9	152.6	153.4	19.1	113.7	98.3	124.2	88.7	100.8	67.2
	SE	15.6	47.8	24.0	35.7	23.1	22.3	19.3	4.1	14.5	11.6	21.1	14.5	17.9	5.5
	n	9	9	8	7	10	10	12	10	9	9	10	10	11	10
♀	Mean	8.1	18.2	17.6	18.6	10.5	14.4	14.6	6.0	14.9	14.4	16.0	13.3	9.9	14.1
	SE	1.6	1.2	2.0	1.5	1.4	1.9	2.7	0.5	1.9	1.2	1.5	3.1	1.4	1.4
	n	8	9	10	10	10	9	8	10	8	11	10	10	10	11
♂	Mean	6.7	14.6	17.1	16.0	8.9	9.7	9.7	5.7	12.9	13.0	15.3	11.6	9.2	8.9
	SE	1.8	2.5	3.6	1.6	1.2	1.5	1.5	0.9	1.1	1.3	1.1	0.9	1.8	1.5
	n	9	9	8	7	10	10	12	10	9	9	9	10	11	10

TABLE 1. Continued.

Statistic	Early												Late											
	0 h				1 h				4 h				0 h				1 h				4 h			
	B	C	G	X	B	C	G	X	B	C	G	X	B	C	G	X	B	C	G	X				
♀	Mean	4.2	5.9	5.5	6.1	6.8	5.1	5.5	3.9	4.0	4.2	4.6	3.1	4.1	3.4									
	SE	0.3	0.9	0.6	0.7	0.7	0.8	0.9	0.3	0.3	0.3	0.4	0.5	0.2	0.3									
	<i>n</i>	8	9	10	10	10	10	8	10	9	11	10	10	10	11									
♂	Mean	5.1	5.9	6.7	7.0	7.5	6.9	7.3	4.5	5.8	6.2	6.2	5.9	5.6	5.9									
	SE	0.5	0.7	0.8	0.3	0.8	0.2	0.7	0.3	0.3	0.3	0.3	0.4	0.5	0.4									
	<i>n</i>	9	9	8	7	10	10	12	9	9	9	10	10	11	10									
♀	Mean	54.6	43.3	43.3	46.7	36.7	33.5	28.2	52.0	43.9	42.9	44.1	30.1	28.2	30.8									
	SE	5.0	5.1	4.2	2.8	3.1	4.6	4.1	3.1	4.2	1.7	1.0	2.6	2.4	2.4									
	<i>n</i>	8	8	10	10	10	10	8	10	8	11	10	10	10	11									
♀	Mean	11.1	10.9	12.2	10.9	12.8	12.0	14.0	13.3	8.4	8.7	10.1	12.2	11.8	9.2									
	SE	2.9	1.3	2.2	1.1	1.5	1.2	1.9	2.4	1.6	1.1	1.4	1.4	1.4	1.1									
	<i>n</i>	8	8	9	10	9	10	8	8	8	11	8	9	10	11									

<https://www.rstudio.com/>) using R (version 3.1.2: R Foundation for Statistical Computing; <http://www.R-project.org>). A series of multivariate ANOVAs (MANOVAs) were used to explore general responses of blood plasma and muscle physiological variables to the tagging treatment scenarios. Separate MANOVAs were used to test for differences in blood plasma variables and muscle metabolite variables among externally and gastrically tagged male and female fish held for 1 or 4 h during both sampling periods. The assumptions of multivariate normality were assessed before employing this parametric multivariate statistical method. One female in the early sampling period that was gastrically tagged and held for 4 h was identified as an outlier due to an aberrant physiological profile with maximum plasma potassium and lactate values and minimum glucose concentrations, likely indicating a severe pre-existing condition. This individual was omitted from the analysis. All possible two-way interactions were included in both the plasma and muscle MANOVAs to account for the relationships that are expected to occur between these variables.

After testing different order combinations of predictor and response variables in the MANOVAs for robustness, it was revealed that tag type (control, external, and gastric) had no effect, either as an individual effect or in a two-way interaction, on the physiological response of blood plasma and muscle metabolite variables. Therefore, tag type was removed from all subsequent analyses. Because tag type as a predictor variable was dropped, the baseline group (0 h) was added as another level to the holding time predictor variable in successive tests to further explore the time course of physiological responses following a capture and tagging event. Cortisol was removed from this MANOVA because it violated the assumption of equal variance required for this test (Quinn and Keough 2002) and was analyzed graphically.

