



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

W.M. Twardek^{a,*}, T.O. Gagne^b, L.K. Elmer^a, S.J. Cooke^a, M.C. Beere^c, A.J. Danylchuk^b

^a Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, 1125 Colonel By Dr., Ottawa, ON, Canada

^b Department of Environmental Conservation, University of Massachusetts Amherst, 160 Holdsworth Way, Amherst, MA 01003, USA

^c BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Fisheries Branch, 3726 Alfred Ave, Smithers, BC, Canada

ARTICLE INFO

Handled by Chennai Guest Editor

Keywords:

Recreational fishing
Rainbow trout
Migration
Freshwater
Salmon
Mortality

ABSTRACT

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. Over-winter 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

* Corresponding author.

E-mail address: WillTwardek@cmail.carleton.ca (W.M. Twardek).

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 km², 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

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 Witsset 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 *lrm*; 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 versus theoretical quartiles, residual versus 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

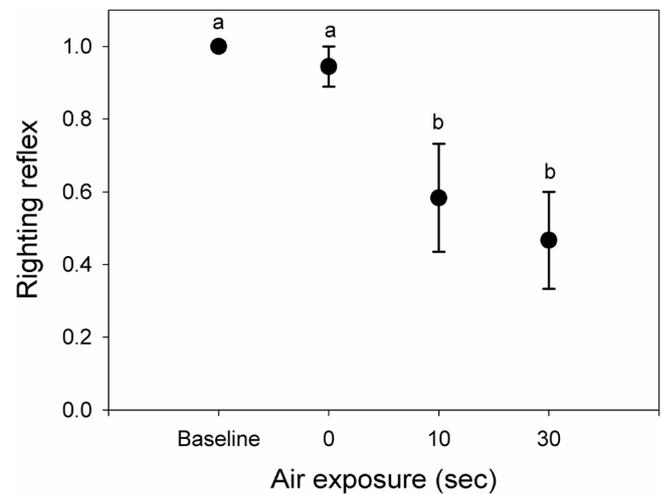


Fig. 2. Presence of the righting reflex in baseline ($N = 14$), 0 s ($N = 18$), 10 s ($N = 12$), and 30 s ($N = 15$) air exposed steelhead following angling. Different letters denote a significant difference ($p < 0.05$).

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 ($^{\circ}\text{C}$) 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 ($^{\circ}\text{C}$)	0.82	39	0.36

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).

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 ($^{\circ}\text{C}$) were included as continuous variables. Significant variables are emphasized with boldface font.

Variable Parameter	Glucose			Lactate			pH		
	Estimate \pm SE	t-value	p	Estimate \pm SE	t-value	p	Estimate \pm SE	t-value	p
(Intercept)	0.44 \pm 1.67	0.26	0.79	6.16 \pm 2.91	2.12	0.04	7.69 \pm 0.29	26.93	< 0.01
Air exposure: 10 s	-0.35 \pm 0.33	-1.06	0.29	0.39 \pm 0.58	0.68	0.50	-0.02 \pm 0.06	-0.29	0.77
Air exposure: 30 s	-0.02 \pm 0.32	-0.05	0.96	0.14 \pm 0.55	0.26	0.80	-0.06 \pm 0.05	-1.19	0.24
Fight time (s)	0.01 \pm 0.01	-0.30	0.77	0.01 \pm 0.01	1.25	0.22	-0.01 \pm 0.01	-0.09	0.93
Sex: Male	0.62 \pm 0.28	2.25	0.03	-0.34 \pm 0.48	-0.71	0.48	-0.01 \pm 0.05	-0.21	0.83
Fork length (mm)	0.01 \pm 0.01	0.10	0.92	-0.01 \pm 0.01	-2.00	0.05	-0.01 \pm 0.01	1.14	0.26
Landing method: Tail-grab	0.88 \pm 0.33	2.68	0.01	0.46 \pm 0.57	0.81	0.42	-0.04 \pm 0.06	-0.63	0.53
Water temperature ($^{\circ}\text{C}$)	0.18 \pm 0.10	1.87	0.07	0.46 \pm 0.17	2.64	0.01	-0.06 \pm 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 $^{\circ}\text{C}$ and remain low and constant from 6.5 to 11.7 $^{\circ}\text{C}$ (Fig. 8). Average daily movement rate also had a significant relationship with

mean discharge ($\text{m}^3 \text{s}^{-1}$; 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

