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Consequences of catch-and-release angling on the physiology, behaviour and survival of wild steelhead *Oncorhynchus mykiss* in the Bulkley River, British Columbia

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A R T I C L E I N F O

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A B S T R A C T

Steelhead, the anadromous form of rainbow trout (*Oncorhynchus mykiss*), is one of the most coveted recreationally targeted salmonids worldwide, and catch-and-release (C&R) is commonly used as a conservation strategy to protect wild stocks. Nevertheless, little research has examined how wild steelhead respond to capture and handling. During a summer-run recreational fishery on the Bulkley River in British Columbia, we used non-lethal blood sampling and radio telemetry to assess the physiological stress response, post-release behaviour, and survival of wild steelhead exposed to either 0 s, 10 s, or 30 s of air exposure, over a range of water temperatures, fight times, and landing methods. Steelhead that were air exposed following landing had greater reflex impairment and moved further downstream immediately following release than fish kept in the water, though there was no observed difference in movement two weeks after capture. Overall, angled fish had significantly greater blood lactate levels than baseline levels (obtained from a subsample of fish dip netted from the river) suggesting a general stress response to angling and handling. Regardless of air exposure treatment, water temperature was positively associated with blood lactate and negatively associated with blood pH. Other variables such as fish body size (mm) and fight time (s) had little influence on any of the physiological or behavioural variables. Estimated 3-day survival of steelhead was 95.5%, with deep-hooking as the primary source of mortality. Overwinter mortality of caught-and-released fish was estimated at 10.5%, with an estimated total pre-spawn mortality of 15.0%. This study is the first to evaluate the factors that influence C&R outcomes in wild steelhead in a recreational fishery. Findings suggest that steelhead anglers should limit air exposure to less than 10 s, and that anglers should be cautious (minimize handling and air exposure) when water temperatures are warmer.

1. Introduction

Oncorhynchus mykiss are an iteroparous fish species that maintain populations with a range of life-history strategies (Moore et al., 2014). These life-history strategies are typically described in terms of the freshwater resident forms (rainbow trout) and the anadromous forms (steelhead). Unlike other iteroparous salmonids with anadromy (e.g. Atlantic salmon; *Salmo salar*), steelhead over-winter in freshwater and spawn in tributaries during the spring, prior to emigrating back to the ocean as kelts (Quinn, 2005). Their spawning migrations often span hundreds of kilometres resulting in considerable energy expenditure (94% loss in lipid content of white muscle tissue; Penney and Moffitt, 2014). This severe energy depletion coupled with down-regulation of feeding hormones during their reproductive cycle may make steelhead particularly susceptible to anthropogenic stressors that result in additional energetic costs (Fenkes et al., 2016). Previous research has highlighted the negative influences of warm water temperatures (Wade et al., 2013), habitat degradation (National Research Center (NRC, 1996), water pollution (Suttle et al., 2004) and fisheries interactions (Andrews and McSheffrey, 1976; Stewart and Lewynsky, 1988) on steelhead populations. Given the multifaceted stressors steelhead face during their upstream migration, Kendall et al. (2015) suggested the need to further evaluate the role of anthropogenic impacts (including fisheries) on steelhead.

Capture by fisheries can be one of the most severe acute stressors imposed on fish throughout their lives (Davis, 2002). Previous work

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investigating commercial net fisheries for salmon has shown significant by-catch mortality of wild steelhead following discard (Thomas and Associates LTD., 2010). Discard may also occur in recreational fisheries (typically termed catch-and-release; herein, C&R) either voluntarily or to comply with regulations (Arlinghaus et al., 2007). Comparatively little is known about recreational fisheries discard mortality (Cooke and Suski, 2005), and even less is known about the impacts of recreational angling practices on steelhead physiology, behaviour, and survival (but see Nelson et al., 2005 for the general effects of angling). Given the widespread decline and conservation status of wild steelhead populations (Gayeski et al., 2011; Good et al., 2005; Smith et al., 2000), recreational fisheries for steelhead have been established as primarily C&R in hopes of conserving wild populations. The efficacy of C&R as a conservation tool, however, is contingent on released fish surviving and incurring negligible fitness consequences (Cooke and Schramm, 2007; Wydoski, 1977).

Fish may be subject to considerable stress and even mortality during a capture event, and this may be related to environmental variables, intrinsic biotic factors (fish condition, disease presence, size, age, sex), and angler behaviour (gear choice, fight time, and air exposure; reviewed by Cooke and Suski, 2005). Prolonged fight times, air exposure, and hooking injury can lead to blood acidosis, hypercapnia, and injury, respectively (Ferguson and Tufts, 1992; Meka, 2004; Wood et al., 1983). Previous work has suggested general guidelines for anglers to adhere to including the minimization of fight times, air exposures, and proper gear choice (Brownscombe et al., 2017). Although generalities can be made, differences exist in species morphology, life-history, and surrounding environments creating the need for species- and context-specific evaluations (Cooke and Suski, 2005). Salmonid species are considered some of the most valuable and coveted species to recreational anglers, and have been subject to numerous studies assessing the extent of sublethal consequences and mortality following recreational fisheries encounters (Boyd et al., 2010; Gjernes et al., 1993; Lennox et al., 2015; Pope et al., 2007; Schreer et al., 2005). Albeit, even amongst salmonids the response to fisheries capture is consistently context- and fishery-specific (Patterson et al., 2017; Raby et al., 2015). As anglers have a considerable role on the outcome of an angling event (Cooke et al., 2017), it is relevant for recreational fisheries to have scientifically based best practices for anglers to follow to minimize harm on released fish. Despite the popularity of steelhead as a recreational fish species (Kelch et al., 2006), little to no research has evaluated the response of wild steelhead to various C&R angling practices. An exception is a study on the Chilliwack River of British Columbia which investigated the movement and survival of winter-run steelhead following catch-and-release, but focused primarily on the differences between fish of hatchery and wild origin (Nelson et al., 2005).

The objectives of this study were to evaluate the sub-lethal impacts and survival of wild steelhead following C&R angling. Steelhead were assessed for the presence of the righting reflex (an effective and non-invasive proxy for stress and mortality following fisheries interactions; Danylchuk et al., 2007b; Davis, 2010) and for physiological indicators, specifically glucose, lactate, and pH (Barton et al., 1998). A separate group of steelhead was monitored for immediate post-release movement, long-term migration rate, and mortality. It was anticipated that air exposure would impair reflexes, increase physiological alterations, and promote downstream post-release movement of angled wild steelhead. Findings from this research will help refine management strategies and identify best handling practices for wild steelhead.

2. Methods

2.1. Study site and collection methods

Steelhead were sampled from the Bulkley River, British Columbia from September 17th to November 7th, 2016. The Bulkley River is located ~250 km inland, stretching an additional 141 km to the Bulkley-Morice confluence (Ministry of Forests, Lands, Natural Resource Operations and Rural Development (FLNRORD), 2013). The Bulkley River watershed drains an area of approximately 12,000 km^2, making it the largest tributary of the Skeena River. The river is considered relatively pristine with no manmade barriers (i.e. dams) to fish migration. As a result, the river has maintained an entirely wild summer-run steelhead population averaging 21,520 (9735 to 41,428) individuals from 1999 to 2016 (Witset [formerly Witset] Mark-Recapture, 2017) and contributes greatly to the world-renowned Skeena recreational fisheries that are estimated to be worth nearly $53 million CAD annually (Counterpoint Consulting, 2008). Recreational anglers can access the river by jet boats, pontoon boats, or walk-in sites and are permitted to use both fly fishing and spin-cast equipment. Starting in 1991, the mandatory C&R of wild steelhead has become part of the B.C. FLNRORD's fishing regulations for the entire Skeena Watershed; the rule was expanded to all of British Columbia in 1997.

