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The consequences of angling, beach seining, and confinement on the physiology, post-release behaviour and survival of adult sockeye salmon during upriver migration

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ABSTRACT

Few studies have examined the effects of fisheries capture on wild fish, particularly in the context of evaluating the sustainability of capture and release methods for Pacific salmon (*Oncorhynchus* spp.) during upriver migration. This study examined the physiological condition, post-release behaviour and survival of adult migrating sockeye salmon (*O. nerka*) in the Fraser River, British Columbia, Canada. Fish were captured by either beach seine or angling and released immediately, or were captured by angling and released following a 24-h recovery period in a net pen. Before release, all salmon were biopsied or tagged with radio telemetry transmitters. Capture by either angling or beach seine with immediate release resulted in >95% survival 24 h after release, whereas net pen recovery after angling resulted in ∼80% survival. This differential in survival was similarly expressed in the percentage of released fish reaching natal sub-watersheds, with 52.2% and 36.3% of fish immediately released by beach seine and angling reaching natal sub-watersheds, respectively, compared with 2.9% of fish released after angling and net pen recovery. Blood plasma stress indices reflected the 10-fold difference in survival, with a ∼4-fold higher plasma cortisol, a ∼2-fold higher plasma glucose and significantly depressed plasma ions and osmolality relative to fish sampled upon capture. Plasma lactate did not differ among groups. Collectively, these results suggest that a 24 h recovery in net pen following angling failed to promote post-release survival experienced with immediate release after angling or beach seining.

1. Introduction

The anadromous reproductive migrations of Pacific salmon are some of the most challenging life history stages of any organism (Dingle, 1996; Dingle and Drake, 2007). The transition into freshwater requires a series of changes in osmoregulatory and ionoregulatory systems (Shrimpton et al., 2005) and physiological and morphological changes associated with the development of secondary sexual characteristics (Brett, 1995; Hendry and Berg, 1999). Environmental conditions in freshwater, particularly high river temperatures, can result in a number of physiological costs, including elevated indices of stress (Macdonald, 2000) and stock-specific collapse of aerobic scope (Farrell et al., 2008). Fisheries interactions are overlaid on these inherent migration-related challenges. As Pacific salmon enter freshwater, they are targeted by recreational (e.g., hook and line), commercial (e.g., gill net) and First Nations (e.g., gill net, beach seine) fisheries.

In the Fraser River, British Columbia, Canada, the sockeye salmon recreational fishery has traditionally been regulated as a

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retention fishery with a bag limit of two fish. However, catch-and-release is common among anglers through either mandated (e.g., non-retention recreational fishery during low abundance years) or voluntary means (e.g., by anglers who reach their bag limit or choose to release undersized or undesirable fish, non-target species, or fish that are beginning to display secondary sexual characteristics; see Kristianson and Strongitharm, 2006). Fisheries and Oceans Canada creel surveys estimated that over 100 000 recreationally caught sockeye salmon were released between 2004 and 2006, along with over 220 000 harvested fish (Mahoney, 2005, 2006), representing an almost 2:1 harvest to release ratio. Similarly, beach seining is traditionally a retention fishery used by First Nations in the Fraser River, but captured non-target species are often released. While the fundamental assumption of catch-and-release is a minimal sublethal impairment and minimal effect on survival (Cooke and Schramm, 2007), little is known about the effects of catch-and-release on physiological condition, post-release behaviour and survival for any anadromous Pacific salmon species. A number of methods for promoting physiological recovery and survival following a capture event have been tested, including the use of recovery boxes (Farrell et al., 2001a,b). The 'Fraser box', which promotes survival of Pacific salmon released from commercial gear, has been validated in the marine environment, but no such method has been reported for use in freshwater.

The limited studies on the consequences of fisheries interactions on migrating Pacific salmon in freshwater reflect the logistic constraints associated with the capture, handling and holding of actively migrating fish and the cost of carrying out large-scale field studies. Recently, there has been a call for more experimental and integrative approaches to catch-and-release research, particularly for studies that use telemetry as a tool to assess behaviour and survival (Donaldson et al., 2008). While field-based fisheries capture studies often preclude the ability to use true 'controls' (Pollock and Pine, 2007), experiments that contrast different capture techniques have been conducted previously (Vander Haegen et al., 2004; Gingerich et al., 2007) and enable the assessment of relative effects of different capture methods. Recent laboratory capture and holding simulations (Donaldson et al., 2010a) and comparative field experiments (Donaldson et al., 2010b) have begun to shed some light on the consequences of fisheries stressors on adult migrating Pacific salmon in the Fraser River, but many questions remain unanswered.

This study addressed one such knowledge gap for sockeye salmon by using previously established protocols for physiological biopsy and radio telemetry (Cooke et al., 2005) to compare the survival consequences of capture from hook-and-line angling and beach seine fisheries in freshwater. The objective was to compare physiological condition, post-release behaviour and survival to natal sub-watersheds for fish that were either immediately captured and released by angling or beach seine with angled fish that were recovered in a net pen for 24 h. This recovery period was chosen because salmonids generally recover physiologically within this time following a stressful encounter (Milligan, 1996; Donaldson et al., 2010a).