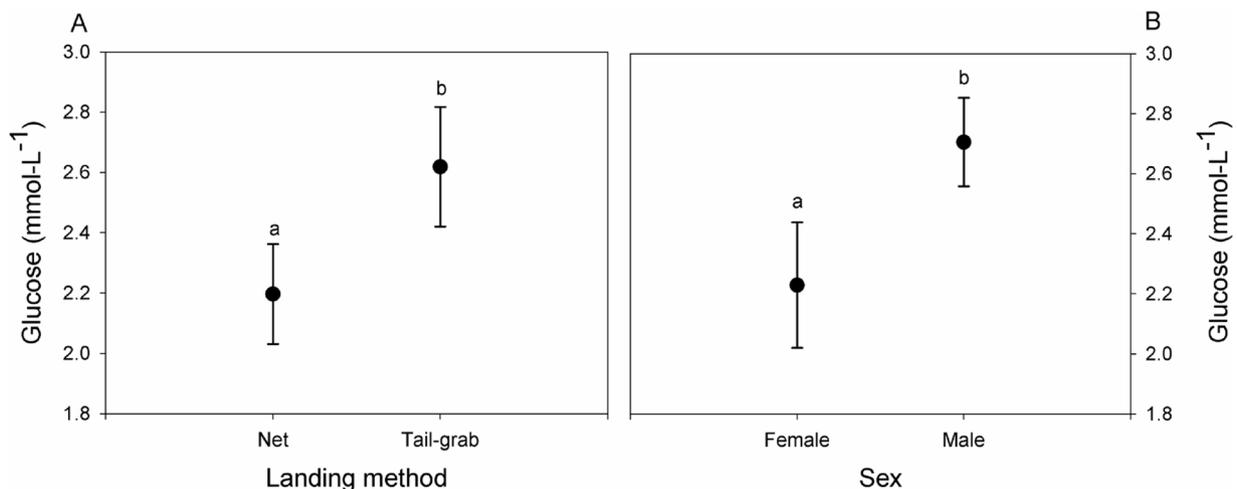


Fig. 3. Mean blood glucose levels of wild steelhead that were angled and A) landed by net ($n = 19$), or tail-grab ($n = 26$) B) female ($n = 25$), or male ($n = 20$). Blood samples were taken approximately 20 min after angling. Different letters denote a significant difference ($p < 0.05$).

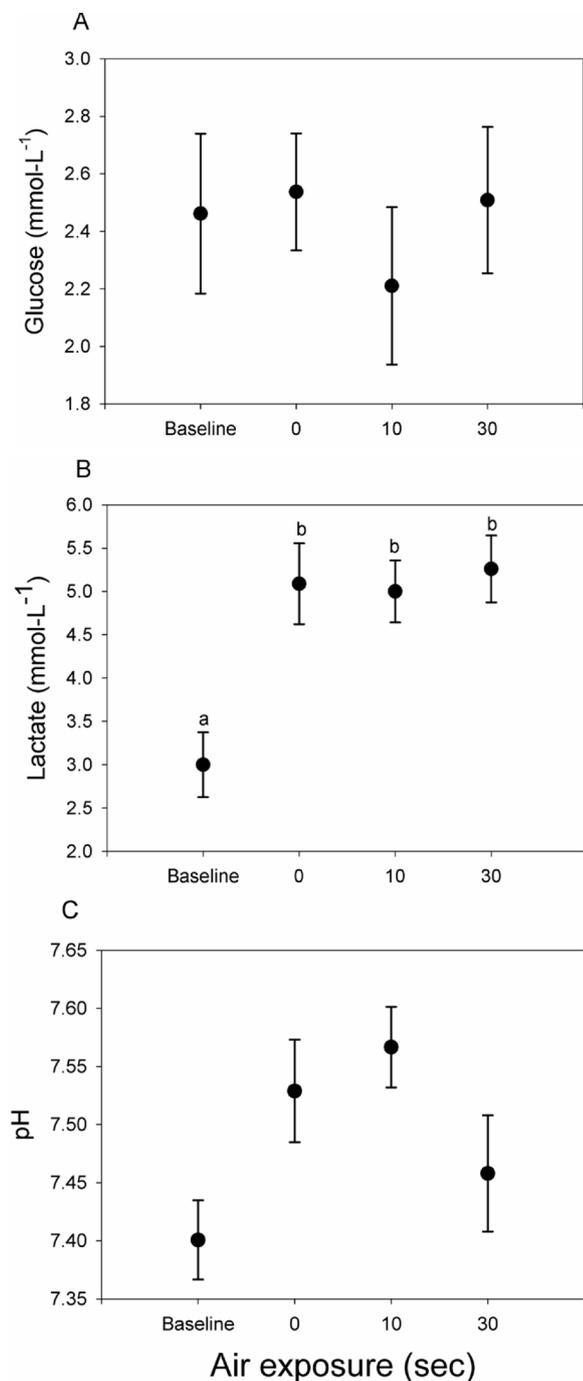


Fig. 4. Blood parameter values of air exposed steelhead following angling and approximately 20 min of holding. A) Blood glucose levels of baseline (n = 14), 0 s (n = 18), 10 s (n = 12), and 30 s (n = 15). B) Blood lactate levels of baseline (n = 14), 0 s (n = 18), 10 s (n = 12), and 30 s (n = 15). C) 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

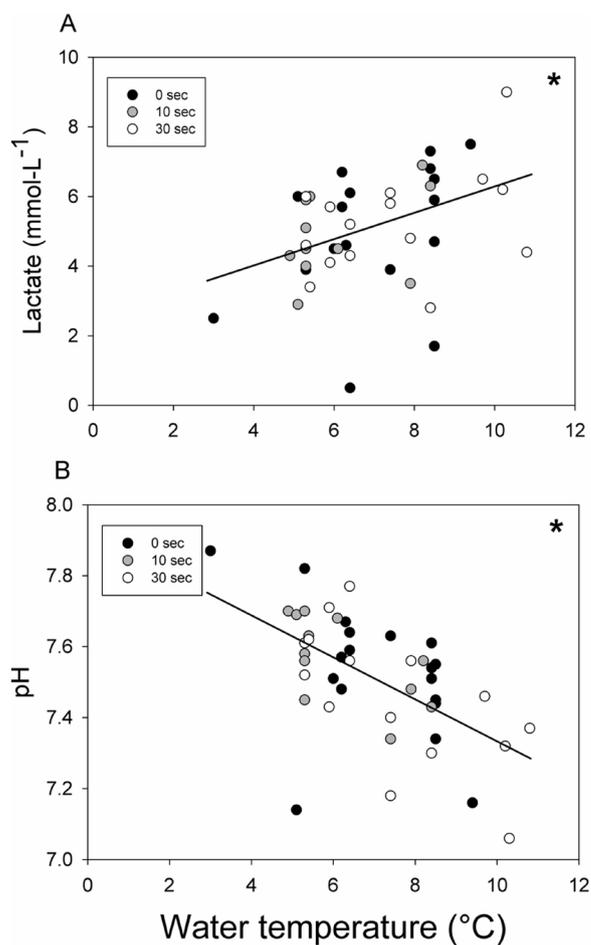


Fig. 5. The relationship between water temperature (°C) and A) blood lactate levels and B) blood pH of steelhead following angling and approximately 20 min of holding (n = 45). Asterisks denote a significant relationship between parameters ($p < 0.05$).

