



Linking environmental factors with reflex action mortality predictors, physiological stress, and post-release movement behaviour to evaluate the response of white sturgeon (*Acipenser transmontanus* Richardson, 1836) to catch-and-release angling

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ABSTRACT

White sturgeon are the largest freshwater fish in North America and are the focus of an intense catch-and-release (C&R) fishery; the effects are largely unknown. We assessed the effect of fight and handling time, water temperature, river discharge rate, and fish size on physiological and reflex impairment responses of wild white sturgeon to angling. Sixty of these fish were tagged with acoustic transmitters to assess survival and post-release behaviour. Survival was high (100%). Water temperature and discharge influenced post-capture blood physiology. Specifically, lactate, chloride, and cortisol concentrations were elevated in individuals fought longer, and captured at higher water temperatures and river discharge. Cortisol was affected by fish size, with lower concentrations found in larger individuals. Only lactate and chloride were positively related to reflex impairment scores. Post-release movements were correlated with physiological state, fight characteristics and the environment. Specifically, higher blood lactate and chloride and those with longer fight times moved shorter distances after release. Contrastingly, higher levels of circulating glucose and potassium, as well as larger fish captured during periods of high discharge moved longer distances. Sturgeon tended to move shorter distances and at slower rates when reflex impairment was high, although reflex impairment in general did not explain a significant proportion of the variance in any movement metric. Our results show intriguing variance in the physiological and behavioural response of individual white sturgeon to C&R angling, with some degree of environmental dependence, and highlights the importance of understanding drivers of such variation when managing fisheries.

1. Introduction

Recreational fishing is an increasingly popular activity, despite often unknown consequences to individual fish and populations

(Brownscombe et al., 2017). Ideally, catch-and-release (C&R) fishing methods promote the sustainable use of fisheries resources by reducing direct mortality, however it has been shown that post-release survival rates are highly variable among species (Arlinghaus et al., 2007;

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Bartholomew and Bohnsack, 2005; Muoneke and Childress, 1994). Despite the perception that C&R is an effective management and conservation strategy (Cooke and Schramm, 2007), fishing-related stressors including hooking, exhaustive exercise, handling, and air exposure, can result in physiological disturbances (e.g., measurable changes in cortisol, glucose, lactate, ions, etc.), physical injury, and behavioural impairments that increase the risk of immediate or delayed mortality, or sub-lethal effects with fitness consequences (Brownscombe et al., 2017; Cook et al., 2018). For example, short-term foraging behaviour of pike (*Esox lucius*) – specifically a delay in interest and attack on prey compared to uncaught controls – has been shown to change following C&R (Stålhammar et al., 2012). A change in feeding habits can affect individual fitness (i.e., reduced growth) and can have broader implications to the fish community (i.e., reduced rates of pike predation). Acute changes in behaviour during spawning migrations is another potential fitness consequence that has been seen in some fish populations. For example, stress-induced fallback (i.e., downstream movements after capture during an upstream migration) and mortality were documented in a population of Atlantic salmon (*Salmo salar*) after C&R at high water temperatures (Havn et al., 2015). Although recommendations for C&R best-practices exist for some species (see Brownscombe et al., 2017 for review), greater knowledge of species-specific stress responses and mortality rates due to acute angling stressors is still needed (Cooke and Suski, 2005; Cooke et al., 2016). Study of sub-lethal disturbances, such as behavioural changes, is also needed; understanding the effects of C&R on movement and distribution patterns is important when estimating population level impacts.

White sturgeon *Acipenser transmontanus* are an economically important species for recreational freshwater fisheries throughout their North American spawning range from the Sacramento-San Joaquin (California, USA) watershed, north to the Fraser River (British Columbia [B.C.], Canada; Hildebrand et al., 2016). Sexual maturity is reached between the ages of 11 to 30 (150–160 cm FL), with males reaching sexual maturity before females (COSEWIC, 2012). White sturgeon are iteroparous broadcast spawners that exhibit varying periods of intermittent spawning; spawning periodicity has been documented to range from 3 to 5 years, with upper limits of 10 years between spawning recorded in northern populations (summarized in Hildebrand et al., 2016). Spawning is latitudinally dependent and occurs from late winter (southern part of the species range) to late summer (northern Canadian populations; Hildebrand et al., 2016). The largest population of white sturgeon in Canada is in the lower Fraser River, B.C. (LFR). The mean 2017 abundance estimate for LFR white sturgeon ranging from 60 to 279 cm FL was 34,860, with evidence to suggest a decline in the total abundance by 38.2% compared to the highest abundance estimate in 2003, and 17.3% lower than 2016 (Nelson et al., 2018). Despite concerns about the species' conservation status, white sturgeon are highly prized game fish and many populations sustain important recreational fisheries.

Catch-and-release fishing of sturgeon is pervasive in Canada, particularly in the LFR where the socioeconomic importance of the fishery to the province of B.C. has increased substantially in recent years (E. Stoddard, Min. Forests, Lands, Natural Resource Operations and Rural Development [FLNRORD], B.C., personal communication). Although the Committee for the Status of Endangered Wildlife in Canada (COSEWIC) gave white sturgeon a 'Threatened' status in 2012, the LFR population has only recently been considered for listing under the Species at Risk Act (SARA). The SARA recovery potential assessment for white sturgeon in the LFR began in 2015 and included discussions on the significant information gaps in sources of mortality and other effects from various fisheries (E. Stoddard, personal communication). Like

most sturgeon, white sturgeon populations were severely overharvested at the turn of the 19th century (Hildebrand et al., 2016). Life history traits like long lifespan and delayed age of maturity make sturgeon susceptible to human-induced impacts. In an extensive review on the status of white sturgeon populations, Hildebrand et al. (2016) outlined the most prominent current threats, and future threats they are likely to face. Fishery "impacts" were listed as an important area for future research given that the biological and population-level effects of repeated capture-and-release are largely unknown (Hildebrand et al., 2016). From a management and fish welfare perspective, research on the behaviour and fate of white sturgeon after C&R is critically needed.

Assessing post-release survival and behaviour of fish is particularly challenging as it is difficult to monitor the fate of individuals via direct observation and without biasing the C&R procedure. Electronic tracking technologies are routinely employed to help fill these gaps. Electronic tracking is also very useful to C&R science when it is combined with physiological sampling, as this allows researchers to identify mechanistic links between fishing stressors and components of fitness (Brownscombe et al., 2017, 2019; Crossin et al., 2017; Donaldson et al., 2008). This method is often complex, however, and can come with potential limitations and biases related to tag attachment (Broell et al., 2016). Another increasingly favoured method employed in C&R science is the use of non-invasive quantifications of post-release mortality and vitality (i.e., the capacity to survive) via a suite of tested reflexes that are deemed either impaired or unimpaired (Davis, 2005, 2007, 2010). Often the method is referred to in the literature as Reflex Action Mortality Predictor (RAMP) scores or reflex impairment indices and has been used to assess individual vitality following a stressful encounter in several fish species (e.g., coho salmon *Oncorhynchus kisutch*, Raby et al., 2012, 2014; sockeye salmon *Oncorhynchus nerka*, Gale et al., 2011, 2014; bonefish *Albula* spp., Brownscombe et al., 2013, 2015; black sea bream *Spondyliosoma cantharus*, Pinder et al., 2017), including white (McLean et al., 2016) and shortnose sturgeon *Acipenser brevirostrum* (Struthers et al., 2018). In short, the presence or absence of specific reflexes that are routinely expressed in unstressed individuals are assessed to predict the likelihood for post-release mortality. Therefore, RAMP provides a quantitative link between the stress response and fitness outcomes or proxies thereof (Davis, 2005, 2007, 2010). Although most commonly used to predict post-release mortality of species targeted by fisheries, studies have also linked reflex impairment with sublethal changes in behaviour. For example, poor RAMP scores have been associated with coho salmon migration failure (Raby et al., 2012) and walleye *Sander vitreus* and sauger *S. canadensis* moved shorter distances when they had poor scores after C&R – however, the fitness implications of the reduced movements were unclear (Eberts et al., 2018). The relationship between reflex impairment, stress physiology, and post-release behaviour after angling has not been assessed for wild white sturgeon.

Our previous work established that longer combinations of exercise and air exposure (i.e., simulated angling stress) can cause greater physiological and behavioural impairments in captive white sturgeon (McLean et al., 2016). Similarly, we recently showed that longer angling durations in a C&R fishery can cause similar physiological impairments in wild white sturgeon, which required sturgeon to undergo some degree of post-release rest (i.e., recovery) after release (McLean et al., 2019). In a holding pen study, Robichaud et al. (2006) also established the immediate hooking mortality from angling for white sturgeon was negligible (0.01%) and the short-term (72 h) mortality after release was low (2.6%). In the LFR, white sturgeon can experience a range of environmental conditions, with seasonal water temperatures ranging from below 0 °C during the winter to > 20 °C in the summer

months. In general, Fraser River maximum water temperatures have risen by $\sim 1.8^\circ\text{C}$ over the past 50 years (Patterson et al., 2007) and the number of summer days exceeding 20°C has doubled (Islam et al., 2019). In our captive study, two sturgeon experienced latent mortality after combined air exposure and exercise during warm temperatures ($> 15^\circ\text{C}$). In addition, we determined that warm water temperatures exacerbated the physiological and reflex impairment responses and increased recovery times for surviving individuals (McLean et al., 2016). The extreme biochemical alterations at high water temperatures have been proposed to be important factors to consider in the latent mortality of released fish (Wilkie et al., 1996). More specifically, higher water temperatures reduce an exhausted fish's ability to replenish intramuscular glycogen and return homeostatic intramuscular pH that changes in response to high levels of lactate that accumulated following anaerobic metabolism (Wood et al., 1983). Indeed, the C&R literature is replete with examples of increased risk of physiological disturbance, incidence of disease, energy expenditure, and mortality during high water temperatures (Crossin et al., 2008; Gale et al., 2013), but the effects of seasonal changes in environmental conditions have not been studied for angled white sturgeon in the wild.