2. Materials and methods

2.1. Study site and fish capture methods

Experimental procedures were conducted on the Fraser River at Grassy Bar, near Chilliwack, British Columbia, Canada over a four week period in August 2009. This location has become one of the more popular locations in the lower Fraser River mainstem for angling sockeye salmon in recent years (Mahoney, 2006). This study was developed as part of a synergistic study investigating the short-term survival of sockeye salmon caught by recreational anglers in 2008 and 2009 by holding salmon in net pens for 24 h (J.O. Thomas and Associates, 2009a,b).

Three treatment groups were established which involved biopsy or telemetry tagging and release following: (1) angling, (2) beach seining, and (3) angling followed by 24 h holding in a net pen. Individuals were biopsied or tagged and released from all treatment groups in equal proportions during each week.

For the angling group, volunteer anglers of varying experience and skill captured sockeye salmon using standard bottom-bouncing gear from either shore or boats anchored near shore. Their angling setup included long leaders (i.e., >3 m), barbless J-shaped hooks sized 1 to 3/0 that were generally bare, and a heavy weight that bounced along the riverbed but suspended the hook in the water column. Capture durations ranged between 1 and 5 min (see Section 3). Fish were generally landed in a long-handled knotless landing net, unhooked, and transferred by hand into a submerged black, flow-through mesh and Hypolon fish transport bag (1.0 m × 0.2 m). Air exposure durations ranged from <15 s to ~1 min, depending largely on the ease by which the barbless hook was removed. Anglers endeavoured to minimize the impact of the capture event on the fish by keeping angling durations short, rapidly removing the hook, and minimizing air exposure durations, factors that can exacerbate stress (Arlinghaus et al., 2007).

Capture by beach seine occurred at the study site using a 64 m × 7.5 m × 5 cm mesh beach seine net that was tied off on shore and dragged in an arc into the middle of the river and drawn closed using a power boat. The seine was then brought to shore and fish were rapidly removed from the net. Throughout the entire process, the net remained completely submerged in water, resulting in only 2–3 s of air exposure as fish were transferred by hand from the net to an individual fish bag. Technicians continually monitored the catches from both capture methods and recorded information about angling durations, air exposure durations, injuries (e.g., hooking location and degree of bleeding), and general condition descriptions. Again, fish were either biopsied or tagged and released immediately as described below.

For the net pen recovery group, angled fish in Hypolon bags were slowly walked in-river from the point of landing to one of three large net pens for holding (4 m × 4 m × 3 m). Before transfer, each fish was first tagged in the dorsal musculature while inside the Hypolon bag with a uniquely numbered anchor tag (Floy Tag & Mfg., Inc., Seattle, WA, USA) and then released into the net pen with the transport bag immersed in the net pen. Each fish swam freely into the pen without any further handling. Net pens were constructed of 125 mm diameter, foam-filled, PVC piping fitted with 25 mm knotless mesh netting. The net pens were located in a low flow (<0.5 m/s) side channel and the bottom corners were anchored with four 14 kg anchors. Sheets of floating Styrofoam and an anti-predator frame were used on the water surface of each net pen to deter predators from entering the pen and to prevent fish from jumping out of the pen. To minimize crowding stress, holding capacities in each net pen were restricted to a maximum of 35 fish (i.e., approximately 1 sockeye salmon per 1.4 m^3 of water; J.O. Thomas and Associates, 2009b). After a 24-h period in the net pen fish were either biopsied or tagged and released.

2.2. Biopsy and tagging methods

Fish were randomly selected for either biopsy or gastric radio telemetry tagging (i.e., tagged fish were not biopsied). Established protocols were used for gastric tagging adult salmon without anaesthetic, since fish that could be harvested for human consumption cannot be anaesthetized (Cooke et al., 2005; Young et al., 2006; Donaldson et al., 2010b). All protocols were approved by the University of British Columbia and Carleton University Animal Care committees in accordance with the Canadian Council of Animal Care.

The entire biopsy or tagging procedures were always completed in ≤2.5 min. For the immediate release groups, fish were either biopsied or tagged while in a Hypolon bag, which was constantly supplied with clean flowing river water that passed through the fish's gills. Biopsy involved a rapid 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, NJ) to assess plasma physiological indices. Individuals from the recovery group were randomly dip-netted from the net pen and placed into a Hypolon bag for biopsy or tagging. Netting individuals for sampling necessitated the possible disturbance of other individuals in the net pen. Dip net capture generally took <30 s per individual. To test for effects of sampling order on physiological variables, a linear regression of each plasma variable was conducted by sample order on each day (see Section 3). For all fish, a scale sample and a 0.5 g adipose fin clip were taken for identification of stock complexes, and fork length (FL) measurements were made.