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 CO₂ and additional lactate accumulate, and the blood's 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 ($^{\circ}\text{C}$) were included as continuous variables. Significant variables are emphasized with boldface font.

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

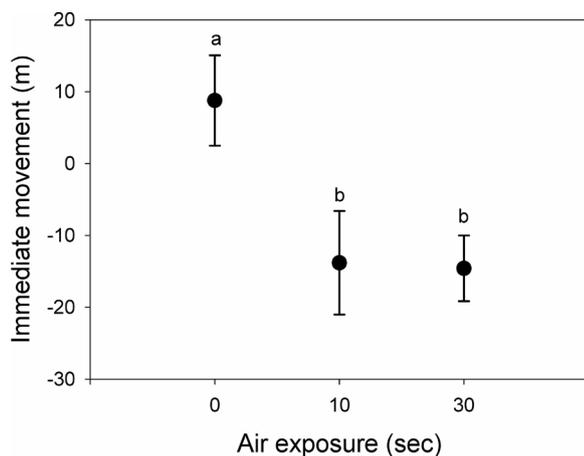


Fig. 6. Immediate post-release movement of steelhead following angling and air exposures of 0 s ($n = 22$), 10 s ($n = 25$), and 30 s ($n = 21$). Different letters denote a significant difference ($p < 0.05$).

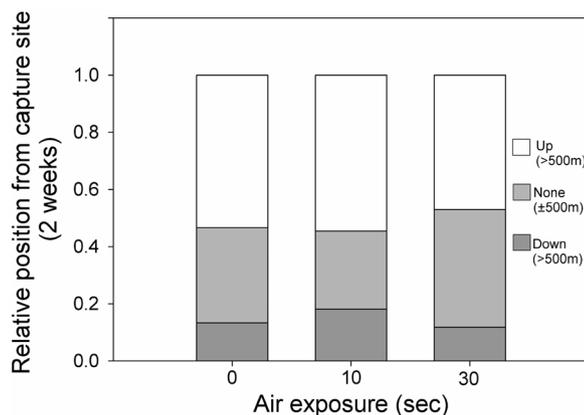


Fig. 7. The 2-week relative position of steelhead following angling and air exposures of 0 s ($N = 15$), 10 s ($N = 22$), and 30 s ($N = 17$). Relative positions of each fish were categorized 2 weeks after capture as down (> 500 m movement downstream of the capture site; dark grey), none (less than 500 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 glucocorticoids 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 $^{\circ}\text{C}$ water had a mortality rate of 9.6% approximately 36-h post-

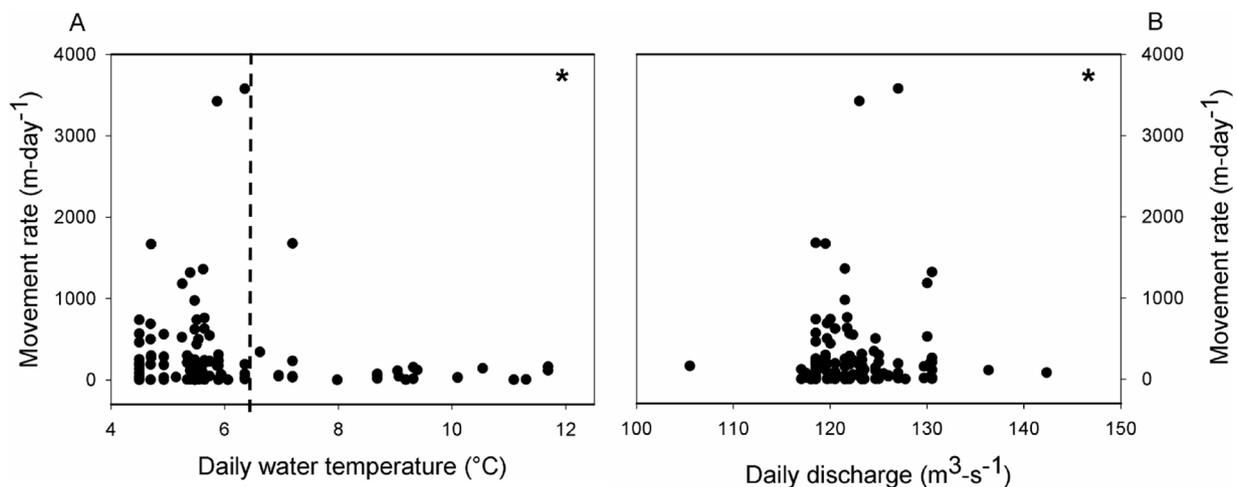


Fig. 8. The relationship between average daily movement rate and (A) average daily water temperature ($^{\circ}\text{C}$) and (B) average daily discharge of steelhead following angling ($n = 121$). The dashed line in (A) indicates the location of 6.5°C , a potential thermal threshold to movement. Asterisks 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 $\sim 6.5^{\circ}\text{C}$, 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 $120\text{ m}^3\text{ s}^{-1}$ and $130\text{ m}^3\text{ s}^{-1}$. 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 $4.06 \pm 0.26\%$ (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 (Valentinčić 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) compared 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 precautionary 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.