In this study, we attempted to isolate and quantify the effects of water temperature and discharge, fight characteristics (e.g., fight duration and handling time) and fish size on physiological stress and reflex impairment in white sturgeon captured in the C&R fishery by working with the charter industry. We had three objectives: 1. to further study post-release survival of capture-tag-release events for white sturgeon in the wild; 2. to assess the physiological stress response of captured white sturgeon under different environmental conditions; and, 3. to assess how post-release state (physiological stress response and reflex impairment) and other factors associated with capture (environmental conditions, fight time, handling, fish size) may influence behaviour. We used a combination of acoustic telemetry data, and mark-recapture information provided by the Fraser River Sturgeon Conservation Society (FRSCS) Passive Integrated Transponder (PIT) volunteer tagging program, to determine survival of white sturgeon that were captured by angling and then released in the LFR. We then investigated factors underlying the physiological stress response and reflex response of white sturgeon, captured over a range of capture temperatures ($\sim 2\text{--}21^\circ\text{C}$) and river discharge rates (1270 to $9430\text{ m}^3\text{s}^{-1}$). Based on our previous work revealing correlations between RAMP scores and physiological stress measures in captive sturgeon (McLean et al., 2016), we predicted that variation in reflex impairment scores would be directly related to physiological status, the duration of the stressor (e.g., fight time/handling time), and environmental conditions. We also predicted variation in post-release movement metrics would be directly related to fight characteristics, stress physiology, and environmental condition at capture.

2. Materials and methods

2.1. Study site

The study took place between 05 May 2014 and 16 September 2016 in the LFR, B.C., Canada (Fig. 1). The LFR spans ~ 200 km from the delta, where the river mouth drains into the Pacific Ocean (Strait of Georgia) to the interior of B.C. at Hell's Gate, a confined canyon section that provides a natural upriver movement barrier to many fish (COSEWIC 2012; Fig. 1). Freshwater discharge varies yearly and seasonally with marked fluctuations noticeable over periods of a few days. Snowmelt constitutes 75% of the total runoff, beginning in April and increasing to a maximum in late May and early June ($\sim 8800\text{ m}^3\text{s}^{-1}$;

McLean et al., 1999). River discharge diminishes throughout the summer and fall and by mid-February the levels are at their lowest ($\sim 880\text{ m}^3\text{s}^{-1}$). The glacial melt and freshet season in the LFR causes periods of high flow and turbidity, with the highest water levels being experienced in mid-May to early June (McLean et al., 1999). The lower portion of the Fraser River up to river km $\sim 80\text{--}94$ near the town of Mission, B.C. (Fig. 1) is tidally influenced, with the maximum intrusion of the salt-wedge being km 20. Resident populations of fish, like white sturgeon, experience a broad range of river temperatures throughout the LFR on an annual basis. Surface water temperatures range seasonally from $< 0^\circ\text{C}$ to $> 20^\circ\text{C}$, with lower temperatures recorded during the winter months (January/February) and highest recorded temperatures occurring during summer, primarily late August. Surface water temperature was measured at the time of capture and daily average river discharge rates were obtained from the Government of Canada's real-time hydrometric data service at the Hope, B.C. location, ~ 50 km downstream of Hell's Gate (Fig. 1; available at <https://wateroffice.ec.gc.ca>).

2.2. Capture and sampling

To ensure relevance of our research, we partnered with the recreational fishing community (Cooke et al., 2013). The following protocols conformed to regulations established by the Canadian Animal Care Committee, via permits issued by the Dalhousie Animal Care Committee (protocol #04-12) and the British Columbia FLNRORD Scientific Fish Collection Permit SU14-94586). White sturgeon ($N = 121$; 65 in May 2014, 5 in October 2014, 10 in December 2014, 16 in January 2015, 19 in May 2015, 1 in June 2015, and 6 in August 2016) were captured by rod-and-reel angling by experienced anglers from a charter vessel in the LFR. Fight times were recorded as the duration between hooking and landing. Upon landing, fish were positioned in a stern-mounted sling that facilitated processing and allowed fish to remain partially suspended in water and limit air exposure to the gills. Once maneuvered into the sling, a blood sample was taken from the caudal vasculature using a lithium heparin coated barrel syringe (4 mL Vacutainer, and 18 G, 3.8 cm needle; Becton-Dickinson, Franklin Lakes, NJ, USA) and placed on an ice-water slurry before processing. Time-to-bleed was recorded from landing to when the blood extraction occurred and averaged (\pm SEM) 3.49 ± 0.35 min (range 1–18 min). Sturgeon were measured (fork length, FL) to the nearest centimeter and in accordance with the FRSCS tagging program, were scanned for the presence of a PIT tag and implanted in the absence of one (reviewed in Nelson et al., 2016). Handling time was recorded from landing to release. Blood was tested for common markers of a physiological stress response following exhaustive exercise in white sturgeon (i.e., lactate, glucose, cortisol, chloride, potassium; see McLean et al., 2016, 2019). Within 15 min of sampling, $\sim 250\ \mu\text{L}$ of whole blood were analyzed for lactate (Lactate Pro LT-1710 portable lactate analyser; Arkray Inc., Kyoto, Japan) and glucose (ACCU-CHEK glucose meter; Roche Diagnostics, Basel, Switzerland) with point of care devices previously validated for use in fish (Stoot et al., 2014). Remaining blood was centrifuged (Portifuge; LW Scientific, Lawrenceville, USA) for 5 min at 3300 rpm. Plasma was transferred to cryovial tubes and frozen onsite on dry ice until it could be stored in a -80°C freezer. Plasma cortisol, chloride (Cl^-) and potassium (K^+), were later processed at the Department of Fisheries and Oceans, West Vancouver facility as detailed in McLean et al. (2016).

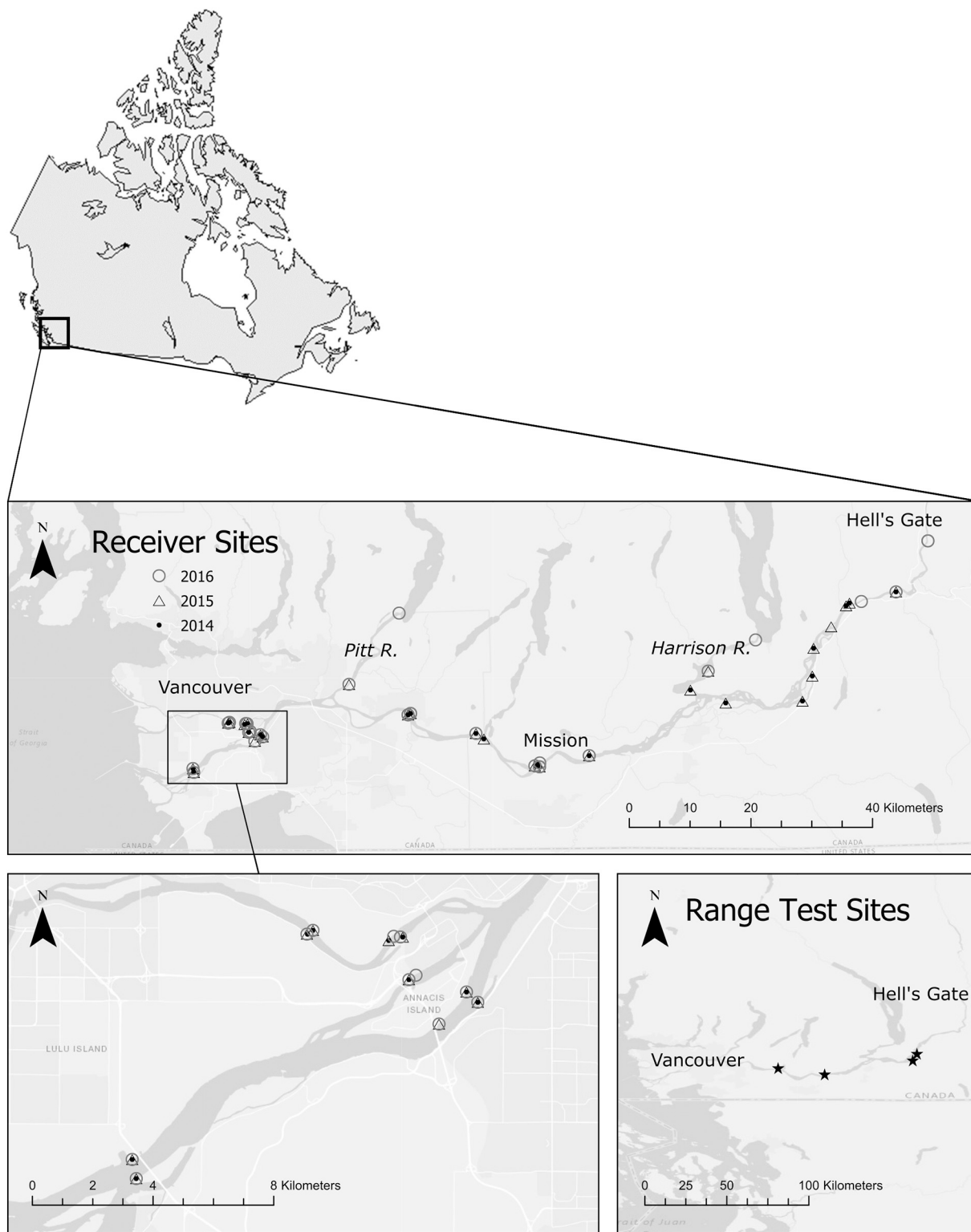


Fig. 1. Acoustic receiver sites for 2014, 2015 and 2016 in the lower Fraser River (LFR), B.C., Canada and tributaries – Pitt and Harrison Rivers. The LFR spans ~200 km from the delta, where the river mouth drains into the Pacific Ocean (Strait of Georgia) to the interior of B.C. at Hell's Gate, a confined canyon section that provides a natural upriver movement barrier to many fish. Range testing was completed at four sites as depicted by stars in the bottom right panel. White sturgeon, *Acipenser transmontanus*, were angled, biopsied and assessed for reflex impairment, implanted with Passive Integrated Transponder tags and acoustic transmitters (V16 series, VEMCO), and passively tracked to assess post-release survival and behaviour.

