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ARTICLE

Consequences of Fishery Gear Type and Handling Practices on Capture and Release of Wild Steelhead on the Bulkley River

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Abstract

Steelhead *Oncorhynchus mykiss* are captured and released during spawning migrations by the commercial, subsistence (Indigenous), and recreational fishing sectors, though the consequences of these fisheries interactions on steelhead migration are poorly understood. This study evaluated injury, reflex impairment, behavior, and survival of released wild adult steelhead following capture in the subsistence dip-net, subsistence beach-seine, and recreational angling fisheries of the Bulkley River, British Columbia. Wild steelhead were captured using common handling practices employed in each fishery and were monitored postrelease using radiotelemetry. A greater proportion of steelhead captured by dip net and seine had impaired righting reflexes compared with angled fish, but only fish captured by dip net had notably higher incidence of injury (i.e., net marks, torn fins, flesh wounds, scale loss). Fish captured by dip and seine net had considerably faster peak migration rates (>4,000 m/d) than angled fish (<1,000 m/d), which likely reflects when the steelhead are encountered during their migration in these fisheries (earlier versus later stages). Air exposure (15–74 s) and water temperature (9.2–15.1°C) at the time of capture had significant negative relationships with 24-h fallback behavior (temperature only), intermediate-term (10–20 d after capture) migration rates, and peak migration rates in dip-net-captured steelhead. There were no significant effects of capture duration or fish length on injury, righting reflexes, or migratory behavior. Immediate mortality upon release was rare and occurred in only one fish captured by dip net. The 3-d survival was 88–97% for dip-net-caught steelhead, 96–100% for seine-caught steelhead, and 68–100% for angled steelhead. Despite inherent differences in timing and location between these fisheries, findings suggest that air exposure and water temperature can decrease steelhead migration rates. Fishers should look for opportunities to avoid or minimize these capture and handling conditions when releasing steelhead.

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Fisheries are often a complex blend of motivations and human–fish interactions (Cooke and Cowx 2006; Young et al. 2016). In many cases, modes of capture are relatively indiscriminate, with fishing gears such as hook and line and nets capturing a wide range of species in the same location (Gray and Kennelly 2017; Northridge et al. 2017). Many of the fish that are landed are released to comply with harvest restrictions or as a voluntary behavior on behalf of the fisher for conservation purposes (Cooke et al. 2013) or because the bycatch is considered low value to the fisher (Arlinghaus et al. 2007; Davies et al. 2009). The underlying assumption of releasing captured fish is that these individuals will survive with minimal fitness consequences from being caught, handled, and released. This is not always the case, however, as capture by fisheries can be one of the most severe acute stressors imposed on fish throughout their lives (Davis 2002). As a result, a considerable amount of research has evaluated both the lethal and sublethal effects of capture and release in commercial, subsistence, and recreational fisheries (Alverson et al. 1994; Bartholomew and Bohnsack 2005; Wilson et al. 2014).

Characteristics associated with a unique species, population, or fishery can influence the severity of the impact that capture has on an individual fish (Cooke and Suski 2005; Raby et al. 2015a; Patterson et al. 2017). Fish captured in net fisheries (gill net, seine net, tangle net, fyke net) may experience physical damage to organs, flesh, scales, and the mucous layer due to entanglement (Vander Haegen et al. 2004; Smith and Scharf 2011; Colotelo et al. 2013; Raby et al. 2015b; Bell and Lyle 2016). Physical damage may also occur for fish captured recreationally due to damage at the hooking location (Hühn and Arlinghaus 2011) and handling (Colotelo and Cooke 2011). In most fisheries there is a degree of exhaustion resulting from anaerobic exercise that can result in physiological changes in the captured fish (Kieffer 2000) and even mortality (Wood et al. 1983). It is also common for captured fish to be lifted in the air (i.e., air exposure) before being returned to the water (Cook et al. 2015). In some net-based fisheries, air exposures can exceed 60 min due to large catches and the time needed to process fish (Davis 2002). In recreational fisheries, air exposures are related to unhooking and admiration of captured fish but typically do not exceed 60 s for salmonid species (Lamansky and Meyer 2016). Air exposure can lead to physiological and behavioral changes in fish (Thompson et al. 2008; Rapp et al. 2014), which can be further exacerbated during certain environmental conditions, such as warm water temperatures (Gingerich et al. 2007). There are multiple factors that can influence capture and release outcomes, and their relative impact can vary on a fishery- and species-specific basis, suggesting the need for context-specific evaluations (Cooke and Suski 2005; Raby et al. 2015a; Brownscombe et al. 2017).

Thus far, few studies have compared the catch-and-release outcomes of beach-seine and angling gear within a single system (but see Donaldson et al. 2011), and to our knowledge no studies have evaluated the consequences of dip-net capture. Dip nets are used to capture Pacific salmon *Oncorhynchus* spp. in the Pacific Northwest (e.g., the Fraser and Thompson rivers of British Columbia and the Copper, Kenai, and Kasilof rivers and Fish and Sweathart creeks of Alaska) but often have bycatch that must be released. These species-specific evaluations are particularly important for species such as steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) that are in decline (Smith et al. 2000; Northwest Fisheries Science Centre 2015; Neilson and Taylor 2018) and that are exploited by multiple fisheries during critical periods of their life history.

Steelhead are one of the world's most iconic salmonid species, serving a keystone function in freshwater ecosystems (Willson and Halupka 1995), while contributing to human culture, economy, and recreation (Counterpoint Consulting 2008). Due to their declining populations across their distribution they are generally not targeted in harvest-oriented fisheries, though some ceremonial harvest still occurs in Indigenous fisheries (e.g., Levy and Parkinson 2014). Despite minimal legal harvest of wild steelhead, the existence of fisheries for other Pacific salmon results in a considerable amount of steelhead bycatch (J. O. Thomas and Associates 2010) as other Pacific salmon and steelhead runs co-occur. For example, in the Skeena River system it is estimated that 1.5% of summer-run steelhead may be captured each year in the gill-net test fishery used to inform real-time management, with apparent short-term mortality rates of 49% (Welch et al. 2009; MFLNRORD 2017a). A substantial proportion of this steelhead stock is then captured in the Bulkley River, as approximately 4% of individuals are captured by seine, 10% by dip net, and 59% by angling (MFLNRORD 2017b, 2018). Capture within commercial, Indigenous, and recreational sectors is common throughout most watersheds in the Pacific Northwest (e.g., Fraser and Columbia rivers), yet the response of steelhead to different modes of capture and release has received little attention.

The purpose of this study was to quantify sublethal impacts and the mortality of steelhead following capture and release by dip net, beach seine, and angling gear on the Bulkley River, British Columbia. Steelhead were assessed for injury, reflex ability, migratory behavior, and survival following fisheries captures during their spawning migrations. This study also evaluated the potential drivers of migratory stress and mortality in each of these fisheries to help inform handling practices and management of steelhead.

