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# Population-Specific Consequences of Fisheries-Related Stressors on Adult Sockeye Salmon\*

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## ABSTRACT

The objective of this study was to determine whether fisheries-related stressors differently influence two populations of adult sockeye salmon (*Oncorhynchus nerka*) with shared migration timing and location but where one population (i.e., Harrison) spawns 1 mo after the other (i.e., Weaver). Four stressor treatments were used following beach seine capture: (1) immediate release, (2) release after 10–15 min in the beach seine, (3) an additional 3-min gill net entanglement and 1-min air exposure, and (4) an additional 3-min tangle net simulation and 1-min air exposure. A comprehensive acoustic telemetry array and manual tracking revealed that survival was low overall, with more Weaver fish (34.2% of 38 tagged) reaching spawning areas compared to Harrison fish (17.8% of 78 tagged). For the Harrison population but not the Weaver, the gill net treatment influenced immediate (i.e., survived treatment) and short-term (i.e., 5-d postrelease) survival as well as survival to reach spawn-

ing areas. Harrison fish were more likely to be injured by the treatment, and reflex impairment predicted their short-term and long-term survival. Physiological condition did not differ between populations at the time of release, although both populations showed signs of severe physiological disturbances from the gill and tangle net simulations. These results suggest that even short durations of gill or tangle net entanglement can result in profound population-specific physiological disturbances and mortality. The notion that there can be population-specific variation in response to fisheries encounters adds complexity to management and provides further evidence for intraspecific differences in migration success.

## Introduction

The fate of fish and other animals released from capture is an increasing conservation concern (Davis 2002; Lewison and Crowder 2003, 2007; Read et al. 2006). However, any lethal or sublethal consequences of bycatch release are undoubtedly context, species, and, perhaps, population specific, making generalities particularly difficult to establish. In freshwater, there is the added difficulty of a paucity of research (Raby et al. 2011). The anadromous reproductive migrations of Pacific salmon (*Oncorhynchus* spp.) into freshwater make them vulnerable to fisheries capture throughout their return to natal spawning grounds. Moreover, they have only one opportunity to spawn and attempt to secure fitness. When adult sockeye salmon (*Oncorhynchus nerka*) enter freshwater, they are targeted by recreational, commercial, and aboriginal fisheries. Commercial fisheries use drift gill nets and aboriginal fisheries use drift and set gill nets, as well as beach seines, to capture river-migrating sockeye salmon. Tangle nets, which are small-mesh gill nets, are also used in fisheries, including research fisheries (Vander Haegen et al. 2004; Donaldson et al. 2010a). Fish may be released from fisheries gear, either intentionally through voluntary or mandated release or unintentionally from individuals that make contact with the fisheries gear but escape prior to being landed. Delayed mortality (i.e., occurring up to several days) following release or escape from fisheries can occur days or weeks after net disentanglement (Davis 2002; Broadhurst et al. 2008; Donaldson et al. 2010a) and has been suggested to be stress related for salmonids (Black 1958; Wood et al. 1983; Kieffer et al. 2002). Postrelease lethal and sublethal effects can contribute to fisheries-induced selection (Baker et al. 2010).

Sockeye salmon have a discrete population structure, where returning adults have high fidelity to natal spawning areas,

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resulting in more than 100 genetically distinct populations in the Fraser River watershed alone (Beacham et al. 2005). Differences in migration timing, upriver migration conditions, and spawning locations have resulted in a suite of population-specific physiological adaptations (Lee et al. 2003; Farrell et al. 2008; Crossin et al. 2004; Eliason et al. 2011). Eliason et al. (2011) showed that cardiorespiratory physiology varies at the population level for Fraser River sockeye salmon, where populations that undergo more challenging migratory conditions are better adapted to cope with these challenges, including having greater aerobic scope, a better coronary supply, and more ventricular  $\beta$ -adrenoceptors compared with populations with less physiologically demanding migrations. Body morphology, gross somatic energy and egg number, and migration behavior likewise differ between populations, depending on migration difficulty (Crossin et al. 2004). Survival and migration rates can also be population specific for sockeye salmon (Hinch and Rand 2000), with certain populations being more vulnerable to predicted changes in climate (Martins et al. 2011) and fisheries effects (Donaldson et al. 2010a).

Previous work developed from comparative physiology studies on exercise stress has highlighted two important factors relevant to understanding how capture affects fish. First, the type and duration of fish capture have consequences to level of stress incurred by fish (Wood 1991; Kieffer 2000). For example, the duration of capture is typically proportional to the magnitude of physiological response (e.g., Gustavson et al. 1991; Chopin et al. 1996), and the magnitude of stress, including interactive effects such as temperature and air exposure, can result in impaired ventilation, equilibrium loss, and mortality (Gingerich et al. 2007). Second, the magnitude of the physiological disturbance shows a typical recovery profile, which, if severe, can have profound consequences (Black 1958; Wood 1983). For example, Donaldson et al. (2010b) found that the duration of fisheries capture simulations influenced the duration of recovery of heart rate to prestress values. For salmon, the magnitude of the physiological disturbance may be predictive of postrelease migration behavior and delayed mortality for certain populations of Fraser River sockeye salmon (i.e., early-entry Adams-Shuswap) but not others (normal-timed Chilko; Donaldson et al. 2010a). Donaldson et al. (2010a) found evidence of a carryover effect, where an event that occurs in one life-history phase (i.e., onset of freshwater migration) profoundly affects a subsequent life-history phase (i.e., spawning). The concept of a carryover effect is well illustrated by migrating taxa, particularly birds, where one event can influence subsequent migratory and reproductive outcomes (Norris and Taylor 2006; Sorenson et al. 2009). However, no known studies have linked the effects of a controlled set of experimental stressors to migration survival among populations.