2.3. Transmitter implant

Sixty white sturgeon were implanted with acoustic transmitters (20 in May 2014, 4 in October 2014, 5 in December 2014, 27 in May 2015, 1 in June 2015, and 3 in August 2016). Following blood sampling, a small incision was made to the ventral surface, anterior to the pelvic girdle. A transmitter (VEMCO, Bedford, N.S. Model V16, 69 kHz, mm length x 16 mm diameter) was inserted into the body cavity following standard surgical protocol and as detailed in [McLean et al. \(2019\)](#). All surgeries were performed by two trained researchers and occurred in < 5 min. Each transmitter was uniquely coded and programmed to emit signals at a frequency of 69.0 kHz at randomly determined intervals varying from 130 to 330 s (V16-3 × and 4 × series, VEMCO). Estimated tag life for 40 of our tags was ~10 years (3393 to 3650 days) and 166 d for 20 tags. Surgical anesthesia was not used prior to surgery because there was not a tested and widely accepted method for anesthetizing adult sturgeon in the wild with minimal post-release consequences at the time. Large sturgeon are not often anesthetized in the field prior to surgical implantation (see [Kessel et al., 2018](#); [McLean et al., 2019](#)). Tagged sturgeon were inverted in the wetted sling with adequate water provided so that they would remain calm during surgeries. Acoustic signals were decoded and archived to memory by fixed VEMCO VR2W acoustic receivers ([Fig. 1](#)) when tags were within the detection range (~545 m; [Figure A1](#)), or by opportunistic active tracking using a VEMCO VR100 mobile receiver with an omnidirectional hydrophone. We utilized an existing array deployed and maintained by FLNRORD and Kintama Research Services. Receiver station coverage was designed for multispecies tracking studies in the system. Active tracking only occurred when fixed VR2W stations were being downloaded or maintained, or on days when we chartered the fishing boat to capture and sample fish.

2.4. Reflex impairment assessments

In 2015 and 2016, 26 of the captured white sturgeon were also tested for reflex impairment. Reflex tested fish included 21 individuals that received acoustic tags (Fish 40–60; [Appendix Table A1](#)). Sample size for acoustically tagged fish and physiologically sampled fish differed from those tested for reflex impairments because most of the wild sampling occurred before the impairment procedure was validated in the lab (see [McLean et al., 2016](#)). Reflex measures that were validated in lab and used subsequently in the field included ventilation, orientation, body flex and tail grab. Using a categorical assessment, individual reflexes were assigned a “0” if the reflex was unimpaired and a “1” if the reflex was impaired. Ventilation was unimpaired if the sturgeon exhibited regular ventilation for 10 s, as observed by watching the number of opercular movements. To test orientation, upon release, each sturgeon was placed upside-down just below the surface. An unimpaired orientation response was noted if the sturgeon righted itself within 3 s. The tail grab response was assessed by the handler attempting to grab the caudal peduncle while the sturgeon was fully submerged in water, with an unimpaired response characterized by an immediate burst-swim response to the grab. Body flex was tested by placing pressure on either side of the body near the pectoral fins. If the sturgeon actively struggled free it was recorded as an unimpaired response. All RAMP assessments were completed in < 30 s. Some sturgeon were too vigorous to allow for complete testing of reflexes and were assigned an overall unimpaired status ($N = 5$). An overall RAMP score was assigned to each fish as a proportion ranging from 0 to 1 of the total reflexes.

2.5. Post-release survival and movements

Post-release survival and movement metrics were determined by using fixed-place receivers ([Fig. 1](#); 31 in 2014, 29 in 2015 and 2016) distributed across several unique locations (17 in 2014, 21 in 2015, 18 in 2016) throughout the LFR. Receiver stations covered the LFR mainstem, the North Arm, and two primary tributaries, the Harrison and Pitt Rivers and the associated lake mouths ([Fig. 1](#)). Stations were considered unique if they were separated by > 1 km, and receivers < 1 km were grouped together. If acoustic tracking data was not available for a fish, we assessed survival by checking the FRSCS PIT database for recapture events. Several thousand PIT-tagged white sturgeon are captured, sampled, and released each year in the LFR as part of the FRSCS mark-recapture monitoring study ([Nelson et al., 2013](#)). In our study, if a fish was identified at two different locations over the course of the study period (865 d), it was considered to have survived the capture-and-release event. If a fish was detected in only one location, then the time between detections was taken into consideration and it was assumed that the fish was alive if the first detection occurred > 72-h after release, or if the first detection was made within 72-h but it also left the area for at least 24-h and then returned to be detected again. If no “movement” away from the station was apparent, and no other subsequent detections were made on other stations, then survival could not be confirmed. If a transmitter was not detected on any fixed VR2W or on the mobile VR100 at any time, the PIT recapture database was consulted to identify whether the fish was recaptured following the tagging event, and if so, that fish was considered to have survived the initial capture event. The LFR is a turbid environment with seasonal high currents, wave action and heavy commercial and recreational boat traffic that can affect the performance of acoustic transmission. Fish may have avoided detection due to poor signal reception during periods of high discharge (i.e., during spring glacial snowmelt) or other loud noise events, or may simply not have been detected due to the nature of their movement ecology (i.e., small home range between widely dispersed receivers).

White sturgeon behaviour in relation to an angling event has only been characterized in the wild for 30 min post-release ([McLean et al., 2019](#)). We analyzed several movement metrics to characterize the longer-term post-release behaviours of acoustically tagged white sturgeon. The linear distance from release site to first detection was calculated for each tagged fish as well as time to first detection (days; time metric). A rate of movement (km/day) and the total number of unique sites visited per day (activity metric) were also calculated and used as proxies of white sturgeon behaviour after release.

2.6. Data analysis

The five physiology variables measured (i.e., cortisol, lactate, glucose, chloride, and potassium) were placed into a varimax rotated principle components analysis (PCA) (‘principal’, package = “psych” and “GPArotation” to manage collinearity among responses). Varimax rotation is used to simplify the interpretation of a regular PCA by changing the coordinates to maximize the sum of the variances of the squared loadings. The goal of a varimax rotated PCA is to generate independent components or composite variables. This approach has been used in other stress physiology studies when there are multiple, presumably correlated, physiological metrics that have been measured in response to a stressor (e.g., [Struthers et al., 2018](#)). The first three rotated principle components axes (RC1, RC2, and RC3) were used as multivariate response variables that captured substantial variation in the blood physiology ([Table 1](#)). There were some missing values in the

Table 1

Parameters for the varimax rotated principal component analysis (PCA) that was performed on the five blood physiology variables collected from angled white sturgeon. RC1 was positively loaded with lactate and chloride, RC2 was positively loaded with glucose and potassium, and RC3 was positively loaded with cortisol.

PCA parameters	RC1	RC2	RC3
SS loadings	1.43	1.09	1.08
Proportion variance	0.29	0.22	0.22
Cumulative variance	0.29	0.50	0.72
Proportion explained	0.40	0.30	0.30
Cumulative proportion	0.40	0.70	1.00

blood physiology that we chose to impute ('imputePCA', package = "missMDA") rather than remove these fish from the dataset.

2.7. Linking angling, stress physiology and reflex impairment

Angling variables (fight time, water temperature, daily average water discharge) and fish size (FL) were fit to the ordinated blood physiology axes (RC1, RC2, and RC3) using the lm function in R to model the influence of factors related to the angling event on the physiological response variables.

Using a quasibinomial logistic regression with a logit link function, we also modelled the relationship between fish size, physiological status, fight characteristics (fight time, handling time), environmental conditions (water temperature, and daily average water discharge), and reflex impairment. Fish size was a fixed effect, fight and handling time were fixed effects representing the fight characteristics and the rotated principle component axes (RC1, RC2 and RC3) represented overall physiological status before release. Residuals were assessed for normality and heteroscedasticity using the Shapiro-Wilks ('shapiro.test') and Breusch-Pagan test ('ncvTest', package = "car"), respectively.

2.8. Post-release movement behaviour

We constructed generalized linear models and used model selection to test relationships between fight characteristics, stress physiology, fish size, environmental conditions, and fish movement metrics: linear distance between release site and first detection, time to first detections, the rate of movement (km/d), and the number of unique sites visited (activity metric). There was a strong correlation ($r > 0.70$) between the total number of days an individual was tracked in the system and the number of unique stations visited. To correct for this, we divided the number of unique locations visited by the total number of days tracked which resulted in an estimate of the number of unique sites visited per day as the activity metric.