Steelhead were captured by approximately 30 different recreational anglers using fly fishing (spey rods, flies size #8+), spin-cast fishing (various sizes of inline spinners and artificial worms), and by centre pin (a free spooling reel, various sizes of inline spinners and artificial worms) while wading from shore. Anglers represented all levels of experience, from first time steelhead anglers to anglers that fish every day for the entire steelhead season. Most fish were captured by experienced steelhead anglers, which is representative of the general angling public of the Bulkley River. All fish were captured upstream of Witset Falls from rkm 314 to 407 (Fig. 1), using single barbless hooks as per the recreational fishing guidelines in the Skeena region (FLNRORD, 2017). Fish were landed with the assistance of another angler, who either netted the fish using a rubber or nylon landing net or grabbed the caudal peduncle of the fish (tail-grab). These conditions allowed anglers to unhook steelhead without lifting them out of the water at any point. Steelhead were selected through random stratification to be measured for blood physiology parameters, or radio-tagged following capture, thus creating two separate groups from here on referred to as the 'physiology' group and the 'movement' group, respectively.

2.2. Quantification of the angling event

For each capture event, the fight duration (s), anatomical hooking location, hook removal difficulty, water temperature (°C), fork length (cm), and sex were recorded. The fight duration was considered the time from hooking to landing by either tail-grab or landing net. Hook removal difficulty was determined by a 1–5 ordinal ranking system that reflected the effort needed by the angler or guide to remove the hook from the fish. A score of '1' indicated the hook was removed with no effort (hook fell out once the fish was landed), while a score of '5' indicated that substantial effort was needed to remove the hook (pliers were required to remove the hook). Water temperatures at the time of capture were taken using a handheld digital thermometer (Taylor Precision Digital Thermometer, #9847, Taylor USA, Oak Brook, IL, USA). Water temperature throughout the season was taken using a data logger (HOBO Water Level Data Logger, #U20L-01, Bourne, MA, USA) that recorded every 15 min. Discharge rates were taken from the Bulkley River at Smithers using Environment and Climate Change Canada's Real Time Hydrometric Data search engine.

2.3. Reflex test

A righting reflex test (equilibrium) was used as an indication of reflex ability after angling and air exposure. To assess the righting reflex, fish were flipped ventral side up and monitored for their ability to return to normal orientation within 3 s (outlined in Raby et al., 2012). To minimize handling of captured steelhead, only the righting reflex test was evaluated. This reflex is typically the one that is most "responsive" when salmonids are exhausted (Raby et al., 2012). Reflex tests were completed immediately following capture for fish that would

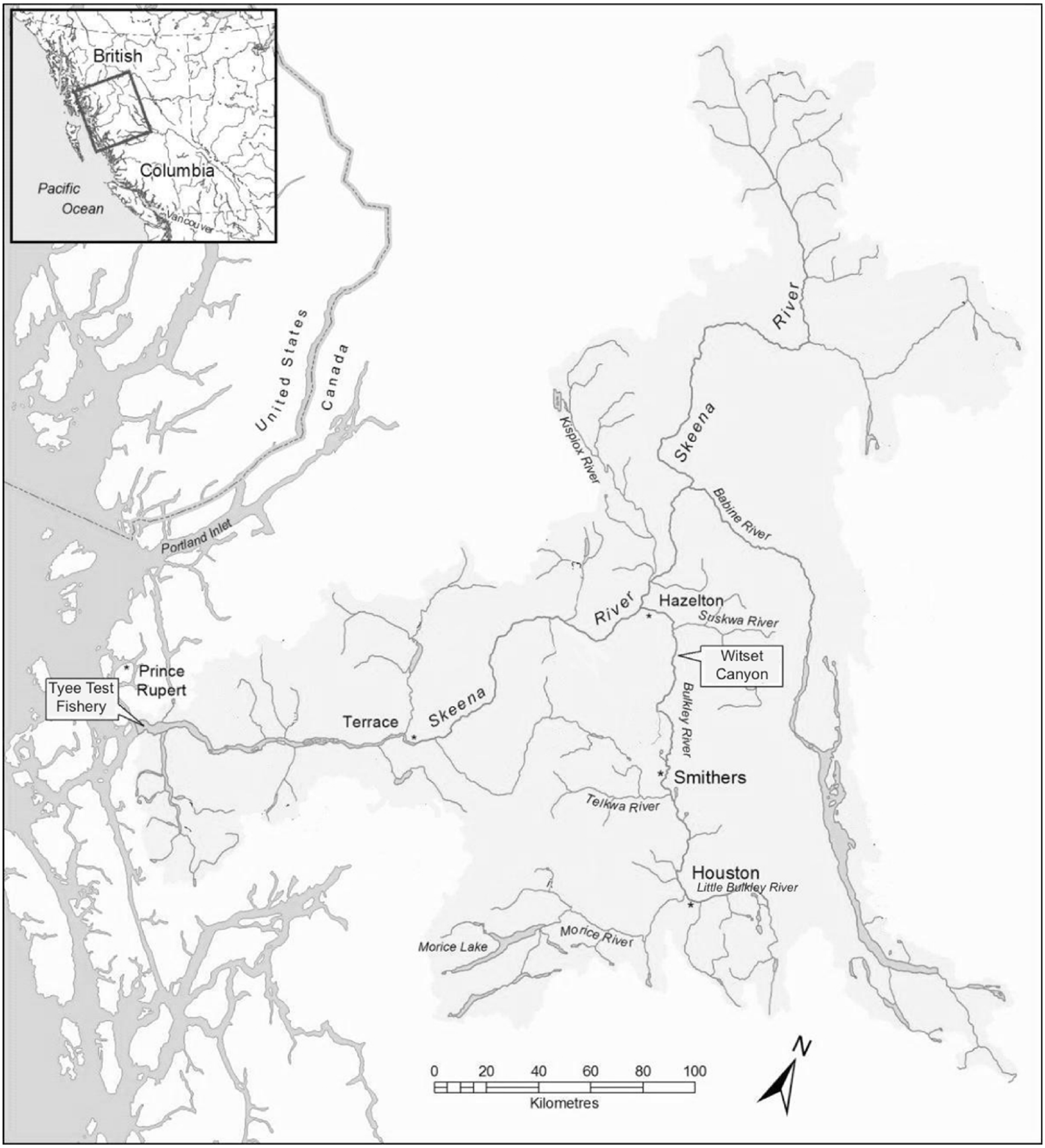

Fig. 1. A map of the Skeena watershed highlighting the Skeena, Bulkley, and Morice Rivers, and their major tributaries. Adopted from www.oceanecology.ca.

be included in the physiology group, and immediately before release for fish in the movement group due to logistical constraints.

2.4. Post-release physiology

Following landing, fish to be included in the physiology group were transferred to a recovery bag and included into one of three air exposure treatment groups; 0 s (N = 18), 10 s (N = 12), and 30 s (N = 15) by lifting the bag out of the water. Treatment groups were selected to be representational of the range of common practices; final selection was based on regional consultation (personal communication with regional anglers and guides, 2016). Fish were then held in the recovery bag for approximately 20 min to obtain elevated values for the blood physiology stress indices. It should be noted that these values peak between 5–15 min for lactate and 120–240 min for glucose in hatchery rainbow trout plasma, although glucose is still significantly elevated compared to baseline values 15 min after stress (López-Patiño et al., 2014; Perrier et al., 1978). As holding steelhead for 120 min was not feasible while working with anglers, we opted to hold fish for 20 min to capture peak lactate, and elevated glucose levels. 2 ml of blood was non-lethally sampled from the caudal vasculature using a 21 g × 1.5” needle (BD Vacutainer needles, #360213, Mississauga, ON, Canada), and a 4 mL Vacutainer (59 USP units of Lithium Heparin, Mississauga, ON, Canada). Blood was analyzed for glucose (mmol L^{-1}, Accu-Check Compact Plus, Roche Diagnostics, Basel, Switzerland), lactate (mmol L-1, Lactate Plus, Nova Biomedical Corporation, Waltham, MA, USA), and pH (HI-99161 w/automated temperature compensation, Hanna Instruments, Woonsocket, Rhode Island, USA) using point-of-care devices that have been previously validated for use on fish (Stoot et al., 2014). The stress responsive values of angled fish were compared to baseline physiology values obtained from steelhead sampled within 3 min of an acute stressor (Cooke et al., 2013; Lawrence et al., in press). This was not feasible for fish captured by angling (5 min fight times), so opportunistic sampling was completed at the Wet'suwet'en salmon fishery/steelhead mark-recapture program at Witset Falls (rkm 314). Here, steelhead captured by dip net were immediately (< 15 s) transported to the sampling trough and measured, as part of the long-term mark-recapture project (< 30 s of handling). Baseline samples were obtained between September 22–29 (8.6 ± 0.5 °C) during the final week of the Wet'suwet'en fishing operations, while samples from angled fish were obtained September 20th-October 29th, 2016 (7.0 ± 0.3 °C).