This study contrasts with several recent observational studies (Vander Haegen et al. 2004; Baker and Schindler 2009; Donaldson et al. 2010a) by adopting an experimental approach (Donaldson et al. 2008) to examine how simulated fishing gear encounters influence the survival of two populations of adult

sockeye salmon that migrate through the same location at the same time, to limit variation in environmental variables. While both populations share a similar migration path and spawn within a few kilometers of one another, peak spawning of Harrison sockeye salmon occurs 1 mo later than that of Weaver salmon. We wished to test the hypothesis that fisheries differentially influence survival of migratory adult salmon in a population-specific manner and used biotelemetry (tagging) to follow fish behavior and survival after release. We predicted that the protracted migration timing and longer freshwater residency of the Harrison population would result in higher migration failure relative to the earlier-timed spawning Weaver population following fisheries-related stress. We place these results in the context of population-specific carryover effects and discuss the relevance of these findings for the conservation of comigrating salmon populations.

## Methods

### *Study Site and Experimental Treatments*

Two populations of Fraser River sockeye salmon, the Weaver Creek and Harrison River populations, were captured in the Harrison River, British Columbia, Canada. Fish capture and experimental procedures were conducted on the Harrison River on Chehalis First Nations land downstream of Harrison Lake on September 10, 11, 14, and 17, 2009. These genetically distinct populations migrate through the lower Fraser River and enter the Harrison River, but Weaver fish spawn either within Weaver Creek proper or in an artificial spawning channel after diversion by Fisheries and Oceans Canada. Harrison fish spawn within Harrison River itself (fig. 1). Although these populations migrate together and spawn within a few kilometers of each other, Harrison fish spawn approximately 1 mo after Weaver fish. Individual population origin cannot be determined visually, so DNA analysis of adipose fin tissue biopsies was required (Beacham et al. 2005). Mean river temperature during experimental treatments was 17.2°C, as determined by iButton thermal loggers distributed throughout the release area. Harrison River temperatures averaged 16.3°C throughout September, 11.6°C throughout October, and 9.4°C throughout November.

Fish were captured by beach seine, using a powerboat to lead the net into the middle of the river in a semicircle pattern and then rapidly drawing the net closed to a vehicle tie-off on shore. The net was brought to shore and closed but remained submerged underwater (~60-cm depth) while individuals were collected using dip nets. Several seine sets were conducted during each day of the study to enable sufficient sample sizes in each treatment group. While the beach seine methods were identical for each set, the number of fish captured ranged from 0 to several hundred. Even still, the time from seine deployment to being closed and brought to shore was always ~5 min, and having additional fish in the seine (i.e., fish not used for experimental treatments) mimics the reality of beach seine fisheries, which can capture several hundred fish per set that typically need to be sorted or released. Netting individuals from the beach seine necessitated the possible disturbance of other

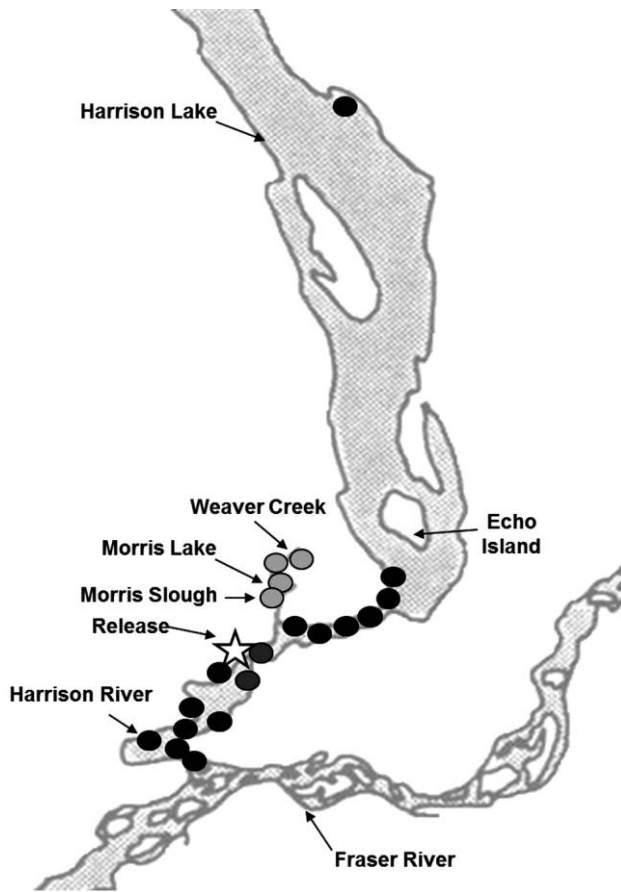


Figure 1. Map of the study area in Harrison River, British Columbia, Canada. The star represents the treatment and release site. Black circles indicate key VR2 receiver coverage. Light gray and dark gray circles indicate receivers at general spawning locations for Weaver Creek and Harrison River sockeye salmon, respectively.

individuals in the seine. Dip net capture generally took <15 s per individual. All fish were either biopsied or tagged, as described below, following one of four experimental treatments.