Acknowledgements

We would like to thank the Freshwater Fisheries Society of BC, Native Fish Society, B.C. Ministry of Forests, Lands, and Natural Resources, Wild Steelhead Coalition, the Steelhead Society of BC Northern Branch, Wet'suwet'en First Nations fisheries team, Oscar's Source for Adventure, River Safety, Headwaters Fish Reproductions, Moldy Chum, Costa Sunglasses, Umpqua Feather Merchants, Yeti Coolers, Patagonia Inc., and anonymous donors for making this project possible. We extend our greatest appreciation to Whitey Evans and Missy Moure for their immense in-kind support, as well as Pat Beahen, Tommy Thomson, Kevin Kish, Emilie Schmidt, Chloë Curtis, Natasha Erbel, Ida Hamhuis, and Dave Hughes from the Bulkley River Lodge for their assistance with fish collection and local knowledge on the fishery. We thank Alexandre Bussmann, Kerry Kilpatrick, and Troy Peters for their helpful advice and support for the project. We thank Jim Simonelli, Mitch Sapizak, Nick Elcheson, Aaron Lau, Chuck Holyk, Matt Chabot, Luke Saffarek and the numerous other volunteer anglers that donated their time to help us tag and sample steelhead. We thank Dean Peard of the B.C. Ministry of Forests, Lands, and Natural Resources for knowledge on the Witset Falls mark-recapture program. Twardek was funded by an NSERC-CGS-M and Ontario Graduate Scholarship. Cooke is further supported by NSERC and the Canada Research Chairs Program. Danylchuk is supported by the National Institute of Food & Agriculture, U.S. Department of Agriculture, the Massachusetts Agricultural Experiment Station and Department of Environmental Conservation.

References

- Aarestrup, K., Jepsen, N., 1998. Spawning migration of sea trout (*Salmo trutta* (L.) in a Danish river. *Hydrobiologia* 371/372, 275–281. <http://dx.doi.org/10.1023/A>.
- Aarestrup, K., Jepsen, N., Rasmussen, G., Økland, F., Thorstad, E.B., Holdensgaard, G., 2000. Prespawning migratory behaviour and spawning success of sea-ranched Atlantic salmon, *Salmo salar* L., in the River Gudena, Denmark. *Fish. Manag. Ecol.* 7, 387–400. <http://dx.doi.org/10.1046/j.1365-2400.2000.00210.x>.
- Afonso, L.O.B., Basu, N., Nakano, K., Devlin, R.H., Iwama, G.K., 2003. Sex-related differences in the organismal and cellular stress response in juvenile salmon exposed to treated bleached kraft mill effluent. *Fish. Physiol. Biochem.* 29, 173–179. <http://dx.doi.org/10.1023/B:FISH.0000035939.81588.09>.
- Andrews, T.R., McSheffrey, H.M., 1976. *Commercial Interceptions of Steelhead Trout*