METHODS

Study site.— The Bulkley River is the largest tributary of the Skeena River, draining an area of approximately 12,000 km^2. The Bulkley River joins the Skeena River at approximately river kilometer (rkm) 266 (measured from the mouth of the Skeena River) and extends 141 km upriver to the Morice River, which then flows an additional 74 km to Morice Lake (Figure 1). Along the Bulkley River there are three relatively larger tributaries that steelhead can migrate into, including the Suskwa River (~rkm 280, measured from the mouth of the Skeena River), the Telkwa River (~rkm 365), and the Little Bulkley River (~rkm 405), as well as a number of smaller tributaries that steelhead may enter during spring runoff. The river is free of manmade barriers, with Witset (formerly Moricetown) Canyon as the greatest hydrological barrier (15-m change in altitude) to fish migration. At Witset Canyon, there is a long-standing Wet'suwet'en Indigenous subsistence fishery. The Wet'suwet'en fishers target migrating salmonids (primarily Pink Salmon *Oncorhynchus gorbuscha*, Coho Salmon *Oncorhynchus kisutch*, and Chinook Salmon *Oncorhynchus tshawytscha*), with most steelhead being released after capture. As of 1999 the Ministry of Forests, Lands, Natural Resource Operations, and Rural Development (MFLNRORD) and the Wet'suwet'en have collaborated to conduct a mark–recapture program (using conventional Anchor-T tags) for all steelhead captured and released in the beach-seine and dip-net fisheries (MFLNRORD 2017b). In addition to these subsistence salmon fisheries, the river also maintains a world-renowned steelhead recreational fishery, with the largest steelhead capture of any stream in British Columbia. Each year an average of 20,873 summer-run steelhead migrate up to the Bulkley River, although the 2017 run was estimated at just 9,234 fish (MFLNRORD 2017b). Recreational anglers can access the river by jet boat, pontoon, and walk-in sites, and use both fly and spin fishing gear. Since 2010, recreational angling effort for steelhead has averaged 12,524 angler days per season (MFLNRORD 2016). All steelhead must be released following recreational capture as per the MFLNRORD's fishing regulations in the province of British Columbia.

Capture methods.— Steelhead sampling was completed on the Bulkley River, British Columbia, from August 24 to October 10, 2017. Wet'suwet'en fishers sampled steelhead from Witset Canyon by dip net and beach seine. Dip-net sampling took place above the canyon just below the top of the falls using dip-net gear (a ~600-cm aluminum pole with 4-cm × 4-cm square nylon mesh) between August 25 and September 30, 2017 (Figure 2A). Steelhead were brought to the surface by the fisher and were placed into a transport cradle that was carried by a runner to the sampling station approximately 20 m away. Steelhead were placed by the runner into a water-filled storage tub that was used to hold the steelhead while other fish were being processed. Steelhead were dipnetted from the storage tub into a sampling trough, where they were measured, sexed, and visually assessed for injuries, tags, and scars. Fish were released by samplers into slow-moving water on the edge of the falls through a plastic slide or were placed into the water directly, depending on the water level.

Beach-seine sampling (~90-m × 8-m × 5-cm stretched-mesh opening size) was conducted in the canyon by jet boat between August 29 and September 22 (Figure 2B). One end of the seine was anchored to shore while the other was pulled by jet boat into an arc and corralled back to shore into an area of approximately 5 m^2, with a mean depth of approximately 20 cm. The beach-seine crew sorted fish species in a sampling trough held within the river. Steelhead were measured, sexed, and assessed for injuries, tags, and scars by workers as part of the MFLNRORD monitoring program. Fishers would typically sort and release steelhead before sorting other species of fish, as most other species were harvested after capture.

Recreational anglers captured steelhead throughout the entirety of the Bulkley River upstream of Witset Falls to the confluence of the Morice–Bulkley rivers (rkm 318–407; Figure 2C). These fish were generally closer to potential spawning sites than fish captured at Witset Falls. Anglers targeted steelhead by fly fishing (spey rods #7, 8, and 9), center-pin fishing (a free-spooling reel), and spin fishing (e.g., 2.6-m rod with medium action). Anglers used various sizes and colors of flies, inline spinners, spoons, and artificial worms on single barbless hooks. Flies were tied to size 1 hooks and smaller, while heavy tackle was used in conjunction with hooks as large as 3/0. Fish were landed in rubberized landing nets or were secured by the caudal peduncle with a bare hand (tail grab). In some cases, anglers lifted steelhead out of the water for an admiration period.

Quantification of the capture event.— Elements of the capture events were recorded that were common across all three fisheries. Capture-related variables included capture duration (s), duration of air exposure (s), and the time to attach the transmitter (s). For dip-netted and beach-seined fish, capture duration was considered the elapsed time from netting the fish to the point that the fish was secured in the water-filled sampling trough. Capture duration was taken as the time elapsed between hooking and landing for angled fish. Air exposure was determined as the time the fish was lifted out of the water prior to entering the sampling trough. Each fish captured was assessed for fish length (fork length; mm), sex, scale loss (presence versus absence), and injury at the time of capture. Injuries were classified binomially as either the presence or absence of flesh wounds, net marks, ripped fins, and bleeding organs. Scars or predator wounds that were inflicted before the capture event were also recorded but were not included as a capture-related injury. We were unable to isolate most