Beach seine capture was a common treatment for all four experimental treatments. After beach seine capture, the following additional interventions were also performed: (1) immediate release, which involved keeping the fish submerged and corralled in the beach seine while they were either tagged or biopsied within 3 min from the closure of the seine; (2) prolonged beach seine capture, involved crowding fish in the fully submerged seine for a period of 10–15 min; (3) tangle net and (4) gill net simulations, which were designed to simulate a selective fishery, where nontarget species would be rapidly removed from a net and released. For both net simulation treatments, fish were rapidly placed in a landing net that was loosely strung with 13.3- or 8.9-cm monofilament mesh netting (representing standard mesh sizes for commercial gill nets and selective harvest tangle nets in the Fraser River, respectively) while underwater for a period of 3 min. The net and fish were then lifted from the water for an additional 1 min while the fish was

untangled and released. The additional 1 min of air exposure was designed to simulate air exposure that occurs during sorting of commercial and native fisheries. In each case, the net soak times and air exposure times were intentionally rapid, to test methods for simulating fisheries-related stressors that could be employed in selective fisheries.

Individuals were randomly assigned to treatments. At the time of capture, populations could not be visually distinguished (i.e., DNA identification was required), ultimately resulting in higher sample sizes for the Harrison population relative to the Weaver. For Harrison fish, the handling time between dip net capture and release did not differ significantly for gill net and tangle net treatments (23 min, 3 s, and 24 min, 54 s, respectively) but was twice as long as the prolonged beach seine (11 min, 26 s) and almost eight times longer than the immediate-release (3 min, 6 s) treatments. Similarly for Weaver fish, handling time did not differ significantly for gill net and tangle net (18 min, 50 s, and 22 min, 49 s, respectively) and was almost twice as long as the prolonged beach seine (12 min, 57 s) and six times longer than the immediate-release (2 min, 52 s) treatments.

#### *Biopsy and Tagging Methods*

Similar to Donaldson et al. (2011), fish were either biopsied (blood sample) or tagged (gastric radio telemetry implant) in an alternative fashion. Established protocols were used for both procedures and have been validated previously for adult salmon (Cooke et al. 2005; Young et al. 2006). All fish were handled in the same manner, with the biopsy and tagging procedures completed in  $\leq 2$  min. Two teams of technicians worked in parallel for sampling and tagging while additional technicians conducted the actual fisheries simulations. Fish were transferred by dip net from the enclosed seine to a cylindrical coarse mesh open-ended Hypolon bag (length, 100 cm; diameter, 20 cm), which was submerged in-river and constantly supplied with clean flowing river water. Biopsy involved a 2-mL blood sample collected using caudal venipuncture with a 3.8-cm, 21-gauge needle and a vacutainer (lithium heparin, 3 mL, Becton-Dickson) to assess plasma physiological indexes.

Acoustic transmitters (V16-1H-R64K coded tags, Vemco; diameter, 16 mm; length, 54 mm; weight, <2% of fish body mass) were inserted gastrically (Cooke et al. 2005). A unique coding system for the transmitters enabled the identification of individual fish as they were detected at receiver stations. For all fish, a scale sample and a 0.5-g adipose fin clip were taken for identification of population complexes, and fork length (FL) measurements were made. All fish-handling procedures were approved by the animal care committees of the University of British Columbia and Carleton University, in accordance with the Canadian Council of Animal Care.

#### *Reflex and Injury Assessments*

A reflex impairment index score, developed from the reflex action mortality predictor method (Davis 2005, 2007), was de-

terminated immediately prior to release of all tagged fish. A scale from 0 for unimpaired to 1 for impaired was assigned based on the following reflexes (Davis 2007): tail grab (i.e., fish successfully burst-swim away from the technician), body flex (i.e., the fish actively attempting to struggle free from the technician when held briefly out of water), head complex (i.e., the fish exhibited a regular pattern of ventilation by opening and closing of the lower jaw), vestibular-ocular response (i.e., the fish's eye rolling to maintain level pitch, tracking the handler), and orientation reflex (i.e., the fish turned upside down on release and righted itself within 3 s). The entire reflex assessment took  $\leq 10$  s to complete. The reflex impairment score was the average of the five measured reflexes.

The severity of net injury by gill and tangle net was assigned either 0 for minor scale loss or other signs of injury or 1 as severe, if they had considerable mucus, scale, or blood loss. Severe scores were typically associated with fish that had wrapped the net either around the gills and head, resulting in damage to the gills and opercula, or around the middle of the body, resulting in scale and mucous loss and gill net marks along the body.

#### *Biotelemetry Methods and Determination of Survival*

To monitor fish movement throughout the Harrison River, Weaver Creek, and Harrison Lake following release and determine survival to the spawning area, we strategically located a fixed array of 20 acoustic telemetry receivers (VR2 and VR2W, Vemco) both downriver and upriver of the release site at locations known to spatially cover the migration route of sockeye salmon from each population, following that used by Mathes et al. (2010). Receivers were distributed to ensure that detection fields overlapped whenever possible to strengthen the likelihood of detection and determine whether fish were no longer actively migrating. Mortality was assigned based on inactivity. Immediate survival represented fish that survived the treatments and migrated away from the release site, short-term survival represented detection of activity for up to 5 d after release, and long-term survival represents detection at spawning areas. DNA population identification enabled the determination of arrival at a potential spawning area for each individual. For Weaver fish, arrival at the spawning area was determined by detection with receivers positioned at Morris Lake, Weaver pool, Lower Weaver raceway, and Weaver Creek spawning channel. Detection at one or more of these locations was used to assign successfully reaching a potential spawning area. Similarly for Harrison fish, detections at receivers that were positioned where the majority of spawning activity is known to occur (Schaeffer et al. 1951) on or after October 20, 2009, were considered to have successfully reached spawning areas. This date represents a time well before the mean spawning date, and fish detected at this time and afterward and confirmed to remain in this location can be considered potential spawners. If Harrison individuals had their last detection at this site prior to October 20 and were not determined to be actively moving in this region again, they were not considered to be survivors (i.e., these were

