Disentangling the Roles of Air Exposure, Gill Net Injury, and Facilitated Recovery on the Postcapture and Release Mortality and Behavior of Adult Migratory Sockeye Salmon (*Oncorhynchus nerka*) in Freshwater*

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ABSTRACT

We sought to improve the understanding of delayed mortality in migrating sockeye salmon (*Oncorhynchus nerka*) captured and released in freshwater fisheries. Using biotelemetry, blood physiology, and reflex assessments, we evaluated the relative roles of gill net injury and air exposure and investigated whether using a recovery box improved survival. Fish ($n = 238$), captured by beach seine, were allocated to four treatment groups: captured only, air exposed, injured, and injured and air exposed. Only half of the fish in each group were provided with a 15-min facilitated recovery. After treatment, fish were radio-tagged and released to resume their migration. Blood status was assessed in 36 additional untagged fish sampled after the four treatments. Compared with fish sampled immediately on capture, all treatments resulted in elevated plasma lactate and cortisol concentrations. After air exposure, plasma osmolality was elevated and reflexes were significantly impaired relative to the control and injured treatments. Injured fish exhibited reduced short-term migration speed by 3.2 km/d and had a 14.5% reduced survival to subnatal watersheds compared to controls. The 15-min facilitated recovery improved reflex assessment relative to fish released immediately but did not affect survival. We suggest that in sockeye salmon migrating in cool water temperatures (~13°–16°C), delayed mortality can result from injury and air exposure, perhaps through sublethal stress, and that injury created additive delayed mortality likely via secondary infections.

Introduction

A selective fishing policy for mixed-stock fisheries is intended to allow the harvest of abundant species or stocks while protecting the vulnerable ones (DFO 2001). Such protective management approaches include spatiotemporal closures, gear restrictions, or modifications that reduce bycatch or live release nontarget species (i.e., discarding). However, a variable proportion of the protected fish that are discarded may subsequently die or sustain serious behavioral or reproductive impairments (e.g., see Chopin and Arimoto 1995; Davis 2002). Losses from delayed mortality and reproductive failures often go unobserved and therefore are unaccounted for, potentially causing significant uncertainties in mortality estimates and management models (e.g., see Chopin and Arimoto 1995; Baker and Schindler 2009; Raby et al. 2012) and potentially increasing cryptic fishing mortality to unsustainable levels (Coggins et al. 2007).

Physical damage from capture gear and from inappropriate handling and release practices involve some degree of internal

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and external injuries that vary in severity and among gear types (e.g., mucous and scale loss, wounding, crushing, net marks, abrasions, fin tear and loss, bleeding, barotrauma). Injury can also cause stress (e.g., through blood loss or problems with water balance) or serve as an entry point for pathogens. Components of the capture experience that result in physiological stress include but are not limited to handling, exercise, crowding, air exposure, and prolonged exposure to warm temperatures (Davis 2002). The physiological stress resulting from capture can result in immediate mortality at the time of capture, suppress immune function, or make fish susceptible to postrelease predation or fallback (i.e., downstream movement of fish) due to impaired behavior or physiological capacity (Cooke and Philipp 2004), which can lead to delayed mortality (Lupes et al. 2006). To date, there has been relatively little direct study comparing the relative impacts of injury and air exposure on delayed mortality of Pacific salmon from a mechanistic perspective. Knowing the relative consequences of injury and air stress on delayed mortality could be useful for shaping management strategies for reducing postrelease mortality in fisheries.

Of further interest to fisheries managers and scientists is the possibility that tools could be developed that facilitate physiological recovery of fish from capture and prevent (or reduce) postrelease mortality. Recovery tools have been developed with coho salmon (*Oncorhynchus kisutch*) in British Columbia, Canada, in the past decade (e.g., Blewett and Taylor 1999; Farrell et al. 2000, 2001*a*, 2001*b*; Buchanan et al. 2002) as an initiative undertaken as part of British Columbia's selective fishing policy. Farrell et al. (2001*a*) demonstrated the possibility that lethargic or seemingly moribund coho salmon captured in marine fisheries can be revived using a specially designed box (known as a Fraser box) that holds fish into flowing water to provide gill ventilation. As a consequence, certain marine commercial fishing vessels releasing coho are now required to carry and use a Fraser box with the aim to increase postrelease survival. Despite positive results using Fraser boxes, they have been tested only in marine waters thus far, which may not reflect the nature of stressors during the in-river phase of migration (e.g., pathogens, water temperature, and different osmotic pressures). It has been demonstrated that facilitated recovery can enhance metabolic recovery for exhausted fish, but it is still unknown whether it can benefit vigorous fish that are physically injured (Milligan et al. 2000; Farrell et al. 2001*a*, 2001*b*). Indeed, earlier studies with coho salmon left out fish that were bleeding, and no evaluation was made of the injuries resulting from gill net entanglement. Last, survival benefits documented in previous work (Farrell et al. 2001*a*, 2001*b*) relied on the use of short holding in protective net pens. In contrast, use of radio-tracking to investigate whether delayed mortality occurs (Donaldson et al. 2008) provides a more realistic assessment of whether the Fraser box would facilitate recovery and survival of salmon caught in freshwater fisheries.