A total of 99 sockeye salmon were radio-tagged for all the three treatment groups. A coded radio transmitter (MCFT-3A-3V, Lotek Wireless Inc., Newmarket, ON) was inserted gastrically with the trailing end of the antenna exiting the mouth and crimped to drift laterally along the individual's body. Coded transmitters enabled the identification of individual fish as they were detected at receiver stations. Transmitters were 16 mm in diameter, 46 mm long with a 460 mm long antenna. As part of another study, a thermal logger was attached to each transmitter and waterproofed using Plasti Dip multi-purpose rubber coating (Plasti Dip International, Blaine, MN), adding ~10 mm in length (Donaldson et al., 2009). The transmitter/thermal logger complex weighed 17 g in air and 7 g in freshwater. Tags were transmitted on the 150 MHz band on six unique frequencies (320, 360, 440, 460, 600 and 800 kHz) with three pulse intervals per frequency (4.5, 5.0, and 5.5 s) to reduce the occurrence of signal collisions.

2.3. Laboratory assays

Individual population origin was determined from DNA analysis of fin clips and scales (Beacham et al., 2004). Plasma cortisol, ions (K^+, Cl^- and Na^+), glucose, lactate and osmolality, were quantified from blood samples based on procedures described in Farrell et al. (2001b), except osmolality analyses were conducted using an AI 3320 Freezing Point Osmometer (Advanced Instruments Inc., Norwood, MA) and K^+ and Na^+ were conducted using a Model 410 Single Channel Flame Photometer (Cole Parmer, Montreal, QC).

2.4. Telemetry methods and determination of survival and migration rate

Fixed radio-telemetry receiver stations (SRX400 or SRX400A, Lotek Wireless Inc., Newmarket, ON) used 3-element or 4-element Yagi antennas (Maxrad Inc., Hanover Park, IL, or Grant Systems Engineering Inc., King City, ON) and were strategically positioned both down-river and up-river of the release site (Fig. 1; Robichaud and English, 2006, 2007). Twenty one receivers were distributed at 18 locations throughout the Fraser River mainstem and into tributaries that lead to natal sub-watersheds (Fig. 1).

Arrival at natal sub-watershed was determined by detection with fixed station telemetry receivers located in tributaries en-route to spawning grounds. Failure of an individual to reach a subsequent receiver location was termed en-route mortality (Robichaud and English, 2006, 2007). Individuals that were reported as fisheries harvest were excluded from this study. For statistical analyses, we evaluated percentage survival >24 h, 48 h, 96 h and ultimate survival to reach spawning areas (Table 1).

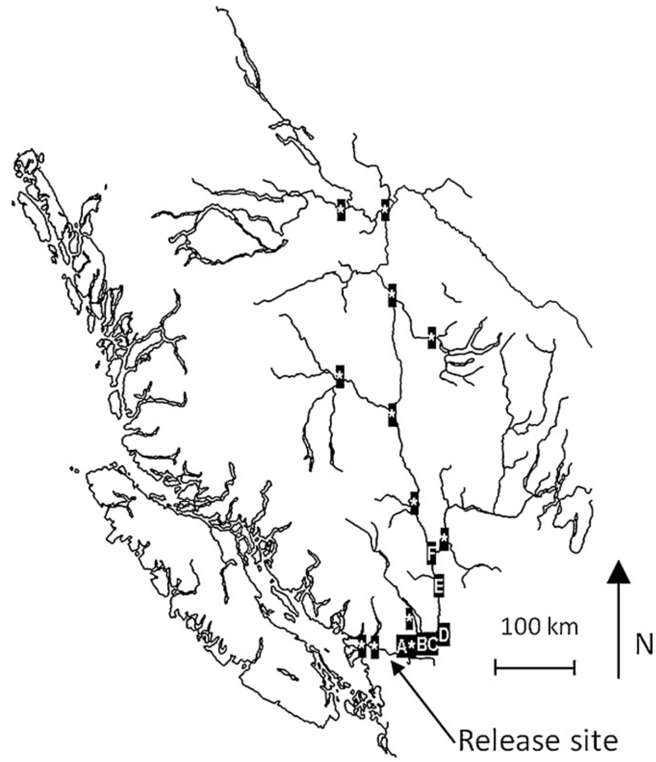

Fig. 1. Map showing the Fraser River, British Columbia, Canada watershed and the study and release site. Asterisks denotes radio receiver stations distributed throughout the Fraser River mainstem and into tributaries throughout the watershed. Letters represent receiver locations used in the calculation of migration rates, as follows: A (Harrison River confluence), B (Hope), C (Qualark), D (Sawmill), E (Hell's Gate), and F (Thompson River confluence).