fish that were present in the area only transiently but ultimately were not detected in the area during the spawning period for this population). Manual tracking by foot and by boat occurred throughout the study period to determine fish position and confirm mortalities or arrival at spawning areas.

#### *Laboratory Assays of Physiological Variables*

Plasma cortisol, ions ( $K^+$ ,  $Cl^-$ , and  $Na^+$ ), glucose, lactate, and osmolality were quantified from blood samples based on procedures described by Farrell et al. (2001), except osmolality analyses were conducted using an AI 3320 freezing-point osmometer (Advanced Instruments) and  $K^+$  and  $Na^+$  were conducted using a model 410 single-channel flame photometer (Cole Parmer).

#### *Statistical Analyses*

Homogeneity of variance was assessed using Levene's test, and variables were log transformed as necessary. Multiple analysis of variance (MANOVA) was used to test for population-specific differences in physiological response to treatments, and one-way ANOVA was used to test for differences in length, longevity, and time to release for each treatment group and population. Where significant differences were found, Tukey-Kramer post hoc tests were used (Zar 1999). Pearson  $\chi^2$  analysis was used to test for differences in postrelease survival between groups and populations. Logistic regression was used for relationships between reflex impairment and survival. Fisher's exact test was used to compare injury score between populations for each of the gill net and tangle net treatments. Additional statistical tests are summarized in "Results." All values presented here represent means  $\pm$  standard errors, unless otherwise noted. Statistical analyses were conducted using JMP, version 8.0.2 (SAS Institute, Cary, NC).

## **Results**

### *Survival*

Independent of treatment groups, surprisingly few salmon (33 of 116 fish [28.5%]) reached their spawning areas after a fisheries treatment (table 1). Furthermore, almost twice as many Weaver fish (13 of 38 [34.2%]) survived to reach spawning areas compared with Harrison fish (14 of 78 [17.8%]). Weaver and Harrison fish had similar short-term survival (23 of 38 [60.5%] and 50 of 78 [64.1%], respectively).

### *Treatment Effects on Survival*

Treatment significantly influenced survival of Harrison sockeye to reach spawning areas ( $\chi^2 = 11.279$ ,  $df = 3$ ,  $P = 0.010$ ). For Harrison fish, individuals in the immediate-release (seven individuals [33.3%]) and beach seine (five individuals [33.3%]) groups were more likely to reach spawning areas relative to the gill net (0 individuals [0.0%]) and tangle net (two individuals [8.7%]) simulations. Weaver fish had proportionately higher

Table 1: Percentage of fish that survived treatment (i.e., immediate survival), survived 5 d, or survived to spawning areas for adult Harrison and Weaver sockeye salmon in the Harrison River, British Columbia, Canada

Population, treatment	<i>N</i>	Survived treatment (% [ <i>N</i> ])	Survived 5 d (% [ <i>N</i> ])	Survived to spawning area (% [ <i>N</i> ])
<b>Harrison:</b>				
Immediate release	21	100.0 (21)	85.7 (18)	33.3 (7)
Beach seine	15	100.0 (15)	80.0 (12)	33.3 (5)
Gill net simulation	19	89.5 (17)	42.1 (8)	.0 (0)
Tangle net simulation	23	91.3 (21)	52.2 (12)	8.7 (2)
Total	78	94.5 (74)	64.1 (50)	17.8 (14)
<b>Weaver:</b>				
Immediate release	7	100.0 (7)	4 (57.1)	14.3 (1)
Beach seine	13	100.0 (13)	7 (53.9)	30.8 (4)
Gill net simulation	12	100.0 (12)	8 (66.7)	41.7 (5)
Tangle net simulation	6	100.0 (6)	4 (66.7)	50.0 (3)
Total	38	100.0 (38)	60.5 (23)	34.2 (13)
Grand total	116	96.6 (112)	62.9 (73)	28.5 (33)

survival in the gill net and tangle net groups relative to the immediate and beach seine groups, but there was no statistically significant relationship between treatment and survival to reach spawning areas for this population ( $\chi^2 = 2.264$ ,  $df = 3$ ,  $P = 0.519$ ).

All but two Harrison individuals from each of the tangle net and gill net simulations survived the treatments, and the immediate-release and beach seine groups resulted in 100% survival. Weaver fish had 100% immediate survival for all treatments. Treatment significantly influenced short-term survival for Harrison ( $\chi^2 = 11.327$ ,  $df = 3$ ,  $P = 0.010$ ) but not Weaver ( $\chi^2 = 0.560$ ,  $df = 3$ ,  $P = 0.905$ ) fish. Longevity (i.e., the amount of time between an individual's first and last detections at a receiver) was not influenced by treatment for either population (one-way ANOVA,  $P = 0.381$  and  $0.786$ , respectively).