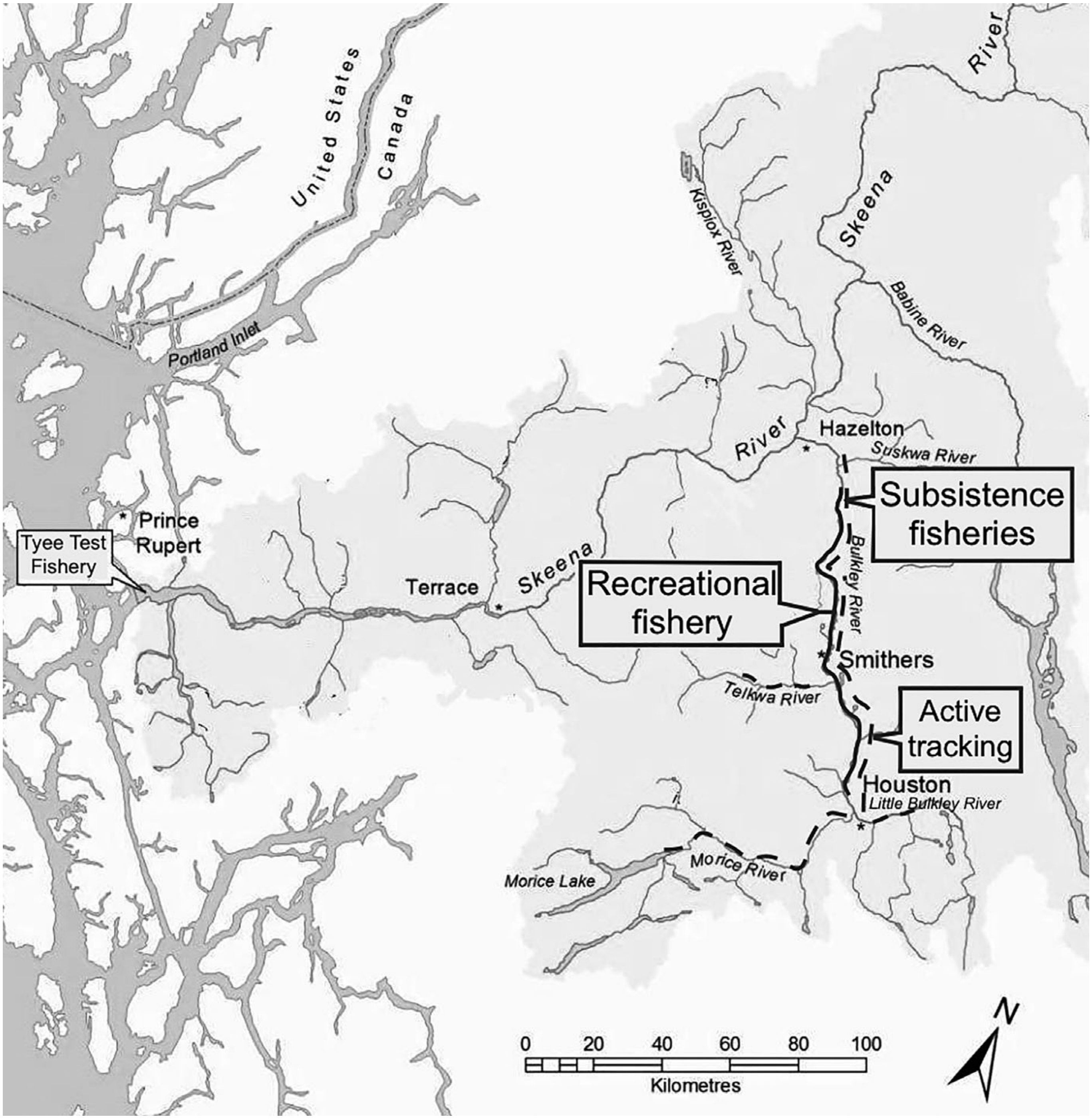

FIGURE 1. A map of the Skeena River watershed highlighting the Skeena, Bulkley, and Morice rivers and their major tributaries. The sampling locations for the subsistence and recreational fisheries (solid bold line) are noted on the map. Active radiotelemetry tracking was completed along the dashed line. Picture sourced from www.oceanecology.ca.

capture injuries from those incurred naturally. This may be particularly important for dip-net-captured fish that are actively trying to ascend steep falls and may collide with canyon walls and rocks. Anatomical hooking location was noted for fish captured by angling. Water temperature (°C) was recorded following each capture using a handheld digital thermometer (Compact Waterproof Digital Thermometer, Taylor USA, Las Cruces, New Mexico).

Radiotelemetry tagging.— Following capture and processing in each of these fisheries, steelhead were secured in

FIGURE 2. Photographs showing steelhead capture by **(A)** dip net, **(B)** beach seine, and **(C)** recreational angling on the Bulkley River, British Columbia. Following capture in the dip net, steelhead were transferred to a transport cradle that was carried by a runner to a sampling station, where steelhead were assessed for sex, length, and injury prior to release. [Color figure can be viewed at afsjournals.org.]

a water-filled (flow-through), v-shaped sampling trough (100 cm in length × 25 cm in width × 20 cm in height) or recovery bag (100 cm in length × 20 cm in diameter). A radiotelemetry transmitter (4.7 g weight in air, 220–441 d battery life, 33 pulses per minute; Series F1970, Advanced Telemetry Systems, Isanti, Minnesota) was attached externally behind the dorsal fin using two stainless steel 18-gauge surgical needles inserted through the dorsal musculature (as per Twardek et al. 2018). Wires were secured to the dorsal musculature on the opposite side of the transmitter using steel crimps and plastic backing plates to reduce tissue irritation. Each tag had contact information and ID to facilitate angler reporting. A previous review on externally attached telemetry tags suggested little impact to physiology and behavior in salmonids (Jepsen et al. 2015), so it was expected that the influence of the 4.7-g tags attached to the steelhead in our study would be minimal. Tagged fish were removed from the sampling trough or recovery bag and were assessed for the presence of the righting reflex prior to release. To assess this reflex, fish were rotated ventral side up and were monitored for their ability to regain normal orientation within 3 s (as per Davis 2010).

Manual radiotelemetry tracking.— Fish were located by zero-point manual tracking (Cooke et al. 2012) using a radiotelemetry receiver and a 3-element Yagi antenna (Lotek Biotracker; Lotek Wireless, Ontario). The positions of each fish were recorded using a handheld GPS instrument (Garmin GP 60 Handheld GPS Device, 010-00322-00; Garmin, Olathe, Kansas) set to Universal Transverse Mercator. Angled fish were located 20 min after release as an indication of immediate postrelease movement following capture. Precise tracking locations could not be determined for beach-seine and dip-net fish due to logistical constraints working along a waterfall and canyon. Dip-net fish were therefore evaluated for their presence above or below the falls 24 h following release. Both dip-netted and beach-seined fish were monitored for their emigration from Witset Falls, defined as movement greater than 500 m above or below the falls. Successive tracking was completed opportunistically by jet boat and raft, based on the section of river that angler volunteers planned to fish that day. The entirety of the Morice–Bulkley system between Morice Lake (headwaters of the Bulkley River) and the Suskwa–Bulkley confluence (20 km below the most downstream tagging site) and the two major tributaries (Telkwa River, Little Bulkley River) were tracked between October 10 and 19, 2017 (Figure 1). Tracking data from this period were used to calculate intermediate-term migration rates (m/d), defined as the displacement of each fish from its release site 10–20 d after release divided by the number of elapsed days (10–20 d) since capture. This tracking data was also used to calculate the peak migration rate (m/d) of each fish, determined as the fastest migration rate observed between successive detections in the fall of 2017. A secondary tracking event was completed between April 7 and 19, 2018, by rafting, hiking, driving, and aircraft. Tracking spanned the entirety of the Morice and Bulkley rivers above the Suskwa River and the majority of the Little Bulkley and Telkwa rivers.