The full candidate models contained fight time (FT), handling time, fish size (FL), surface water temperature at capture, the daily average water discharge on the date of capture, and ordinated blood physiology axes RC1, RC2 and RC3. All candidate models, including the null model (movement metric ~ 1) were compared using the bias-corrected Akaike Information Criterion (AICc) ('glmulti', package = "glmulti") and normalized evidence weights (AICw). According to this criterion, the model with the lowest AICc value is the most parsimonious in describing the data (Burnham and Anderson, 2002). Further, models with delta AICc < 2 and the highest AICw are considered to have the most substantial support (Burnham and Anderson, 2004). Because of the number of parameters used for model selection ($N = 8$), we had 256

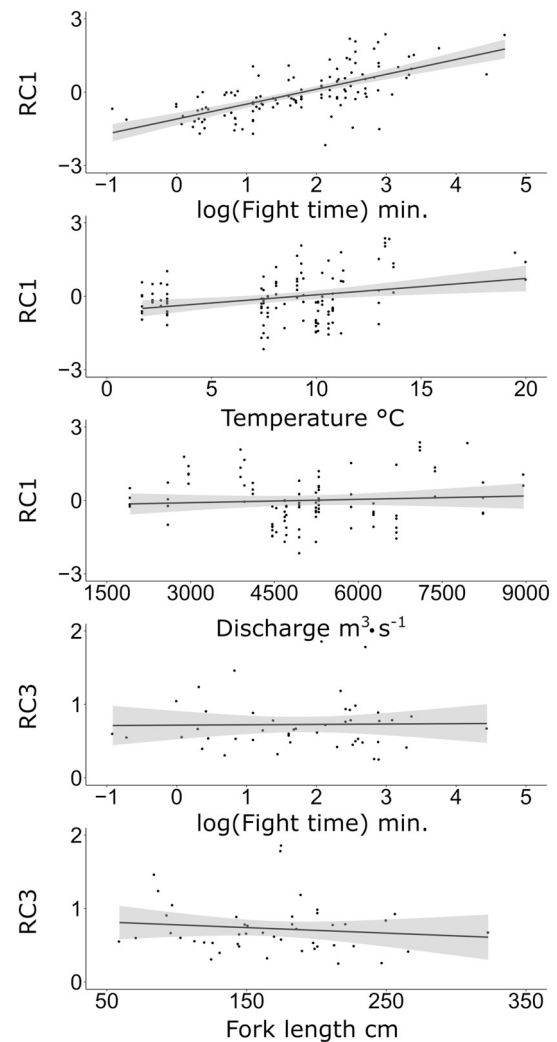


Fig. 2. Significant explanatory variables for ordinated blood axes RC1 and RC3 are shown. All variables were assessed for predictability of stress physiology via linear models. Ordinated blood axes RC1 (lactate + chloride) and RC3 (cortisol) are unitless. Capture temperature was measured at the time of capture, and river discharge rates were measured and reported as a daily average on the date of capture. There were no significant explanatory variables for RC2 (glucose + potassium). The solid line represents the fitted linear model and shaded areas are the 95% confidence limits.

possible models per movement metric (e.g., 2^8). In cases where multiple models had delta AICc < 2 , and for exploratory purposes, we considered all the models as part of a multi-model inference approach and obtained model-averaged parameter estimates and variances – or weighted averages of the model coefficients (terms) across the various models (with weights equal to the model probabilities). The single, most parsimonious model (highest AICw), was then chosen and model parameters were assessed at a significance of $P = 0.05$. The relationship between RAMP score and post-release movement metrics were explored via several analysis of variance tests and post-hoc comparisons were made using a Tukey-HSD test. All statistical analyses were conducted using RStudio (v. 1.1.456) and R (v. 3.5.3; R Core Development Team, 2019).

Table 2

Multiple regression outputs of wild white sturgeon blood physiology (n = 121), ordinated axes RC1 (lactate + chloride), RC2 (glucose + potassium), and RC3 (cortisol).

Dependent variable	Fixed effect	Value \pm SEM	t-value	P-value
RC1	(Intercept)	-1.82 ± 0.38	-4.84	< 0.001*
	Fork length	0.00 ± 0.00	1.38	0.17
	Log(Fight time)	0.35 ± 0.16	2.17	0.03*
	Temperature	0.01 ± 0.002	5.17	< 0.001*
	Daily average water discharge	-0.00 ± 0.00	-2.51	0.01*
RC2	(Intercept)	0.03 ± 1.02	0.03	0.97
	Fork length	-0.01 ± 0.01	-0.67	0.51
	Log(Fight time)	0.35 ± 0.37	0.94	0.35
	Temperature	-0.02 ± 0.03	-0.50	0.62
	Daily average water discharge	0.00 ± 0.00	-0.40	0.70
RC3	(Intercept)	-0.21 ± 1.03	-0.21	0.84
	Fork length	-0.02 ± 0.01	-2.35	0.02*
	Log(Fight time)	0.95 ± 0.45	2.12	0.04*
	Temperature	0.01 ± 0.06	0.16	0.87
	Daily average water discharge	0.00 ± 0.00	1.62	0.11

Blood sampling occurred immediately after capture by angling in the lower Fraser River, B.C. Water temperature at the time of capture ranged from ~2 to 20 °C and the daily average water discharge on the day of capture ranged from 1270 to 9430 m³·s⁻¹.

* Significance at $P \leq 0.05$ is denoted by an asterisk.

3. Results

3.1. Linking angling capture, stress physiology, and reflex impairment

A total of 121 juvenile, subadult, and adult white sturgeon ranging from 59 to 323 cm FL (164.0 ± 4.4 cm FL, mean \pm SEM; Appendix Table A1) were angled at water temperatures ranging from 1.7 to 20.4 °C (8.7 ± 0.4 °C) with daily average water discharge ranging from 1270 to 9430 m³·s⁻¹. The mean fight duration was 9.8 ± 1.3 min (range 36 s – 110 min) and mean handling time was 13.6 ± 0.8 min (range 3–49 min). Mean blood lactate concentration after angling was 2.9 ± 0.2 mmol·L⁻¹ (range 0.2–10.0), glucose was 2.9 ± 0.1 mmol·L⁻¹ (range 1.4–5.7), plasma cortisol was 22.8 ± 4.2 ng·mL⁻¹ (range 4.9–357.1), plasma chloride was 127.4 ± 0.5 mmol·L⁻¹ (range 111.7–147.0), plasma potassium was 2.8 ± 0.1 mmol·L⁻¹ (range 1.6–6.6). RC1 was positively loaded with chloride and lactate, RC2 was positively loaded with glucose and potassium, and RC3 was positively loaded with cortisol. Together these axes explained 72% of the variation in blood physiology (Table 1). Fight time, capture temperature, and daily average water discharge on the date of capture were all significant explanatory variables of the first ordinated blood physiology dependent variable (Fig. 2; RC1; $t = 2.26$, $P = 0.03$; $t = 4.45$, $P < 0.001$; $t = -2.51$, $P = 0.01$, respectively; see Table 2 for full model). Specifically, longer fight times, higher water temperature, and increased rates of water discharge were positively related to higher values of RC1 (lactate + chloride). There were no significant individual explanatory variables of the second axis, RC2 (full model in Table 2). For the third ordinated blood physiology dependent variable, RC3, both fish size and fight time were significant explanatory variables (Fig. 2; $t = -2.35$, $P = 0.02$ and $t = 2.12$, $P = 0.04$, respectively; Table 2). Specifically, RC3 (cortisol) was higher in larger fish and when fight times were longer.

Of the 26 white sturgeon tested for reflex impairment, 18 showed partial impairment with RAMP scores ranging from 0.25 (1 reflex impaired) to 0.75 (3 reflexes impaired), three exhibited complete

impairment (RAMP score = 1), and 5 were unimpaired (RAMP score = 0; Appendix Table A1). Orientation was the most prevalent reflex lost in impaired sturgeon, with 95% of tested fish unable to re-orient themselves following capture. Forty-two percent experienced abnormal ventilation, and 35% did not respond to a tail and/or body stimulus. There was no immediate mortality of any sturgeon captured by anglers. Only RC1 was significantly related to RAMP score with higher lactate + chloride concentrations resulting in a higher RAMP score (Fig. 3; $t = 2.54$, $P = 0.02$; full model is presented in Table 3). RC2 (glucose + potassium) and RC3 (cortisol) were not significantly related to RAMP score (Table 3).

3.2. Post-release survival and movements

In total, 60 (mean \pm SEM 195.6 ± 29.5 cm FL, range 150–269) sub-adult/adult white sturgeon were implanted with V16 acoustic transmitters to assess post-release survival and movement patterns (Appendix Table A1). Only sturgeon large enough (> 150 cm FL) to carry V16 tags were selected for surgery. Due to the apparent sedentary nature of some individuals of this population (Robichaud et al., 2017), using a minimum cut-off for travel distance or number of unique stations visited to assess survival was not appropriate, as has been done in previous studies (e.g., Atlantic sturgeon, Beardsall et al. 2013). Instead each movement profile was considered along with additional data from the PIT recapture database supplied by the FRSCS. The first detection or recapture event was used in subsequent analysis. For example, one fish (Fish 18) had a low post-release linear movement (0.1 km) based on acoustic detections, however, it was detected in the same location over multiple years, and was also recaptured in the fishery 37 km from the original release site 5 months after it was released for this study. Another (Fish 11) had a particularly unusual detection pattern, which suggested to us it may have originated upstream of the LFR. It was not detected on any fixed station post-release; however, it was recaptured in the fishery 824 d following the initial capture, and then detected on the mobile VR100 4 d after the recapture event. We believe this fish to be natal to the upper portion of the LFR, or even a middle Fraser River fish, since the original release, recapture, and detection on the mobile receiver occurred upstream of our last fixed-station south of Yale, B.C. (Fig. 1), and no detections were made on downstream stations. Another individual (Fish 44) was detected 18 days after release on the mobile receiver, 5 km from the release location and downstream of the last fixed VR2W station in our study system (Appendix Table A1). At the time of analysis, only one fish (Fish 3) was not detected on any of the fixed-stations, during mobile tracking, or recaptured in the FRSCS PIT database (Appendix Table A1), however, the recapture database was consulted a final time during preparation of this manuscript (April 2019), and it had been recaptured in 2018 and reported in the 2019 database. It was therefore considered to have survived the original C&R event. Overall, 100% of the fish tagged in our study were confirmed to have survived the original capture-tag-release event and were detected or recaptured within an average (\pm SEM) of 98 ± 32 days, ranging from 0.7 to 1641 days (Appendix Table A1).