The FL of Harrison fish was significantly smaller than that of Weaver fish (mean  $\pm$  SEM,  $56.8 \pm 0.4$  and  $63.1 \pm 0.6$  cm, respectively;  $t$ -test,  $t = 82.527$ ,  $df = 1$ ,  $P < 0.001$ ). Even so, FL did not differ among treatment groups for either Harrison ( $F = 1.348$ ,  $df = 3$ ,  $P = 0.265$ ) or Weaver ( $F = 0.259$ ,  $df = 3$ ,  $P = 0.855$ ) fish. FL had no effect on short-term survival for either Harrison or Weaver fish ( $F = 3.886$ ,  $df = 1$ ,  $P = 0.052$  and  $F = 0.079$ ,  $df = 1$ ,  $P = 0.780$ , respectively) or survival to reach spawning areas ( $F = 1.924$ ,  $df = 1$ ,  $P = 0.170$  and  $F = 0.121$ ,  $df = 1$ ,  $P = 0.297$ , respectively).

#### Migration Behavior

Seventeen Harrison and 19 Weaver sockeye fell back downriver and were detected at the farthest downriver receiver, located at the Harrison River/Fraser River confluence. Treatment had no effect on the likelihood of falling back for either population (Harrison,  $\chi^2 = 3.634$ ,  $df = 3$ ,  $P = 0.304$ ; Weaver,  $\chi^2 = 2.029$ ,  $df = 3$ ,  $P = 0.566$ ). However, Weaver sockeye that did

not fall back were significantly more likely to reach spawning areas ( $\chi^2 = 9.471$ ,  $df = 1$ ,  $P = 0.002$ ; table 2). This trend was not apparent for Harrison fish ( $\chi^2 = 0.023$ ,  $df = 1$ ,  $P = 0.879$ ).

Twelve fish (six Harrison and six Weaver) were detected entering Harrison Lake. Treatment had no effect on the duration or likelihood of fish reaching Harrison Lake for either population ( $P > 0.05$  in each case). Of these, only one Harrison and two Weaver sockeye ultimately reached spawning areas.

#### Physiological Condition

Each treatment produced a physiological stress response, but this response did not differ significantly between the two populations, as evidenced by a significant treatment effect but no significant effect for population or their interaction (two-way MANOVA, whole model:  $F_{50,207.5} = 2.059$ ,  $P < 0.001$ ; treatment effect:  $F_{21,115.47} = 3.336$ ,  $P < 0.001$ ; population effect:  $F_{7,40} = 0.965$ ,  $P = 0.469$ ; interaction:  $F_{21,115.41} = 0.978$ ,  $P = 0.496$ ).

#### Treatment Effects on Physiological Condition

The gill net and tangle net simulations induced a more severe physiological disturbance, including increases in plasma cortisol, lactate, glucose, osmolality, and ions ( $\text{Na}^+$  and  $\text{Cl}^-$ ) compared with the immediate-release group. Specifically, significant relationships were detected among treatment groups for plasma cortisol ( $F_{3,50} = 4.771$ ,  $P = 0.005$ ; Tukey-Kramer HSD test,  $P < 0.05$ ), glucose ( $F_{3,50} = 11.262$ ,  $P < 0.001$ ; Tukey-Kramer HSD test,  $P < 0.05$ ), lactate ( $F_{3,50} = 10.496$ ,  $P < 0.001$ ; Tukey-Kramer HSD test,  $P < 0.05$ ), osmolality ( $F_{3,50} = 20.203$ ,  $P < 0.001$ ; Tukey-Kramer HSD test,  $P < 0.05$ ), sodium ( $F_{3,50} = 5.775$ ,  $P = 0.002$ ; Tukey-Kramer HSD test,  $P < 0.05$ ), and chloride ( $F_{3,50} = 5.057$ ,  $P = 0.004$ ; Tukey-Kramer HSD test,  $P <$

Table 2: Fallback and survival to reach spawning areas for adult Harrison and Weaver sockeye salmon in the Harrison River, British Columbia, Canada

Population, fell back to the		Survived to spawning area (% [N]) <sup>a</sup>
Harrison/Fraser River confluence	N	
Harrison:		
Fell back	17	17.7 (3)
Did not fall back	57	19.3 (11)
Total	74	18.9 (14)
Weaver:		
Fell back	19	10.5 (2)
Did not fall back	19	57.9 (11)
Total	38	34.2 (13)
Grand total	112	23.3 (27)

<sup>a</sup>Excludes immediate mortalities.

0.05) but not potassium ( $F_{3,50} = 0.729$ ,  $P = 0.539$ ; Tukey-Kramer HSD test,  $P > 0.05$ ; fig. 2).

Physiological condition is likely reflective of the time course of stress response rather than simply the treatment itself, since a significant relationship was found between treatment and the time between seine net closure and sampling for both Harrison ( $F_{3,82} = 34.065$ ,  $P < 0.001$ ; Tukey-Kramer HSD test,  $P < 0.05$ ) and Weaver ( $F_{3,41} = 19.606$ ,  $P < 0.001$ ; Tukey-Kramer HSD test,  $P < 0.05$ ) fish. Thus, these measures should be interpreted as an indicator of physiological condition at the time of release, rather than as an absolute measure of the stress response to the treatment itself.