Here, we examined sources of delayed fisheries-related mortality in relation to three known factors influencing postrelease behavior and mortality in fish: physiological exhaustion (stress through air exposure), physical damage (via gill net entanglement), and facilitated recovery (using Fraser boxes). We used sockeye salmon (*Oncorhynchus nerka*) in the lower Fraser River as a model for this research, given conservation concerns regarding a number of sockeye populations (see Cooke et al. 2012). The study was designed to simulate gill net fisheries because high levels of delayed mortality may have important implications for harvest management in exploited and nontarget salmon populations. Our primary objective was to distinguish the relative consequences of physical injury and air exposure stress using an experimental approach coupled with reflex assessments (Davis 2010), physiological sampling (nonlethal blood samples; see Cooke et al. 2005), and telemetry tracking of postrelease migration success (Donaldson et al. 2008). Specifically, we used assessments of reflex impairment and blood physiology to characterize the relative impacts of our experimental treatments. Our secondary objective was to test whether Fraser recovery boxes could reduce delayed mortality and improve migration speed for captured fish exposed to varying degrees of stress and injury.

Material and Methods

Study Area and Fish Capture

Sampling occurred on three days (September 14, 15, and 17, 2010) at Gill Road fishing bar located near Rosedale, on the south shore of the lower Fraser River, British Columbia (fig.

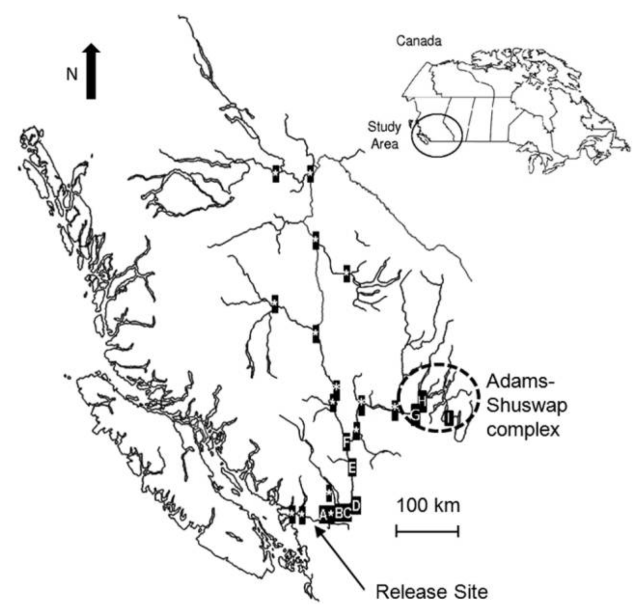

Figure 1. Map displaying the Fraser River watershed, British Columbia, Canada, and the study, release, and natal subwatersheds. Asterisks denote most of the radio receiver stations distributed throughout the Fraser River mainstem and into tributaries throughout the watershed. Letters represent receiver locations used in the calculation of migration rates, as follows: A, Harrison River confluence; B, Hope; C, Qualark; D, Sawmill; E, Hell's Gate; F, Thompson River confluence; G, Little River; H, Adams River; and I, Lower Shuswap River.

1), at or below the seasonal average river temperature (13.2°–15.6°C). Sockeye salmon were captured using beach seine nets (described in Donaldson et al. 2011). The net was kept in sufficient water depth to minimize net contact, fish crowding, and air exposure and thereby minimized physical and physiological disturbances. All fish were subsequently transferred using soft knotless nylon dip nets into two large in-river net pens (1.2 m × 1.2 m × 2.4 m) for holding. The entire capture and transfer process took up to 15 min. The two net pens minimized crowding of fish and allowed sufficient sample size, given that the number of fish caught in each seine set was unpredictable. Only two or three fish could be processed (i.e., experimentally treated and tagged) at a time, which resulted in fish being held for up to 5 h (mean ± SD time, 81 ± 85 min) and the introduction of a potential net pen effect (Portz et al. 2006). However, the net pen effect is dispersed among all treatments, allowing relative comparison among treatments. In addition, our team has conducted numerous studies where we have captured and temporarily held fish in this manner. Seine capture does elicit stress; however, injury is rare based on how we conduct the seining (i.e., keep the seine in the water and minimize crowding). Moreover, individuals captured with injuries and/or visible infections were excluded from the study, and all remaining fish that were not sampled were released.

Experimental Treatments

Fish, randomly selected from net pens, were subjected to experimental treatments that simulated capture stress and injury. The four treatments groups were as follows (table 1).

1. Captured only (C; $n = 57$). A low-stress, low-injury group where fish were captured by beach seine and handled but not subjected to any additional experimental manipulations.

2. Captured and air exposed (A; $n = 61$). A high-stress, low-injury treatment that consisted of handling plus air exposure for 2 min. Air exposure was performed in black Hypalon fish bags to minimize physical damage. When fish are being sorted and/or disentangled from netting, air exposure can last from a few seconds to >60 min for large catches.