Survival estimates.— Steelhead survival rates were estimated for the first 3 d following capture to ensure short-term mortality (i.e., 24 h) was accounted for (Carbines 1999) and to remain consistent with previous catch-and-release evaluations on steelhead (Nelson et al. 2005; Twardek et al. 2018). If a fish moved upstream after 3 d, it was designated as having survived. If a fish moved during the winter it was also considered alive based off previous evidence that dead Bulkley River steelhead tagged in the fall cease drifting prior to winter (W. M. Twardek, unpublished data). This is consistent with the observation that salmonids approach complete decomposition 6–7 weeks following mortality (Johnston et al. 2004). Only movements greater than 500 m were considered true movements to account for imprecision in our tracking locations. A lack of movement over winter did not indicate mortality given that Bulkley River steelhead may remain within the same run or pool all winter before entering spawning tributaries (Twardek, unpublished data). Therefore, if a fish failed to move upstream or make delayed downstream movements during intermittent tracking over the 7-month study period, its fate was considered unknown. Survival estimates were therefore presented as a range (minimum to maximum percent). Minimum estimates assumed all fish with an unknown fate died, while maximum estimates assumed all fish with an unknown fate survived. Only one mortality could be confirmed, limiting the precision in our mortality estimates. Fish that were not detected after a certain time point (until the end of the study) were assigned an unknown fate, as the possibilities of tag malfunction, emigration from the study system, illegal harvest, predation, and missed detections could not be discerned. Tag malfunction is generally uncommon (Townsend et al. 2006) and was likely extremely low in our study given the maximum length of our monitoring period (238 d) compared with the tag battery life (441 d). Previous work with externally attached tags on adult Brown Trout *Salmo trutta* (Økland et al. 1996; Aarestrup and Jepsen 1998; Thorstad et al. 2014), Atlantic Salmon *Salmo salar* (Aarestrup et al. 2000), and steelhead (Twardek et al. 2018) suggests tag loss and tagging-related mortality are also low.

Data analysis.— Spatial analyses were conducted in ARCMAP GIS 10.5.1 for all location data. Location data were projected into Universal Transverse Mercator Zone 9 and were snapped to river lines of the Bulkley and Morice rivers using the "near" function. Distances between fish locations were quantified using the "create routes" and "distance along a route" functions in the "linear referencing tools" menu.

All statistical analyses were conducted in R (R Core Team 2015). Differences in fish length, sex ratio (% male and female), water temperature, air exposure duration, and tagging time across each capture group were evaluated using analysis of variance models (ANOVA; R function *aov*) and a chi-square test (R function *chisq.test*). Injuries, scale loss, and maintenance of the righting reflex were classified as a binomial categorical response (presence versus absence) and were compared across capture groups using chi-square tests, while differences in intermediate-term and peak migration rates across capture groups were modelled using ANOVAs. A post hoc Tukey's test for chi-square tests (R function *chisq.post.hoc*; package *fifer*) and general linear hypotheses (R function *TukeyHSD*) was used when statistically significant differences existed across capture groups. Each capture group was then analyzed separately for each response variable. All models included capture duration, water temperature, and fish length as explanatory variables, with additional variables included when relevant to the fishery. These additional variables included air exposure for models restricted to dip-netted fish and gear choice (fly versus spin) for models restricted to angled fish. Incidence of injury and reflex impairment were modelled by logistic regression (R function *glm* specifying *family = binomial*) for dip-netted fish only, as the sample sizes for these variables were too low to facilitate further analysis in the other capture groups. Logistic regression was also used to model presence above or below the falls for dip-netted fish and to evaluate the factors contributing to emigration times of dip-netted and seined fish from the falls. Emigration from the falls was treated as a factor and separated into three levels (<3, 3 to 9, and ≥10 d) to account for gaps in tracking data. These levels were ordered and modeled by ordinal logistic regression with the *rms* package (R function *lmr*). The relationship between presence above and below the falls for dip-netted fish and emigration timing was modelled using a chi-square test. Multiple linear regression (R function *lm*) was used to model immediate postrelease movement of angled fish and the intermediate-term (10–20 d postcapture) and peak migration rates of all fish. An intermediate-term migration rate model was not created for seine-caught fish due to the low sample size for this response variable.

Goodness-of-fit tests and diagnostic plots were evaluated to ensure models did not violate fundamental assumptions of each statistical test. One fish was removed from movement analyses as it died immediately after release in the dip-net fishery. Two fish that had evidence of a previous capture event (gill-net, dip-net, or general net marks) were also removed from analyses on injury, reflex ability, and movement as the influence of previous capture events could not be discerned from the most recent tagging event. Fish recaptured within any of the three fisheries following tagging and release were included in all movement analyses up until the time point that the fish was recaptured and it was then excluded from all further movement analyses. Recapture events were either observed by researchers or reported by fishers, though the true proportion of captured, tagged fish reported by fishers is unknown. Telemetry data was analyzed and interpreted under the assumption that tag loss, tag malfunction (Townsend et al. 2006), predation, and illegal harvest did not occur, and that the tagged fish behavior was reflective of the target population (Jepsen et al. 2015). Where appropriate, descriptive statistics are reported as mean ± SE. Statistical significance was considered at $\alpha < 0.05$. No adjustments were made for multiple statistical comparisons (type I; falsely rejecting null associations), as a trade-off exists between minimizing type I and II errors (Rothman 1990).

RESULTS

A total of 94 wild steelhead were captured during this study, distributed among dip-net ($n = 35$), beach-seine ($n = 25$), and angling ($n = 34$) gear. There were no significant differences in the lengths of fish (F-value = 1.26, df = 89, $P = 0.29$) captured via each method (dip net = 633 ± 16 mm, beach seine = 671 ± 21 mm, or angling = 664 ± 18 mm) or in sex ratios ($\chi^2 = 0.61$, df = 2, $P = 0.74$) across dip-netted (73% female), seined (72% female), and angled (65% female) groups. At least 13% ($n = 12$) of steelhead included in this study were captured multiple times during their spawning migrations (Table A.1 in the Appendix).

Capture Conditions

Differences in environmental and capture conditions were examined across each capture group. Water temperature was higher for fish caught by dip net (mean ± SE = 10.9 ± 0.4°C) and seine (11.6 ± 0.4°C) than by angling (9.3 ± 0.3°C), and angled fish were caught later in the season. Dip-net fish were captured and processed within 25–840 s (261 ± 42 s), while seine fish were captured and processed within 270–1,020 s (530 ± 41 s). Angled fish were caught by both fly fishing ($n = 21$) and spin-casting or centerpin angling ($n = 13$). Angling duration ranged from 85 to 835 s (230 ± 28 s) and was longer for fish caught by fly fishing (258 ± 41 s) than spin-casting or centerpin angling (185 ± 29 s). Air exposure was higher for dip-netted fish (41 ± 7 s) than seined fish (<1 s) and angled fish (4 ± 1 s). Dip-net (199 ± 14 s) and seine-caught (173 ± 15 s) fish had longer tagging times than angled fish (86 ± 4 s).

Injury

A significantly higher proportion of dip-netted fish (48%) were injured (flesh wounds, net marks, fin and tail damage) compared with seined (8%; $\chi^2 = 12.50$, df = 89, $P < 0.01$) and angled fish (3%; $\chi^2 = 17.01$, df = 89, $P < 0.01$; Figure 3A). Flesh wounds were present in 3% of dip-netted fish and 4% of seined fish. Net marks were present in 18% of dip-netted fish and 4% of seined fish, while damage to the fins and tails was also present in dip-netted (42%) but not seined fish (0%). There was no incidence of visible organ damage in dip-netted or seined fish. Angled fish had no incidences of flesh wounds, net marks, or fin damage, but one fish (3%) had an organ wound (nicked gill). Fish were hooked almost exclusively in the corner of the mouth (97%), but one fish was hooked in the interior of the mouth (3%). No fish was classified as deeply hooked in the gills, esophagus, or tongue. Neither capture duration (z-value = 0.01, df = 28, $P = 0.99$), air exposure duration (z-value = 1.33, df = 28, $P = 0.19$), water temperature (z-value = 0.90, df = 28, $P = 0.37$), or fish length (z-value = 0.97, df = 28, $P = 0.33$) had a significant influence on the occurrence of injury in dip-netted fish. The occurrence of scale loss was also significantly greater in dip-netted (73%) than seined (24%; $\chi^2 = 14.50$, df = 89, $P < 0.01$) and angled fish (18%; $\chi^2 = 24.63$, df = 89, $P < 0.01$).