2.5. Post-release movement

Following C&R, landed steelhead included in the movement group were secured in the river in a flow through tagging trough and had a radio-transmitter (4.7 g weight in air, 220–441 day battery life, 33 pulses per minute; Series F1970, Advanced Telemetry Systems, Isanti, MN, USA) attached externally (Jepsen et al., 2015). Transmitters were attached using two stainless steel 18 Ga. surgical needles inserted into the dorsal musculature posterior to the dorsal fin. Wire attached to the tag was then threaded through the needles, and the needles were removed. The wire was then secured to the fish using steel crimps, with small plastic backing plates separating the crimps from the body of the fish to minimize tissue irritation. Fish were then included into one of three air exposure treatment groups; 0 s (N = 22), 10 s (N = 25), or 30 s (N = 21). To conduct air exposures, tagged fish were lifted out of the water for the duration of the air exposure treatment. Fish were returned to the water and were assessed for the righting reflex and released. If a fish did not swim away immediately, it was held loosely by the caudal peduncle until it was able to swim away on its own (all < 15 s). Presence of an externally-attached telemetry tag (7.0 g) had little to no influence on swimming performance or blood physiology of Atlantic salmon (450–590 mm; Thorstad, 2000) so it was expected that the tag effect (4.7 g) was negligible for the wild steelhead in our study (508–870 mm). Further, tags weighed approximately 0.1% of average steelhead body mass and were therefore well below the recommended tag to fish weight ratio of 2.0% (Smircich and Kelly, 2014).

Fish were tracked manually using a radio telemetry receiver and a 3-element Yagi antenna (Lotek Biotracker, Lotek Wireless, Ontario, Canada). Fish were located using zero-point tracking (successive gain reductions; Cooke et al., 2012), and had their positions saved using a handheld GPS instrument (Garmins GP 60 Handheld GPS Device, 010-00322-00, Garmin, Olathe, KS, USA) set to Universal Transverse Mercator projection (UTM). The location of fish 20 min after release was recorded as an indication of immediate post-release movement. Tracking was completed opportunistically by jet-boat and raft depending on the stretch of river anglers visited that day. Most sections of the river were tracked weekly (September 17th–November 6th). The entirety of the Bulkley and lower 50 km of the Morice River were tracked by raft between October 23rd–27th, 2016 and November 2nd–6th, 2016. For fish that were found twice within a 3-day period, average daily movement rate was calculated as the absolute movement rate regardless of up or downstream direction (Richard et al., 2014). A post-winter season relocation was conducted from April 6th–12th, 2017 by rafting, hiking, driving, and aircraft (Cessna-185 fixed wing telemetry attachment) to identify mortalities. Tracking spanned the entire Bulkley River study site and the lowermost 70 km of the Morice River, as well as the first 30 km of the Telkwa River (a tributary of the Bulkley River). A final tracking was completed by raft between August 21st-30th, 2017 to identify in-river mortalities and emigration rates from the 141 km study site.

Survival was estimated at four time intervals; 3-day survival, survival to winter, overwinter survival, and survival to emigration. Survival estimates were adjudged based on individual fish movement patterns (Donaldson et al., 2008). If a fish moved upstream at any point it was considered alive at that point and all previous points in time. If a fish moved upstream, and maintained its position in the river it was considered alive at that point and all previous points in time. If a fish moved multiple kilometers downstream within the first few days after capture and never moved back upstream it was considered a mortality. These mortality designations were confirmed by the presence of a radio-transmitter in the study site during tracking in August, 2017, when surviving steelhead would have emigrated to the ocean. Fish that were not located at a certain time point were considered inconclusive as the potential outcomes of long distance migrations, tag malfunction, and predation events could not be discerned. As some fish could not be designated as true mortalities (Bird et al., 2016), survival rates are presented as estimated (removes unlocated fish from the survival calculation), maximum (assumes all fish not located in the spring emigrated the system and survived), minimum (assumes all fish not located in the spring died) survival (example Gagne et al., 2017). Based on the wide-ranging movements of steelhead (including downstream movement) during migration on the Bulkley River (Kintama, 2008), it seems likely that most undetected fish would be survivors that emigrated from the study area. If they were dead fish they would have still been detected in the river after the spawning period, given that movement rates of dying/dead fish were low (< 10 km downstream).

2.6. Data analysis

Separate multiple regression models were created for the blood glucose, blood lactate, and blood pH response variables that included air exposure, fight time, sex, fork length, landing method, and water temperature as predictor variables. A logistic regression model was used to predict the presence of the righting reflex with the same variables listed above (R function *glm*, specifying *family = 'binomial'*; R Core Team 2015). Only angled fish (0, 10, and 30 s air exposure groups) were included for the reflex impairment and blood physiology candidate models as many angling-related variables were not relevant to fish collected via dip net (e.g. fight time, air exposure, landing method). In addition, only reflex assessments conducted on 'physiology' fish were included as a response variable in the righting reflex model. To compare physiology values across air exposure groups and baseline fish, a one-way Analysis of Variance (ANOVA) was conducted for each blood parameter, while the Chi-square test was used to evaluate the righting reflex.

ARCMAP GIS 10.0 was used to plot all location data onto a river line of the Bulkley and Morice Rivers, and potential spawning tributaries. Fish locations that fell adjacent to the river line were snapped to the nearest edge of the river using the 'near' function. The distances from the release sites to successive fish locations were determined using the 'create routes' and 'distance along a route' functions in the 'linear referencing tools' menu. All data were first projected into the UTM Zone_9 projection.

A multiple regression model was used to evaluate the influence of air exposure, fight time, sex, fork length, landing method, and water temperature on immediate post-release movement. The relative position of fish approximately 2 weeks after capture (10–19 days) was available for most fish and was treated as a categorical variable with three levels of either upstream (> 500 m up), no change (± 500 m), or downstream (> 500 m down) movement from the capture site. This variable was modeled using ordinal logistic regression with the *rms* package and included the same predictor variables used for the immediate movement model (R function *lmr*; R Core Team 2015). This model was created to evaluate any longer term impacts of catch-and-release practices on behaviour, and only included surviving fish. Ordinal logistic regression was used to evaluate the relationship between immediate post-release movement and relative position after 2 weeks. Reflex tests completed on 'movement' fish were used to predict future movement using one-way ANOVAs and Chi-square tests. Daily movement rate was modeled using a generalized linear model and the

Poisson distribution for right skewed count data and included average daily water temperatures and discharge as explanatory variables. Given the number of variables that varied across each angling event, we conducted Chi-square tests and ANOVAs across air exposure treatments to evaluate whether there were significant differences in fork lengths, fight times, water temperatures, anatomical hooking locations, sex proportions, capture methods, capture dates, or landing methods across air exposure treatments for both physiology and post-release movement groups. Our final models were restricted to include the variables considered most relevant to the outcome of an angling event, while minimizing the number of variables per observation (Brownscombe et al., 2017; Austin and Steyerberg, 2015). Further, variance inflation factors were used to evaluate the extent of collinearity between variables but little evidence of collinearity existed (all VIF < 3.0). Model assumptions were evaluated by analyzing diagnostic plots of residuals (standardized residuals verse theoretical quartiles, residual verses fitted values, variance of residuals, and Cook's distance). Based on Cook's distance values, and the fact that deeply hooked fish died shortly after release and floated downstream, the two deeply hooked radio-tagged fish were removed from further analyses on post-release movement. One fish that died a few days after release was only included for immediate post-release movement. One fish was dragged onto shore during capture and was removed from behavioural assessments, but was included for post-release mortality. One fish was only detected upon release, and was therefore included for the immediate movement model, but was excluded for assessment of longer-term movement and post-release mortality. An additional two fish were excluded that had faulty tags producing unreliable location data. Significant differences between factored levels were evaluated using the Tukey post-hoc test at an alpha level of 0.05.