3. Captured and injured (I; $n = 61$). A low-stress, high-injury treatment where fish were handled and entangled in gill net for approximately 30 s. Fish were injured using multifilament gill net material of 13.34-cm mesh size, widely used for sockeye commercial gill net fishing in British Columbia, but mounted on a handheld dip net frame. Fish were tangled and disentangled for approximately 30 s while submerged in a perforated plastic tub (239 L, 93.7 cm × 53.98 cm × 47.27 cm) placed in the river, allowing fresh river water to pass through the tub throughout the treatment. If the entanglement period was longer than 30 s, the net was cut to disentangle the animal and maintain relatively consistent entanglement duration among treatments and minimize exhaustive stress relative to the air exposure treatment. Following entanglement, sockeye were examined for severity, location, and type of injuries that were inflicted from the experimental injuring procedures. Injuries were categorized as (i) minor injuries, which consisted of fish with very faint net marks and minimal scale loss (<5%); (ii) moderate injuries, which included visible and shallow net marks and 5%–20% scale loss; and (iii) severe injuries, which included deep and dark net marks and >20% scale loss. Any bleeding from the gills was considered a severe injury. Location of injuries included the mouth, nose, head, occiput, body, and fins, whereas types of injuries consisted of scale loss, net marks, bruising, bleeding, and fin tear. A pilot study was conducted with six fish to ensure that the procedures selected to injure the fish were rapid enough to isolate injury by minimizing stress.

4. Captured and injured plus air exposed (IA; $n = 59$). A high-stress, high-injury group where fish were handled, subjected to gill net entanglement for ~30 s, and then exposed to air (2 min).

After the treatment, all fish were quickly measured (fork length [FL] to the nearest centimeter), tagged, assessed for reflex impairment, and released.

Table 1: Summary of number of radio-tagged Fraser River sockeye salmon (*Oncorhynchus nerka*) used in each of the experimental treatments

Treatment group	Recovered	Not recovered	Total	Treatment description	Justification
Capture only: low stress, low injury	29 (26)	28 (26)	57 (52)	Captured by beach seine, minimal handling, not subjected to treatments	Control
Air exposed: high stress, low injury	31 (28)	30 (29)	61 (57)	Captured by beach seine, 2 min air exposure, minimal handling	Attempt to distinguish stress from injury
Injured: low stress, high injury	31 (29)	30 (28)	61 (57)	Captured by beach seine, gillnetted for ~30 s, minimal air exposure	Attempt to distinguish injury from stress
Injured plus air exposed: high stress, high injury	30 (29)	29 (28)	59 (57)	Captured by beach seine, gillnetted for ~30 s, 2 min air exposure	Control for interactions and cumulative effects

Note. Values in parentheses are the number of tags included in statistical analyses; see “Material and Methods” for explanations.

Recovery Treatment

Half of the fish were released immediately after the treatment, while the other half of each treatment group (total $n = 121$; see below) was subjected to a 15-min recovery period prior to release. Recovery took place in a Fraser box, which assists gill ventilation by jetting river water toward the mouth of the fish (at 0.6 L s^{-1}, following Farrell et al. 2001*a*). Fraser boxes followed the blueprint of those used in marine fisheries, a 40 × 40 × 90-cm marine-grade plywood box with a center divider that allowed fish to be placed on both sides, a fastened lid to prevent fish from escaping, and a water inflow and outflow on each end of the channel (Blewett and Taylor 1999; Farrell et al. 2001*a*). Boxes were painted black to minimize sensory stimuli. Our Fraser box eliminated the rubber chute for releasing fish back into the water without handling. Instead, fish were dipnetted (using a wet knotless nylon net) and quickly released into the river.

Tagging Procedures

Following each experimental treatment and prior to any recovery, sockeye were gastrically implanted with coded radio transmitters using methods previously validated for migratory salmon in the Fraser River system (Cooke et al. 2005) and technology described in Donaldson et al. (2010, 2011). A yellow spaghetti tag (Floy Manufacturing, Seattle, WA) was inserted into the dorsal musculature adjacent to the dorsal fin for easy visual identification if a fish was recaptured, and a 0.5-g DNA adipose fin clip was taken for stock identification. However, the DNA clip was not used in this study, as telemetry results and parallel stock assessment activity by management agencies indicated that the majority (i.e., >95%) of sockeye in the river at sampling time were Adams-Shuswap stock (Pacific Salmon Commission, unpublished data).

Blood Sampling

Handling fish for blood sampling introduces an additional stress beyond the four treatments that were used, which could bias the survival results. Therefore, rather than sampling all treatment fish, an additional 36 untagged fish were sampled after 15 min in the recovery boxes to characterize differences in physiological disturbances resulting from air exposure and gill net injury and account for the delay in the physiological response of blood variables (e.g., Milligan 1996; Barton 2002; Cook et al. 2011). The experimental treatments (C, A, I, IA) were replicated and an additional subgroup of fish was sampled immediately and directly from the seine net, which represented a baseline postseine group (B). Following treatment and recovery, individuals were placed in supine position and submerged in a V-shaped trough that was manually supplied with fresh river water for a rapid 1.5-mL blood sample taken via caudal venipuncture (3 mL, lithium-heparinized vacutainer, 38-mm, 21-gauge, 3.8-cm needle; Cooke et al. 2005). Plasma was immediately separated via centrifuge for 5 min at 10,000 *g* (Compact II Centrifuge, Clay Adams, Parsippany, NJ) prior to being frozen in liquid nitrogen and eventual storage in an ultracold (−80°C) freezer at the laboratory. Plasma assays included plasma cortisol, ions (K^+, Cl^-, and Na^+), glucose, lactate, and osmolality, based on procedures described in Farrell et al. (2001*b*) and Donaldson et al. (2011), and were conducted at the Department of Fisheries and Oceans West Vancouver Laboratory. For logistical reasons, physiological sampling occurred as a separate study on the Harrison River at Chehalis Park (near Harrison confluence receiver; fig. 1) from September 20 to September 24, 2010, at water temperatures of 14°C and would have represented a mix of Harrison and Weaver populations of sockeye.