Migration rates were calculated from release to detection at the Thompson River Confluence. Some populations have divergent migration paths after passing this location, which resulted in sample sizes that were too low for such analysis for receivers located further up-river. Migration rate was calculated by dividing the distance between two fixed receiver sites by the difference in time from the first detection at a downriver receiver or release site to the first detection at the subsequent upriver site. In instances where an individual failed to be detected at a particular site, that individual was excluded from the migration rate calculation for that section of the river.

2.5. River temperature monitoring

A temperature logger (resolution ±0.1 °C, accuracy ±0.2 °C, Onset Computer Corporation, Pocasset, MA), programmed to record temperatures every 15 min, was deployed in the net pen offshore at the angling site. An additional temperature logger (resolution ±0.1 °C, accuracy ±0.2 °C, Vemco-Amirix Systems, Inc., Halifax, NS; resolution ±0.1 °C, accuracy ±0.2 °C, Onset Computer Corporation, Pocasset, MA), programmed to record temperature every hour, was deployed in-river near the release site at Whonnock (Fig. 1). This location is representative of the range of temperatures encountered by all individuals during the capture and tagging procedure, as the Fraser River is a large, well-mixed system (Patterson et al., 2007) and temperatures in the lower river are generally correlated with upper river temperatures (Hague et al., 2008). However, we cannot exclude minor variations in temperature exposures that may

Table 1
Survival of sockeye salmon captured by beach seine or angling and immediately released or confined in a net pen for 24 h.

Capture method	Survived >24 h	Survived >48 h	Survived >96 h	Reached natal sub-watershed
Beach seine (immediate release)	21 of 22 (95.5%)	20 of 22 (90.9%)	16 of 22 (72.7%)	12 of 23 (52.2%)
Angling (immediate release)	31 of 32 (96.9%)	25 of 32 (78.1%)	19 of 32 (59.4%)	12 of 33 (36.3%)
Net pen recovery (holding for 24 h)	29 of 36 (80.6%)	22 of 36 (61.1%)	12 of 36 (33.3%)	1 of 35 (2.9%)

Survival to reach natal sub-watersheds represents only individuals that were detected by fixed station receivers at terminal areas. Total numbers do not include unreported fisheries harvest.

have been behaviourally exploited by fish but unresolved by our telemetry array (Donaldson et al., 2009).

2.6. Statistical analyses

Homogeneity of variance was assessed using Levene's test. One-way analysis of variance (ANOVA) was used to test for differences in physiological variables for each treatment group (beach seine, angling, 24 h net pen holding). Where significant differences were found, Tukey–Kramer post hoc tests were used (Zar, 1999). Pearson Chi-square analysis was used to test for differences in post-release survivorship between groups. Wilcoxon univariate survival analysis was used to determine the time to mortality and one-way ANOVA was used to determine longevity between groups. Wilcoxon/Kruskal–Wallis tests were used to compare migration rates between groups at each receiver location, followed by pairwise comparisons for significant relationships. Additional statistical tests are summarized in Section 3. All values presented here represent means ± S.E., unless otherwise noted. Statistical analyses were conducted using JMP v. 8.0. (SAS Institute, Cary, NC).

3. Results

3.1. Fish characteristics and capture details

All sockeye salmon were silver-coloured and without overt signs of secondary sexual characteristics to visually determine individual sex. DNA stock analysis of tagged individuals revealed that the majority were destined for mid- and upper-Fraser River spawning areas. Mean fork length was 58.6 ± 0.4 cm.

Capture time with angling, from hooking to landing was 2.7 ± 0.1 min. Capture time was not associated with fork length (Pearson's correlation analysis, $P > 0.05$) or with survival to reach natal sub-watersheds (logistic regression, $P > 0.05$). Fish captured by anglers were generally hooked in or around the mouth. However, two fish were foul-hooked in the body or head, and some individuals bled from their hook wounds or from the fishing line tangling around their gill arch.

The time for the beach seine to be closed and brought to shore took 6.0 ± 0.1 min. The required time to remove an individual from the seine and complete all biopsy or tagging procedures took up to 4 min. Fish captured by beach seine appeared to be in good physical condition, although some individuals had visible scale loss and fresh net mark bruising.

For the net pen treatment, pairwise correlations revealed that plasma cortisol increased with sampling order ($r = 0.317$, d.f. = 56, $P = 0.015$), but this was not the case for any other plasma variable (all $P > 0.05$). The length of time to mortality was not influenced by sampling order (linear regression, $r^2 = 0.002$, SS = 7375.3, d.f. = 34, $P = 0.815$). Migration rates between receiver locations were not influenced by sampling order (linear regression, all $P > 0.05$). Low survival of the net pen group precluded the ability to make statistical comparisons between sampling order and survival to reach natal sub-watersheds.

Both capture gears resulted in fish showing signs of exhaustion (e.g., difficulty maintaining equilibrium, few attempts to burst swim away from the sampling team). Fish released immediately were in these states. In contrast, fish released from the net pen after 24 h were typically vigorous and were able to burst swim away from the sampling team. It was difficult to assess whether or not the fresh scale loss observed on several individuals was due to net pen holding, initial capture, or pre-capture conditions.