Righting Reflex

A significantly lower proportion of dip-netted fish (73%; $\chi^2 = 7.91$, df = 89, $P = 0.02$) and seined fish (76%; $\chi^2 = 6.01$, df = 89, $P = 0.05$) maintained the righting reflex after capture compared with angled fish (97%; Figure 3B). There was no significant influence of capture duration (z-value = 0.17, df = 28, $P = 0.86$), air exposure duration (z-value = −1.28, df = 28, $P = 0.20$), water temperature (z-value = −1.01, df = 28, $P = 0.31$), or fish length (z-value = 1.06, df = 28, $P = 0.29$) on the presence of the righting reflex in dip-netted fish.

Behavior

Dip-netted fish were monitored for their presence above or below the falls within 24 h. Approximately 44% of dip-netted steelhead dropped back below the falls, while 12.5% of fish tagged below the falls by other capture methods migrated above and then dropped back down the falls. This estimate of 12.5% reflects the combined rates of drop-down behavior associated with tagging and natural overshoot and indicates that the rate of drop down for fish captured by dip net at the falls is much higher. Whether a fish dropped down the falls or remained above the falls was not correlated with their emigration time from Witset Falls ($\chi^2 = 0.05$, df = 2, $P = 0.98$). Steelhead that fell down the falls were captured at warmer water temperatures (11.6 ± 0.6 °C) than those that remained above (10.1 ± 0.3°C; z-value = −2.14, df = 31, $P = 0.03$). No other variables, including capture duration (z-value = −1.01, df = 31, $P = 0.32$), air exposure duration (z-value = 0.48, df = 31, $P = 0.63$), or fish length (z-value = −1.10, df = 31, $P = 0.27$), had a significant effect on the presence of steelhead above or below the falls within 24 h of capture. Approximately 48% of dip-netted steelhead left the falls (500-m displacement upstream or downstream) in 2 d or less following capture, while 38% of steelhead left between 3 and 9 d, and 14% of fish took greater than 10 d to leave the falls. Seined fish had similar emigration rates from Witset Falls, with 60% leaving in 2 d or less, 25% leaving between 3 and 9 d, and 15% taking greater than 10 d. Approximately 9% of dip-net and 12% of beach-seine steelhead did not migrate upstream of Witset Falls following capture. Immediate movement

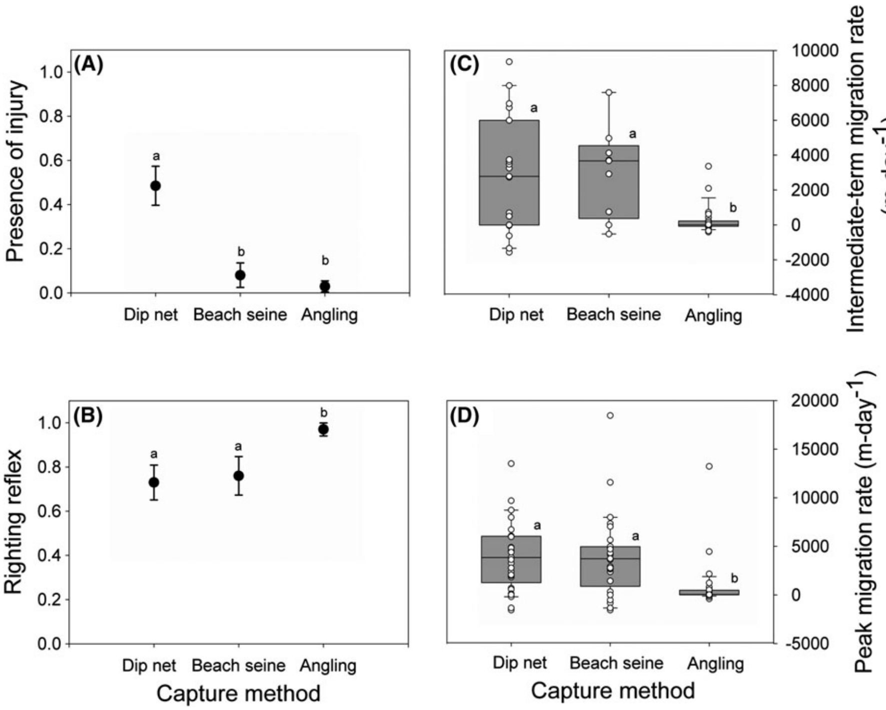

FIGURE 3. Differences in **(A)** the proportion of fish with injuries, **(B)** the proportion of fish maintaining the righting reflex, **(C)** intermediate-term migration rates, and **(D)** peak migration rates following capture and release by dip net (n = 33, 33, 19, 29, respectively), beach seine (n = 25, 25, 9, 21, respectively), and angling (n = 34, 34, 23, 32, respectively). Intermediate-term migration rate reflects the migration rate of a fish 10–20 d after capture, while peak migration rate reflects the fastest migration rate of a fish observed between successive detections. In the box plots for migration rates, the horizontal lines in each box indicate the medians, the box dimensions represent the 25th–75th percentile ranges, the whiskers indicate the 10th–90th percentile ranges, and the circles are individual data points. Within each panel, different letters denote a statistically significant difference ($P < 0.05$).

(20 min following release) of angled steelhead ranged from 28 m downstream to 33 m upstream. Immediate movement of angled fish was not significantly influenced by capture duration (t-value = 1.40, df = 13, $P = 0.19$), gear choice (t-value = −0.05, df = 13, $P = 0.96$), water temperature (t-value = 0.76, df = 13, $P = 0.46$), or fish length (t-value = −1.17, df = 13, $P = 0.26$).

Steelhead movement ranged from 38 km downstream to 145 km upstream from release sites during the study period. The migration rate of steelhead ranged from 1,562 m/d downstream to 18,460 m/d upstream. The intermediate-term (10–20 d) migration rates of dip-netted fish (2,856 ± 575 m/d; t-value = 3.53, df = 48, $P < 0.01$) and seine-caught fish (3,025 ± 518 m/d; t-value = 2.96, df = 48, $P < 0.01$) were significantly greater than that of angled fish (285 ± 144 m/d; Figure 3C). Air exposure duration (t-value = −3.16, df = 14, $P < 0.01$) and water temperature at the time of capture (t-value = −2.86, df = 14, $P = 0.01$) were significantly and negatively correlated with the intermediate-term migration rate of dip-netted fish (Figure 4A, B). Neither capture duration nor fish length had significant correlations with intermediate-term migration rates in the dip-net or angling groups (multiple linear regression; all $P > 0.05$; Table 1). Neither was there a significant influence of gear choice (fly fishing versus spinning or centerpin rod; t-value = −1.34, df = 18, $P = 0.20$) or water temperature (t-value = −0.12, df = 18, $P = 0.91$) on the intermediate-term migration rate of angled fish.