Reflex Assessments

Reflex action mortality predictors (RAMP; Davis 2007, 2010) characterized fish vitality in response to our capture simulation treatments by testing for reflex impairment, where reflex impairment is defined as any decrease or complete inhibition of normal baseline reflex action (Davis and Ottmar 2006). Five reflexes, which were adopted from previous RAMP studies with coho salmon (Raby et al. 2012), were tested after experimental treatments and tagging procedures and scored as unimpaired or impaired. Fish were rapidly tested (<15 s) in the following order for (1) body flex, where fish were restrained for ~3 s by holding the body out of water with two hands and observed for signs of vigorous whole-body response to restraint; (2) tail grab, where the fish's tail was grabbed while in water, inside a fish bag, and observed for startle or burst-swim response; (3) vestibular ocular response, where fish were rotated out of water on a body length axis and noted for presence or absence of the eye rolling and tracking the handler; (4) head complex, for which fish were held out of water and examined for a pattern of regular ventilation; and (5) orientation, which was conducted on release by turning each fish upside down just below river surface and scoring reequilibration after 3 s. Each reflex was scored as either 0 or 0.2 (i.e., proportion of reflexes that were impaired out of the five reflexes tested), so that a RAMP index score of 0 indicated no reflex impairment and 1 indicated all reflexes impaired (Davis and Ottmar 2006; Davis 2007).

Biotelemetry and Determination of Migration Failure and Behavior

Postrelease behavior and mortality were assessed by 27 fixed radiotelemetry receiver stations strategically placed (fig. 1) between the release site and the Adams-Shuswap spawning area (as described in English et al. 2005; Donaldson et al. 2011; Robichaud et al. 2011). Detection of tagged fish at an upstream station receiver was scored as successful migration to that point. Failure to detect an individual upstream of this receiver was scored as en route mortality (Robichaud et al. 2011). Individuals either reported as fisheries harvest or detected in tributaries different from Adams-Shuswap were excluded.

Mean migration speeds (km d^{-1}) and mortality were cal-

Table 2: Relative effects of experimental treatments (baseline, captured only, air exposed, injured, injured plus air exposed; mean ± SD) on plasma variables in mature wild sockeye salmon

Plasma variables	Baseline (N = 6)	Control (N = 9)	Air exposed (N = 10)	Injured (N = 6)	Injured plus air exposed (N = 5)	F	P
Lactate (mmol L^{-1})[a]	5.7 ± .9[A]	12.6 ± 4.8[B]	17.3 ± 2.7[B]	14.0 ± 1.1[B]	18.4 ± 2.6[B]	28.8	<.01*
Glucose (mmol L^{-1})	4.9 ± .5	5.6 ± .9	6.8 ± .7	6.2 ± 2.1	6.4 ± 1.2	2.96	.04
Osmolality (mOsm kg^{-1})	315.2 ± 2.7[A]	340.8 ± 13.8[B]	349.9 ± 17.2[B]	328.8 ± 20.3[A]	346.1 ± 4.0[B]	6.66	.01*
Chloride (mmol L^{-1})	129.8 ± 4.3	135 ± 4.1	133.3 ± 6.2	129.1 ± 9.8	130.7 ± 4.6	1.3	.29
Potassium (mmol L^{-1})[a]	3.0 ± 2.2	1.3 ± .4	1.2 ± 1.0	2.0 ± .8	2.2 ± .8	2.59	.06
Sodium (mmol L^{-1})	143.2 ± 3.9	153.4 ± 10.9	143.9 ± 14.7	138.3 ± 13.8	142.3 ± 7.1	1.85	.15
Cortisol (ng mL^{-1})[a]	35.7 ± 23.7[A]	111.8 ± 133.6[AB]	331.5 ± 186.0[C]	369.9 ± 118.5[C]	231.4 ± 103.7[BC]	16.1	<.01*

Note. Fish were captured on the Harrison River and measured 15 min poststressor, except for a baseline value measured immediately from the seine net. Significant effects are denoted by dissimilar capital letters.

[a]Values were logged transformed for statistical tests.

*False discovery rate significance at $\alpha = 0.02$.

culated from release site to Hope, to the Thompson confluence, and to the natal subwatershed (Little River receiver location) using calculations described by Donaldson et al. (2011). Short-term (24–48 h) mortality was assessed for fish reaching Hope (~38 river km upstream from release site), long-term (~7 d) mortality and behavior were assessed for fish reaching the Thompson confluence (~145 river km upstream from release site), and migration success was assessed for fish detected at the Adams-Shuswap subwatershed (~400 river km upstream from release site).