Univariate ANOVAs revealed which predictor variables and interactions had a significant effect on each blood plasma and muscle metabolite response variables. Where statistical differences were detected, box plots were used to visually assess the nature of the differences between two-level variables (i.e., sex, sampling period). Tukey's honest significant difference (HSD) tests assessed significant differences in the three-level variable (i.e., holding time with levels 0, 1, and 4 h).

A MANOVA was also used to assess differences in physiological variables between fish in the late sampling period with a perforated or intact stomach. Little to no stomach perforations occurred in the early period. For the analysis, physiological results from fish in the late period with an intact stomach in all three tagging treatments were pooled and compared with those from gastrically tagged fish with a perforated stomach.

RESULTS

The tagging and initial processing took an average of 15 ± 6 s (mean \pm SD) for the gastric procedure, which was significantly faster ($t = 19.54$, $df = 144.49$, $P < 0.001$) than the 43 ± 14 s required for the external procedure. Changes in male and female plasma and female only muscle physiological variables following the tagging and holding treatments are summarized in Table 1. Despite differences in tagging time, the plasma and muscle physiological variables did not significantly differ among control, gastrically tagged, and externally tagged Sockeye Salmon (MANOVA; Table 2). Furthermore, no significant interactions of tag type were observed. As such, we dropped tag type from subsequent analyses.

Pooling data from the tag type treatment groups allowed for a focused assessment of variance in plasma and muscle variables across all three holding times (0, 1,

TABLE 2. Results from MANOVAs for Sockeye Salmon blood plasma variables and muscle metabolites. The MANOVA for muscle metabolites did not include Sex as a predictor variable as these data were available for females only. Significant values ($P \leq 0.05$) are indicated in bold italics.

Predictor variable	Blood plasma			Muscle metabolites		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Tag Type	0.64	2	0.784	0.02	2	0.999
Sampling Period	21.75	1	<0.001	5.09	1	0.009
Time	63.02	1	<0.001	23.06	1	<0.001
Sex	86.95	1	<0.001			
Tag Type \times Sampling Period	0.82	2	0.611	0.29	2	0.878
Tag Type \times Time	0.45	2	0.918	0.79	2	0.530
Tag Type \times Sex	0.63	2	0.791			
Sampling Period \times Time	3.18	1	0.009	0.07	1	0.929
Sampling Period \times Sex	4.23	1	0.001			
Time \times Sex	1.05	1	0.389			

and 4 h), while still accounting for the potential main and interactive effects of sex and sampling period (early and late) following capture and handling. The overall physiological response was significantly influenced by sex, sampling period, and holding time (MANOVA; Tables 3 and 4). In addition, there were significant interactions between sex and sampling period, as well as between sampling period and holding time (MANOVA; Tables 3 and 4).

Female fish had plasma lactate values that were approximately 20% greater than male fish (Figure 1A); plasma lactate increased in both sexes after time 0 h and remained elevated (Table 1; Figure 1B). Cortisol values increased from time 0 h, and concentrations for female fish were consistently greater than those for male fish (Table 1; Figure 2). The plasma glucose levels increased with time; however, the response profile was significantly influenced by the interactions of sex and sampling period, as well as sampling period and time (Table 1; Figure 3A, B).

Plasma sodium levels were significantly higher in the late sampling period than in the early sampling period (Table 1; Figure 4A). This response variable significantly increased from 0 to 1 h and then decreased to values below 0-h values at the 4-h measurement (Table 1;

Figure 4B). Plasma potassium levels changed with holding time; however, the holding time and sampling period interaction had a significant disordinal effect on the plasma potassium values (Table 1; Figure 5). Female muscle lactate concentrations were highest in the 0-h group and displayed a significant decrease over time (Figure 6). The concentrations of female muscle glycogen did not vary with time.

Notes on the integrity of the stomach were recorded for gastrically tagged individuals throughout the experiment. We observed perforated stomachs in 66% and 70% of gastrically tagged females and males, respectively, in the late sampling period. No gastrically tagged females and only 1 of 18 (5.6%) gastrically tagged males exhibited signs of stomach perforation in the early sampling period; this is consistent with our observations of thin stomach walls in the late sampling period. However, stomach perforation had no significant impact on the physiological response profiles of adult Sockeye Salmon in the late sampling period compared with fish for which the stomach was not perforated (MANOVA: $F = 1.71$, $df = 1$, $P = 0.138$). During the late sampling period, there was one occurrence of a gastrically tagged female regurgitating the tag in the net-pen. This individual was kept in the analysis, as it

TABLE 3. Results from the MANOVA and subsequent ANOVAs indicating the response of Sockeye Salmon blood plasma variables (Na^+ , K^+ , lactate, glucose; omitting cortisol) to main effects and interactions. Tag types were pooled and baseline group (0 h) was added. Significant values ($P \leq 0.05$) are indicated in bold italics. The ANOVAs did not include the Sex \times Time interaction because it was not significant in the MANOVA.