#### Reflex Impairment

For Harrison fish but not Weaver, reflex impairment score was influenced by treatment ( $F_{3,74} = 5.302$ ,  $SS = 0.510$ ,  $P = 0.002$ ; fig. 3). Harrison mean reflex impairment score was higher for gill net (0.365) and tangle net (0.275) treatments relative to immediate-release (0.133) and beach seine (0.175) treatments. Logistic regressions revealed that reflex impairment score was predictive of both short-term survival ( $r^2 = 0.117$ ,  $\chi^2 = 11.925$ ,  $df = 1$ ,  $P < 0.001$ ) and survival to reach spawning areas ( $r^2 = 0.153$ ,  $\chi^2 = 11.212$ ,  $df = 1$ ,  $P < 0.001$ ) for Harrison fish but not Weaver. Reflex impairment score had no relationship with fallbacks ( $P > 0.05$  for both populations).

#### Injury Score

All four (100%) fish that did not survive the treatments had an injury score of 1, suggesting severe injury due to the net simulations. Treatment type (i.e., gill vs. tangle net) did not influence injury score for Weaver ( $\chi^2 = 0.529$ ,  $df = 1$ ,  $P = 0.4669$ ) or Harrison ( $\chi^2 = 4.325$ ,  $df = 1$ ,  $P = 0.055$ ) fish, so

both treatments were combined into a single variable for subsequent comparisons of injury score. Harrison fish (35.7% of individuals with an injury score of 1) were significantly more likely to have an injury score of 1 relative to Weaver fish (5.6% of individuals with an injury score of 1;  $\chi^2 = 5.860$ ,  $df = 1$ ,  $P = 0.016$ ). Injury score had no relation to short-term survival for either population (Weaver,  $\chi^2 = 0.529$ ,  $df = 1$ ,  $P = 0.467$ ; Harrison,  $\chi^2 = 1.909$ ,  $df = 1$ ,  $P = 0.167$ ). Injury score did not influence the likelihood of Weaver fish to reach spawning areas ( $\chi^2 = 1.324$ ,  $df = 1$ ,  $P = 0.250$ ). The two Harrison fish reaching spawning areas after either gill or tangle net simulation had injury scores of 0.

#### Discussion

While overall survival for all treatment groups combined appears low, the survival of Weaver fish to reach spawning areas in this study is similar to survival of telemetry-tagged sockeye salmon released from a recreational fishery (i.e., ~36%) but lower than those released from a beach seine in the Fraser River (i.e., 52.2%; Donaldson et al. 2011). The survival observed here also falls within the range observed by Donaldson et al. (2010a), who found that survival ranged between 18% and 42% for sockeye released from tangle nets in the Fraser River. The much lower survival of the Harrison fish is driven largely by the gill and tangle net simulations, whereas survival from the beach seine treatments is comparable to that of the recreational fishery survival from Donaldson et al. (2011). For the Weaver population, the result that the immediate-release group has the lowest survival is unexpected and may simply be the result of low sample sizes (i.e.,  $n = 7$ ) in that group, but it must be noted that treatment had no significant influence on survival to reach spawning areas for Weaver fish, whereas treatment did affect survival for Harrison fish.

The mechanism of delayed mortality from fisheries-related stress has been suggested to be linked to injury and physiological stress, but the proximate causes of delayed fisheries-related mortality are not always apparent (Wood et al. 1983; Davis 2002). We found that the net simulation treatments resulted in a significantly greater proportion of fish from the Harrison population exhibiting severe injury. The four immediate mortalities from the tangle and gill net treatments for Harrison fish were all related to the fact that gill net (and occasionally tangle net) fisheries function by entangling fish around the gills and preventing their escape. Each immediate mortality was assigned an injury score of 1, where the net mesh had bound the individual's opercula and gills, causing damage to the gill tissue and preventing normal ventilation throughout the duration of the treatment. We can only speculate that the dermal injuries sustained during the treatments may have likewise influenced short-term survival and survival to reach spawning areas. Individuals either may have died due to the injuries themselves or were more susceptible to secondary disease development, particularly when coupled with presumed stress-mediated immunosuppression (Lupes et al. 2006).