Peak migration rates were significantly faster for dip-net (4,149 ± 605 m/d) and seine (4,460 ± 880 m/d) fish than for angled fish (755 ± 419 m/d; dip net versus angled: t-value = 3.87, df = 78, $P < 0.01$; seined versus angled: t-value = 3.89, df = 78, $P < 0.01$; Figure 3C, D). The peak migration rate of dip-netted fish was negatively correlated with air exposure duration (t-value = −3.94, df = 23, $P < 0.01$) and water temperature at the time of capture (t-value = −3.14, df = 23, $P < 0.01$; Figure 4C, D), but these variables were not correlated with peak migration rates of beach-seine and angled steelhead (all $P > 0.05$; Table 2). Neither capture duration nor fish length had a significant influence on the peak migration rate of fish in any of the three capture groups (multiple linear regression; all $P > 0.05$). Gear type was not significantly correlated with the peak migration rate of angled fish (multiple linear regression; $P = 0.58$).

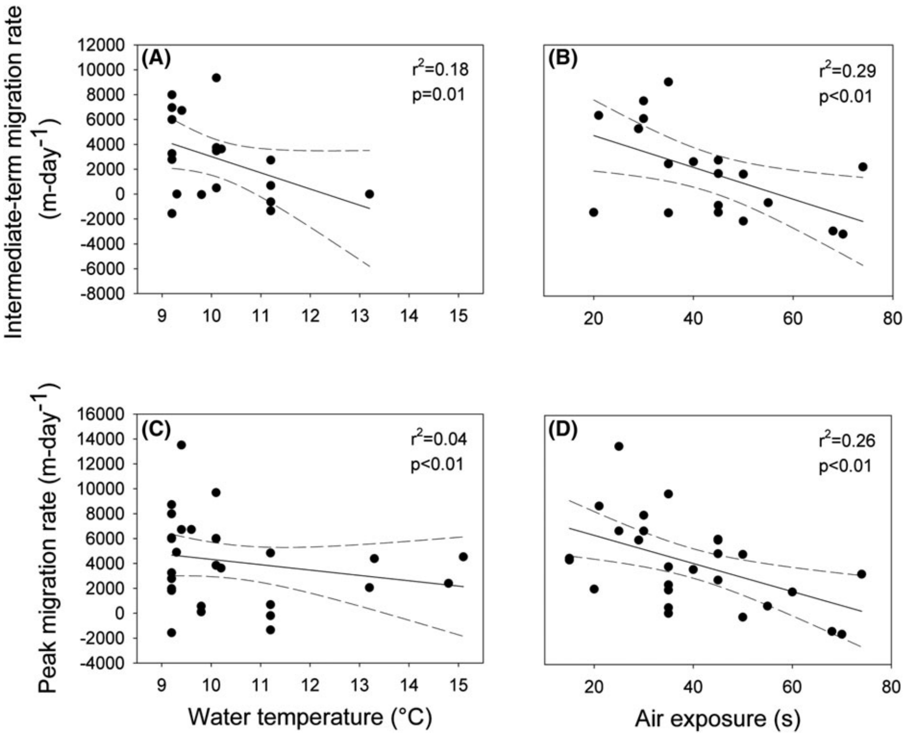

FIGURE 4. Influence of water temperature (°C) and air exposure (s) on **(A)**, **(B)** intermediate-term migration rates (*n* = 19) and **(C)**, **(D)** peak migration rates (*n* = 29) for steelhead captured by dip net. Intermediate-term migration rate reflects the migration rate of a fish 10–20 d after capture, while peak migration rate reflects the fastest migration rate of a fish observed between successive detections. The solid lines indicate the line of best fit, while dashed lines indicate 95% confidence intervals.

TABLE 1. Multiple linear regression outputs predicting intermediate-term (2-week) migration rates in steelhead (*n* = 50) after a capture event. Models were developed for each capture group and included capture duration, water temperature, and fish length as continuous variables. In the dip-net capture group air exposure was included as a continuous variable, and in the angling group gear choice (fly versus spinning or center-pin fishing) was included as a categorical variable. A model for fish captured by beach seine was not included due to insufficient sample size. Asterisks denote statistical significance.

Parameter	*t*-value	df	*P*-value
Dip net			
Air exposure (s)	−3.16	14	<0.01*
Capture duration (s)	−1.85	14	0.09
Water temperature (°C)	−2.86	14	0.01*
Fish length (fork length; mm)	0.21	14	0.84
Angling			
Capture duration (s)	−1.11	18	0.28
Gear choice	−1.34	18	0.20
Water temperature (°C)	−0.12	18	0.37
Fish length (fork length; mm)	1.12	18	0.36

Survival

The immediate mortality of steelhead was low across all capture groups, with only one dip-net fish succumbing to mortality at release. The 3-d survival of dip-net steelhead was 88–97% (*n* = 32) and was 96–100% (*n* = 23) for seine steelhead, compared with 68–100% (*n* = 31) for angled steelhead. These survival estimates exclude 9% of dip-net, 8% of beach-seine, and 9% of angled steelhead that were never detected again shortly after release as the fate of these fish is unknown. The fate of some fish could not be determined based on their movement patterns, so mortality estimates are presented as a range under the assumptions that all fish died (minimum survival) or all survived (maximum survival). It seems likely that the survival of angled steelhead would be closer to the maximum survival estimate of 100% based on the absence of deep-hooking in these fish and the high survival (98.5%) of steelhead that were not deeply hooked during a previous investigation on the Bulkley River (Twardek et al. 2018).

DISCUSSION

This study evaluated both the sublethal and lethal consequences of capture and release from three different fishery gear types on steelhead of the Bulkley River. Inherent differences existed across fisheries beyond the capture gear itself (seine versus dip net versus angling), related to the timing of operation, location, and handling conditions

TABLE 2. Multiple linear regression outputs predicting peak migration rates in steelhead (n = 80) after a capture event. Models were developed for each capture group and included capture duration, water temperature, and fish length as continuous variables. In the dip-net capture group air exposure was included as a continuous variable, and in the angling group gear choice (fly versus spinning or centerpin fishing) was included as a categorical variable. Asterisks denote statistical significance.

Parameter	*t*-value	df	*P*-value
Dip net			
Air exposure (s)	−3.94	23	<0.01*
Capture duration (s)	−1.79	23	0.09
Water temperature (°C)	−3.14	23	<0.01*
Fish length (fork length; mm)	0.06	23	0.95
Beach seine			
Capture duration (s)	−0.91	17	0.18
Water temperature (°C)	−0.28	17	0.78
Fish length (fork length; mm)	−1.30	17	0.21
Angling			
Capture duration (s)	−0.83	27	0.41
Gear choice	−0.60	27	0.58
Water temperature (°C)	−0.32	27	0.75
Fish length (fork length; mm)	0.60	27	0.56

that may have influenced our findings. When possible, we have evaluated the influence of these variables (e.g., water temperature, air exposure) and otherwise discuss the potential influence that these differences (e.g., location, timing of fishery) could be having on the response of steelhead to capture.