Predictor variable	MANOVA			Na^+ (mmol/L)			K^+ (mmol/L)			Lactate (mmol/L)			Glucose (mmol/L)		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Sex	19.49	1	<0.001	2.14	1	0.144	0.57	1	0.451	14.79	1	<0.001	52.91	1	<0.001
Sampling Period	27.44	1	<0.001	14.40	1	<0.001	7.24	1	0.008	3.68	1	0.056	48.45	1	<0.001
Time	46.50	2	<0.001	101.05	2	<0.001	41.89	2	<0.001	46.92	2	<0.001	10.31	2	<0.001
Sex \times Sampling Period	4.15	1	0.003	0.55	1	0.450	3.59	1	0.059	0.65	1	0.420	5.07	1	0.025
Sex \times Time	1.08	2	0.379												
Sampling Period \times Time	5.57	2	<0.001	2.35	2	0.097	8.54	2	<0.001	1.77	2	0.173	3.40	2	0.0348

TABLE 4. The MANOVA and ANOVA results indicating the response of muscle metabolites (glycogen, lactate) for female Sockeye Salmon to main effects and interactions. Tag types were pooled and baseline group (0 h) was added. Significant values ($P \leq 0.05$) are indicated in bold italics. The ANOVAs did not include the Sampling Period main predictor variable and the Sex \times Time interaction because they were not significant in the MANOVA.

Predictor variable	MANOVA			Glycogen (mmol/kg)			Lactate (mmol/kg)		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Sampling Period	3.27	1	0.413						
Time	17.69	2	<0.001	2.34	2	0.100	42.38	2	<0.001
Sampling Period \times Time	0.85	2	0.492						

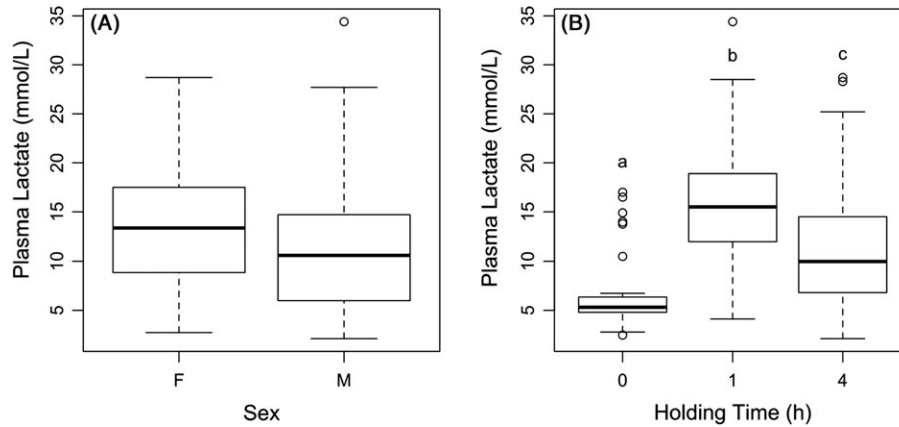


FIGURE 1. (A) Sex and (B) Holding Time had significant main effects on plasma lactate concentrations in Sockeye Salmon. Data were pooled for all tag-type treatments. Lowercase letters indicate significant differences ($P < 0.05$) between holding time groups, as assessed by Tukey's HSD test. On the box plot, the bold horizontal line in the rectangular box indicates the median, the box bounds the first and third quartiles, and the whiskers extend to include all values within the $1.5\times$ interquartile range.