Statistical Analysis

Homogeneity of variance on migration speed and physiological and covariate metrics among treatments was assessed using Levene's test and visual plots. These variables were subsequently $\log_{10}$ transformed to reduce heteroscedasticity where necessary. A one-way ANOVA was used to check for among-treatment differences in fish size (FL) and time held in the net pen. Using a false discovery rate (FDR)–corrected alpha level of 0.019 (Pike 2011), one-way ANOVA was also used to test for differences in seven physiological variables (plasma lactate, glucose, ions, osmolality, and cortisol) among the five treatment groups (i.e., B, C, A, I, IA). Subsequently, Tamhane post hoc tests were used for variables that did not meet the assumption of equal variances (even after transformations) and Tukey-Kramer post hoc tests were used for all other variables. Because RAMP scores are ordinal, a nonparametric Kruskal-Wallis ANOVA compared RAMP scores among nonrecovered treatment groups followed by Mann-Whitney U post hoc tests. Wilcoxon signed-rank tests compared RAMP scores between fish immediately released and those allowed to recover in a Fraser box.

General linear models with binomial error structures were used to test for the effects of stress, injury, and recovery treatments on migration success from release to Hope, release to Thompson confluence, and release to spawning grounds. In each analysis, the initial model contained all possible first- and second-order interactions among variables. The interactions were sequentially removed if not significant (i.e., backward selection) until only the main effects remained in the model. Similarly, a three-way ANOVA was used to test for differences among treatment groups in migration speed (km d^{-1}) from release to Hope, to the Thompson River confluence, and to Little River spawning grounds. The binomial generalized linear model and three-way ANOVA were FDR corrected ($\alpha = 0.027$) and were performed in R 2.14. All remaining analyses were performed in PASW 18.0.

Results

Capture and Experimental Details

Thirteen tagged fish were captured in fisheries, and two were detected in a different tributary, resulting in a sample size of 223 tagged fish (FL ranged from 45 to 69 cm). The average (±1 SD) time required to remove fish from the net pen and conduct experimental procedures, including removal from the net pen, treatments, gastric tagging, measuring FL, inserting spaghetti tag, and performing RAMP, was 3.7 ± 1.2 min for C fish, 5.5 ± 1.5 min for A fish, 5.1 ± 1.7 min for I fish, and 6.9 ± 2.0 min for IA fish. Covariates were similar among treatment groups (FL, ANOVA, log transformed: $F_{7,216} = 0.238$, $P = 0.975$; time held in net pen: $F_{7,216} = 0.539$, $P = 0.805$).

Physiological Variables

Significant differences were detected among groups for plasma cortisol ($F_{4,31} = 16.09$, $P < 0.01$), lactate ($F_{4,38} = 28.76$, $P < 0.01$), and osmolality ($F_{4,31} = 6.66$, $P < 0.01$) but not plasma glucose, Cl^-, K^+, and Na^+ (table 2). Relative to the baseline values for fish sampled immediately, all treatment groups had a significantly elevated plasma lactate, and all, except the I group, had significantly elevated plasma osmolality. All treatment groups except group C had significantly higher elevated plasma cortisol relative to the B group, but the difference in plasma cortisol levels for groups C and IA did not reach statistical significance (table 2).

Reflex Impairment

RAMP scores among treatment groups that were not recovered differed significantly ($H_3 = 23.1$, $P < 0.01$, $n = 247$), where the C and I groups had similar RAMP scores, as did the A and IA groups (fig. 2). RAMP scores indicated that reflex impairment decreased significantly following 15 min in the Fraser box across all treatment groups (C: $z = -3.6$, $P < 0.01$, $n = 26$; A: $z = -3.9$, $P < 0.01$, $n = 28$; I: $z = -3.8$, $P < 0.01$, $n = 26$; IA: $z = -3.3$, $P < 0.01$, $n = 24$; fig. 2).

Postcapture and Release Mortality

Twenty-three of the 223 fish (10.3%) were either undetected or detected near or downstream of the release site. Thus, 200 fish survived to Hope (table 3), of which two (one IR and one IAR) were first detected downstream of the release site, indicating that downstream fallback on release does not preclude subsequent upstream migration.

A FDR-adjusted alpha of 0.03 was used for analyses of migration success among the three river reaches. Since no significant interactions were detected between the three treatment effects (injury, air stress, recovery) on postcapture and release mortality, only main effects were tested. Postrelease mortality to Hope was unaffected by injury (deviance [dev] = 0.14, df = 1, $P = 0.11$), air stress (dev = 2.8, df = 1, $P = 0.09$), and recovery (dev = 0.04, df = 1, $P = 0.84$; table 3). Similarly, survival to the Thompson confluence was unaffected by injury (dev = 0.74, df = 1, $P = 0.39$), air stress (dev = 0.10, df = 1, $P = 0.75$), and recovery (dev = 0.24, df = 1, $P = 0.62$; table 3). Delayed mortality to the Adams-Shuswap spawning area was negligible from air stress (dev = 0.39, df = 1, $P = 0.53$) or recovery (dev = 1.3, df = 1, $P = 0.26$; table 3). However, mortality at the Adams-Shuswap spawning area was 14.5% greater for injured fish compared to fish from uninjured treatments (36.0% vs. 50.5%); the effect was significant after the FDR correction (dev = 4.88, df = 1, $P = 0.03$).