Injuries may have been more detrimental for Harrison fish

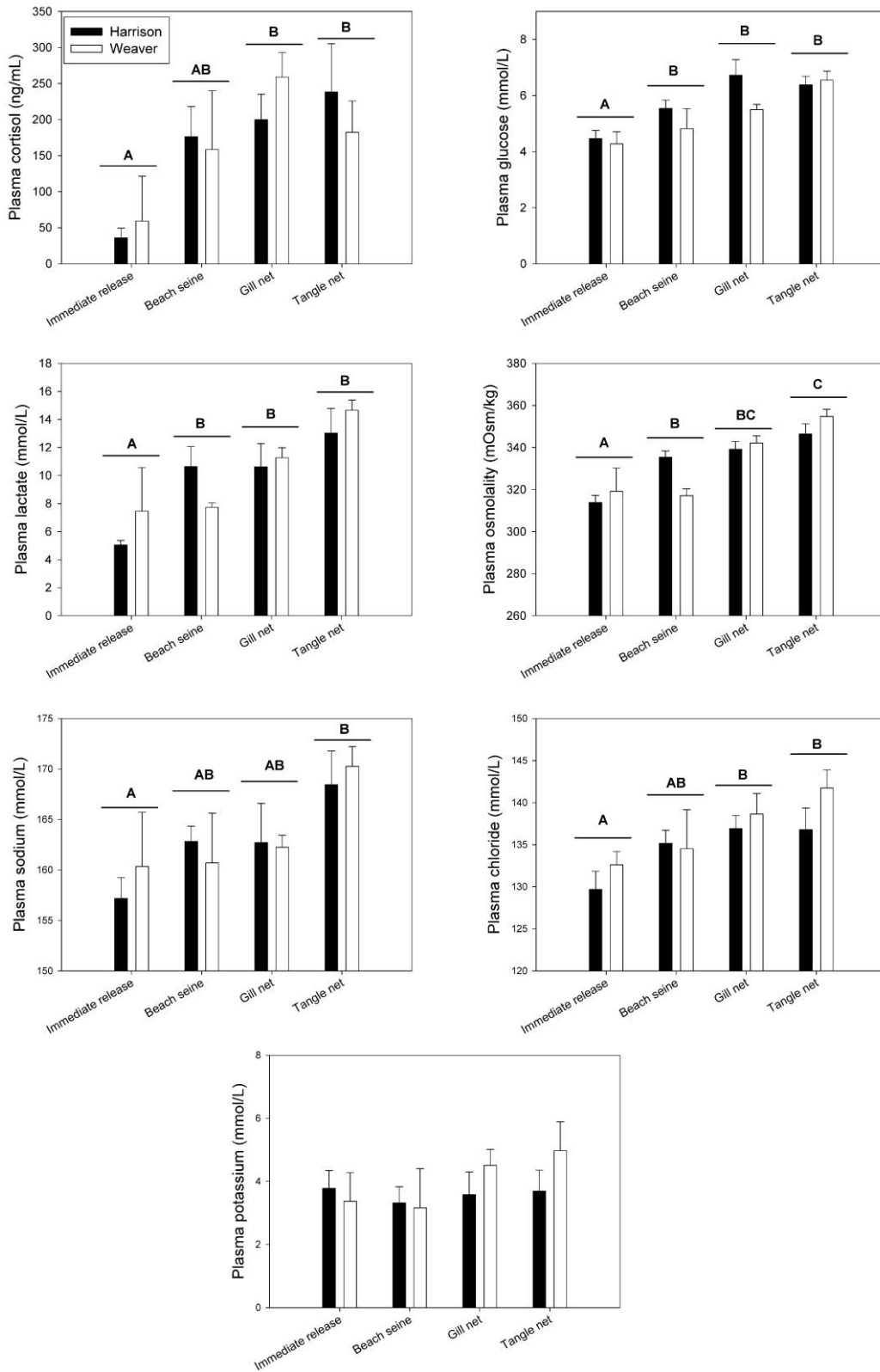


Figure 2. Plasma physiological variables for four experimental treatment groups for adult Harrison and Weaver sockeye salmon in the Harrison River, British Columbia, Canada. Populations did not differ significantly among treatments for all variables and were pooled for analysis. Dissimilar letters represent significant differences between treatments.



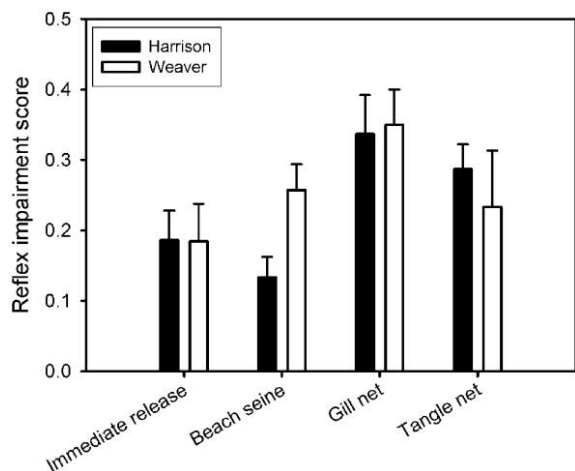


Figure 3. Reflex impairment score versus treatment for adult Harrison and Weaver sockeye salmon in the Harrison River, British Columbia, Canada.

because they had to continue holding in the Harrison River for up to 2 mo after release, allowing more time for disease development, whereas Weaver fish had only 3–4 wk remaining until peak spawning. Peak spawning for Weaver fish occurs about 1 mo after the treatments (~October 20), whereas Harrison fish spawn 1 mo afterward (~November 20). This would allow more time for latent mortality to manifest in Harrison fish than in Weaver fish and would be in line with recent data indicating that Pacific salmon may be more resilient to fisheries encounters at later stages in their migration (Donaldson et al. 2010a; G. Raby, personal communication). Because sockeye salmon reabsorb their scales during reproductive maturation, they may have been less likely to be affected by net abrasion and susceptibility to fungal development, which may have been the case for Weaver fish. If disease development is indeed a factor influencing latent mortality, Harrison Lake is a thermal refuge that is available to both populations and has been shown to improve survival for early entrants (Farrell et al. 2008). Neither Weaver nor Harrison populations need to enter Harrison Lake to reach spawning areas; however, they may do so voluntarily to mitigate thermal stress, which has been shown to increase the likelihood of survival in warm-temperature years (Mathes et al. 2010). Temperatures were moderate in 2009, and few individuals from either population entered the lake in this study. Of those that entered, few ultimately returned to spawning areas.