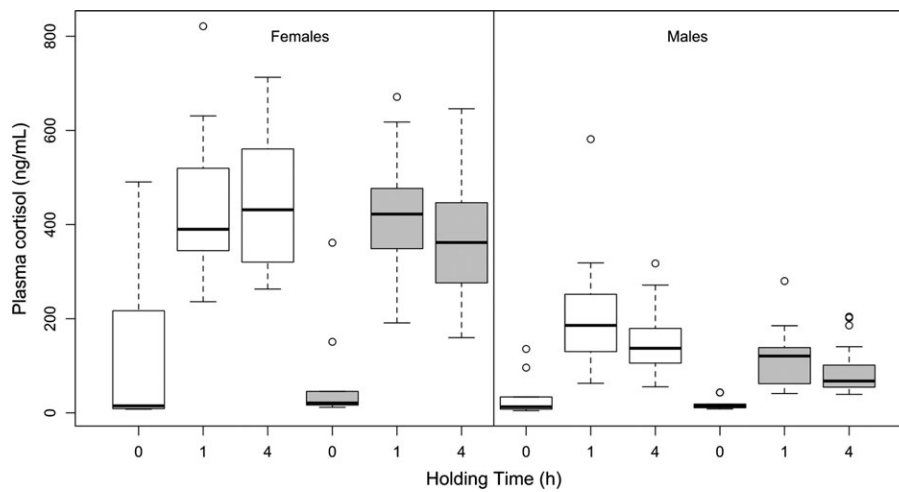


FIGURE 2. Average plasma cortisol values for each Sockeye Salmon treatment group. Data for females are to the left of the vertical line and data for males are to the right. White box = early sampling period, gray box = late sampling group. Data were pooled for all tag-type treatments. On the box plot, the bold horizontal line in the rectangular box indicates the median, the box bounds the first and third quartiles, and the whiskers extend to include all values within the $1.5\times$ interquartile range.

could not be determined when the tag was lost, but data from this individual was still valuable in exploring the physiological consequences of gastric tagging. There was no loss of external tags during the experiment.

DISCUSSION

Our evaluation of the short-term physiological response of wild, adult, Sockeye Salmon to experimental tagging scenarios indicated no significant differences between

gastric and external approaches. Furthermore, tagged fish displayed the same physiological response as untagged, control individuals. This suggests that the observed recovery profile was primarily associated with capture and handling of the fish and that tagging had no additive effect. To our knowledge, this is the first study to report and compare quantitative measures of the blood and muscle physiological responses of tagged adult Pacific salmon affixed with either external or gastric tags to controls in their natural environment. Thus, this work represents an

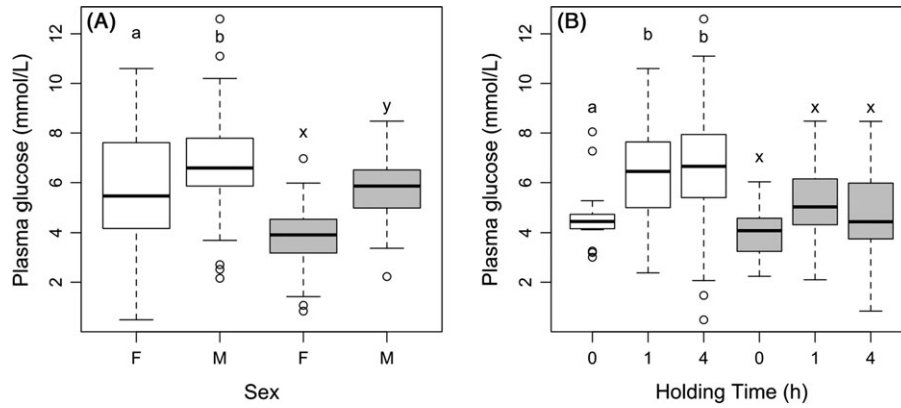


FIGURE 3. Significant interaction effects of (A) Sampling Period and Sex and (B) Sampling Period and Holding Time on plasma glucose concentrations in Sockeye Salmon. White box = early sampling period, gray box = late sampling period. Data were pooled for all tag type treatments. Lowercase letters indicate significant differences ($P < 0.05$) between Sex (A) and Holding Time groups (B) within the sampling periods, as assessed by Tukey's HSD test. On the box plot, the bold horizontal line in the rectangular box indicates the median, the box bounds the first and third quartiles, and the whiskers extend to include all values within the 1.5 \times interquartile range.

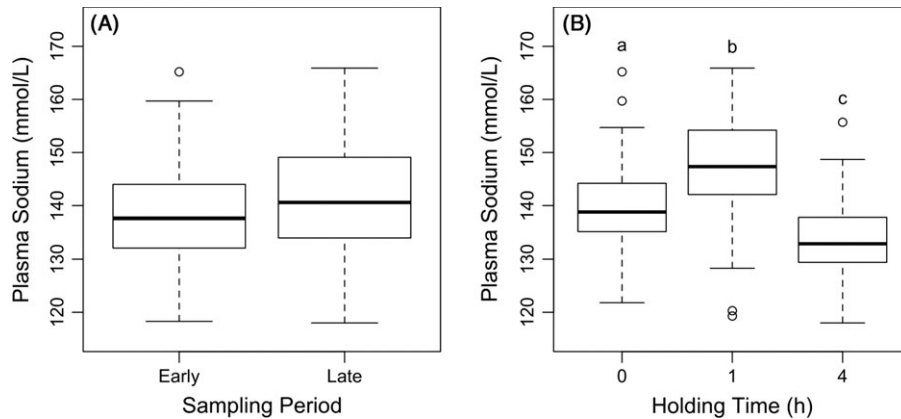


FIGURE 4. (A) Sampling Period and (B) Holding Time had significant main effects on plasma sodium concentrations in Sockeye Salmon. Data were pooled for all tag-type treatments. Lowercase letters in (B) indicate significant differences ($P < 0.05$) between groups, as assessed by Tukey's HSD test. On the box plot, the bold horizontal line in the rectangular box indicates the median, the box bounds the first and third quartiles, and the whiskers extend to include all values within the 1.5 \times interquartile range.

important step towards understanding the physiological mechanisms underlying the impacts of the overall tagging event.