To assess post-release movements we used a cut-off of 365 d, resulting in the removal of 3 of 60 acoustically tagged fish from further analysis (Appendix Table A1). The remaining 57 tagged fish were first detected within an average (\pm SEM) of 47 d (± 5.9) after their initial release. Average (\pm SEM) linear river distance from release site to first detection was 13.4 km (± 2.1). Fish were detected on an average of 7.5 (± 0.8) VR2W receivers and visited an average of 4.5 (± 0.4) unique stations. Rate of movement ranged from 0.01 to 5.4 km/d but averaged (\pm SEM) 0.7 (± 0.1) km/d. The most parsimonious model to predict

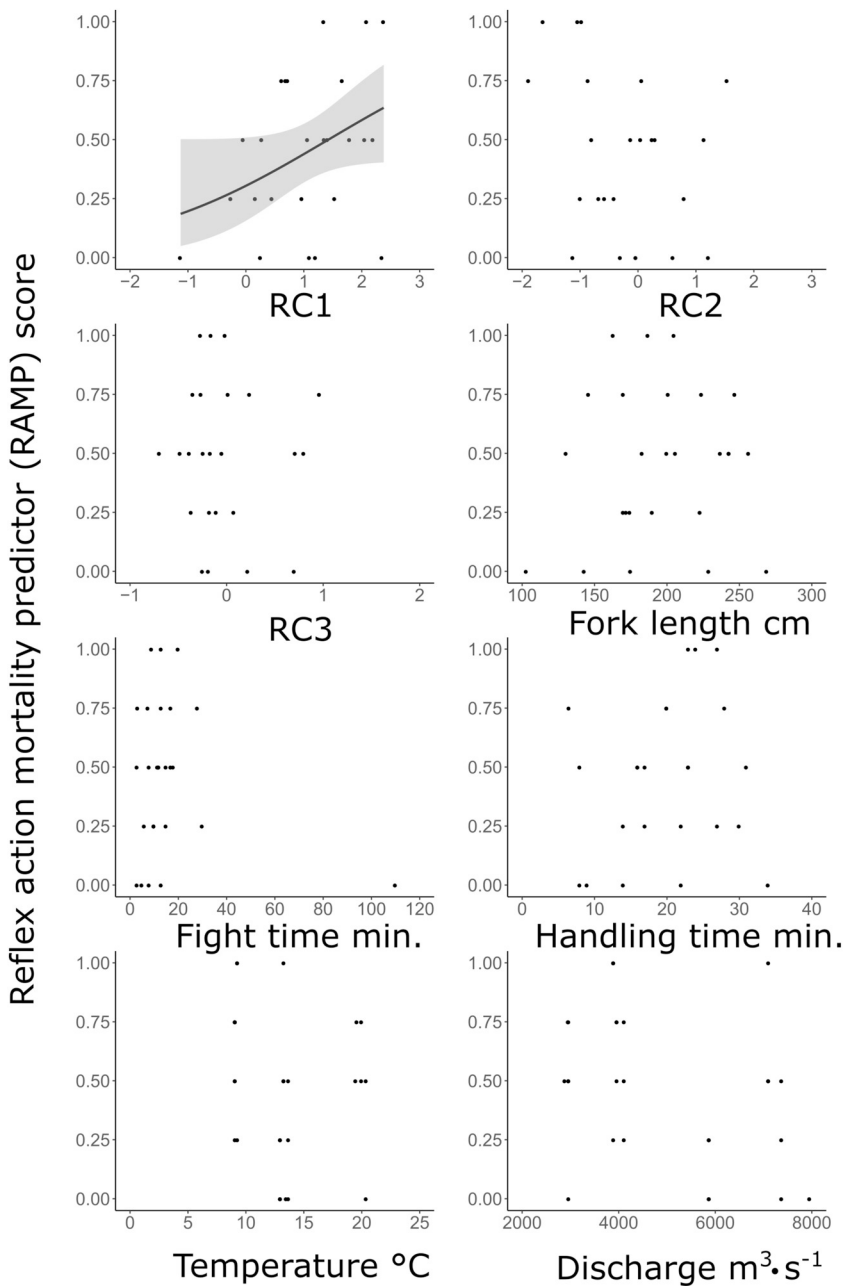


Fig. 3. Raw data of each explanatory variable plotted for reflex action mortality predictor (RAMP) scores collected from 26 white sturgeon after a catch-and-release angling event in the lower Fraser River, British Columbia. Explanatory variables were assessed for predictability of RAMP score via generalized linear model (GLM; family = quasibinomial, link = logit). Ordinated blood axes RC1 (lactate + chloride), RC2 (glucose + potassium), and RC3 (cortisol) are unitless. Surface temperature was measured at the time of capture, and river discharge rates were reported as a daily average on the date of capture. Only RC1 was a significant explanatory variable ($t = 2.65$, $P = .02$). The solid line represents the fitted GLM and shaded areas are the 95% confidence limits.

post-release linear distance included the ordinated blood parameters, RC1, RC2, fight time, fish size, and daily average water discharge (Table 4). Specifically, higher RC1 (lactate + chloride) and longer fight times resulted in reduced linear distances ($t = -4.83$, $P \leq .001$, and $t = -2.76$, $P = .01$, respectively). Contrastingly, higher RC2 (glucose + potassium) resulted in higher linear distance ($t = 3.37$, $P = 0.001$). Larger fish and those caught during periods of higher discharge, also resulted in higher linear distance ($t = 3.55$, $P = 0.001$, and $t = 2.63$, $P = 0.01$, respectively). Model-averaging of the importance of terms revealed average daily water discharge and RC1 were the top explanatory variables of linear distance across all 256 models (Appendix Fig. A2).

The null model was the most parsimonious for days to first detection

(~1), although handling time, fork length, RC1, RC2 and RC3 appeared in lower order models (Table 4). Model-averaging revealed that fish size was the most important term for predicting the days to first detection (Appendix Fig. A2) but no variable was significant.

The most parsimonious model for predicting the number of unique sites visited/day (activity metric) included ordinated blood parameters RC1, RC2, and RC3 (Table 4). All variables explained a large proportion of the variance when model-averaging was used to assess the importance of terms across all models (Appendix Fig. A2). RC1, RC2, and RC3, however, were not found to be significant explanatory variables of the activity metric ($t = 1.47$, $P = 0.15$, $t = -1.40$, $P = 0.17$, $t = 1.43$, $P = 0.16$, respectively). Daily average water discharge and fish size also appeared in lower order models (Table 4).

Table 3

Multiple generalized logistic regression (quasibinomial with logit link function) outputs of wild white sturgeon reflex impairment, or reflex action mortality predictor (RAMP), scores ($n = 26$).

Dependent variable	Fixed effect	Value \pm SEM	t-value	P-value
RAMP score	(Intercept)	1.60 \pm 2.22	0.72	0.48
	RC1	1.13 \pm 0.43	2.65	0.02*
	RC2	-0.21 \pm 0.31	-0.69	0.50
	RC3	-0.07 \pm 0.25	-0.29	0.78
	Fork length	0.002 \pm 0.01	0.21	0.83
	Fight time	-0.04 \pm 0.08	-1.12	0.28
	Temperature	-0.12 \pm 0.08	-1.46	0.16
	Daily average water discharge	-0.00 \pm 0.00	-1.48	0.16
	Handling time	0.01 \pm 0.05	0.14	0.89

Testing of reflexes occurred immediately prior to release following a catch-and-release by angling event in the lower Fraser River, B.C. Water temperature at the time of capture ranged from ~ 2 to 20 °C and the daily average water discharge on the day of capture ranged from 1270 to 9430 $m^3 \cdot s^{-1}$.

* Significance at $P = 0.05$ is denoted by an asterisk.

Table 4

We constructed generalized linear models and used model selection based on AIC to test relationships between fight characteristics, stress physiology, fish size, environmental conditions, and fish movement metrics: linear distance between release site and first detection, time to first detections, the rate of movement (km/d), and the number of unique sites visited (activity metric).

Dependent variable	Fixed effects	AICc	AICw
Linear distance (km)	RC1 + RC2 + FT + FL + Daily average water discharge	456.149	0.144
	RC1 + RC3 + FL + Daily average water discharge	456.818	0.103
	RC1 + RC2 + RC3 + FL + Daily average water discharge	457.733	0.065
	NULL	586.022	0.051
Time to first detection (d)	FL	586.697	0.037
	RC1	586.807	0.035
	RC2 + FL	587.370	0.026
	RC2	587.777	0.021
	RC3	587.817	0.021
	Handling	587.954	0.020
Unique sites visited/day	RC1 + RC2 + RC3	-41.922	0.104
	RC2 + RC3 + FL + Daily average water discharge	-41.330	0.078
	RC1 + RC2 + RC3 + FL	-41.229	0.074
	RC1 + RC2 + RC3 + FT	-41.229	0.074
	RC1 + RC2 + RC3 + Daily average water discharge	-41.229	0.074
Rate of movement (km/d)	RC1 + RC2 + RC3 + Temperature	-41.229	0.074
	RC1 + RC2 + RC3 + Handling	-41.168	0.072
	RC2	157.544	0.053
	NULL	157.939	0.044
	RC2 + FT + FL	158.505	0.033
	RC2 + FL	158.742	0.029
	FT + FL	159.152	0.021
	RC2 + Temperature	159.412	0.021
	RC2 + Handling	159.443	0.021
	FT	159.498	0.020

A total of 256 models were assessed per movement metric. Independent variables included ordinated axes RC1 (lactate + chloride), RC2 (glucose + potassium), RC3 (cortisol), daily average water discharge ($m^3 \cdot s^{-1}$), fish size (fork length; FL), fight time (FT), handling time, and water temperature at the time of capture (°C). The top models ($\Delta AICc < 2$) are presented. To explore the relationship between all parameters in the top models, we used a multi-model inference approach. The single most parsimonious model had the highest normalized evidence weight (AICw) and is indicated in boldface.