At the time of telemetry tagging, river temperatures were stable throughout the duration of the study (17.4–18.9 °C; mean = 18.3 °C). There was no relationship between tagging temperature and survival to reach natal sub-watersheds for any of the treatment groups (Student's *t*-test, all $P > 0.05$). Water temperatures measured in the net pen were similar to those measured in river (17.6–19.6 °C; mean = 18.6 °C).

3.2. Physiological responses to capture and net pen recovery

Significant relationships were detected among treatment groups for plasma cortisol ($F_{2,108} = 99.0$, $P < 0.001$; Tukey–Kramer HSD test, $P < 0.05$), glucose ($F_{2,108} = 16.2$, $P < 0.001$; Tukey-Kramer HSD test, $P < 0.05$), sodium ($F_{2,108} = 16.3$, $P < 0.001$; Tukey–Kramer HSD test, $P < 0.05$), chloride ($F_{2,108} = 37.3$, $P < 0.001$; Tukey–Kramer HSD test, $P < 0.05$), and osmolality ($F_{2,108} = 10.3$, $P < 0.001$; Tukey–Kramer HSD test, $P < 0.05$), but not lactate ($F_{2,108} = 3.0$, $P = 0.051$). For each of these significant relationships, Tukey–Kramer post hoc tests revealed that the net pen group contributed significantly to the relationship (denoted by dissimilar letters in Fig. 2), but that the angling and beach seine groups were not significantly different (all $P > 0.05$). Relative to fish sampled immediately after capture, individuals that were held in the net pen for 24 h had significantly elevated plasma cortisol and glucose levels, and sodium and chloride ions and osmolality were all significantly decreased relative to fish sampled immediately after beach seining and angling (Fig. 2).

3.3. Behaviour and survival

Migration rate from the release site to Harrison River confluence site (Fig. 3), the first up-river detection location, was significantly different between groups ($\chi^2 = 7.893$, d.f. = 2, $P = 0.019$), with the post-angling net pen recovery group traveling faster relative to those released immediately ($\chi^2 = 7.868$, d.f. = 1, $P = 0.005$), but not those released immediately after beach seining ($\chi^2 = 1.524$, d.f. = 1, $P = 0.217$). No significant differences in migration rates between groups were detected in passage between the following sites: Harrison to Hope ($\chi^2 = 1.566$, d.f. = 2, $P = 0.457$), Hope to Qualark ($\chi^2 = 3.793$, d.f. = 2, $P = 0.150$), Qualark to Sawmill ($\chi^2 = 1.130$, d.f. = 2, $P = 0.568$), and Sawmill to Hell's Gate ($\chi^2 = 1.337$, d.f. = 2,