The lack of significant differences in the acute physiological responses among the tag types and control suggests that the cumulative effect of capture, handling, and holding in addition to tagging was antagonistic, meaning the sum of the effects was less than what would be expected from the sum of the individual components (Johnson et al. 2012). The stress of capture and handling likely masked the incremental impact of the tagging procedures. If the fish had been allowed to recover from the capture stress prior to the tagging treatment, this may have reduced the influence of capture on the stress response profile and helped isolate the incremental effects of the tagging

procedures themselves. However, this would not be comparable with field studies that employ tagging techniques for assessing fish in the wild. In addition, confinement in the net-pen during the 1 or 4 h holding period may have influenced the response profile and thus the ability to detect an incremental tagging effect (Portz et al. 2006; Donaldson et al. 2011). Disentangling the effects of capture, handling, tagging, and confinement/holding on wild fish is an inherent challenge in evaluations of tagging effects (Jepsen et al. 2015) and, conversely, in evaluations of capture and handling effects when using telemetry techniques (Patterson et al. 2017). The evidence herein suggests that the short-term physiological effect of tagging may be minimal when assessed in conjunction with the acute stressors of capture, handling, and holding.

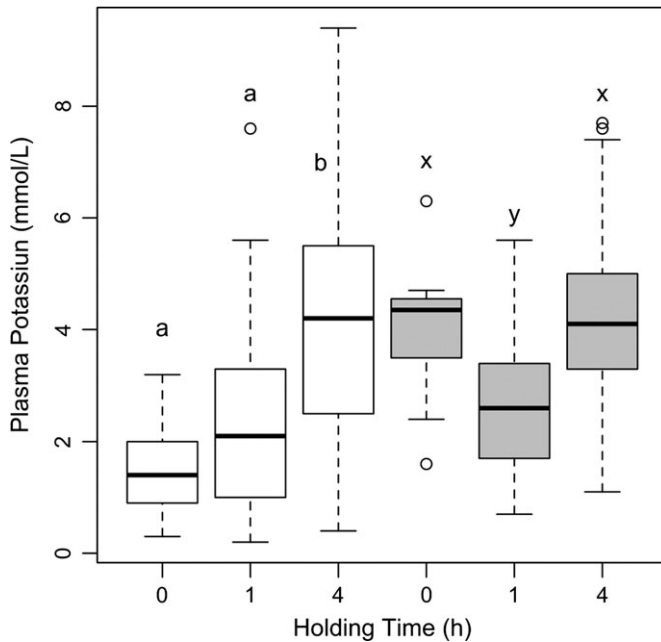


FIGURE 5. Sampling Period and Holding Time had a significant interaction effect on plasma potassium in Sockeye Salmon. White box = early sampling period, gray box = late sampling period. Data were pooled for all tag type treatments. Lowercase letters indicate significant differences ($P < 0.05$) between holding time groups within the sampling periods, as assessed by Tukey's HSD test. On the box plot, the bold horizontal line in the rectangular box indicates the median, the box bounds the first and third quartiles, and the whiskers extend to include all values within the 1.5 \times interquartile range.

However, we cannot eliminate the possibility that tagging effects may play a greater and more dynamic role in sub-lethal or chronic consequences that may only become apparent outside of the 4-h holding period or under different tagging or environmental conditions.

The average tagging times of 15 s for the gastric procedure and 43 s for external attachment in this study were rapid relative to other studies tagging adult Pacific salmon without anesthesia (e.g., 2 min: Mathes et al. 2010; 3 min: Roscoe et al. 2011; 2.5 min: Corbett et al. 2012). Also, the environmental conditions in the Harrison River at the time of this study were benign, with normal water flows and water temperatures that were within the predicted optimal thermal window for aerobic scope (Eliason et al. 2013) for Harrison River Sockeye Salmon. Longer tagging times and the addition of a biopsy during tagging or less favorable environmental conditions may elicit more profound tagging effects, although tag and biopsy procedures of 150 s or less in favorable water quality conditions do not cause significant deleterious effects on travel times and survival (Cooke et al. 2005). Similarly, our results showed no incremental effect on acute physiology for tagging that took place in under 100 s, but we caution that similar