The predictive power of the reflex index was population specific, where reflex impairment was influenced by the severity of the stressor for Harrison fish but not Weaver. Reflex impairment score is an established measure of fish vitality (Davis 2010) and has been used previously to monitor animal condition and to predict delayed mortality (Davis and Ottmar 2006; Davis 2007, 2010; Humborstad et al. 2009). Of the reflexes used to develop the reflex impairment score, the tail grab response (i.e., failure to engage in burst swimming when stim-

ulated), orientation (i.e., inability to maintain equilibrium), and head complex (i.e., inability to maintain rhythmic ventilation) are all indexes that may be suggestive of exhaustive exercise (Davis 2010). This assertion was corroborated by elevated plasma lactate and cortisol, two indexes of exhaustive exercise stress (Wood 1991; Milligan 1996; Kieffer 2000), in the prolonged beach seine, gill net, and tangle net treatments. Our finding that reflex score predicted mortality even several weeks after treatment suggests that a response to a stressor that is presumed acute can still have long-term consequences on survival.

Physiological condition did not differ between populations for any of the treatments. The net simulation treatments resulted in a greater stress response relative to the immediate-release and beach seine groups; however, this may simply reflect the fact that these variables were changing on a fixed time course, rather than the severity of the treatments themselves. Most of the plasma variables measured here typically continue to increase after the stressor until they peak and begin to recover (generally between 30 min and 2 h; Wood et al. 1983; Milligan 1996; Barton 2002). This response pattern has indeed been shown in adult migrating Pacific salmon in freshwater (e.g., coho salmon *Oncorhynchus kisutch*; Donaldson et al. 2010b). While the values obtained from our longer treatments (net simulations and prolonged beach seine treatments and all treatments required initial beach seine capture) may reflect the duration between capture and sample collection, they provide an indication of physiological condition at the time of release and suggest that a major stress response was being mounted at that time. The physiological stress response in fishes has previously been linked with latent mortality due to bacterial or fungal disease development (Mazeaud et al. 1977; Schreck et al. 2000; Lupes et al. 2006). For the immediate-release group, plasma values were similar to plasma collected from postexercise (Hinch et al. 2006) or rapidly captured sockeye salmon in freshwater (i.e., dip net [Young et al. 2006], tangle net of identical mesh size [Donaldson et al. 2010a], angling [Donaldson et al. 2011]).

The treatment effect observed for Harrison survival to reach spawning areas contributes to a growing body of ecological research identifying latent mortality and carryover effects. A carryover effect refers to an event that occurs at a discrete time point that influences subsequent migratory and reproductive outcomes (Sorenson et al. 2009). This phenomenon has been described previously for migratory birds (Norris and Taylor 2006) as well as nonmigratory (O'Connor et al. 2010) and migratory (Donaldson et al. 2010a) fish. By traditional definition, carryover effects typically have a seasonal component, but growing evidence for Pacific salmon suggests that carryover effects may emerge in discrete life-history stages. For adult migrating Pacific salmon, latent mortality has been linked with a range of stressors, including navigating challenging migration barriers (Budy et al. 2002; Caudill et al. 2007), capture stress (Donaldson et al. 2010a), and confinement stress (Donaldson et al. 2011). Donaldson et al. (2010a) found that physiological condition at the time of capture was predictive of fate for the

Adams-Shuswap population complex but not Chilko. Comparable to the results of this study, Donaldson et al. (2010a) found that Adams-Shuswap fish had slower migration rates and were less likely to reach natal subwatersheds relative to the Chilko population. Interestingly, both the Chilko and Weaver populations migrate directly to spawning areas (i.e., within days), while the Adams-Shuswap and Harrison populations tend to spend weeks in freshwater prior to spawning. Remarkably similar to the findings of the twofold difference in survival for Weaver fish versus Harrison fish in this study, Chilko fish had a nearly twofold higher survival to reach spawning areas relative to Adams-Shuswap fish.

Regardless of the mechanisms of mortality, the population-specific treatment effects highlight the need to better understand population-specific mechanisms for migration mortality in sockeye salmon. Our finding that even a short-duration net simulation resulted in elevated mortality suggests that selective fisheries aimed at releasing nontarget Pacific salmon could still encounter high mortality rates. Other methods, such as the immediate-release beach seine, which involved less handling and potentially less mucous and scale loss, could be a more viable means of reducing mortality of released fish. Our results indicate that in addition to a diversity of behavioral and physiological traits (Lee et al. 2003; Farrell et al. 2008; Mathes et al. 2010; Eliason et al. 2011), Fraser River sockeye salmon populations show diversity in their resilience to fisheries encounters. The differences between populations suggest that mortality associated with release from capture fisheries is context dependent, meaning that management regimes must be careful applying generalizations across comigrating populations. This is particularly relevant to vulnerable populations of sockeye salmon (e.g., Cultus Lake sockeye salmon; Rand 2010). While the fishery is already managed on a population-specific basis, comigrating populations are typically simultaneously targeted during fisheries openings. This suggests that even if fisheries were selective and nontarget populations could be released, there may be reduced population-specific postrelease survival. Future research needs to identify the factors that contribute to postrelease mortality, including an assessment of the effects of dermal injury and metabolic stress, and disease/fungal development. Given that even short durations of gear entanglement can result in delayed mortality, further research is required to test methods for promoting recovery and improving methods for handling and releasing fish to reduce postrelease mortality. This study is one of the first involving an experimental approach using physiological measurements and telemetry in a fisheries bycatch context. The findings provide a cautionary note: researchers and managers should consider the potential role of interpopulation variation when interpreting research findings and making management decisions related to fisheries.

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