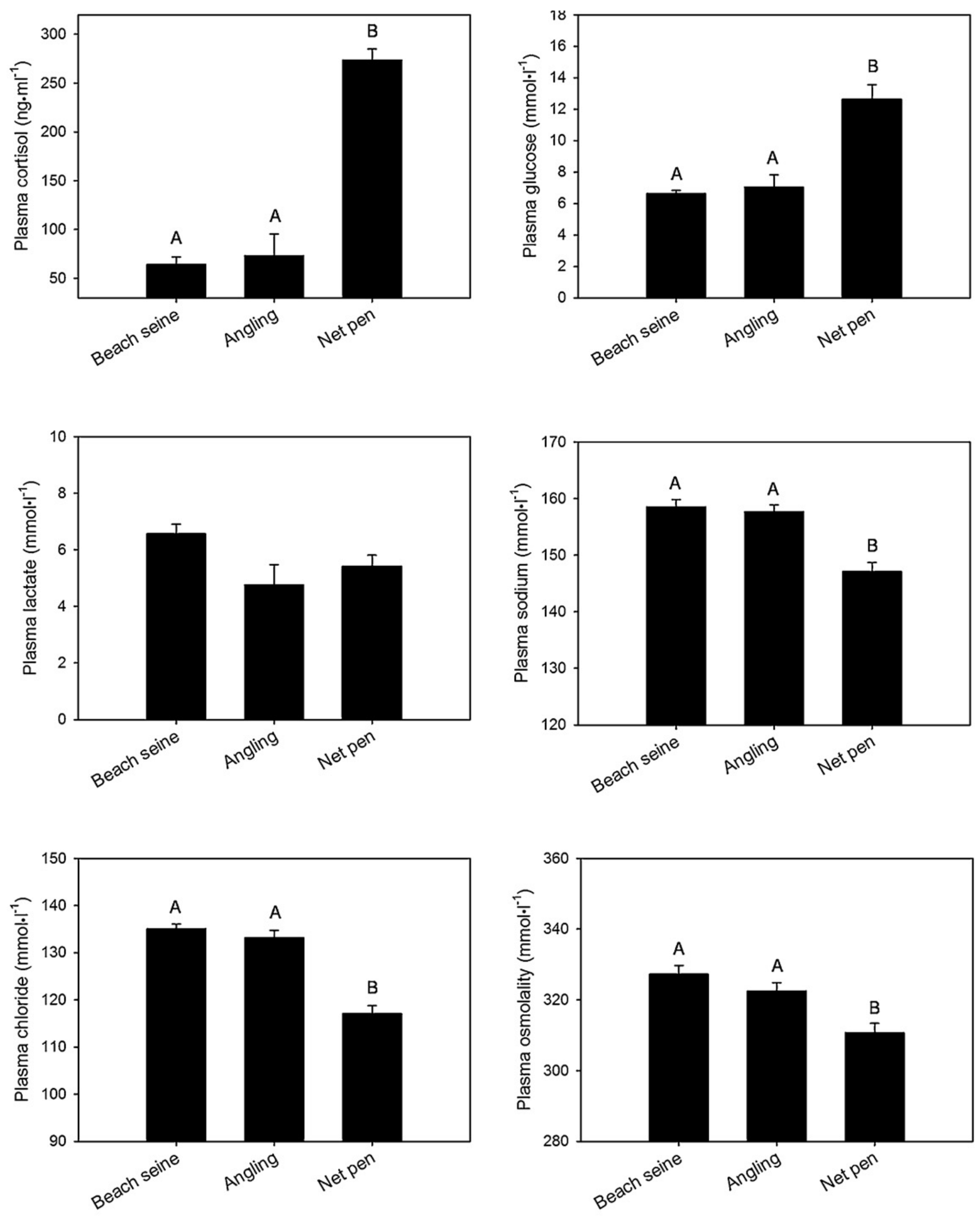

Fig. 2. Mean (±S.E.) for plasma indices by beach seine, angling, or net pen confinement treatment group for adult Fraser River sockeye salmon. Statistical details for one-way analysis of variance (ANOVA) and Tukey–Kramer post hoc tests are presented above each panel.

P = 0.512). Migration rates between the Hell's Gate and Thompson River confluence sites differed (χ^2 = 9.071, d.f. = 2, P = 0.011), with the angling group traveling faster relative to the beach seine group (χ^2 = 7.788, d.f. = 1, P = 0.005) but not the net pen group (χ^2 = 3.788, d.f. = 1, P = 0.052; Fig. 3).

In total, 8 individuals (8.8%) were never detected at up-river fixed station receivers and were considered to be mortalities. The net pen holding had significantly more individuals that were not detected up-river (18.9%) relative to either beach seine or angling (0.0% and 2.7%, respectively; Pearson Chi-square analysis; χ^2 = 9.490, d.f. = 2, P = 0.009). Within the first 24 h after release, net pen recovery resulted in lower survival (80.6%; Table 1) compared with immediate release (>95%). For fish that were detected at up-river fixed stations, survivorship analysis revealed a significant difference in the length of time to mortality among the treatment groups (Wilcoxon univariate survival analysis; χ^2 = 11.326, d.f. = 2, P = 0.004). Pairwise comparisons revealed that the net pen group succumbed to mortality faster than the beach seine group (χ^2 = 8.739, d.f. = 1, P = 0.003) and angling group (χ^2 = 4.354, d.f. = 1, P = 0.037) but there was no difference between the angling and beach seine groups (χ^2 = 3.410, d.f. = 1, P = 0.065).

Survival to natal sub-watersheds after net pen recovery was only 2.9%. In contrast, survival to natal sub-watersheds after immediate release was over 10-times higher, being 52.2% and 36.3%, respectively, for beach seining and angling (Table 1).

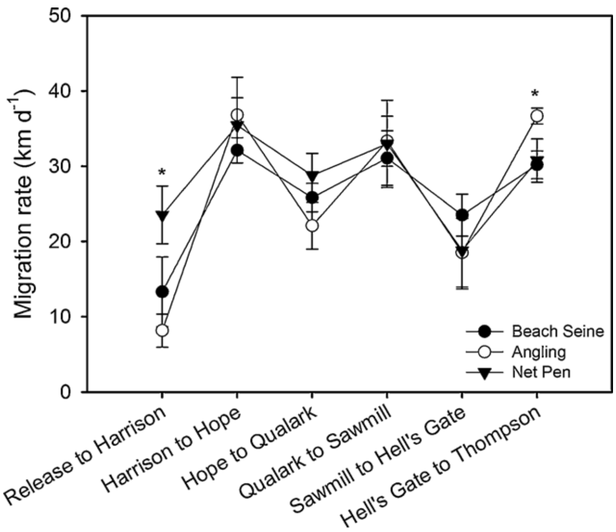

Fig. 3. Migration rates (km d^{-1}) of adult sockeye salmon detected at each radio telemetry receiver location through the Fraser River mainstem across three treatment groups (beach seine, angling, and 24 h net pen recovery).