3. Results

A total of 129 wild steelhead (687 ± 7 mm FL) were captured by fly angling (n = 92), spin-casting/centre pin angling (n = 23), and dip net (n = 14). Fight time ranged from 100 to 960 s (299 ± 15 s), and was positively correlated with the size of the fish ($p < 0.01$). Fish were primarily hooked in the corner of the mouth (61%) but were also hooked in the interior of the mouth (17%), snout (8%), tongue (4%), tail (< 1%), and under the jaw (< 1%). Seven percent of hooks fell out prior to visual assessment so no location could be determined. No fish were hooked in the gills or esophagus. Three of five fish hooked in the tongue were considered deep hooked due to the extent of bleeding from the hooking site.

3.1. Righting reflex

Presence of the righting reflex in physiology fish was significantly lower for 10 s (0.58 ± 0.15; p = 0.03, 0.01) and 30 s (0.47 ± 0.13; $p < 0.01$, < 0.01) air exposed groups, than for 0 s (0.94 ± 0.06), and baseline groups (1.0 ± 0; $\chi^2 = 17.03$, df = 3, $P < 0.01$; Fig. 2). No other variable of fork length, fight time, water temperature, sex, or landing method had a strong influence on reflex ability (df = 39, all $p > 0.05$; Table 1). Radio-tagged steelhead that failed the righting reflex test tended to have further immediate movement downstream than steelhead that passed the reflex test (F-value = 4.66, df = 65, p = 0.03). However, this reflex test was not a significant predictor of glucose (F-value = 0.11, df = 43, p = 0.74), lactate (F-value = 1.63, df = 43, p = 0.21), or pH (F-value = 1.84, df = 43, p = 0.18), or relative position after 2 weeks ($\chi^2 = 2.35$, df = 2, p = 0.31).

3.2. Physiology

The timing of blood sampling after the angling event was not significantly different (F-value = 0.92, df = 42, p = 0.92) for the 0 s (1116 ± 49 s), 10 s (1148 ± 45 s), and 30 s (1133 ± 63 s) air exposed groups. Blood samples were taken in less than 3 min for the baseline group (151 ± 24 s; N = 14). There was no significant difference in fork lengths (p = 0.31), fight times (p = 0.63), water temperatures (p = 0.15), anatomical hooking location (p = 0.22), sex proportions (p = 0.43), capture method (p = 0.80), capture date (p = 0.80), or landing method (p = 0.76) across air exposure treatments. There was no significant difference in the blood glucose levels among baseline (2.5 ± 0.3 mmol L^{-1}), 0 s (2.5 ± 0.2 mmol L^{-1}), 10 s (2.2 ± 0.3 mmol L^{-1}), and 30 s (2.5 ± 0.3 mmol L^{-1}) air exposed fish (F-value = 0.32, df = 3, p = 0.81). Blood glucose levels were significantly higher for steelhead that were tail-grabbed (2.6 ± 0.2 mmol L^{-1}) compared to those landed by net (2.2 ± 0.2 mmol L^{-1}; t-value = 2.68, p = 0.01; Table 2, Fig. 3A). Males (2.7 ± 0.1 mmol L^{-1}) also had significantly higher blood glucose levels than females (2.2 ± 0.2 mmol L^{-1}) regardless of treatment (t-value = 2.25, p = 0.03, Fig. 3B). Blood lactate levels of fish that were angled and air exposed for 0 s (5.1 ± 0.5 mmol L^{-1}; $p < 0.01$), 10 s (5.0 ± 0.4 mmol L^{-1}; p = 0.01), or 30 s (5.3 ± 0.4 mmol L^{-1}; $p < 0.01$) were significantly higher than baseline lactate levels (3.0 ± 0.4 mmol L^{-1}). There was no significant difference in blood lactate levels among air exposure groups (F-value = 0.09, df = 42, p = 0.92, Table 2, Fig. 4A). Blood lactate was positively correlated with water temperature (t-value = 2.64, df = 37, p = 0.01; Table 2, Fig. 5A). There was no significant difference in blood pH between the baseline (7.40 ± 0.03), 0 s (7.53 ± 0.04), 10 s (7.57 ± 0.03), or 30 s (7.46 ± 0.05) air exposure groups (F-value = 2.76, df = 3, p = 0.05, Fig. 4C), although pH was negatively correlated with water temperature (t-value = −3.52, df = 37, $p < 0.01$; Table 2, Fig. 5B).

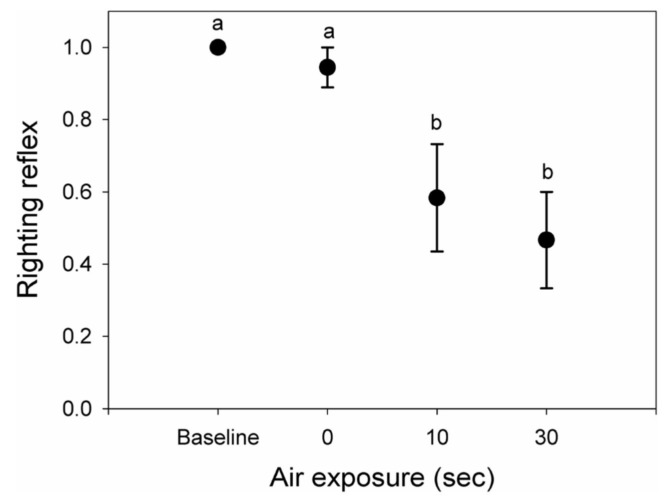

Fig. 2. Presence of the righting reflex in baseline (N = 14), 0 s (N = 18), 10 s (N = 12), and 30 s (N = 15) air exposed steelhead following angling. Different letters denote a significant difference ($p < 0.05$).

Table 1
Logistic regression output predicting presence of the righting reflex in steelhead (n = 45) immediately after an angling event. The model includes air exposure (s), sex, and landing method as categorical variables. Fight time (s), fork length (mm), and water temperature (°C) were included as continuous variables. Significant variables are emphasized with boldface font.

Parameter	Chisq	df	P-value
Air exposure	**10.42**	**39**	**< 0.01**
Fight time (s)	1.82	39	0.18
Sex	1.23	39	0.27
Fork length (mm)	0.80	39	0.37
Landing method	2.33	39	0.13
Water temperature (°C)	0.82	39	0.36

Table 2
Multiple regression model output predicting steelhead (n = 45) blood glucose, lactate, and pH after approximately 20 min of holding following the angling event. The model includes air exposure (s), sex, and landing method as categorical variables. Inferences for factors are presented relative to reference levels, which were 0 s for air exposure, female for sex, and netted for landing method. Fight time (s), fork length (mm), and water temperature (°C) were included as continuous variables. Significant variables are emphasized with boldface font.