- Stocks in British Columbia: a Preliminary Review. B.C. Marine Resources Branch, Fisheries Management Report No. 1, Victoria.
- Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Schwab, A., Suski, C., Sutton, S.G., Thorstad, E.B., 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Rev. Fish. Sci.* 15, 75–167.
- Austin, P.C., Steyerberg, E.W., 2015. The number of subjects per variable required in linear regression analyses. *J. Clin. Epidemiol.* 68, 627–636.
- Bartholomew, A., Bohnsack, J.A., 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Rev. Fish Biol. Fish.* 15, 129–154.
- Barton, B.A., 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. *Integr. Compar. Biol.* 42, 517–525.
- Barton, B.A., Morgan, J.D., Vlajay, M., 1998. Physiological and condition-related indicators of environmental stress in fish. In: Adams, S.M. (Ed.), *Biological Indicators of Aquatic Ecosystem Stress*. American Fisheries Society, Bethesda pp. 111–148.
- Barwick, D.H., 1985. Stocking and hooking mortality of planted rainbow trout in Jocassee Reservoir, South Carolina. *North Am. J. Fish. Manag.* 5, 580–583. [http://dx.doi.org/10.1577/1548-8659\(1985\)5<580:SAHMOP>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(1985)5<580:SAHMOP>2.0.CO;2).
- Bird, T., Lyon, J., Wotherspoon, S., King, R., McCarthy, M., 2016. Accounting for false mortality in telemetry tag applications. *Ecol. Modell.* 355, 116–125. <http://dx.doi.org/10.1016/j.ecolmodel.2017.01.019>.
- Boyd, J.W., Guy, C.S., Horton, T.B., Leathe, S.A., 2010. Effects of catch-and-release angling on salmonids at elevated water temperatures. *North Am. J. Fish. Manag.* 30, 898–907. <http://dx.doi.org/10.1577/M09-107.1>.
- Brett, J.R., 1995. Energetics. In: Groot, C., Margolis, L., Clarke, W.C. (Eds.), *Physiological Ecology of Pacific Salmon*. University of British Columbia Press, Vancouver pp 3–68.
- Brett, J.R., 1971. Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* 11, 99–113.
- Brownscombe, J.W., Danylchuk, A.J., Chapman, J.M., Gutowsky, L.F.G., Cooke, S.J., 2017. Best practices for catch-and-release recreational fisheries: angling tools and tactics. *Fish. Res.* 186, 693–705. <http://dx.doi.org/10.1016/j.fishres.2016.04.018>.
- Cook, K.V., Lennox, R.J., Hinch, S.G., Cooke, S.J., 2015. Fish out of water: how much air is too much? *Fisheries* 40, 452–461. <http://dx.doi.org/10.1080/03632415.2015.1074570>.
- Cooke, S.J., Donaldson, M.R., O'Connor, C.M., Raby, G.D., Arlinghaus, R., Danylchuk, A.J., Hanson, K.C., Hinch, S.G., Clark, T.D., Patterson, D.A., Suski, C.D., 2013. The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation, and relevance to stakeholders. *Fish Manag. Ecol.* 20, 268–287.
- Cooke, S.J., Hinch, S.G., Lucas, M.C., Lutcavage, M., 2012. Biotelemetry and biologging. In: Zale, A.V., Parrish, D.L., Sutton, T.M. (Eds.), *Fisheries Techniques*, third ed. American Fisheries Society, Bethesda, Md Chapter 18, pp. 819–860.
- Cooke, S.J., Schramm, H.L., 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fish. Manag. Ecol.* 14, 73–79. <http://dx.doi.org/10.1111/j.1365-2400.2007.00527.x>.
- Cooke, S.J., Suski, C.D., 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodivers. Conserv.* 14, 1195–1209. <http://dx.doi.org/10.1007/s10531-004-7845-0>.
- Cooke, S.J., Palensky, L.Y., Danylchuk, A.J., 2017. Inserting the angler into catch-and-release angling science and practice. *Fish. Res.* 186, 599–600.
- Counterpoint Consulting, 2008. Economic Dimensions of Skeena Watershed Salmonid Fisheries. Report submitted to the Pacific Salmon Foundation (Accessed 25 August 2017). <http://skeenawatershedinitiative.com/libraryfiles/lib248.pdf>.
- Danylchuk, A.J., Danylchuk, S.E., Cooke, S.J., Goldberg, T.L., Koppelman, J.B., Philipp, D.P., 2007a. Post-release mortality of Bonefish, *Albula vulpes*, exposed to different handling practices during catch-and-release angling in Eleuthera, the Bahamas. *Fish. Manag. Ecol.* 14, 149–154.
- Danylchuk, S.E., Danylchuk, A.J., Cooke, S.J., Goldberg, T.L., Koppelman, J., Philipp, D.P., 2007b. Effects of recreational angling on the post-release behaviour and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. *J. Exp. Mar. Biol. Ecol.* 346, 127–133.
- Danylchuk, A.J., Danylchuk, S.C., Kosiarski, A., Cooke, S.J., Huskey, B., 2018. Keepemwet Fishing—An emerging social brand for disseminating best practices for catch-and-release in recreational fisheries. *Fish. Res.* 205, 52–56.
- Davis, M.W., 2010. Fish stress and mortality can be predicted using reflex impairment. *Fish Fish.* 11, 1–11.
- Davis, M.W., 2002. Key principles for understanding fish bycatch discard mortality. *Can. J. Fish. Aquat. Sci.* 59, 1834–1843.
- Dedual, M., Jowett, I.G., 1999. Movement of rainbow trout (*Oncorhynchus mykiss*) during the spawning migration in the Tongariro River, New Zealand. *New Zeal. J. Mar. Freshw. Res.* 33, 107–117. <http://dx.doi.org/10.1080/00288330.1999.9516861>.
- Donaldson, M.R., Arlinghaus, R., Hanson, K.C., Cooke, S.J., 2008. Enhancing catch-and-release science with biotelemetry. *Fish Fish.* <http://dx.doi.org/10.1111/j.1467-2979.2007.00265.x>.
- Dotson, T., 1982. Mortalities in trout caused by gear type and angler-induced stress. *North Am. J. Fish. Manag.* 2, 60–65. [http://dx.doi.org/10.1577/1548-8659\(1982\)2<60:MITCBG>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(1982)2<60:MITCBG>2.0.CO;2).
- DuBois, R.B., Kuklinski, K.E., 2004. Effect of hook type on, trauma, and capture efficiency of wild, stream-resident trout caught by active baitfishing. *North Am. J. Fish. Manag.* 24, 617–623. <http://dx.doi.org/10.1577/M02-172.1>.
- Fenkes, M., Shiels, H.A., Fitzpatrick, J.L., Nudds, R.L., 2016. The potential impacts of migratory difficulty, including warmer waters and altered flow conditions, on the reproductive success of salmonid fishes. *Comp. Biochem. Physiol. - Part A Mol. Integr. Physiol.* 193, 11–21. <http://dx.doi.org/10.1016/j.cbpa.2015.11.012>.