Migration Speed

Again, an FDR-adjusted alpha of 0.027 was used for analyses of migration speed. Since no interactions among injury, air stress, and recovery treatments were detected in migration speed (km d^{-1}), only main effects were tested. Log-transformed migration speed from release site to Hope was significantly reduced by gill net injury ($F_{1,161} = 13.0$, $P < 0.01$) but not by air exposure ($F_{1,161} = 2.6$, $P = 0.11$) or recovery ($F_{1,161} = 4.4$, $P = 0.04$; table 3) treatments. There were no significant factors affecting migration speed between release and the Thompson confluence after FDR adjustments (injury: $F_{1,135} = 4.7$, $P = 0.03$; stress: $F_{1,135} = 1.7$, $P = 0.19$; recovery: $F_{1,135} = 3.1$, $P = 0.08$; table 3) or between release and the Little River receiver (injury: $F_{1,92} = 1.5$, $P = 0.23$; stress: $F_{1,92} = 0.9$, $P = 0.37$; recovery: $F_{1,92} = 2.7$, $P = 0.10$; table 3).

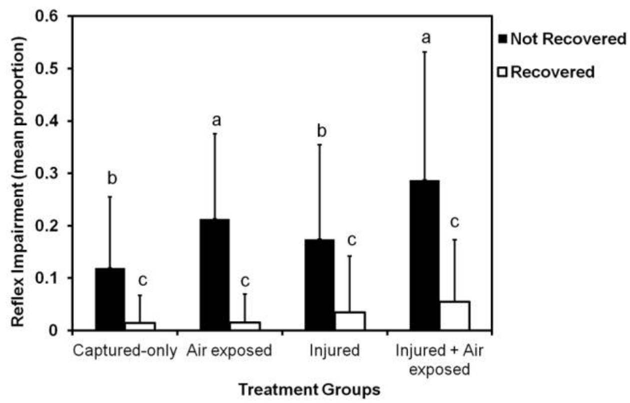

Figure 2. Impairment (proportion) of a suite of five reflexes (orientation, vestibular ocular response, tail grab, head complex, and body flex) in free-swimming adult sockeye for all experimental treatments. Values are presented in mean ± SD proportion of reflex impairment. Dissimilar letters denote a significant difference at $\alpha = 0.05$.

Discussion

Physiology

The large increases in plasma lactate and cortisol levels relative to baseline values for A and I groups, combined with the elevated levels of plasma variables for both groups relative to handling alone (C group), indicate that injury and air exposure are inherently and incrementally stressful to fish, as expected. Clearly, the fish collection (beach seine) and holding (net pen) caused added physiological disturbances to the experimental treatments. However, these disturbances were spread among all treatment groups, and the additive captures stress from the beach seine is relevant to the Fraser River fisheries, as recaptures are common among released and escaped adult migratory salmon. Concern therefore exists that such stress associated with fisheries interactions decreases disease resistance, swimming performance, and even reproductive endocrinology and maturation (Pickering 1993) in the long term. Gill net entanglement, a common capture method known to injure adult sockeye salmon (Thompson et al. 1971; Baker and Schindler 2009), also elicits struggling and associated anaerobic exercise (Kieffer 2000). Clearly, our I treatment did not isolate injury and generated some physiological disturbances even though we had hoped to maintain a low level of stress. However, we believe the level of stress to be less than that obtained during the air exposure in the high-stress treatment. Indeed, the I group remained vigorous compared with both air-exposed groups and displayed smaller changes in mean concentrations of plasma osmolality (relative to C fish). This suggests that the injury treatment was less intense and less disruptive to the immediate ionic balance of salmon, relative to other stressors. This occurrence was also reported by Farrell et al. (2001*b*), where

Table 3: Migration failure and migration rate (mean ± 95 CI) of tagged Fraser River sockeye salmon (*Oncorhynchus nerka*) from release site to three locations of interest: Hope, Thompson River confluence, and Adams-Shuswap complex, including the Little River, Adams River, and Lower Shuswap telemetry receivers

Treatment effects[a]	Tagged fish (N)	Hope: Migration failure N_{mort}	Hope: Migration failure %	Hope: Migration rate (km d^{-1}) N	Hope: Migration rate (km d^{-1}) Mean ± 95 CI	Thompson River confluence: Migration failure N_{mort}	Thompson River confluence: Migration failure %	Thompson River confluence: Migration rate (km d^{-1}) N	Thompson River confluence: Migration rate (km d^{-1}) Mean ± 95 CI	Adams-Shuswap complex (Little River, Adams River, and Lower Shuswap): Migration failure N_{mort}	Adams-Shuswap complex: Migration failure %	Adams-Shuswap complex: Migration rate[b] (km d^{-1}) N	Adams-Shuswap complex: Migration rate[b] (km d^{-1}) Mean ± 95 CI
Injury:													
1	114	11	9.6	86	17.9 ± 1.1**	45	40	68	17.9 ± 1.0*	73	64.0*	41	19.7 ± 1.2
0	109	12	11	79	21.1 ± 1.2	37	34	71	19.4 ± .8*	54	49.5	55	20.6 ± 1.0
Stress:													
1	114	8	7	85	18.8 ± 1.2	43	38	71	18.4 ± 1.1	67	58.8	47	20.0 ± 1.2
0	109	15	14	80	20.1 ± 1.3	39	36	68	18.9 ± .7	60	55	49	20.4 ± .9
Recovery:													
1	112	12	11	85	18.7 ± 1.3*	43	38	68	18.0 ± 1.0	68	60.7	44	19.6 ± 1.1
0	111	11	9.9	80	20.3 ± 1.2	39	35	71	19.3 ± .9	59	53.2	52	20.8 ± 1.0