Variable	Glucose			Lactate			pH		
Parameter	Estimate ± SE	t-value	p	Estimate ± SE	t-value	p	Estimate ± SE	t-value	p
(Intercept)	0.44 ± 1.67	0.26	0.79	**6.16 ± 2.91**	**2.12**	**0.04**	**7.69 ± 0.29**	**26.93**	**< 0.01**
Air exposure: 10 s	−0.35 ± 0.33	−1.06	0.29	0.39 ± 0.58	0.68	0.50	−0.02 ± 0.06	−0.29	0.77
Air exposure: 30 s	−0.02 ± 0.32	−0.05	0.96	0.14 ± 0.55	0.26	0.80	−0.06 ± 0.05	−1.19	0.24
Fight time (s)	0.01 ± 0.01	−0.30	0.77	0.01 ± 0.01	1.25	0.22	−0.01 ± 0.01	−0.09	0.93
Sex: Male	**0.62 ± 0.28**	**2.25**	**0.03**	−0.34 ± 0.48	−0.71	0.48	−0.01 ± 0.05	−0.21	0.83
Fork length (mm)	0.01 ± 0.01	0.10	0.92	−0.01 ± 0.01	−2.00	0.05	−0.01 ± 0.01	1.14	0.26
Landing method: Tail-grab	**0.88 ± 0.33**	**2.68**	**0.01**	0.46 ± 0.57	0.81	0.42	−0.04 ± 0.06	−0.63	0.53
Water temperature (°C)	0.18 ± 0.10	1.87	0.07	**0.46 ± 0.17**	**2.64**	**0.01**	**−0.06 ± 0.02**	**−3.52**	**< 0.01**

3.3. Post-release movement

The average tagging time from landing to tag attachment was 283 ± 16 s, and did not differ significantly between treatments (F-value = 1.67, df = 64 p = 0.20). There was no significant difference in fork lengths, fight times, water temperatures, anatomical hooking location, sex proportions, capture method, capture date, or landing method, across air exposure treatments (all $p > 0.05$). Movement of fish 20 min after release (immediate post-release movement) ranged from 149 m downstream to 99 m upstream. Fish air exposed for 10 s (−13.8 ± 7.2 m; movement t-value = −2.64, p = 0.01) and 30 s (−14.6 ± 4.6 m; t-value = −2.47, p = 0.02) moved downstream significantly further than 0 s fish (8.8 ± 6.3 m) during their immediate post-release movement (Table 3, Fig. 6). No other variables (fight time, landing method, sex, fork length, water temperature) had a significant influence on immediate movement following release (Table 3). Long-term (7 month) migration of steelhead ranged from 11.3 rkm downstream to 60.1 rkm upstream. The relative position of steelhead after 2 weeks was not significantly influenced by air exposure (s), fight time (s), sex, fork length (mm), landing method, or water temperature (Table 3; Fig. 7). Immediate post-release movement was not significantly correlated with the relative position of steelhead after 2 weeks (F-value = 1.00, df = 51, p = 0.38).

The average daily movement rate of fish during the fall was significantly influenced by mean daily water temperature (z-value = −43.36, df = 118, $p < 0.01$), and tended to increase from 4.5 to 6.5 °C and remain low and constant from 6.5 to 11.7 °C (Fig. 8). Average daily movement rate also had a significant relationship with mean discharge ($m^3 s^{-1}$; z-value = 5.14, df = 118, $p < 0.01$; Fig. 8), and appeared to peak at intermediate discharge rates.

3.4. Survival

Steelhead survival within the first 3 days of capture was estimated at 95.5% (N = 67). Estimated steelhead survival to winter was slightly lower than 3-day survival at 94% (N = 67). Steelhead overwinter survival was estimated at 85% with a maximum survival of 87% and a minimum survival of 75.0%. Similarly, emigration from the study site following spawning was estimated at 85% with a maximum emigration rate of 87% and a minimum estimate of 75%.

4. Discussion

4.1. Angling-related factors

During an angling event fish are forced to exercise that requires the use of anaerobic metabolism (Ferguson and Tufts, 1992). Longer angling durations (fight times) typically increase blood acidosis as secondary metabolites such as lactate are produced and free protons (H+) accumulate in the blood stream (Milligan and Wood, 1986; Wood, 1991). Indices of metabolic stress (glucose, lactate, pH) were not influenced by fight times in the steelhead caught-and-released on the Bulkley River, but blood lactate values were significantly greater in fish that were angled compared to baseline levels. This result is consistent with Meka and McCormick (2005), who found little relationship between blood glucose and fight time, but found lactate values to be

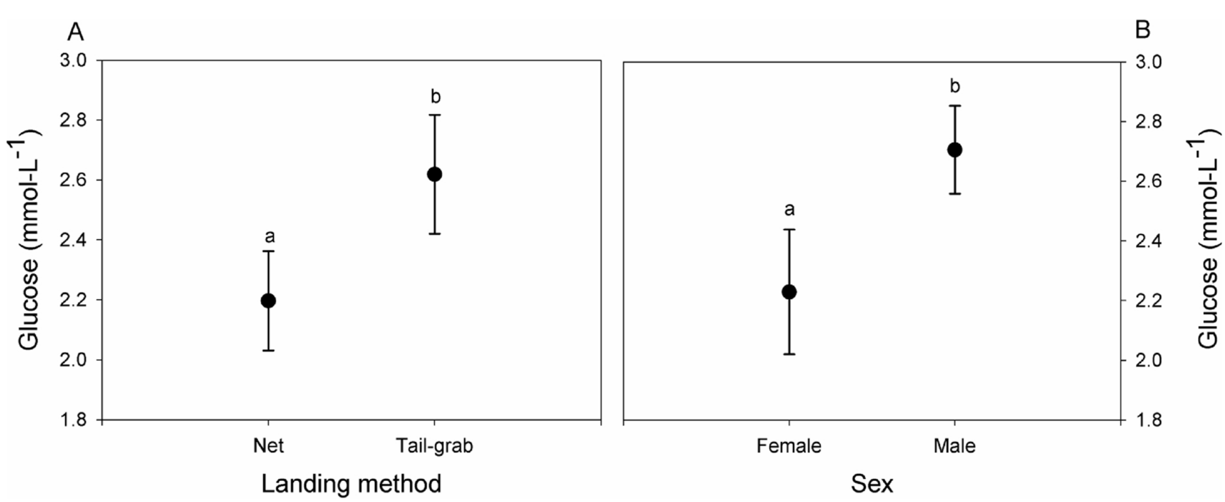

Fig. 3. Mean blood glucose levels of wild steelhead that were angled and A) landed by net (n = 19), or tail-grab (n = 26) B) female (n = 25), or male (n = 20). Blood samples were taken approximately 20 min after angling. Different letters denote a significant difference ($p < 0.05$).

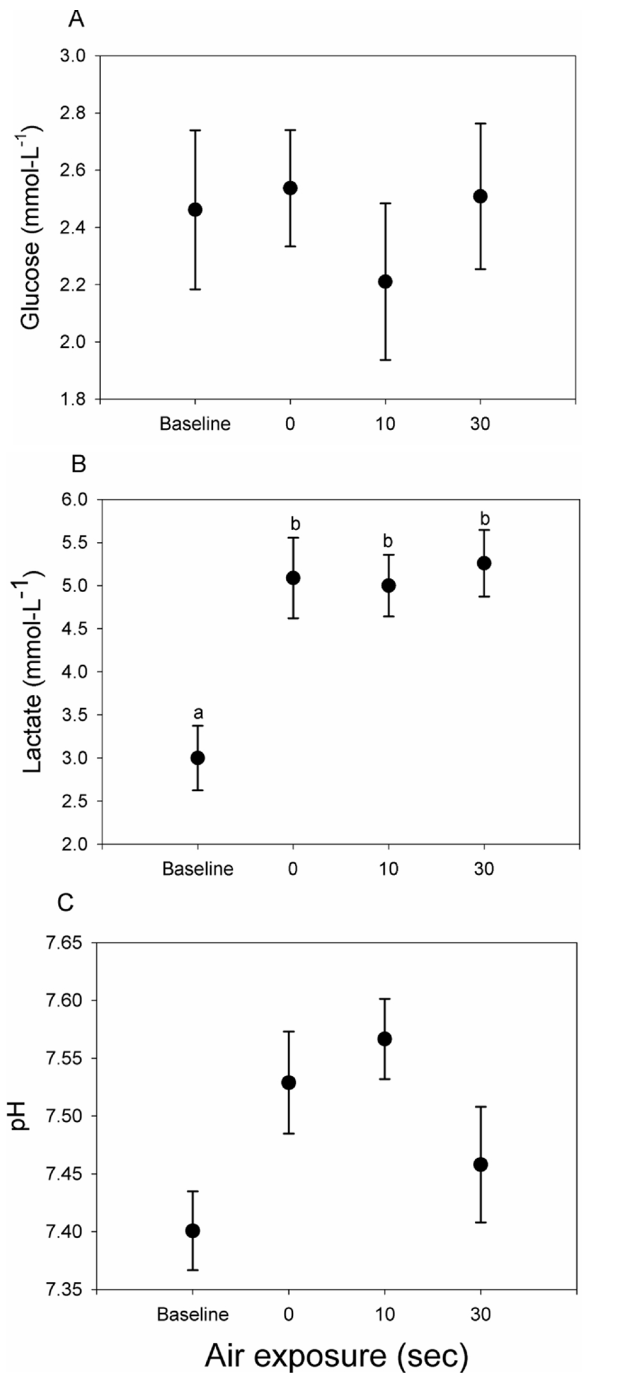

Fig. 4. Blood parameter values of air exposed steelhead following angling and approximately 20 min of holding. A) Blood glucose levels of baseline (n = 14), 0 s (n = 18), 10 s (n = 12), and 30 s (n = 15). B) Blood lactate levels of baseline (n = 14), 0 s (n = 18), 10 s (n = 12), and 30 s (n = 15). C) Blood pH of baseline (n = 14), 0 s (n = 18), 10 s (n = 12), and 30 s (n = 15). Different letters denote a significant difference ($p < 0.05$).