- Ferguson, R.A., Tufts, B.L., 1992. Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for “catch and release” fisheries. *Can. J. Fish. Aquat. Sci.* 49, 1157–1162. <http://dx.doi.org/10.1139/f92-129>.
- Gagne, T., Ovitiz, K., Griffin, L., Brownscombe, J.W., Cooke, S.J., Danylchuk, A.J., 2017. Evaluating the consequences of catch-and-release recreational angling on golden dorado (*Salminus brasiliensis*) in Salta, Argentina. *Fish. Res.* 186, 625–633.
- Gale, M.K., Hinch, S.G., Donaldson, M.R., 2013. The role of temperature in the capture and release of fish. *Fish Fish.* 14, 1–33. <http://dx.doi.org/10.1111/j.1467-2979.2011.00441.x>.
- Gayeski, N., McMillan, B., Trotter, P., 2011. Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. *Can. J. Fish. Aquat. Sci.* 68, 498–510. <http://dx.doi.org/10.1139/F10-166>.
- Gingerich, A.J., Cooke, S.J., Hanson, K.C., Donaldson, M.R., Hasler, C.T., Suski, C.D., Arlinghaus, R., 2007. Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released. *Fish. Res.* 86, 169–178.
- Gjernes, T., Kronlund, A.R., Mulligan, T.J., 1993. Mortality of chinook and coho salmon in their first year of ocean life following catch and release by anglers. *North Am. J. Fish. Manag.* 13, 524–539. [http://dx.doi.org/10.1577/1548-8675\(1993\)013<0524:MOCACS>2.3.CO;2](http://dx.doi.org/10.1577/1548-8675(1993)013<0524:MOCACS>2.3.CO;2).
- Good, T.P., Waples, R.S., Adams, P., 2005. Updated Status of Federally Listed ESUs of West Coast Salmon and Steelhead. U. S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-66 pp. 356.
- Guckian, M., Danylchuk, A.J., Cooke, S.J., Markowitz, E.M., 2018. Peer pressure on the riverbank: assessing catch-and-release anglers' willingness to sanction others' (bad) behavior. *J. Environ. Manage.* 219, 252–259.
- Hagelin, A., Calles, O., Greenberg, L., Piccolo, J., Bergman, E., 2016. Spawning migration of wild and supplementary stocked landlocked Atlantic Salmon (*Salmo Salar*). *River Res. Appl.* 32, 383–389. <http://dx.doi.org/10.1002/rra.2870>.
- Hooton, R.S., 1987. Catch and release as a management strategy for steelhead in British Columbia. In: Barnhart, R., Roelofs, T. (Eds.), *Proceedings of Catch and Release Fishing – A Decade of Experience*. September 30–October 1, Humboldt State University, Arcata, California.
- Hooton, R.S., 2001. Facts and Issues Associated With Restricting Terminal Gear Types in the Management of Sustainable Steelhead Sport Fisheries in British Columbia. Report for the Ministry of Lands, Forestry, and Natural Resources pp 28.
- Hühn, D., Arlinghaus, R., 2011. Determinants of hooking mortality in freshwater recreational fisheries: a quantitative meta-analysis. *Am. Fish. Soc. Symp.* 75, 141–170.
- Thomas, J.O., Associates Ltd, 2010. Steelhead Bycatch and Mortalities in the Commercial Skeena Net Fisheries of British Columbia from Observer Data: 1989 to 2009. Report prepared for the Pacific Salmon Foundation and British Columbia Ministry of Environment, Skeena Region.
- Jeffries, K.M., Hinch, S.G., Gale, M.K., Clark, T.D., Lotto, A.G., Casselman, M.T., Li, S., Rechisky, E.L., Porter, A.D., Welch, D.W., Miller, K.M., 2014. Immune response genes and pathogen presence predict migration survival in wild salmon smolts. *Mol. Ecol.* 23, 5803–5815. <http://dx.doi.org/10.1111/mec.12980>.
- Jepsen, N., Thorstad, E.B., Havn, T., Lucas, M.C., 2015. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. *Anim. Biotelemetry*. <http://dx.doi.org/10.1186/s40317-015-0086-z>.
- Keefer, M.L., Boggs, C.T., Peery, C.A., Caudill, C.C., 2008. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. *North Am. J. Fish. Manag.* 28, 81–96. <http://dx.doi.org/10.1577/M07-011.1>.
- Kelch, D., Lichtkoppler, F., Sohngen, B., Daigneault, A., 2006. The value of steelhead (*Oncorhynchus mykiss*) angling in Lake Erie tributaries. *J. Great Lakes Res.* 32, 424–433. [http://dx.doi.org/10.3394/0380-1330\(2006\)32](http://dx.doi.org/10.3394/0380-1330(2006)32).
- Kendall, N.W., McMillan, J.R., Sloat, M.R., Buehrens, T.W., Quinn, T.P., Pess, G.R., Kuzishchin, K.V., McClure, M.M., Zabel, R.W., 2015. Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. *Can. J. Fish. Aquat. Sci.* 72, 319–342.
- Kerr, S.M., Ward, T.D., Lennox, R.J., Brownscombe, J.W., Chapman, J.M., Gutowsky, L.F.G., Logan, J.M., Twardek, W.M., Elvidge, C.K., Danylchuk, A.J., Cooke, S.J., 2017. Influence of hook type and live bait on the hooking performance of inline spinners in the context of catch-and-release brook trout *Salvelinus fontinalis* fishing in lakes. *Fish. Res.* 186, 642–647. <http://dx.doi.org/10.1016/j.fishres.2016.10.001>.
- Kieffer, J., Currie, S., Tufts, B., 1994. Effects of environmental temperature on the metabolic and acid-base responses of rainbow trout to exhaustive exercise. *J. Exp. Biol.* 194, 299–317.
- Kintama, 2009. Acoustic Telemetry Measurements of Survival and Movements of Adult Steelhead (*Oncorhynchus mykiss*) Within the Skeena and Bulkley Rivers, 2008. PROJECT # 5310-30 Skeena LR (Sonic Telemetry Investigations-2008) pp 52.
- Lawrence, M.J., Jain-Schlaepfer, S., Zolderdo, A., Algera, D., Gilmour, K., Gallagher, A., Cooke, S.J., 2018. Are 3-minutes good enough for obtaining baseline physiological samples from teleost fish. *Can. J. Zool.* in press.
- Lennox, R.J., Uglem, I., Cooke, S.J., Næsje, T.F., Whoriskey, F.G., Havn, T.B., Ulvan, E.M., Solem, Ø., Thorstad, E.B., 2015. Does catch-and-release angling alter the behavior and fate of adult Atlantic salmon during upriver migration? *Trans. Am. Fish. Soc.* 144, 400–409.
- Lirette, M.G., 1988. Telemetric Studies of Summer and Winter Steelhead in the Stamp and Somass Rivers, 1984–85. Ministry of Environment Lands and Parks, Fisheries Program, Nanaimo, B.C Fisheries Report No. VI 881.
- Lirette, M.G., 1989. Monitoring of Tagged Summer Steelhead in the Campbell River, 1988–89. Ministry of Environment Lands and Parks, Fisheries Program, Nanaimo, B.C Fisheries Report No. VI 892.
- Liu, S., Gao, G., Palti, Y., Cleveland, B., Weber, G., Rexroad, C., 2014. RNA-seq analysis of