[a]1 = presence of experimental treatment; 0 = absence of experimental treatment.
[b]Migration rate for the Adams-Shuswap complex was calculated from release site to the Little River receiver station.
*Significant effect at $\alpha = 0.05$.
**Significant effect with false discovery rate correction at $\alpha = 0.03$.

lethargic fish appeared to undergo a greater ion osmoregulatory disturbance than vigorous fish. It is unknown how severe our experimental treatment was relative to normal fisheries operations; however, the physiological response recorded after 15 min from our treatments resulted in similar physiological values as those measured in coho salmon sampled immediately after capture from an experimental commercial gill net vessel (Farrell et al. 2001*a*).

Similar cortisol values for the IA treatment compared with control fish was surprising, given that the interaction of stressors is generally cumulative (e.g., Barton and Iwama 1991; Davis 2002; Gale et al. 2011). This result could be misleading if poststress cortisol values for the two treatments peaked at slightly different times. Future studies might consider a time series of plasma assessment to test for such an effect.

Characterizing Reflex Impairment

RAMP is intended to be a rapid, simple, and inexpensive means of assessing fish vitality (Davis 2010). It has also been validated as a predictive measure for delayed mortality in coho salmon caught in beach seine fisheries (Raby et al. 2012). RAMP scores indicated sublethal effects resulting from the A treatment but not from the I treatment. Thus, either RAMP may not capture sublethal effects from injuries, even though fish were clearly stressed (elevated plasma lactate and cortisol), or the I treatment used here was not severe enough to impair reflexes. Further research investigating a large range of physical injury might be useful in resolving this issue. Until this is done, we believe it is unwise to rely solely on a RAMP score for predicting delayed mortality of injured migrating adult sockeye salmon. Previous studies show that RAMP scores are positively correlated with intensity of capture stressors (e.g., Davis 2005, 2007; Davis and Ottmar 2006; Humborstad et al. 2009; Raby et al. 2012), but none considered the potential linkage between RAMP and physical injury. Nonetheless, wounds inflicted in fish during capture, which can be highly variable, are a major source of mortality for discards and escapees (Trumble et al. 2000; Suuronen et al. 2005). In the interim, quantitative indexes for physical injuries in fishes have been developed and used in field settings such as visual assessments (e.g., Trumble et al. 2000; Davis 2005; Baker and Schindler 2009) or use of forensic techniques (e.g., fluorescein) to detect nonmacroscopic injuries (Noga and Udomkusonsri 2002; Davis and Ottmar 2006; Colotelo et al. 2009) and might be useful to include when predicting mortality.

Postcapture Release Mortality

Postrelease mortality did not differ among treatments, except for the increased mortality for injured fish reaching the Adams-Shuswap spawning area. This is a novel finding for injury, as we are unaware of previous comparable studies contrasting injury and stress. Our estimates do not account for either unreported fisheries capture or natural mortality. Natural mortality has been suggested to be 5% for adult migrating Fraser River sockeye experiencing river temperatures similar to those of our study (Martins et al. 2011), and our estimates far exceed this value, sometimes by an order of magnitude. Even so, our mortality estimates were for experimental simulations rather than real fishing scenarios, which might be more severe (e.g., a gill net or seine soak time of >30 min). In accordance with our animal care requirement, we were especially careful removing fish from gear, perhaps more so than actual fishers (V. M. Nguyen et al., personal observations).

The sublethal disturbances evident with the A treatment caused no additional mortality, a result comparable to previous studies examining effects of air exposure on fate of fish (e.g., Schreer et al. 2005; White et al. 2008; Gale et al. 2011). For example, 60 s of air exposure on top of exhaustive exercise did not affect short-term mortality (within 72 h) of sockeye salmon at 13°, 19°, and 21°C during a laboratory holding study, but mortality, physiological disturbances, and loss of equilibrium increased at warmest temperatures (Gale et al. 2011). The lack of capture effect on survival suggests that Pacific salmon in freshwater can recover from a substantial acute lactic acidosis at low temperatures (Gale et al. 2011). Our work was performed at 16°C, which is the optimum temperature for aerobic scope of this sockeye salmon population (Eliason et al. 2011).