4. Discussion

4.1. Immediate release after capture

Capture by beach seine and angling resulted in a similar physiological response, likely due to the comparable, rapid duration between capture and sampling for both groups. Plasma values were characteristic of previous results for salmonids sampled immediately following exercise and capture-related stressors (Hinch et al., 2006; Young et al., 2006). Many of the plasma parameters measured here typically continue to increase with time after a stress, and would likely reach peak values between 30 min and about 2 h following the stressor (e.g., plasma cortisol; Barton et al., 2002).

The short-term survival of fish in each treatment reflected the general trends that emerged from the plasma physiology results. Over 95% of individuals released from the beach seine and angling groups survived for an additional 24 h following release. Parallel studies were conducted in 2008 (J.O. Thomas and Associates, 2009a) and 2009 (J.O. Thomas and Associates, 2009b) that investigated the 24 h survival of sockeye salmon captured by both angling and beach seine by monitoring fish in net pens, where adjusted survival was 98.8% and 98.3% in 2008 and 2009, respectively. Adult sockeye that were held in pens in a saltwater harbour for 24 h following capture by purse seine showed similar survival trends, where 100% survival was observed (Cooke et al., 2005). Survival was similar for the angling and beach seine groups over a 24 h period, but we observed general decreasing survival over time in each of the treatment groups after 24 h.

The trend in decreasing survivorship over time was reflected in ultimate survivorship to reach natal sub-watersheds, where 52.2% and 36.3% of fish immediately released by beach seine and angling, respectively, reached spawning areas. Martins et al. (2011) modelled survival of radio-tagged adult migrating Fraser River sockeye salmon released from purse seine in the marine environment and from tangle net (i.e., a fine mesh gill net) or fishwheel in the freshwater environment between 2002 and 2007. They found >70% survival to spawning areas for marine-tagged fish, whereas river-tagged survival ranged between 30 and 50%. These marine-tagged fish may represent the best available telemetry survival data that approach true baseline survivorship values for the freshwater migration since they exclude capture and handling effects that occur in freshwater. Based on this 70% survival value, our results show 20–35% mortality associated with capture and immediate release by either beach seine or angling in the lower Fraser River.

Capture and handling at warm river temperatures (relative to cooler marine temperatures) is proposed to account for much of the difference in survival, compounded by the possibility that individuals are still undergoing physiological changes associated with osmoregulatory preparedness for freshwater during their transition through the lower Fraser River (Shrimpton et al., 2005; Donaldson et al., 2010b; Martins et al., 2011). Interestingly, post-release survival was not correlated with river temperatures in this study despite previous findings that high water temperatures may contribute to stress and disease for migrating sockeye salmon (Macdonald, 2000; Wagner et al., 2005). Throughout the tagging period, river temperatures were consistently moderate to high for the mainstem Lower Fraser River (Patterson et al., 2007) yet they did not vary appreciably throughout the study, which may explain why a temperature effect on survival was not detected for any treatment group.

Catch-and-release could be a viable in-river practice provided that best practices as exemplified in this study are used in the capture, handling, and release of Pacific salmon. Rapid angling durations (i.e., ~3 min in the present study), careful handling that minimizes physical injury and rapid release are likely all factors that reduce the sublethal and potentially lethal consequences of catch-and-release. While it is not possible to account directly for the effects of tagging or sampling procedures based on our study design, these factors did contribute to handling time.

4.2. Net pen recovery post-angling

Despite the intention of using the net pen to enable physiological recovery like similar approaches (e.g., Farrell et al., 2001a,b), this treatment actually resulted in a significantly greater physiological disturbance relative to the beach seine and angling groups. Net pen holding for 24 h resulted in depressed plasma osmolality and ions, a ~4-fold elevation of plasma cortisol and a ~2-fold elevation of plasma glucose relative to both the beach seine and angling groups, similar patterns to those observed for juvenile coho salmon (*O. kisutch*) subjected to a confinement stressor and transferred to either seawater or freshwater (Redding and Schreck, 1983). The elevated plasma stress could be a consequence of either the net pen itself contributing to chronic stress, or fish being stressed further when they were dip-netted from the net pen prior to sampling or release. We found that sampling order did influence plasma cortisol values, but had no effect on the other plasma variables or on post-release behaviour or short-term survival. Even so, lowest plasma cortisol value recorded for the net pen group (92.2 ng mL^{-1}), which was one of the first fish sampled on that day, was still higher than the mean plasma cortisol values of the freshly caught angled (89.1 ± 73.0 ng mL^{-1}) or beach seine (64.2 ± 44.3 ng mL^{-1}) fish, suggesting that the net pen contributed to the physiological disturbance but that the secondary netting further elevated this variable. These results make it difficult to draw specific conclusions on whether the plasma cortisol response was caused by the net pen itself, the secondary dip-netting of fish from the net pen, or a combination of the two stressors. Short-term confinement typically results in some degree of stress (Portz et al., 2006). The stress response observed here could be related to the fact that sockeye salmon were artificially prevented from resuming their normal spawning migrations, and unable to maintain normal up-river swimming behaviour.