Table 5

Reflex Action Mortality Predictor (RAMP) scores (four tested reflexes represented as a proportion ranging from 0 to 1, where 0 = unimpaired, 1 = impaired) for white sturgeon after a capture-tag-release event were compared across three movement metrics: linear distance from release site to first detection, time to first detection (days), and the number of unique sites visited per day.

Dependent variable	RAMP score (n)	Mean \pm SEM	$F_{(DF)}$ -value	P-value
Linear distance (km)	0.00 (2)	31.40 \pm 16.30	1.12 _(4,16)	0.38
	0.25 (5)	19.76 \pm 7.50		
	0.50 (7)	13.54 \pm 6.28		
	0.75 (4)	22.45 \pm 11.20		
	1.00 (3)	1.76 \pm 0.69		
Time to first detection (d)	0.00 (2)	72.85 \pm 39.55	1.70 _(4,16)	0.20
	0.25 (5)	23.34 \pm 4.93		
	0.50 (7)	30.60 \pm 7.37		
	0.75 (4)	25.55 \pm 14.74		
	1.00 (3)	56.03 \pm 26.09		
Rate of movement (km/d)	0.00 (2)	0.78 \pm 0.65	0.91 _(4,16)	0.48
	0.25 (5)	1.00 \pm 0.36		
	0.50 (7)	0.58 \pm 0.25		
	0.75 (4)	1.24 \pm 0.73		
	1.00 (3)	0.07 \pm 0.05		
Unique sites visited/day	0.00 (2)	0.05 \pm 0.05	1.88 _(4,16)	0.16
	0.25 (5)	0.35 \pm 0.20		
	0.50 (7)	0.09 \pm 0.04		
	0.75 (4)	0.06 \pm 0.02		
	1.00 (3)	0.52 \pm 0.28		

Analysis of variance and post-hoc Tukey-HSD tests revealed that RAMP did not explain a significant proportion of the variance in any tested movement metric. Significance assessed at $P \leq 0.05$.

RC2 (glucose + potassium) was the only explanatory variable included in the most parsimonious model for significantly predicting rate of movement. Specifically, higher RC2 resulted in increased rates of movement ($t = 2.36$, $P = 0.02$). Although RC2 explained the most variance, model-averaging of terms showed fish size and fight time were important in lower order models (Table 4; Appendix Fig. A2).

Reflex Action Mortality Predictor (RAMP) scores (four tested reflexes represented as a proportion ranging from 0 to 1, where 0 = unimpaired, 1 = impaired) for white sturgeon after a capture-tag-release event were compared across four movement metrics: linear distance from release site to first detection, rate of movement (km/d), time to first detection (days), and the number of unique sites visited per day. Despite the lack of significance some trends were observed. There was a general trend toward smaller distances moved post-release and a reduced rate of movement when white sturgeon had poor outcomes for the RAMP test. For example, fully impaired (RAMP score = 1) fish moved an average (SEM) of 1.8 km from release site, whereas unimpaired (RAMP = 0) moved 31.4 km. The release locations could not be standardized in relation to their proximity to a receiver, however, so rate of movement is likely a better proxy for examining post-release behavioural consequences and although rate of movement for the fully impaired fish was lower (0.07 ± 0.04 km/d, mean \pm SEM) than unimpaired (0.8 ± 0.6 km/d), there was high variability in the rates of movement of sturgeon experiencing a range of RAMP scores. In general, RAMP did not explain a significant proportion of the variance in any fish movement metric (Table 5) and sturgeon that experienced reflex impairment (RAMP score > 0) did have rates of movement that were



Fig. 4. Example of a physiologically exhausted adult female white sturgeon (205 cm FL; captured May 26, 2015) being pulled into shore after capture (20 min fight time, $7110\text{ m}^3\text{ s}^{-1}$ river discharge, $13.3\text{ }^\circ\text{C}$ capture temperature) with a reflex action mortality predictor (RAMP) score of 1 (fully impaired). Post-release survival was confirmed via acoustic transmitter detections made ~ 2 months after release, despite the poor RAMP outcome.

the same as the population average of 0.7 km/d.

4. Discussion

From previous work, we know that the duration of an angling event (i.e., fight time) is related to increased levels of circulating metabolites (e.g., lactate; McLean et al., 2019). In the current study, we also investigated an environmental effect (water temperature and discharge). Recovery of captured and released fishes varies substantially among species (Muoneke and Childress, 1994) as do sublethal effects and temperature thresholds (Spicer and Gaston, 1999). For example, Wilkie et al. (1996) found that angling at temperatures above $20\text{ }^\circ\text{C}$ resulted in complete exhaustion of anaerobic muscle fuels in Atlantic salmon. Here, white sturgeon had higher measures of physiological disturbance at higher water temperatures, when discharge rates were higher, and when they fought longer. Specifically, longer fight times at higher water temperatures and higher discharge resulted in higher values of RC1 – the ordinated blood physiology axis positively loaded with lactate and chloride (Fig. 2). These results corroborate our previous findings in a lab study that found higher levels of lactate were associated with higher water temperatures, and that treatment time (forced exercise and air exposure) exacerbated the effect (McLean et al., 2016). Water temperature has been recognized as being a significant risk factor in C&R fisheries for salmon (reviewed in Gale et al., 2013; Lennox et al., 2017), and has been suggested as being partly responsible for the latent mortality of two of the captive sturgeon from our previous holding study (McLean et al., 2016). In this study, all fish survived the initial C&R event but only three were captured in water temperatures $> 19\text{ }^\circ\text{C}$ so survival above this threshold is unknown. Our results are important in the context of fisheries management, however, since during the warmest months (e.g., $> 20\text{ }^\circ\text{C}$ in summer) and during the highest levels of river discharge (e.g., up to $9430\text{ m}^3\text{ s}^{-1}$ in May 2014 during our study), fish are exposed to environmental conditions that may exacerbate their response to additional stressors. Seasonal or threshold-based closures as a management practice have been adopted by some fisheries in an effort to reduce the impact during physiologically sensitive warm-water periods (Lennox et al., 2017; Patterson et al., 2017), but relevant data that can contribute to estimates of survival for fish captured during these periods is often limited, as is the case for white sturgeon.

The impairment scores for white sturgeon angled in the wild were similar to those for captive white sturgeon (McLean et al., 2016), with orientation being the most impacted reflex, followed by ventilation, and finally tail and body flex. The significant positive relationship between

RC1 (lactate + chloride) and RAMP score (Table 3) was not surprising since lactate concentration has been shown to be related to increased reflex impairment in numerous studies (e.g., Raby et al., 2012; McArley and Herbert, 2014; Brownscombe et al., 2015), including our previous lab study on white sturgeon (McLean et al., 2016). Although we were unable to assess the efficacy of RAMP scores as predictors of post-release mortality rates in the wild, the relationship we found between stress physiology and post-release movement patterns (Table 4), as well as RC1 and RAMP (Table 3), suggests RAMP may be useful in providing a connection between stress physiology after capture and post-release behaviour. Assessments would be further improved if sample sizes were large enough to account for individual and seasonal variations, especially since most of our RAMP tested fish were captured in the Spring. Although white sturgeon moved much smaller distances and had lower rates of movement when they had poor outcomes for the RAMP test, RAMP scores in general did not explain a significant proportion of the variance in any fish movement metric (Table 5).

The inability for white sturgeon to reorient themselves following an angling event could be related to their open swim bladders (physostomous – connected directly to the oesophagus) and the change in pressure during the fight. Since sturgeon are primarily bottom feeders and often bottom-dwelling, angling gear is weighted to lay on the substrate while the bait attracts the fish. Depending on capture location and angler behaviour, the likelihood of impacts on swim bladder volume (Fertter et al., 2013) and reflex impairment may vary with the changes in depth experienced. Lake sturgeon (*A. fulvescens*) have been reported to experience tonic immobility, like sharks (Kessel and Hussey, 2015) when placed ventrally (Kessel et al., 2018). This could also explain the reaction in wild white sturgeon; however, this behaviour was not recorded in white sturgeon from our previous captive study (McLean et al., 2016), nor with unimpaired individuals from the current study, unless they were supported in a sling. The inability to reorient – and reflex impairment in general – could also be associated with complete exhaustion following angling. In our experience, white sturgeon that fought to exhaustion released air bubbles – presumably from the swim bladder – followed by a “belly-up” position as they were towed toward the boat or shoreline (Fig. 4). This observed response (e.g., release of gas from the swim bladder) should be further investigated in that it appears to be associated with a state of physical collapse in white sturgeon following angling. This could be associated with the higher concentrations of lactate found in fully impaired individuals; however, lactate is unlikely to be a causative agent and likely a by-product of the complex physiological pathways more directly responsible for inducing

impairment (Raby et al., 2013).