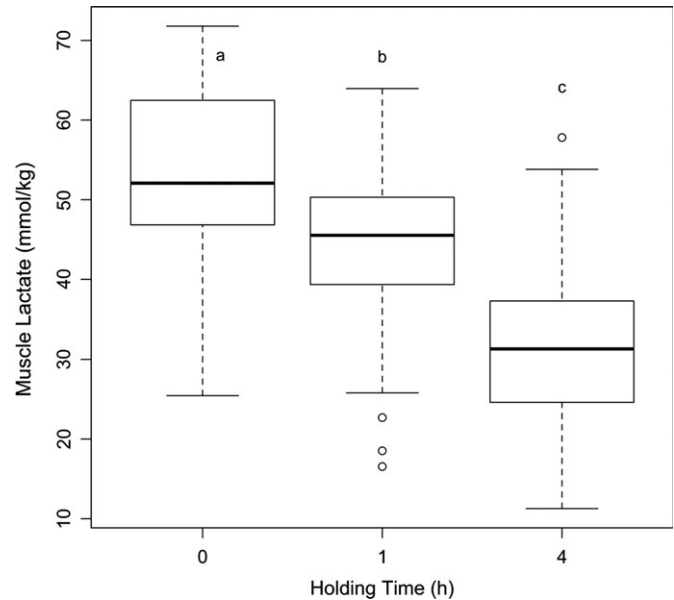


FIGURE 6. Significant main effect of Holding Time on muscle lactate values in female Sockeye Salmon. Data were pooled for all tag type treatments. Lowercase letters indicate significant differences ($P < 0.05$) between holding time groups, as assessed by Tukey's HSD test. On the box plot, the bold horizontal line in the rectangular box indicates the median, the box bounds the first and third quartiles, and the whiskers extend to include all values within the 1.5 \times interquartile range.

results may not occur if the environmental conditions during the study are not ideal.

Consistent with our expectations, sex, sampling period, and holding time had an effect on the overall physiological response. In several cases there were interactions between the main predictors; these interactions are often not explicitly stated in previous stress physiology work. The multivariable design of this study allowed us to demonstrate the importance of biological context for interpreting the stress response under realistic conditions. An additional benefit to the design of this study was the opportunity to collect physiological data from tagged and control individuals at 1 and 4 h; this allowed for a direct comparison amongst treatments at two short-term holding periods, the latter of which is novel to the literature on exhaustive exercise physiology in fish.

A typical beach seine event for salmon involves crowding in the net, struggling, and anaerobic swimming, which are associated with the depletion of energy reserves, physiological dysfunction, and even death (Wood et al. 1983; Wang et al. 1994; Milligan 1996). The physiological status of baseline (0 h) fish from both sampling periods was similar to that of Sockeye Salmon collected by beach seine in other studies on the same river system (Mathes et al. 2010; Donaldson et al. 2012). The temporal response profiles of the physiological variables in this study were

similar to those reported in other field studies examining the recovery of adult Pacific salmon following an acute capture stressor (Farrell et al. 2001; Raby et al. 2015). Plasma lactate, cortisol, glucose, and sodium all increased in response to capture and handling (see Figures 1B, 2, 3B, 4B, and Table 1 in Farrell et al. 2001; see Figures 3 and 4 in Raby et al. 2015). Plasma potassium concentrations continued to rise over time, which is consistent with the response profile of exercised Rainbow Trout (Wood et al. 1983) in which plasma potassium continued to increase to approximately twice the resting values after 2–4 h, and resting levels were not restored until 12 h after exercise. The pronounced and prolonged rise in plasma potassium is thought to reflect the loss of this ion from muscle cells due to exercise (Wood et al. 1983; Sejersted and Sjøgaard 2000).

Lactate is the metabolic end product of anaerobic glycolysis, which initially rapidly accumulates in muscle tissue but can also leak into the circulatory system (Wood 1991; Kieffer et al. 1994; Wang et al. 1994; Milligan 1996). Previous studies have linked delayed mortality with elevated plasma lactate levels (see Black 1958), and plasma lactate levels of ~18–20 mmol/L were associated with increased mortality in Sockeye Salmon tagged in the ocean environment (Crossin et al. 2009). A plasma lactate threshold of 10 mmol/L has been proposed, above which swimming performance is impaired (Farrell et al. 1998). In our study, 64% of the fish still had plasma lactate concentrations exceeding 10 mmol/L after 4 h, and 14% had concentrations surpassing 20 mmol/L (Figure 7). This suggests that the Sockeye Salmon were still experiencing a high level of circulating lactate indicating muscle fatigue that may severely limit burst-swimming ability even 4 h after treatment and potentially reduce survival over the long term (Jain and Farrell 2003; Crossin et al. 2009). Our results show that >4 h was required for plasma cortisol (Figure 2) and plasma lactate (Figure 1B) levels to return to basal values. This prolonged recovery duration has implications on postrelease behavior, survival, and predator avoidance.