greater in wild *O. mykiss* experiencing extended (> 2 min) angling events. Fight times also had little influence on immediate movement, or migration rate, suggesting that steelhead are relatively resilient to angling-induced exercise. This resilience likely stems from their capacity to complete several hundred-kilometer freshwater migrations (Penney and Moffitt, 2014), while burst swimming to traverse high velocity flow segments (waterfalls, rapids, creeks). Relative to other anadromous salmonids, steelhead are considered strong swimmers with the highest burst velocity (m/s), prolonged velocity (m/s) and maximum jumping

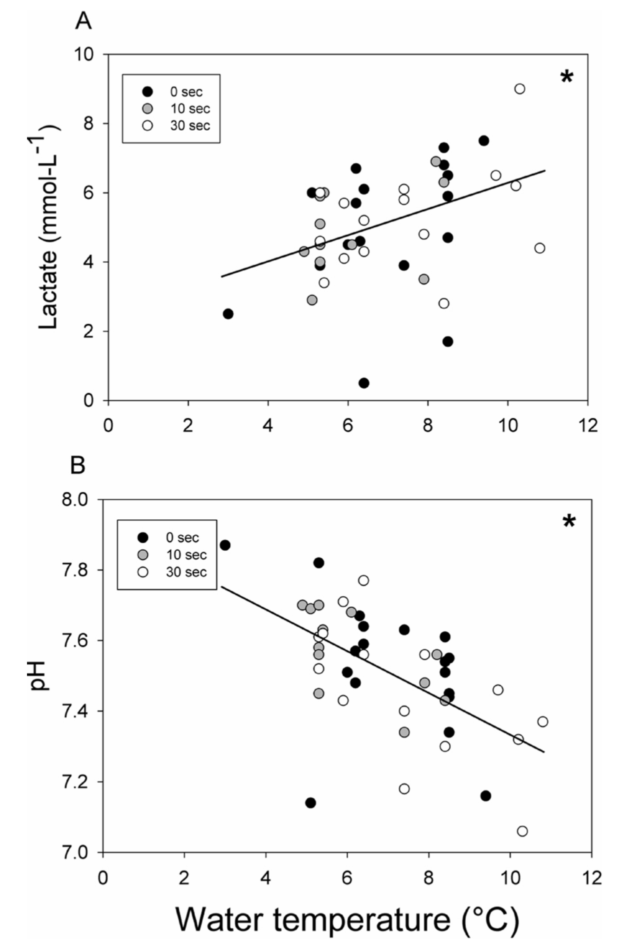

Fig. 5. The relationship between water temperature (°C) and A) blood lactate levels and (B) blood pH of steelhead following angling and approximately 20 min of holding (n = 45). Asterisks denote a significant relationship between parameters ($p < 0.05$).

height (m; Reiser et al., 2006). It is possible however, that there were other sub-lethal consequences of exercise that were not measured in this study. However, offspring survival to the eyed egg stage in hatchery steelhead did not differ greatly between steelhead that were angled and released compared to controls (Pettit, 1977).

Following exercise, steelhead in our study were landed by a fishing net designed for anglers or by hand (tail-grab). Few studies consider landing method as a potential contributor to angling-related outcomes, yet the steelhead in our study had greater blood glucose levels when tail-grabbed. Glucose and other carbohydrates are not major sources of energy in the white muscle of salmonids (Brett, 1995). Nonetheless, glucose has been shown to respond to acute stressors such as stocking density and hypoxia in farmed rainbow trout (Polakof et al., 2012). Landing by tail-grab resulted in longer fight times than netting, but the increase in glucose was not influenced by fight time, suggesting it was likely greater handling stress that resulted in the elevated glucose (Liu et al., 2014).

Air exposure is an angling-related stressor that occurs in virtually all recreational fisheries even though in most cases it can be avoided. Immediately following the angling and air exposure event, fish are subject to decreased pH in the blood as CO_2 and additional lactate accumulate, and the bloods ability to retain oxygen declines by over 80% (Ferguson and Tufts, 1992). It is suggested that intracellular acidosis of the muscles is responsible for mortality within the hours following exhaustive exercise and air exposure (Wood et al., 1983). The sensitivity of fish to removal from the water is highly dependent on both the species and environmental conditions (e.g. water temperature;

Table 3
Multiple regression model output predicting immediate post-release movement (n = 67), and 2-week relative position of steelhead (n = 54). The model includes air exposure (s), sex, and landing method as categorical variables. Inferences for factors are presented relative to reference levels, which were 0 s for air exposure, female for sex, and netted for landing method. Fight time (s), fork length (mm), and water temperature (°C) were included as continuous variables. Significant variables are emphasized with boldface font.

Variable	Immediate post-release movement			2-week relative position		
Parameter	Estimate ± SE	t-value	P	Estimate ± SE	t-value	P
(Intercept)	3.41 ± 40.83	0.08	0.94	–	–	–
Air exposure: 10 s	**−24.10 ± 8.91**	**−2.64**	**0.01**	0.03 ± 0.67	0.05	0.96
Air exposure: 30 s	**−23.95 ± 9.60**	**−2.45**	**0.02**	0.25 ± 0.74	0.33	0.74
Fight time (s)	0.01 ± 0.03	0.03	0.71	−0.01 ± 0.01	−0.85	0.40
Sex: Male	−5.78 ± 7.77	−0.74	0.46	−0.77 ± 0.57	−1.34	0.18
Fork length (mm)	0.02 ± 0.06	0.31	0.76	0.01 ± 0.01	0.08	0.94
Landing method: Tail-grab	−9.61 ± 9.29	−1.03	0.31	0.19 ± 0.70	0.27	0.79
Water temperature (°C)	−0.64 ± 1.59	−0.41	0.69	0.20 ± 0.39	1.78	0.08

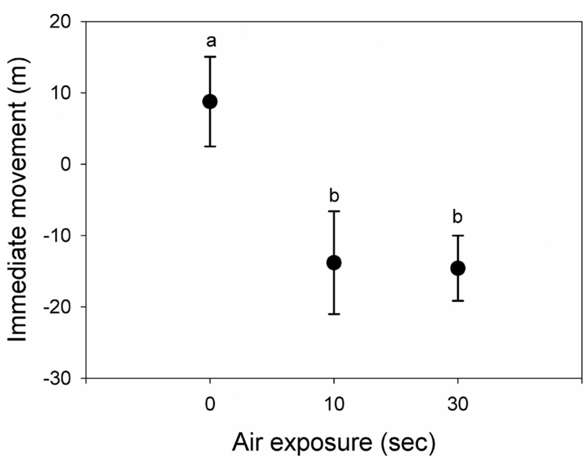

Fig. 6. Immediate post-release movement of steelhead following angling and air exposures of 0 s (n = 22), 10 s (n = 25), and 30 s (n = 21). Different letters denote a significant difference ($p < 0.05$).