Our small sample size at higher temperatures ($> 15^{\circ}\text{C}$, $N = 5$) made it difficult to draw useful conclusions from the comparison of reflex impairment across different temperatures. The upper thermal tolerance for green sturgeon (*A. medirostris*) has been identified as $\sim 33^{\circ}\text{C}$, above which normal ventilatory function is inhibited (Lankford et al., 2003). Though they inhabit similar habitats, this is presumably beyond the range of white sturgeon thermal tolerance – especially for northern cooler-water populations like that in the LFR, but as far as we know a substantiated upper thermal tolerance threshold for white sturgeon has not been previously reported. In the current study, ventilation impairment was prominent (42% lost normal ventilatory function) but it occurred across a range of temperatures. Captive white sturgeon have been shown to have impaired ventilation in warmer water temperatures ($\sim 15^{\circ}\text{C}$), independent of treatment time (McLean et al., 2016), but small sample size likely made finding a relationship difficult in this case. Although longer fight times were associated with full reflex impairment, there were a few exceptions. For example, one individual fought for 110 min, did not show any visible signs of exhaustion (i.e., swim bladder release), and demonstrated a complete lack of reflex impairment upon release. This large (FL = 269.0 cm) female was captured when the water temperature was mild (13°C) and despite the long fight time at high river discharge ($7960\text{ m}^3\text{s}^{-1}$), experienced the population average for physiological disturbance. The same reduced physiological response was seen in the largest white sturgeon we captured (FL = 323.0 cm) despite being fought for 85 min, again at a mild temperature (13°C) but high discharge ($8240\text{ m}^3\text{s}^{-1}$). The cause of individual variability in physiological and impairment response to angling is unknown for white sturgeon. Several species have shown a reduction in stress responsiveness with increasing age (Andrews et al., 2017), so biological age, or simply even life-stage, may explain some of the individual variation seen in the white sturgeon stress response since we sampled across all life-stages (juvenile, sub-adult, and adult). Indeed, we found a negative relationship between the ordinated blood axis RC3 (cortisol) and fish size (Fig. 2) and for the acoustically tagged adults, fish size played a significant role in the post-release behaviours observed. Specifically, larger fish had longer post-release movements and although fish size was not significant, it appeared in lower order models as an explanatory variable for rate of movement and activity (unique sites visited per day; Table 4). The relationships between fish size, life-stage, previous experience, stress physiology, and post-release movement behaviour is a relationship that warrants further consideration.

On average, the 57 white sturgeon we analyzed were detected on 7.5 unique VR2W receivers and visited 4.5 unique locations. However, the range for unique locations visited was also broad (range 1–12) and supports previous findings that suggest there is high individual variability in the movement ecology of white sturgeon in the LFR (Robichaud et al., 2017). This finding is likely partially explained by the season they were captured and tracked since white sturgeon have been recorded as being less active during the colder, winter months (Robichaud et al., 2017). Additionally, water temperature and discharge change seasonally, and both appeared in lower order predictive models explaining some of the variance in three of the four movement metrics we analyzed (Table 4). In our previous study, we used calibrated acoustic transmitters equipped with accelerometer sensors and identified that white sturgeon locomotor activity was variable but lower activity was observed 10 + minutes post-release with few burst swim events (McLean et al., 2019). This is likely partially related to the increase in lactate that occurs during anaerobic exercise (Wood, 1991). Following physical exhaustion, a surplus of oxygen needs to be

delivered to tissues to cope with the increase in lactate via glycogen resynthesis. During this recovery process, there is a deficit of oxygen available for normal behaviour and other movements such as startle reactions and anti-predation behaviours (i.e., flight response) are inhibited. Although three white sturgeon that experienced full reflex impairment following capture were determined to have survived the capture-tag-release event, they had higher blood lactate concentrations than unimpaired fish and overall, higher physiological disturbance (higher RC1) was associated with a lower post-release movement distance (km) to first detection (Table 4). Although our results suggest there could be reduced locomotor activity that extends beyond the 50 min. observation period from previous work (see McLean et al., 2019), the results are somewhat equivocal. As mentioned above, there is high intraspecific variability in the movement patterns of white sturgeon in the LFR, including highly migratory and active individuals that cover large areas, as well as what appear to be more localized, sedentary individuals that consistently inhabit a smaller section of the river (Robichaud et al., 2017; E. Stoddard, FLNRORD, unpublished data). The array design used in this study was likely too coarse to allow precise estimates of angling-induced behaviour without biases associated with capture and release location and season. We suggest future work examining the long-term behavioural patterns of sturgeon utilize fine-scale arrays (e.g., Vemco Positioning System – VPS) where receiver ranges overlap and the time between release and first detection, or subsequent detections, are closer together to account for seasonal variability in movements. Nonetheless our work highlighted intriguing variance in the post-release behaviours that warrants future consideration.

Overall, an understanding of how different components of catch-and-release angling (handling, fight time, water temperature, water discharge, fish size) contribute to post-release survival is imperative to the development of scientifically based guidelines and regulations for the recreational angling of all fish species (Brownscombe et al., 2019; Cooke and Suski, 2005), including white sturgeon. This is particularly important for imperiled species to ensure that fishing activities do not impede population recovery and where optimal fishing and fish handling practices are needed. Reduced fight and handling times, and fishing in water temperatures below thresholds for thermal stress are likely to reduce sublethal consequences and potential latent mortality associated with the capture event. More work is needed to understand the thermal limits for northern populations of coldwater white sturgeon, but our previous work has shown ventilation impairment at 15°C (McLean et al., 2016) and LFR white sturgeon regularly experience in-river temperatures $> 20^{\circ}\text{C}$ during summer. Our study also highlighted the importance of water discharge rates on the stress physiology and post-release behaviours of white sturgeon. Because lactate and chloride were independently affected by high discharge, warmer river temperatures, and longer fight times, we suggest these factors are all important to the future management of this species.

5. Conclusion

Our results revealed a high degree of intraspecific variation in physiological and reflex impairment responses. Often in the field of comparative and ecological physiology there is a focus on central tendencies (“Tyranny of the Golden Mean”, Bennett, 1987; Williams, 2008) but individual variability in the physiological stress and reflex impairment responses of wild white sturgeon is prominent and identifying other drivers behind this variation is an important area of future research. How the individual was fought (i.e., angler skill and experience) and how the fish fought back should also be considered in future

work. The amount of time an individual fish spends using anaerobic high-speed burst swimming vs aerobic sustained swimming would likely help explain some of the variation highlighted in the current study and may be influenced by fish age, sex, life-stage, and experience. Angler behaviour – which includes gear selection, time and location of fishing, and how the angler interacts with the fish when it is on the line (e.g., fight time, fight intensity) – has also been recently recognized as being an important factor to consider when assessing an outcome (e.g., fish condition, health, fitness and survival; [Brownscombe et al., 2017](#); [Cook et al., 2018](#)). We worked aboard a charter vessel with much experience in fish capture and handling. It is possible that anglers fishing from shore or those with less experience (including improper gear) may fight fish for much longer periods and in doing so lead to a potential greater level of fish exhaustion. Lastly, although our work highlighted the sub-lethal changes in physiology, reflex impairment, and behaviour after angling there is still much to be done. We suggest future work investigate the long-term impacts of repeated capture and release since research on other species has shown that changes in behaviour following angling can have serious fitness implications (e.g., disruption to foraging and/or spawning migrations). Taken together, studies like this may help in the support or development of guidelines or regulations to enhance the sustainability of targeted white sturgeon populations and the fishery-based economies that rely on them.

Contributions

MFM, MKL, SGH, SJC, and GTC, secured funding for this project. All coauthors contributed to the initial study design. DAP oversaw blood physiology assays. ES and DWW provided infrastructure and technical support. MFM and ES performed field work and contributed to data generation. MFM, with support from MKL, analyzed the data. All authors provided critical feedback and approved the final version of this.

Funding information

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Appendix A

Includes detailed methods and results for range testing performed in the lower Fraser River before transmitter deployment. Also included:

1. Summary table of the original capture-tag-release events and subsequent detection/recapture information
2. Figure of the range detection results.
3. Figure of the model-averaged importance of terms (predictor variables) for each movement metric (dependent variables).

A.1. Detection range testing of acoustic receivers

The range an acoustic receiver can detect a transmitter can be impacted by multiple factors, including background noise and turbidity ([Kessel et al., 2014](#)). The glacial melt and freshet season in the LFR causes periods of high flow and turbidity, with the highest water levels being experienced in mid-May to early June ([McLean et al., 1999](#)). To establish the effective detection range for passive acoustic receiver stations, extensive range testing was conducted at four stations ([Fig. 1](#)) in the third week of May 2015. Testing was completed by deploying a V16 test transmitter (fixed delay of 6 s) from a vessel on a weighted cable while drifting downstream past the receiver. The tag was positioned so that it was just above the bottom and drifts were conducted in mid-channel and on the bank opposite of each receiver site. A VR100 mobile receiver was also deployed from the vessel during each drift to confirm the transmitter could be detected at short range and to record the GPS location of the boat in relation to the receiver site. The distance from VR100 recorded GPS and the fixed VR2W station was calculated. For each VR2W station, the VR100 and VR2W detections were sorted by distance and then the number of detections made by each within the study period were recorded. We used the number of detections on the VR100 as the expected number of detections, given the proximity of the VR100 to the transmitter, and those made on the VR2W as the observed number of detections. We used the average distance for each drift. For each distance, the proportion of detections was calculated as the ratio of observed to expected detections. The proportion of detections at each distance was calculated for four VR2W stations and plotted in R for visualization. A loess regression was fitted to the data and the distance associated with a 95 and 50% proportion of detection was estimated from the curve.

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Declaration of Competing Interest

The authors declare no conflict of interest.

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Table A1
 Summary of the original capture-tag-release event and subsequent first detection/recapture information for 60 white sturgeon *Acipenser transmontanus* in the lower Fraser River, British Columbia, Canada, arranged in chronological order of the capture and release event. White sturgeon were angled, biopsied for physiological indicators of stress, internally implanted with acoustic transmitters (V16 series) and Passive Integrated Transponder tags and monitored post-release using a series of fixed passive receivers, occasional active tracking using a mobile receiver, and by volunteer anglers as part of the Fraser River Sturgeon Conservation Societies mark-recapture program (see Nelson et al., 2016).