- early hepatic response to handling and confinement stress in rainbow trout. *PLoS One* 9, e88492.
- López-Patiño, M., Hernández-Pérez, J., Gesto, M., Librán-Pérez, M., Míguez, J., Soengas, J., 2014. Short-term time course of liver metabolic response to acute handling stress in rainbow trout, *Oncorhynchus mykiss*. *Compar. Biochem. Physiol. Part A: Mol. Integr. Physiol.* 168, 40–49.
- Lough, M.J., 1980. Radiotelemetry Studies of Summer-Run Steelhead Trout in the Skeena River Drainage, 1979, With Particular Reference to Morice, Suskwa, Kispiox, and Zymoetz River Stocks. British Columbia Fish and Wildlife Branch, Skeena Fisheries Report 79-05, Smithers pp. 82.
- Meka, J.M., 2004. The influence of hook type, angler experience, and fish size on injury rates and the duration of capture in an Alaskan catch-and-release rainbow trout fishery. *North Am. J. Fish. Manag.* 24, 1309–1321. <http://dx.doi.org/10.1577/M03-108.1>.
- Meka, J.M., McCormick, S.D., 2005. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fish. Res.* 72, 311–322. <http://dx.doi.org/10.1016/j.fishres.2004.10.006>.
- Milligan, C.L., Wood, C.M., 1986. Tissue intracellular acid-base status and the fate of lactate after exhaustive exercise in the rainbow trout. *J. Exp. Biol.* 123, 123–144.
- Ministry of Forests, Lands, and Natural Resource Operations, 2013. Bulkeley River Angling Management Plan. (Accessed 29 June 2017). http://www.env.gov.bc.ca/skeena/fish/AMPs/Bulkeley_AMP.pdf.
- Ministry of Forests, Lands, and Natural Resource Operations, 2017. 2017–2019 Freshwater Fishing Regulations Synopsis: Region 6 – Skeena. (Accessed 26 July 2017). http://www.env.gov.bc.ca/fw/fish/regulations/docs/1719/fishing_synopsis_2017-19_region6.pdf.
- Mongillo, P.E., 1984. A Summary of Salmonid Hooking Mortality. Washington Department of Game, Fish Management Division, Olympia, Washington pp. 45.
- Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., Beere, M., 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.* 83, 1035–1046.
- National Research Center (NRC), 1996. Upstream: Salmon and Society in the Pacific Northwest. National Academies Press, Washington, D.C.
- Nelson, T.C., Rosenau, M.L., Johnston, N.T., 2005. Behavior and survival of wild and hatchery-origin winter steelhead spawners caught and released in a recreational fishery. *North Am. J. Fish. Manag.* 25, 931–943. <http://dx.doi.org/10.1577/M04-192.1>.
- Økland, F., Jensen, A.J., Johnsen, B.O., 1996. Winter habitat and seaward migration of a Norwegian brown trout population. In: Baras, E., Philippart, J.C. (Eds.), *Underwater Biotelemetry. Proceedings of the First Conference and Workshop on Fish Telemetry in Europe*. April 4–6, 1995, Liege, Belgium: University of Liege. pp. 161–171.
- Patterson, D.A., Robinson, K.A., Lennox, R.J., Nettles, T.L., Donaldson, L.A., Eliason, E.J., Raby, G.D., Chapman, J.M., Cook, K.V., Donaldson, M.R., Bass, A.L., Drenner, S.M., Reid, A.J., Cooke, S.J., Hinch, S.G., 2017. Review and evaluation of fishing-related incidental mortality for Pacific Salmon. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2017/010. pp. 155.
- Penney, Z.L., Moffitt, C.M., 2014. Proximate composition and energy density of stream-maturing adult steelhead during upstream migration, sexual maturity, and kelt emigration. *Trans. Am. Fish. Soc.* 143, 399–413.
- Perrier, C., Terrier, M., Perrier, H., 1978. A time-course study of the effects of angling stress on cyclic AMP, lactate and glucose plasma level in the rainbow trout (*Salmo gairdnerii* Richardson) during a 64 hour recovery period. *Compar. Biochem. Physiol.* 60, 217–219.
- Pettit, S., 1977. Comparative reproductive success of caught and released and unplayed hatchery female steelhead (*Salmo gairdnerii*) from the Clearwater River. *Idaho. Trans. Am. Fish. Soc.* 106, 431–435.
- Polakof, S., Panserat, S., Soengas, J.L., Moon, T.W., 2012. Glucose metabolism in fish: a review. *J. Comp. Physiol. B.* 182, 1015–1045.
- Pope, K.L., Wilde, G.R., Knabe, D.W., 2007. Effect of catch-and-release angling on growth and survival of rainbow trout, *Oncorhynchus mykiss*. *Fish. Manag. Ecol.* 14, 115–121. <http://dx.doi.org/10.1111/j.1365-2400.2007.00531.x>.
- Quinn, T.P., 2005. The Behavior and Ecology of Pacific Salmon and Trout. *Am. Fish. Soc., Bethesda, Maryland*.
- Raby, G.D., Donaldson, M.R., Hinch, S.G., Clark, T.D., Eliason, E.J., Jeffries, K.M., Cook, K.V., Teffer, A., Bass, A.L., Miller, K.M., Patterson, D.A., Farrell, A.P., Cooke, S.J., 2015. Fishing for effective conservation: context and biotic variation are keys to understanding the survival of pacific salmon after catch-and-release. *Integr. Compar. Biol.* 55, 554–576. <http://dx.doi.org/10.1093/icb/ictv088>.
- Raby, G.D., Donaldson, M.R., Hinch, S.G., Patterson, D.A., Lotto, A.G., Robichaud, D., English, K.K., Willmore, W.G., Farrell, A.P., Davis, M.W., Cooke, S.J., 2012. Validation of reflex indicators for measuring vitality and predicting the delayed mortality of wild coho salmon bycatch released from fishing gears. *J. Appl. Ecol.* 49, 90–98. <http://dx.doi.org/10.1111/j.1365-2664.2011.02073.x>.