In contrast to the high survival of the beach seine and angling groups in the first 24 h post-release, only 80% of the individuals released from the net pen survived the same time period and only

2.9% successfully reached natal sub-watersheds. The survival analysis similarly revealed that the net pen group succumbed fastest with no differences in the time to mortality found for the immediately released groups. A trend emerged in survival between the immediately released and net pen angling groups, where the net pen group survival pattern appeared offset by 24 h, due to the fact that they were held in the net pen for that time. If examined on the same time trajectory, nearly all individuals in both of these groups survived the first 24 h from both treatments, then by 48 h survival was ~80%, and by 96 h survival was ~60% (Table 1). However, a large difference in ultimate survival to reach spawning grounds was observed, where mortality was nearly absolute for the 24 h net pen group. The trend in decreasing survival over time is likely due to natural mortality rates as found by previous telemetry studies on adult migrating sockeye salmon (e.g., English et al., 2005; Cooke et al., 2006; Crossin et al., 2009), but latent mortality associated with the stressor of the capture and/or net pen holding treatments is possible and has been suggested previously (Donaldson et al., 2010b).

While the survivorship of the beach seine and angling groups is similar to other sockeye salmon studies conducted in freshwater, survival of the net pen holding group is much lower than observed previously (Martins et al., 2011). Fish in the net pen treatment clearly had higher elevations of physiological indices of stress, which can be linked with an increase in mortality due to bacterial or fungal disease development long after the stressor occurred and may have contributed at least in part to the high mortality rates observed here (Mazeaud et al., 1977; Pickering and Pottinger, 1989; Schreck, 2000; Budy et al., 2002). While not replicated for the beach seine group, results could have been similar given the remarkable post-capture similarities with immediate release both for survival and physiology.

The net pen group migrated significantly faster than either of the immediately released groups from the release site to the next-closest up-river receiver station at the Harrison River confluence, and in general migration rates were slowest through this region. In response to fisheries capture stress, both increased swimming activity for Atlantic salmon (*Salmo salar*, Mäkinen et al., 2000), sulking and deep-diving behaviour in sockeye salmon (Quinn and terHart, 1987) and decreased swimming activity for largemouth bass (*Micropterus salmoides*, Thompson et al., 2008) have been reported. Being unable to seek cooler water at depth may have in fact have contributed to the stress observed here post-capture (Quinn and terHart, 1987). In salmonids, decreased activity has been suggested as a result of compromised performance while fish recover physiologically from the stressor (Milligan, 1996); however increased activity has been proposed as a behavioural response to escape from a stressor (Mäkinen et al., 2000). At subsequent locations, migration rates did not vary between groups and were consistent with previous studies on Fraser River sockeye salmon (e.g., Hanson et al., 2008). The only subsequent location where migration rate differed between treatment groups was in the reach leading from Hell's Gate to the Thompson River confluence, where the angling group traveled at faster speeds than the other groups. Hell's Gate is a river constriction with high flows and difficult areas of passage that are energetically and physiologically costly to migrating salmon (Hinch and Bratty, 2000; Hinch and Rand, 1998). A previous radio-telemetry study on adult sockeye salmon found that co-migrating individuals retain their rank in swimming speed throughout much of the migration through the lower Fraser River, but the passage through Hell's gate results in a reshuffling of ranks (Hanson et al., 2008). The finding that the angling group migrated faster as they moved past this migration segment is unexpected, but the differences between groups suggests potential latent treatment effects that emerged following passage through this difficult segment of the river.

4.3. Conclusions and future directions

We found that differences in physiological condition between treatments were reflected by both short-term survival and survival to reach natal sub-watersheds. A small, but important difference in survivorship was observed between the beach seine and angling groups, where angled fish had 15.9% lower survival to reach natal sub-watersheds. Importantly, these data also illustrate the fact that recreational, commercial and aboriginal fisheries are not inherently different in that fish that are captured and released tend to be exposed to similar stressors which should promote common strategies to improve survival (Cooke and Cowx, 2006). Relative to adult sockeye salmon tagged in the marine environment, which is the best telemetry data we have to assess baseline mortality, handling and releasing fish in the lower Fraser River is associated with mortality in the range of 20–35%; however we recommend that this finding be tested empirically by tagging fish in the marine and freshwater environments concurrently. While 24 h holding of migrating salmon in net pens is useful for documenting initial and short-term mortality, there may be considerable mortality in the days and weeks following release, which cannot be assessed directly using net pen holding studies and requires approaches such as biotelemetry. The poor physiological condition and high post-release mortality of the 24 h net pen group suggests that future research is required to improve methods for promoting recovery from capture stress in freshwater, particularly ones where fish can be released without the necessity of secondary handling.

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