We anticipated that muscle tissue would provide a more direct and sensitive measure of the anaerobic response in the fish (Pon et al. 2012) and thus identify potential differences between gastric and external tagging techniques. The external tag attachment method required longer handling times that may have entailed higher levels of anaerobic metabolism. However, muscle lactate values were similar for control, external, and gastric tagging scenarios (Table 1). The response profile and maximum muscle lactate concentrations in this study (52.0–54.6 mmol/kg) were similar to those reported in an exercise physiology study in a marine field setting with adult Coho Salmon *O. kisutch* (53.7 mmol/kg; Farrell et al. 2001). In addition, we expected muscle glycogen to decrease following capture

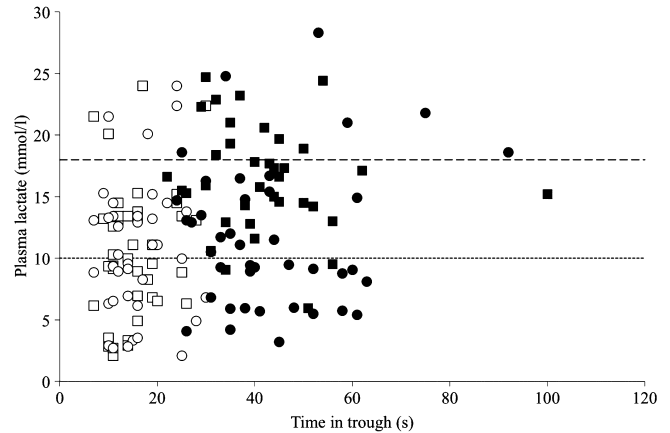


FIGURE 7. Plasma lactate concentrations in Sockeye Salmon and time in trough in seconds. Fish tagged via gastric insertion are represented by white symbols, and fish tagged via external attachment are represented by black symbols. Squares represent blood samples taken 1 h posttagging, and circles represent samples taken 4 h posttagging. Dotted line indicates the plasma lactate threshold of 10 mmol/L indicated by Farrell et al. (1998) for which Sockeye Salmon failed further repetitive swimming within an hour. Dashed line indicates the plasma lactate threshold of 18 mmol/L indicated by Crossin et al. (2009) as increasing mortality before river entry of ocean-caught Sockeye Salmon.

stress and then to be slowly replenished; however, there was no effect of time on the response profile for glycogen (range: 9–13.5 mmol/kg; Table 4). Replenishment was not observed likely due to the short time frame of the experiment, given that peak of replenishment for muscle glycogen in Rainbow Trout occurred 8 h postexercise (Milligan and Wood 1986; Milligan 1996). Also, continued elevation of plasma cortisol limits the restoration of muscle glycogen as well as the clearance of muscle lactate following exercise (Pagnotta and Milligan 1991; Eros and Milligan 1996); both of these limitations could contribute to prolonged recovery durations and delayed migration.

The interpretation of cortisol concentrations following a stressor in migrating adult Pacific salmon can be challenging because plasma cortisol increases progressively with maturation and independently of stress and because females have higher circulating cortisol levels than males (Carruth et al. 2002; Hinch et al. 2006). In this study, plasma cortisol levels increased from 0 h to about 4.5-fold for females and to approximately fivefold for males and remained elevated 4 h after the stressor (Figure 2). Concentrations of plasma cortisol can stay elevated for 6 h or more after a stressor, and increasing plasma cortisol after exercise can have negative consequences to the fish in terms of metabolic recovery (Milligan 1996) and migration success (Cook et al. 2014). There was an appreciable difference in plasma cortisol between sampling periods and sex; lower concentrations were observed in the late sampling period, and the greatest magnitude of difference

between males and females occurred at the 4-h holding times (Figure 2); however, levels remained considerably greater than 0-h values for both males and females after 4 h. High circulating cortisol levels may have hindered muscle lactate and glycogen recovery, but knowing whether this was a long-term or chronic elevation could not be assessed in this study.