Fishery-Specific Differences

Fishery-specific conditions varied across capture groups, which influenced the occurrence of injury, reflex impairment, migratory behavior, and survival of migrating steelhead. Fish captured by dip net had greater incidence of injury (48%) compared with seined (8%) and angled fish (3%), which may be related to difficult handling conditions and gear type. Dip-net fish were entangled and in some cases were dropped or scraped along rocks during capture, which typically did not occur with the other capture groups. This may also explain why reflex impairment was most common for fish captured by dip net. Seine fish had the same incidence of net mark injuries (4%) as steelhead caught by seine in the Columbia River (3.5%; Rawding et al. 2016), suggesting consistently low levels of injury from this capture method. Mesh sizes were considerably smaller in the beach seine than the dip net, which prevented fish from being entangled. Injuries may have had consequences to reproductive fitness, such as delayed or inhibited maturation, that were not measured in this study (Baker et al. 2013). For instance, a study on the Wood River, Alaska, estimated that over half of the Sockeye Salmon *Oncorhynchus nerka* that reached spawning grounds with gill-net injuries failed to reproduce (Baker and Schindler 2009). If steelhead are similarly affected by net-related injuries, then the fish captured by dip net would suffer the greatest declines in reproductive fitness.

The migration rates of fish captured in nets were significantly greater than that of angled fish. Slow migration rates following catch-and-release angling is consistent with findings on Bulkley River steelhead (Twardek et al. 2018), River Alta Atlantic Salmon (Thorstad et al. 2007), and Upsalquitch River Atlantic Salmon (Tufts et al. 2000). However, given minimal physiological disturbance and the high survival of angled steelhead subject to catch and release (Twardek et al. 2018), it is likely that differences in migration rates are related to the migratory phase steelhead were undertaking at the time of capture (Karppinen et al. 2004). Steelhead captured in the dip-net and seine fisheries were sampled further downstream and earlier in the season, suggesting that they were in the active migratory phase, while those captured by angling were sampled later in the season, upstream of netting sites and in holding water typically near spawning tributaries. There are many factors that can contribute to the observed differences in injury, reflex impairment, and migration rates of fish captured in each fishery related to the inherent characteristics of the capture method, environmental variables, and intrinsic biotic factors.

Capture-Related Variables

For the dip-net and beach-seine fisheries, differences in capture duration were primarily related to differences in the time taken to process fish after netting. In both fisheries, steelhead were confined to a small, shallow area that was likely hypoxic given the moderate to high levels of excess postexercise oxygen consumption in Pacific salmon (Farrell et al. 2003; Raby et al. 2014). Air saturation went from 90% to less than 60% after 10 min in a crowded beach-seine net targeting Pacific salmon on the Fraser River, which corresponded to physiological changes in Coho Salmon (Raby et al. 2014, 2015b). Nonetheless, capture duration (i.e., time spent in these confined and likely hypoxic areas) was not correlated with immediate reflex impairment or migratory behavior in net-captured steelhead.

The duration of capture is one of the primary factors considered when evaluating the response of fish to catch-and-release angling (Brownscombe et al. 2017). Longer capture durations correspond to greater anaerobic exercise and physiological disturbance, including metabolic, acid-base, and ionic changes (Holeton et al. 1983; Wood et al. 1983), though this has not been observed in the blood physiology of angled Bulkley River steelhead (Twardek et al. 2018) nor was it correlated with reflex ability or behavior in the current study. A study on steelhead angled to exhaustion in a hatchery indicated that the proportion of offspring reaching the eye-up stage was nearly identical (86.5% versus 86.2%) for angled and control females (Pettit 1977). Nonetheless, it is likely beneficial to capture, process, and release steelhead from these fisheries promptly (Raby et al. 2014).

Following capture fish may be lifted out of the water to facilitate hook removal or processing before release. Air exposure can induce metabolic changes as cortisol, glucose, and lactate are released into the blood stream (Ferguson and Tufts 1992; Arends et al. 1999; Cook et al. 2015), although blood glucose and lactate concentrations were not different for steelhead lifted out of the water for 0, 10, or 30 s on the Bulkley River (Twardek et al. 2018). In the current study, both the beach-seine and angling fisheries had average air exposure durations of less than 5 s, which likely had little influence on the response of steelhead to capture. Steelhead captured by dip net had longer air exposures that averaged 41 s and extended up to 90 s. Air exposure was not associated with immediate impairment but was negatively correlated with the longer-term migration rates of dip-netted steelhead during the fall. Migratory delay may provide an indication of impairment, which could have energetic consequences at the time of spawning when energy is limited (Penney and Moffitt 2014; Raby et al. 2015b). Even short air exposure durations of just 10 s have resulted in decreased offspring production in Atlantic Salmon, with further reductions as the duration increased (Richard et al. 2013). Rainbow Trout angled from Idaho streams displayed lower recapture rates (a proxy for survival) as air exposures increased from 0 s (0.63) to 60 s (0.51), but these differences were not statistically significant (Roth et al. 2018). It should be noted, however, that the influence of air exposure duration cannot be completely discerned from the influence of entanglement in the dip net as both stressors occurred concurrently before transfer to the transport cradle.

Environmental Variables

Environmental conditions at the time of capture can modulate the severity of a capture event (Gale et al. 2013). Steelhead are a coldwater species that are particularly sensitive to warm water temperatures (Wade et al. 2013). Water temperature has been correlated with physiological indices of metabolic stress in angled fish, including steelhead (Twardek et al. 2018), which could impact reflex ability and behavior (Wootton 1998; McLean et al. 2016). Dropping back below the falls in dip-net-captured steelhead was more common in warmer temperatures. This fallback rate of 44% is higher than that recorded for steelhead ascending hydroelectric dams on the Columbia–Snake River system (20.5%; Keefer et al. 2008). The consequences of this fallback may be minimal, as there was no significant delay in the time to emigrate out of the Witset Falls area for fish that fell below the falls relative to those that remained above. It should be noted however that 9% of dip-netted steelhead fell down the falls and never migrated back up the falls. This behavior may reflect a stress response to dip-net capture (e.g., Mäkinen et al. 2000) or may reflect natural searching behavior that is common in anadromous salmonids (Karppinen et al. 2004; Richard et al. 2014). It was suggested that 25% of Columbia–Snake River steelhead fall backs were due to “overshoot” (Boggs et al. 2004) as they reentered tributaries below the fallback site (Keefer et al. 2008).