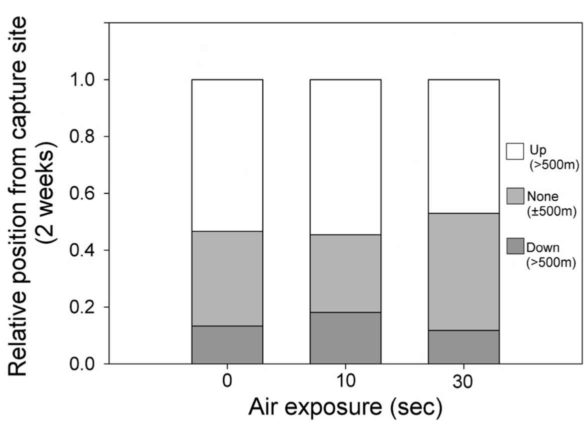

Fig. 7. The 2-week relative position of steelhead following angling and air exposures of 0 s (N = 15), 10 s (N = 22), and 30 s (N = 17). Relative positions of each fish were categorized 2 weeks after capture as down (> 500 m movement downstream of the capture site; dark grey), none (less than 500 m movement from the capture site; grey), up (> 500 m movement upstream of the capture site; white).

Cook et al., 2015; Gingerich et al., 2007). For example, black bass *Micropterus* spp. can survive 10-min air exposure periods (White et al., 2008), while hatchery rainbow trout have shown considerable mortality after just 30 and 60 s air exposures in controlled settings, albeit those fish were also cannulated (Ferguson and Tufts, 1992).

In addition to physiological stress, air exposure can also result in behavioural changes. The steelhead in our study that were air exposed for 10 and 30 s had greater immediate post-release fallback and reflex impairment than fish kept wet. Similar results have been observed in brook trout (*Salvelinus fontinalis*; Schreer et al., 2005), coho salmon (*Oncorhynchus kisutch*; Raby et al., 2012), and bonefish (*Albula vulpes*; Danylchuk et al., 2007a) that had impaired swimming capabilities immediately after short air exposures. This immediate fallback may have been greater due to the additional stress associated with the tagging procedure, but evaluation of similar tagging procedures on Atlantic salmon suggested little difference in blood physiology or short-term swimming performance compared to untagged controls (Thorstad, 2000). Although these differences in immediate movement are likely minimal on the scale of a several hundred kilometer migration, they still provide an indication of acute post-release impairment over a short-term period, similar to other immediate measures such as the reflex action mortality predictors (RAMP; Davis, 2010). Impairments from air exposures appear to return to normal over longer-term monitoring periods as air exposure was not related to relative position after 2 weeks in steelhead. In addition, fish that fell back further immediately after capture had no changes in their relative position after 2 weeks compared to fish that held position or moved upstream after release. It should be noted that air exposures could have had sub-lethal effects on steelhead that were undetected based on their movement. Richard et al. (2014) found no relationship between air exposures of 0–30 s and movement in wild Atlantic salmon but found that air exposures of just 10 s decreased offspring production, with even greater reductions as air exposure duration increased (Richard et al., 2013). As C&R practices were highly responsible in the Bulkley River, it is likely that environmental and intrinsic factors may have had greater influences on physiology and movement.

4.2. Environmental factors

Temperature is often considered the 'master factor' for fishes due to its highly influential role on physiological processes (Brett, 1971). As temperatures increase, physiological indices of stress such as glucorticoids also tend to increase (Barton, 2002; Wendelaar Bonga, 1997). As a result, water temperatures have been a major consideration in C&R studies. A meta-analysis on the capture and release of fish indicated that warmer water temperatures increased sub-lethal stress and/or mortality in 70% of reported articles (Gale et al., 2013). For Bulkley River steelhead, water temperature at the time of capture had a positive correlation with blood lactate and negative correlation with blood pH. Numerous C&R studies conducted on wild and hatchery rainbow trout have found greater stress (Kieffer et al., 1994; Meka and McCormick, 2005; Wydoski et al., 1976), impaired behaviour (Simpkins et al., 2004), and enhanced mortality rates (Dotson, 1982; Schisler and Bergersen, 1996) with warmer water temperatures. Steelhead angled in 8–23 °C water had a mortality rate of 9.6% approximately 36-h post-

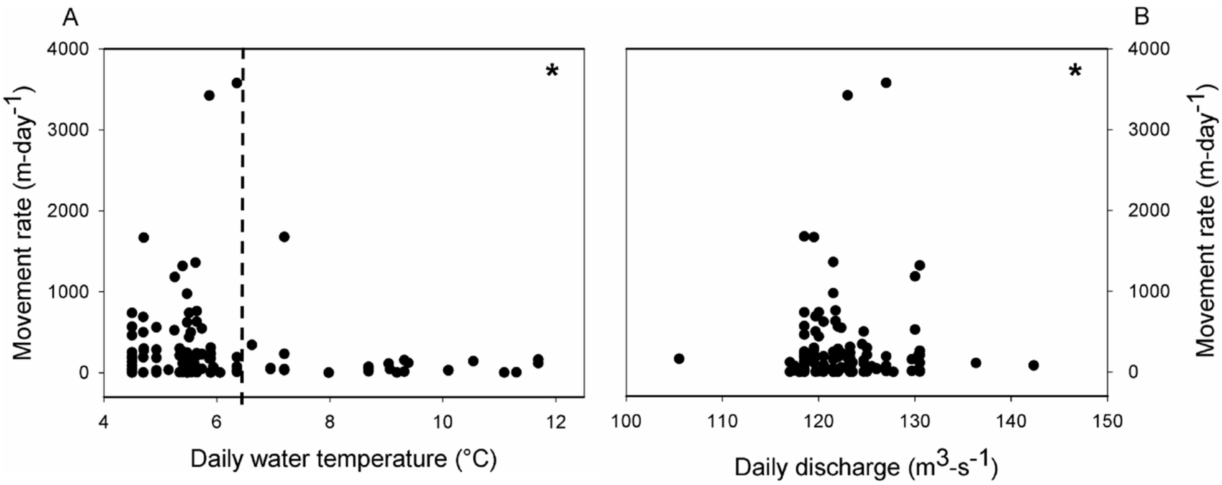

Fig. 8. The relationship between average daily movement rate and (A) average daily water temperature (°C) and (B) average daily discharge of steelhead following angling (n = 121). The dashed line in (A) indicates the location of 6.5 °C, a potential thermal threshold to movement. Asterisks denote a significant correlation ($p < 0.05$).

release, with 83% of mortalities occurring in temperatures above 21 °C (Taylor and Barnhart, 1997). This sensitivity to warmer water temperature, may be particularly salient in the face of global climate change. Neither reflex impairment, nor immediate post-release movement was affected by water temperatures. This suggests that immediate behavioural and reflex impairment may be driven primarily by the angling-related factors discussed previously. Water temperatures also appear to be important in the daily movement of steelhead.

Water temperatures were correlated with the average daily movement rate of steelhead during the fall, with movement considerably higher from 4.5 to ~6.5 °C, compared to 6.5 to 12 °C. Modeling suggested that stocked steelhead movement increases past a threshold temperature averaging 3.8 °C in Lake Michigan tributary streams (Workman et al., 2002). While Columbia-Snake River steelhead (wild and hatchery) halted their upstream movement at 4 °C and re-initiated upstream movement at about 7 °C, with potential impacts of both photoperiod and discharge (Keefer et al., 2008). Perhaps most relevant, Skeena River (mainstem of the Bulkley River) wild steelhead resumed migrating at temperatures of 2–5 °C (Lough, 1980), suggesting that Bulkley and Skeena River steelhead may have similar temperature thresholds. Average daily movement was also correlated with average daily discharge, with movement appearing to peak at approximately 120 $m^3 s^{-1}$ and 130 $m^3 s^{-1}$. Similarly, Atlantic salmon movement was also significantly influenced by both water temperature and discharge (negative correlation), but not C&R (Richard et al., 2014). Although environmental factors such as temperature and discharge can be important determinants of fish physiology and movement, intrinsic biological properties related to the individual can also be highly influential.