Adult Sockeye Salmon undergo profound morphological and physiological changes as the processes of both sexual maturation and senescence proceed during the spawning migration. Over time, energy stores are depleted, GSI increases, secondary sexual characteristics develop, and immune function becomes compromised (Hruska et al. 2010). As expected, physiological profiles differed between fish captured in the early and late sampling periods. Specifically, plasma sodium, potassium, glucose, and cortisol differed between periods suggesting that the absolute values of recovery profiles from salmon will change with maturity. Further, the capacity for physiological recovery in Sockeye Salmon is directly influenced by water temperature (Prystay et al. 2017), which differed by $\sim 5^{\circ}\text{C}$ between the early and late sampling periods. Differences in initial physiologies across timing groups have been identified in other studies (Cooke et al. 2004; Crossin et al. 2009). The elevated potassium levels measured in the late sampling period have been associated with exercise and periods of hypoxia, possibly indicative of cell damage or muscle depolarization (Sejersted and Sjøgaard 2000; Matey et al. 2008). Plasma glucose concentrations were significantly influenced by the interaction of sex and sampling period, with values decreasing from the early to the late period for both males and females but decreasing more significantly for females in the late period than for males (Figure 3A). Plasma glucose was also influenced by the interaction of holding time and sampling period. Similar plasma glucose values were evident for both sampling periods in the 0-h treatment group; levels then showed an overall increasing trend over time in the early sampling period, but then first increased after 1 h then decreased after 4 h in the late sampling period (Figure 3B). Plasma glucose levels typically increase alongside rising cortisol levels (Kubokawa et al. 1999); however, our results indicated that despite high levels of cortisol occurring in females at the 1- and 4-h holding times (Figure 2), plasma glucose in the late sampling period did not reach the relatively elevated levels observed in the early sampling period (Figure 3A). The decreased magnitude of the plasma glucose response in the late sampling period may be attributed to the muting effect of senescence on the stress response of semelparous salmon during this period (McConnachie et al. 2012).

Interestingly, we did not detect an immediate physiological disturbance caused by stomach perforation. The high occurrence of stomach perforation in the late sampling period is similar to some reports of injury to the

gastrointestinal tract for gastrically tagged fish in other studies evaluating tagging effects on adult migrating salmonids (Gray and Haynes 1979; Corbett et al. 2012). In all cases, it was unknown whether damage occurred immediately upon insertion of the tag or at some time after tagging (e.g., during handling and postmortem sampling procedures). Even still, the increased level of gastric tag perforation in the late sampling period could be problematic even though our short-term assessment of the physiological responses to perforation did not indicate physiological dysfunction. A tagging effects study by Corbett et al. (2012) found that gastric tagging of adult Chinook Salmon in the late stages of their spawning migration resulted in 90% mortality when the fish were held for 50 d in captivity, compared with 30% and 10% mortality of control and externally tagged fish, respectively. Furthermore, Corbett et al. (2012) reported that death of fish tagged gastrically only started to occur 16 d posttagging (50% mortality after 22 d) suggesting that any immediate or acute trauma associated with the tagging event did not lead to immediate mortality. Further, reports from a field study suggested that gastrically tagged Sockeye Salmon with perforated stomachs appeared to die prematurely and were less successful spawners (i.e., higher levels of egg retention) compared with those that were found dead with an intact stomach (Schubert and Scarborough 1996). Further research is needed to determine the mechanisms underlying low survival of gastrically tagged fish as reported in Corbett et al. (2012) and to understand whether and how stomach perforation and gastric insertion, in general, adversely affect fish health over a longer period of time. The creation of an index of the progression of gastrointestinal tissue atrophy and risk of perforation based on river-entry timing would be beneficial for researchers when considering tagging options for a telemetry study. Until the long-term consequences of stomach perforation are better understood, we recommend that researchers use the gastric insertion method with caution if tagging migrating Pacific salmon that are nearing sexual maturity and/or have been in the freshwater environment for an extended period.

In summary, this study found that capture by beach seine was physiologically stressful for Sockeye Salmon, but the addition of a tagging stressor, regardless of external or gastric tagging methods, did not influence the recovery profile. We measured acute changes in plasma levels of ions, cortisol, and metabolites as well as muscle metabolites to assess the effects of tag attachment methods (as expressed in Corbett et al. 2012) using multivariable approaches (Johnson et al. 2012). The incorporation of sex and sampling period as main effects and interaction terms in this study design allowed us to better explore the short-term physiological stress response of wild migrating adult Sockeye Salmon to a tagging event. Using this “realistic” study design under field conditions, we did not

identify differences in the physiological response between tagging methods despite a high incidence of gastric perforation during the late sampling period. The equivocal acute physiological results for tagging effects were not consistent with the long-term differences in survival reported in other studies. This potential disconnect between acute stress and long-term survival highlights the need for comparative field studies to understand the long-term consequences of different tagging methods on fish behavior and survival.

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