Temperature at the time of capture also had an influence on the intermediate-term and peak migration rates of steelhead following capture. Physiological status following capture is related to water temperature in both steelhead (Twardek et al. 2018) and Coho Salmon, though most physiological changes return to baseline levels within 24 h (Raby et al. 2015b). Steelhead caught in warmer temperatures earlier in the season would have experienced warmer temperatures following capture as well. This makes it difficult to discern whether it is indeed the temperature at the time of capture driving this relationship through an exacerbated stress response (Gale et al. 2013) or simply greater thermal exposure following capture. Accumulated thermal units have been correlated with slower migration rates in Chinook Salmon and steelhead (High et al. 2006). However, Atlantic Salmon in the Escoumins River had faster migration rates in 22°C than in 14°C (Richard et al. 2014). As water temperature was not a significant predictor of movement in angled or beach-seined fish, it is suggested that the temperature-related movement in dip-netted steelhead is a response to increased capture stress rather than accumulated thermal units.

Location-specific consequences of capture have rarely been considered in fisheries studies (but see Bass et al. 2018) despite potential influences of location on precapture physiological status and therefore the response of fish to capture. Beach seining and angling were conducted in considerably slower moving water compared with the dip netting that occurred at Witset Falls. Prior to capture in the dip-net fishery, fish would have undertaken burst swimming, which requires anaerobic metabolism (discussed in Hinch et al. 2002). This could have exacerbated the stress response to dip-net capture and resulted in increased reflex impairment and fall back in these fish (Davis 2010). Nonetheless, the longer-term migration rates of dip-net fish were similar to that of beach-seine fish, which were caught in a deep, slow-moving pool and were likely less reliant on anaerobic metabolism prior to capture. These physical differences in location are inherent to appropriate use of these gear types and would be common across all fisheries where these gears are used. In addition to the sublethal consequences of capture on steelhead migration, these capture events may also result in immediate and delayed mortality.

Survival

Survival of dip-net fish within 3 d of capture was 88–97%; seine fish survival was 96–100%. Beach-seine survival estimates for steelhead have been conducted in the Columbia River (97% survival over 11 d; Rawding et al. 2016) and Rogue River (96% survival upon release; Everest 1973) and previously at Witset Falls (78–100%; Welch et al. 2009). To date, there are no studies that have evaluated catch-and-release mortality in dip-net fisheries for adult fish.

Estimates of survival of angled steelhead 3 d after capture were imprecise (68–100%) though previous catch-and-release investigations on the Bulkley River found approximately 5% mortality over 3 d (Twardek et al. 2018). Angled fish were captured later in the season and closer to spawning sites, which generally resulted in low rates of upstream movement and uncertainty in the fate of these fish. The absence of deep hooking would suggest that mortality was likely very low (<2%) based on the reported mortality of shallow-hooked steelhead from the Bulkley River (Twardek et al. 2018). Low rates of hooking mortality in this fishery are a likely result of the angling restrictions imposed by the MFLNRORD for Skeena Region 6 that only permit the use of artificial baits on single, barbless hooks. Moreover, water temperatures during the angling season are cool, which may decrease mortality relative to other steelhead recreational fisheries (Taylor and Barnhart 1997). The average catch-and-release angling mortality rate for steelhead is low at approximately 4% (Mongillo 1984; Hooton 1987; Lirette 1988, 1989; J. O. Thomas and Associates 1995; Nelson et al. 2005; MFLNRORD, unpublished data). Nonetheless, catch-and-release regulations may be ineffective at halting population declines in the face of high angling pressure and external stressors (e.g., extreme flow events and whirling disease) as has been observed in the Rainbow Trout fishery of the Bow River, Alberta (Cahill et al. 2018). Although no whirling disease was detected in Bulkley River steelhead in 2016 (Twardek, unpublished), extreme flow events have occurred in recent years and angling effort is high (MFLNRORD 2016) indicating similar processes could be occurring on the Bulkley River.

Conclusions

Inherent differences in capture gear, handling procedures, environmental conditions, timing, and locations may exist across fisheries that can have a varying influence on sublethal stress and survival for captured fish. Steelhead captured by dip net experienced greater levels of entanglement, air exposure, and difficult handling (dropped and scraped along rocks) that likely increased the occurrence of injury and reflex impairment relative to the other capture groups. Migration rates in dip-net-captured fish tended to decrease with greater air exposure durations and warmer water temperature at the time of capture, suggesting that handling practices and capture conditions within the fishery can have sublethal consequences on steelhead migration.

Findings from our study suggest potential changes that managers can implement as part of a safe operating space approach to fisheries management (Carpenter et al. 2017). Gear restrictions could be implemented for fisheries using dip nets, such as decreased mesh sizes (Sangster et al. 1996) and the use of materials that may be less injurious to fish such as knotless rubber (Lizée et al. 2018). As fish caught by beach seine had low injury rates with 5-cm stretch mesh, using a similar mesh size may be an effective gear restriction for fisheries using dip nets. In recreational angling fisheries, managers may restrict terminal tackle to single, barbless hooks with artificial bait as we have shown over 2 years that critical hooking injuries are very low for steelhead angled with this gear (Twardek et al. 2018). Similarly, managers may consider implementing effort restrictions to reduce the total number of steelhead captured within the recreational fishery as an average of 59% of the run has been intercepted each year (1999–2015; MFLNRORD 2018). Across all fisheries, managers may consider warm-weather closures (discussed in Caissie et al. 2017) as water temperatures were correlated with migration rates in dip-netted fish and the physiology of angled fish (Twardek et al. 2018) on the Bulkley River.

Managers may also encourage the voluntary adoption of these potential gear and fishing changes (i.e., best practices; Guckian et al. 2018). Educational programs can be implemented to ensure that fishers are aware that water temperature, air exposure, and general handling practices influence the outcome of steelhead capture and release (Adams 2017). Other gear restrictions could be adopted that are better suited as voluntary “best practice” actions. For example, a water aerator (Boyd 1998) could be used during beach seining to minimize the oxygen deprivation that is associated with longer sorting times (Raby et al. 2014) and warmer water temperature. Greater communication amongst stakeholder groups may enhance responsible shared use of the resource and improve management efforts (Crona and Bodin 2006). Future work should evaluate whether there are sublethal consequences of capture and repeat capture events on reproductive fitness, such as offspring production (e.g., Richard et al. 2014).

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Appendix: Additional Data

TABLE A.1. Capture history for fish subject to multiple capture events during their spawning migrations. Previously incurred net marks could not be discerned as either gill-net, dip-net, or seine-net injuries and are classified as “Net.” The 3-d fate of the fish is assigned as alive, harvested, or unknown.

Capture event 1	Capture event 2	3-d fate
Dip net	Angling	Unknown
Dip net	Angling	Alive
Dip net	Beach seine	Alive
Beach seine	Angling	Alive
Beach seine	Dip net	Alive
Beach seine	Beach seine	Alive
Angling	Gill net	Harvested
Angling	Angling	Alive
Angling	Angling[a]	Unknown
Angling	Gill net	Harvested
Net	Angling	Alive
Net	Dip net	Alive

[a] Fish was captured by angling twice on the same day resulting in three capture events total.