Similar to previous work involving gill net capture of salmon (e.g., Thompson et al. 1971, 1973; Baker and Schindler 2009), our simulated gill net injury suggested that fish that experienced a modest 30-s gill net entanglement had relatively higher post-release mortality (14.5%) to spawning grounds. This suggests that injury may have played the primary role in causing delayed mortality. The mortality estimate for adult Chinook released from tangle nets (a more benign capture method) in the Columbia River was 7%, while fish released from 20.3-, 14-, and 11.4-cm mesh gill nets had elevated mortalities of 49%, 43%, and 32%, respectively. Physical damage is known to cause fish mortality (Thompson and Hunter 1973; Kaimmer and Trumble 1998; Olsen et al. 2012), with the degree and location of injury, fish size, and temperature being significant determining factors (reviewed in Chopin and Arimoto 1995). The most frequent injuries here were net marks, descaling, and abrasions around the occiput (just behind the head/gills) and on the head (V. M. Nguyen et al., unpublished data). Injury can lead to secondary responses that are fatal (Olsen et al. 2012) and also increases the susceptibility to parasite, bacterial, and fungal infections, particularly following gill damage (Trust 1986). *Saprolegnia* spp. is a facultative fungal infection common in freshwater ecosystems and is associated with damaged epidermal tissue (Hatai and Hoshiai 1994; Pickering 1994) and results in further tissue damage, loss of epithelial integrity, and osmoregulatory failure (Bruno and Wood 1999). Fish with gill net injuries are particularly susceptible to such fungal infections (Baker and Schindler 2009), which also have been highly correlated with high (up to 93%) prespawning mortality in Alaskan sockeye salmon (Baker and Schindler 2009). Baker and Schindler (2009) also observed that 11%–29% of fish reaching the spawning grounds had sustained injuries, and half of those failed to reproduce. We observed a lower mortality rate, likely associated with a lower severity of injury. Nevertheless, the fact that we detected significant effects of injury only close to the spawning area may mean that injury-induced prespawning mortality is slow to develop. As such, long-term effects from capture-induced injuries on en route and prespawn mortality should be considered in management strategies to help maintain viable populations and sustainable fisheries.

Migration Behavior

An important novel observation made here was that injury slowed the initial but not the subsequent migration rate of salmon. There has been laboratory evidence that severely ill fish cannot perform repeated swimming tests (Tierney and Farrell 2004), but the relationship between stress response and swimming activity in nature is unclear. Decreased activity in salmonids has been suggested to be a result of compromised performance during physiological recovery from a stressor (Milligan 1996), and increased activity has been proposed as a behavioral escape response (such as deep diving) in an attempt to find more favorable conditions (e.g., Quinn et al. 1989; Candy and Quinn 1999; Mäkinen et al. 2000). Recent work on the effects of descaling of Atlantic herring from purse seine fisheries showed altered swimming and schooling behaviors due to possible damage caused by the injuries (Olsen et al. 2012). Further work in this area is clearly warranted.

Recovery

The 15-min recovery in the Fraser box was neither beneficial nor detrimental. We suggest several hypotheses for the lack of benefits derived from the Fraser box treatment in our study. First, fish were not severely stressed here, perhaps precluding the need for assisted recovery. Farrell et al. (2001*a*) noted that cortisol levels in coho remained high throughout the recovery experiment, implying that confinement in the recovery box could cause additional stress in vigorous fish, and they recommended immediate release of vigorous fish. Also, a 15-min recovery period was chosen to reflect the realism of what we felt a fisher might commit toward revival efforts rather than the full time course of the physiological stress response. For example, Farrell et al. (2001*a*) noted signs of physiological recovery after 1 h and further improvements in hematocrit, muscle lactate concentrations, plasma osmolality, cortisol, and ion concentrations after 2 h. Even so, Donaldson et al. (2013) documented partial recovery of plasma cortisol after just a 15-min recovery period using a cylindrically shaped mesh-ended recovery bag oriented into the high river current. The Fraser box was designed with coho salmon in mind and may not be the best design for smaller sockeye salmon. We did observe a number of fish facing into the corner of the box rather than directly into the water flow, which may have meant that they were not benefiting fully from ram ventilation. Despite the uncertainty surrounding facilitated physiological recovery, our RAMP score unequivocally shows that recovery significantly improved the recovery of impaired reflexes after just 15 min relative to unrecovered fish. This is important, as improvements in vitality (by giving time to recover) could prevent fallback and predation and potentially aid in conserving energy for migration. Unfortunately, we do not know the extent to which this improvement can be attributed directly to the 15-min assisted recovery treatment because we have no data on fish sampled at 15 min without assisted recovery. Clearly, much remains to be done regarding the effectiveness of facilitated recovery methods for maturing salmon in freshwater.

Conclusions and Management Implications

We adopted an integrative approach to assess the effects of fishing practices on wild Pacific salmon in freshwater by combining several tools from the conservation physiology toolbox (Wikelski and Cooke 2006), including biotelemetry, nonlethal physiological biopsies, and reflex impairment assessment. These approaches have proved useful for the study of a variety of applied conservation and management problems for Pacific salmon in the Fraser River, including understanding of the impacts of climate change, disease, and fisheries interactions on migration success (reviewed in Cooke et al. 2012). Here we found that air exposure and facilitated recovery had no discernible effects on the migration success of adult sockeye salmon, while gill net injuries significantly reduced short-term but not long-term river migration speed and substantially reduced successful migration to the natal spawning area. However, further research into understanding fish susceptibility to disease and secondary responses following injury is needed before management strategies that consider fisheries-related delayed mortality can be formulated (Van West 2006; Miller et al. 2011). The failure of facilitated recovery to reduce mortality or improve migration speed for the air exposure treatment was surprising, especially given previous studies that have seen these improvements at least during the short term. Facilitated recovery could have improved impaired reflexes and may still prove to be beneficial with fisheries-related stresses that are more severe than those tested here since our observations are potentially species and context specific (e.g., Davis 2002; White et al. 2008). Selective harvesting as a fisheries management tool will require further research on the short- and long-term consequences for fish, including delayed mortality associated with gear encounters for a variety of fish species, life history stages, gears, and environmental conditions.

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