- Reiser, D.W., Huang, C.-M., Beck, S., Gagner, M., Jeanes, E., 2006. Defining flow windows for upstream passage of adult anadromous salmonids at cascades and falls. *Trans. Am. Fish. Soc.* 135, 668–679. <http://dx.doi.org/10.1577/T05-169.1>.
- Richard, A., Bernatchez, L., Valiquette, E., Dionne, M., 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic Salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 71, 1730–1739.
- Richard, A., Dionne, M., Wang, J., Bernatchez, L., 2013. Does catch and release affect the mating system and individual reproductive success of wild Atlantic Salmon (*Salmo salar* L.). *Mol. Ecol.* 22, 18710.
- Schill, D.J., 1996. Hooking mortality of bait caught rainbow trout in an Idaho stream and a hatchery: implications for special-regulation management. *North Am. J. Fish. Manag.* 16, 348–356. [http://dx.doi.org/10.1577/1548-8675\(1996\)016<0348:HMOBCR>2.3.CO;2](http://dx.doi.org/10.1577/1548-8675(1996)016<0348:HMOBCR>2.3.CO;2).
- Schisler, G.J., Bergersen, E.P., 1996. Postrelease Hooking mortality of rainbow trout caught on scented artificial baits. *North Am. J. Fish. Manag.* 16, 570–578. [http://dx.doi.org/10.1577/1548-8675\(1996\)016<0570:PHMORT>2.3.CO;2](http://dx.doi.org/10.1577/1548-8675(1996)016<0570:PHMORT>2.3.CO;2).
- Schreer, J.F., Resch, D.M., Gately, M.L., Cooke, S.J., 2005. Swimming performance of brook trout after simulated catch-and-release angling: looking for air exposure thresholds. *North Am. J. Fish. Manag.* 25, 1513–1517.
- Simpkins, D.G., Hubert, W.A., Martinez del Rio, C., Rule, D.C., 2004. Factors affecting swimming performance of fasted rainbow trout with implications of exhaustive exercise on overwinter mortality. *J. Freshw. Ecol.* 19, 657–666. <http://dx.doi.org/10.1080/02705060.2004.9664748>.
- Smirich, M.G., Kelly, J.T., 2014. Extending the 2% rule: the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. *Anim. Biotelem.* 2, 16.
- Smith, B.D., Ward, B.R., Welch, D.W., 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance in British Columbias indexed by angler success. *Can. J. Fish. Aquat. Sci.* 57, 255–270.
- Stewart, R.W.J., Lewinsky, V.A., 1988. Interception of Steelhead Trout (*Salmo gairdnerii*) in the Indian Fishery of the Fraser River, September Through November, 1986. Report for Ministry of Environment and Parks, BC pp. 150.
- Stoot, L.J., Cairns, N.A., Cull, F., Taylor, J.J., Jeffrey, J.D., Morin, F., Mandelman, J.W., Clarke, T.D., Cooke, S.J., 2014. Use of portable blood physiology point-of-care devices for basic and applied research on vertebrates: a review. *Conserv. Physiol.* 2, cou011.
- Suttle, K.B., Power, M.E., Levine, J.M., McNeely, C., 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecol. Appl.* 14, 969–974.
- Taylor, G., Barnhart, R.A., 1997. Mortality of angler caught and released summer steelhead. Steelhead Trout Catch Report. California Cooperative Fishery Research Unit and Humboldt State University pp. 1–31.
- Thomas, J.O., 1995. 1995 Skeena River Sport Fish Coho and Steelhead Catch and Release Study. Unpublished report, J.O. Thomas and Associates Ltd. Contract No. FP 95-5049-170H-0315. Department of Fisheries and Oceans, Prince Rupert, B.C.
- Thorstad, E., 2000. Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *J. Fish Biol.* 57, 531–535. <http://dx.doi.org/10.1006/jfbi.2000.1315>.
- Thorstad, E.B., Foldvik, A., Lo, H., Bjørnå, T., Stensli, J.H., 2014. Effects of handling adult sea trout (*salmo trutta*) in a fishway and tagging with external radio transmitters. *Boreal Environ. Res.* 19, 408–416.
- Valentinčič, T., Caprio, J., 1997. Visual and chemical release of feeding behavior in adult rainbow trout. *Chem. Senses* 22, 375–382. <http://dx.doi.org/10.1093/chemse/22.4.375>.
- Wade, A.A., Beechie, T.J., Fleishman, E., Mantua, N.J., Wu, H., Kimball, J.S., Stoms, D.M., Stanford, J.A., 2013. Steelhead vulnerability to climate change in the Pacific Northwest. *J. Appl. Ecol.* 50, 1093–1104.
- Wendelaar Bonga, S.E., 1997. The stress response in fish. *Physiol. Rev.* 77, 591–625.
- White, A.J., Schreer, J.F., Cooke, S.J., 2008. Behavioral and physiological responses of the congeneric largemouth (*Micropterus salmoides*) and smallmouth bass (*M. dolomieu*) to various exercise and air exposure durations. *Fish. Res.* 89, 9–16.
- Wood, C.M., 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in rainbow trout. *J. Exp. Biol.* 160, 285–308.
- Wood, C.M., Turner, J.D., Graham, M.S., 1983. Why do fish die after severe exercise? *J. Fish Biol.* 22, 189–201. <http://dx.doi.org/10.1111/j.1095-8649.1983.tb04739.x>.
- Workman, R., Hayes, D., Coon, T.A., 2002. Model of steelhead movement in relation to water temperature in two Lake Michigan tributaries. *Trans. Am. Fish. Soc.* 131, 463–475.
- Wydoski, R.S., Wedermeyer, G.A., Nelson, N.C., 1976. Physiological response to hooking stress in hatchery and wild rainbow trout (*Salmo gairdnerii*). *Trans. Am. Fish. Soc.* 105, 601–606.
- Wydoski, R.S., 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management. In: Barhardt, R. (Ed.), *Proceedings of a National Symposium on Catch-and-Release Fishing*. Humboldt State University, Arcata, CA. pp 43–87.