4.3. Intrinsic biotic factors

Intrinsic biotic factors such as size and sex can have impacts on fish physiology and movement during migration (Jeffries et al., 2014; Penney and Moffitt, 2014). Although there was no difference in blood lactate and pH between sexes, males had significantly higher blood glucose levels than females. Previous work on juvenile chinook salmon indicated that males had greater levels of plasma glucose and cortisol following 30-day exposure to mill effluent (Afonso et al., 2003). However, the angling-related stressors (aside from landing method) had little influence on blood glucose values, suggesting values observed here may be similar to their free-swimming physiological levels during migration, rather than a response to the acute angling stressor. Penney and Moffitt (2014) found that sexually mature steelhead males had greater protein content than females, suggesting differences in energy allocation prior to reproduction. It is therefore possible that males rely more on glycogen/glucose as an energy source, though the contribution of carbohydrates to energy in salmonids is generally considered low (Brett, 1995; Polakof et al., 2012). In Bulkley River steelhead, sex did not predict migration rate. Sex also had little influence on the movement of wild rainbow trout during their spawning migrations in Tongariro River, New Zealand, migration rate of caught and released Atlantic salmon in the River Klaralven, Sweden (Dedual and Jowett, 1999; Hagelin et al., 2016), or spawning success of Chilliwack River steelhead (Nelson et al., 2005). For the steelhead in our study, fork length showed no relationship with any of the blood physiology, or movement variables. Although size was not a predictor of migration distance in Bulkley River steelhead, it may have advantages for caught-and-released fish during kelt emigration, when larger sized individuals have higher protein content and energy density (Penney and Moffitt, 2014).

4.4. Survival

Steelhead survival within the first three days and several weeks following C&R was high at an estimated 95.5, and 94.0% respectively. Two fish that were deeply-hooked appeared to die within the first three days of capture, while one other fish that was air exposed for 30 s seemed to die shortly after three days. Deep-hooking rupturing vital organs (tongue) was the primary source of short-term mortality for wild steelhead captured and released on the Bulkley River. The rate of deep-hooking mortality was 3.0% which is comparatively low relative to the average hooking mortality of 16% estimated across the Salmonidae (Hühn and Arlinghaus, 2011). *O. mykiss* alone have been subject to countless C&R evaluations with hooking mortality estimates ranging from 0 to 88.5% depending on the hook type, use of bait, fish length, and water temperature (Hühn and Arlinghaus, 2011). Immediate hooking mortality estimates for bait-angled steelhead range from 0.31 to 11.00% with a total mean across studies of 4.06 ± 0.26% (Hooton, 1987; Lirette, 1988, 1989; Ministry of Lands, Forestry, and Natural Resources, unpublished data; Mongillo, 1984; Nelson et al., 2005; Thomas, 1995). These estimates are likely an underestimate of total C&R mortality as delayed mortalities were not accounted for. Nelson et al. (2005) provides the most comparable C&R evaluation as the wild steelhead captured were of similar size (782–940 mm vs. 508–870 mm), and water temperatures were similar in range (4.0–7.0 °C vs. 4.5–11.7 °C), and had a correspondingly similar 3-day mortality of 4.8% vs. 4.5% in our study. The high level of survival to emigration (85%) for steelhead in the Bulkley River recreational fishery could, in part, be attributed to the strict angling regulations imposed on terminal tackle that have historically been associated with greater hooking mortality (Hooton, 2001).

Anglers fishing on the Bulkley River, B.C. are restricted to C&R only using single, barbless hooks, without the use of natural baits (B.C. Ministry of Forests, Lands, and Natural Resource Operations, 2017). Alternative hook types such as treble hooks are typically assumed to cause greater anatomical damage and mortality although evidence suggests little difference compared to single hooks (Bartholomew and Bohnsack, 2005; Kerr et al., 2017). Barbed hooks however, have been shown to increase hooking injury in wild rainbow trout compared to barbless hooks (Meka, 2004; but see DuBois and Kuklinski, 2004). The use of live-bait is also generally implicated with higher rates of deep-hooking in steelhead (Hooton, 2001). Live bait provides both visual and chemical stimuli that excite the central nervous system and increase feeding behaviour (increased swimming and biting/snapping actions) in farmed rainbow trout that feed using both visual and olfactory systems (Valentinčič and Caprio, 1997). Live bait angling in an Idaho stream resulted in 17% of hatchery-reared rainbow trout being hooked in the gills or esophagus and a 16% mortality rate (Schill, 1996), while stocked rainbow trout angled by live bait in a South Carolina reservoir had 39% hooking mortality, compared to just 5% mortality for fish caught by artificial bait (Barwick, 1985). Cool water temperatures (4.5–12 °C) during the angling season could also be maintaining high pre-winter survival of steelhead in the Bulkley River. Wild rainbow trout captured at maximum daily water temperatures greater than 23 °C had up to 16% mortality while mortality on days with maximum temperatures of 20.8 °C was 0% (Boyd et al., 2010).

Mortality of caught-and-released steelhead over-winter was approximately 10.5% (one of these appeared to die several weeks after capture but prior to the onset of winter). This rate is consistent with the 11% over-winter mortality of Sustut river steelhead, (Skeena system), and lower than the 18–38% mortality of Columbia-Snake River steelhead prior to spawning (Keefer et al., 2008). Survival to spawning was higher in Chilliwack River wild winter-run steelhead Chilliwack River steelhead at 95% (Nelson et al., 2005) comapred to the 85% pre-spawn survival for steelhead in the Bulkley River though Bulkley River fish travel significantly further inland and have to survive several extra months in freshwater. Our estimates are based on the assumption that there was no tag loss throughout the 7-month study period. Mortality estimates may therefore include any fish that shed their tags throughout their migration, causing the tag to remain stationary within the river. However, based on the high number of fish observed to emigrate from the river, it is clear that tag loss was not common. Previous work with externally attached tags on adult brown trout (Thorstad et al., 2014; Økland et al., 1996; Aarestrup and Jepsen, 1998) and Atlantic salmon (Aarestrup et al., 2000) in low-vegetation rivers (similar to the Bulkley) suggests little to no tagging-related mortality or tag loss. Although mortality related to deep hooking can be directly attributed to the angling event, other mortalities may also be partly explained by the stress imposed during catch-and-release. Of the 7 non-deeply hooked fish that died, some were subject to an extreme component of an angling event that may explain their delayed mortality. One dead fish was air exposed for 30 s, one was fought for nearly 15 min and air exposed for 30 s, one was caught at the upper temperature limit for our study (13 °C), and one was caught at the upper temperature limit and dragged onto shore during capture. Despite a low number of mortalities, they provide some evidence that various components of an angling event may contribute to long-term survival. Although precautious angling restrictions and cool water temperatures during the majority of the angling season are likely reducing short-term mortality of steelhead in the Bulkley River C&R recreational fishery, it is clear that sub-lethal stress still occurs as a result of other angling-related factors.

5. Conclusions

Angling-related factors such as air exposure, increased reflex impairment and immediate downstream movement, while angling in general increased blood lactate values compared to baseline levels. None of the angling-related variables had any apparent long-term consequences on the migration rate, or pre-spawn distances to potential spawning sites. It is still possible however, that angling-related variables could have sub-lethal impacts at the time of spawning. Water temperature had a strong correlation with metabolic indices of anaerobiosis (lactate and pH) and was correlated with average daily movement rates during fall migration. Findings from this study suggest the C&R regulations on the Bulkley River are an effective conservation strategy for steelhead given high post-release survival to emigration (85–87%). The minimal amount of short-term mortality we observed tended to be associated with deep hooking to the tongue. Results from this study suggest that anglers should limit air exposure to less than 10 s, and that anglers should be conscious of water temperature while they are angling. We will communicate these findings to the Bulkley River angling community based on their existing perceptions and knowledge on catch-and-release angling for steelhead (Guckian et al., 2018), in partnership with Keepemwetfishing, an emerging social brand to communicate best angling practices (Danylchuk et al., 2018). Fisheries managers may consider implementing a regulation similar to Washington that prohibits the removal of wild steelhead and salmon from the water.

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