Fish no.	Acoustic ID	Size (FL, cm)	Season	Water temp. (°C)	Discharge (m ³ s ⁻¹)	RAMP score	First detection or recapture date	First detection/recapture (days)	Linear distance (km) between release and first detection/recapture	Last detection	(d) Tracked	# fixed VRWs detected on	# unique locations visited
1	25056	166	Spring	8.1	5300	-	2014-05-05	0.7	0.1	2016-08-04	821.7	2	2
2	25057	227	Spring	8.1	5300	-	2014-05-16	11.4	0.4	2016-11-13	912.5	11	5
3 ^a	25058	266	Spring	8.1	5300	-	2018-11-01	1641	-	-	-	0	0
4	25059	181	Spring	8.1	5300	-	2014-07-22	78.5	7.2	2014-07-26	4	1	1
5	25060	156	Spring	8.1	5300	-	2014-07-13	69.8	3.3	2016-10-17	826.4	15	9
6	25061	216	Spring	8.1	5300	-	2014-08-06	93.3	4.4	2015-09-06	395.9	2	2
7	25062	221	Spring	7.4	5250	-	2014-05-15	9.9	16.3	2016-10-03	871.2	11	5
8	25063	162	Spring	7.4	5250	-	2014-06-05	30.5	2	2016-09-16	834	4	4
9	25064	150	Spring	7.4	5250	-	2014-06-19	45	20.1	2016-10-04	837.9	16	8
10	25065	183	Spring	7.5	4950	-	2014-07-08	62.2	33.1	2016-10-05	820	13	7
11	25066	172	Spring	7.5	4950	-	2016-08-08 (recap.); 2016-08-12 (detect)	828	7.2	2016-08-12	1	0	1
12	25067	186	Spring	7.5	4950	-	2014-06-27	51.6	55.7	2016-10-24	850.3	9	4
13	25068	212	Spring	7.5	4950	-	2014-06-02	26.9	41	2014-06-07	4.6	1	1
14	25069	213	Spring	7.5	4950	-	2014-06-25	49.6	50	2016-11-09	867.5	7	3
15	25070	165	Spring	7.7	4690	-	2014-09-09	124.2	5.1	2016-12-20	833.5	14	8
16	25071	160	Spring	10	4470	-	2014-07-22	72.2	26.7	2016-10-18	819.3	18	11
17	25072	199	Spring	10	4470	-	2016-06-02	753.3	20.3	2016-06-09	7	2	2
18	25073	190	Spring	10.1	4720	-	2014-05-16	4.9	0.1	2016-10-31	898.5	22	12
19	25074	183	Spring	10.3	5300	-	2014-06-08	25.4	14.3	2016-11-03	879	5	4
20	25075	250	Spring	10.3	5300	-	2014-09-06	115.1	4	2016-11-29	815.1	4	4
21	25419	174	Fall	9.4	2600	-	2015-03-23	143.8	4.9	2016-12-31	649.2	19	10
22	25420	168	Fall	9.4	2600	-	2015-04-10	161.2	4.9	2016-10-14	552.8	15	8
23	25421	151	Fall	9.4	2600	-	2015-02-06	98.1	4.9	2016-12-30	693.2	13	6
24	25422	201	Fall	9.4	2600	-	2015-04-11	162.1	4	2016-08-26	503.2	8	4
25	25423	162	Winter	2.6	1340	-	2014-12-03	1.1	0.5	2016-11-08	706.1	3	3
26	25424	194	Winter	1.7	1270	-	2014-12-03	1.5	2	2016-09-09	646	3	3
27	25425	198	Winter	1.7	1270	-	2014-12-22	19.2	0.5	2016-10-05	653	13	8
28	25426	201	Winter	1.7	1270	-	2014-12-04	1.6	1.5	2016-07-08	581.8	2	2
29	25427	194	Winter	1.7	1270	-	2014-12-09	6.6	1.5	2016-12-31	753.4	3	3
30	25433	192	Winter	2.9	1270	-	2015-05-18	116.5	5.1	2016-12-01	562.7	15	9
31	25434	180	Winter	2.9	1270	-	2015-05-30	128.3	19.2	2016-12-05	555.4	2	2
32	25435	211	Winter	2.9	1270	-	2015-02-14	23.6	5.1	2016-11-19	644.2	3	2
33	25436	191	Winter	2.9	1270	-	2015-01-22	2.2	5.1	2016-11-29	675.3	10	6

(continued on next page)

Table A1 (continued)

Fish no.	Acoustic ID	Size (FL, cm)	Capture date	Season	Water temp. (°C)	Discharge (m ³ s ⁻¹)	RAMP score	First detection or recapture date	First detection/recapture (days)	Linear distance (km) between release and first detection/recapture	Last detection	(d) Tracked	# fixed VRWs detected on	# unique locations visited
34	25437	183	2015-01-22	Winter	2.9	1270	-	2015-02-14	23.5	5.1	2016-10-06	599.7	13	7
35	25438	182	2015-01-22	Winter	2.9	1270	-	2015-04-07	75.7	5.1	2016-12-07	609.4	10	6
36	25439	177	2015-01-22	Winter	2.9	1270	-	2015-01-23	1.4	7.6	2016-12-31	708.6	11	6
37	25447	175	2015-01-30	Winter	2.2	1920	-	2015-03-22	51.2	7.6	2016-12-31	650.5	4	2
38	25448	181	2015-01-30	Winter	2.2	1920	-	2015-02-09	10.6	7.6	2016-11-28	657.5	8	4
39	25449	167	2015-01-30	Winter	2.2	1920	-	2015-02-04	5	7.6	2016-12-06	671.7	17	10
40	19587	172	2015-05-01	Spring	9.3	3900	0.25	2015-05-18	17.5	36.4	2015-10-10	144.9	11	6
41	19588	163	2015-05-01	Spring	9.3	3900	1	2015-08-15	106.5	0.6	2015-08-17	1.9	1	1
42	19589	187	2015-05-01	Spring	9.3	3900	1	2015-05-20	19.3	3	2015-10-08	140.9	6	5
43	19590	224	2015-05-05	Spring	9.1	4120	0.75	2015-05-19	14.7	1	2015-09-25	128.4	5	4
44	19591	190	2015-05-05	Spring	9.1	4120	0.25	2015-05-22	17	5.1	2015-05-22	1	0	1
45	19592	200	2015-05-05	Spring	9.1	4120	0.5	2015-06-19	45.2	7.3	2015-07-13	24.1	1	1
46	19593	201	2015-05-06	Spring	9.1	3970	0.75	2015-05-18	12.4	41.8	2015-09-06	111	17	9
47	19594	247	2015-05-06	Spring	9.1	3970	0.75	2015-07-14	69.4	41.8	2015-08-01	18	3	2
48	19595	243	2015-05-06	Spring	9.1	3970	0.5	2015-06-08	33.6	3.8	2015-10-19	132.5	7	5
49	19596	223	2015-05-22	Spring	13	5880	0.25	2015-06-23	32.2	38.1	2015-11-04	134.1	4	3
50	19597	170	2015-05-22	Spring	13	5880	0.25	2015-06-03	12.2	16.3	2015-09-29	118.4	6	5
51	19598	183	2015-05-26	Spring	13.3	7110	0.5	2015-07-12	47.9	20.1	2015-10-03	82.6	14	7
52	19599	205	2015-05-26	Spring	13.3	7110	1	2015-07-07	42.3	1.7	2015-07-07	1	1	1
53	19600	256.5	2015-05-26	Spring	13.3	7110	0.5	2015-05-26	0.9	1.7	2015-07-08	42.4	2	2
54	19601	243	2015-05-27	Spring	13.7	7380	0.5	2015-07-11	45.5	47.7	2015-11-09	120.8	5	4
55	19602	229	2015-05-27	Spring	13.7	7380	0	2015-06-29	33.3	47.7	2015-08-08	40.5	7	4
56	19603	174.5	2015-05-27	Spring	13.7	7380	0.25	2015-07-03	37.8	2.9	2015-07-05	1.6	1	1
57	22492	269	2015-06-03	Summer	13.5	7960	0	2015-09-23	112.4	15.1	2016-09-12	354.9	3	3
58	19562	237	2016-08-10	Summer	19.5	2890	0.5	2016-08-15	5.5	0.4	2016-09-15	30.6	3	2
59	19604	170	2016-08-11	Summer	19.6	2960	0.75	2016-08-16	5.7	5.2	2016-12-21	127	1	1
60	19563	206	2016-08-12	Summer	20	2970	0.5	2016-09-16	35.6	13.8	2016-11-15	59.8	1	1

^a Denotes a fish that was not detected using acoustic telemetry.

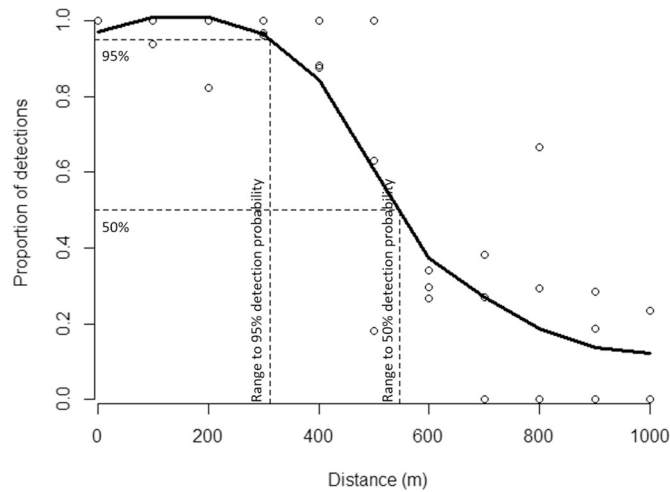


Fig. A1. Range metrics for acoustic receiver data. *Black circles* represent proportions of detections received on four VR2W passive acoustic receivers stationed throughout the mainstem channel of the lower Fraser River in May 2015. The *solid black line* is the logistic regression through data points and the *dotted black lines* represent the range metrics, labelled accordingly.

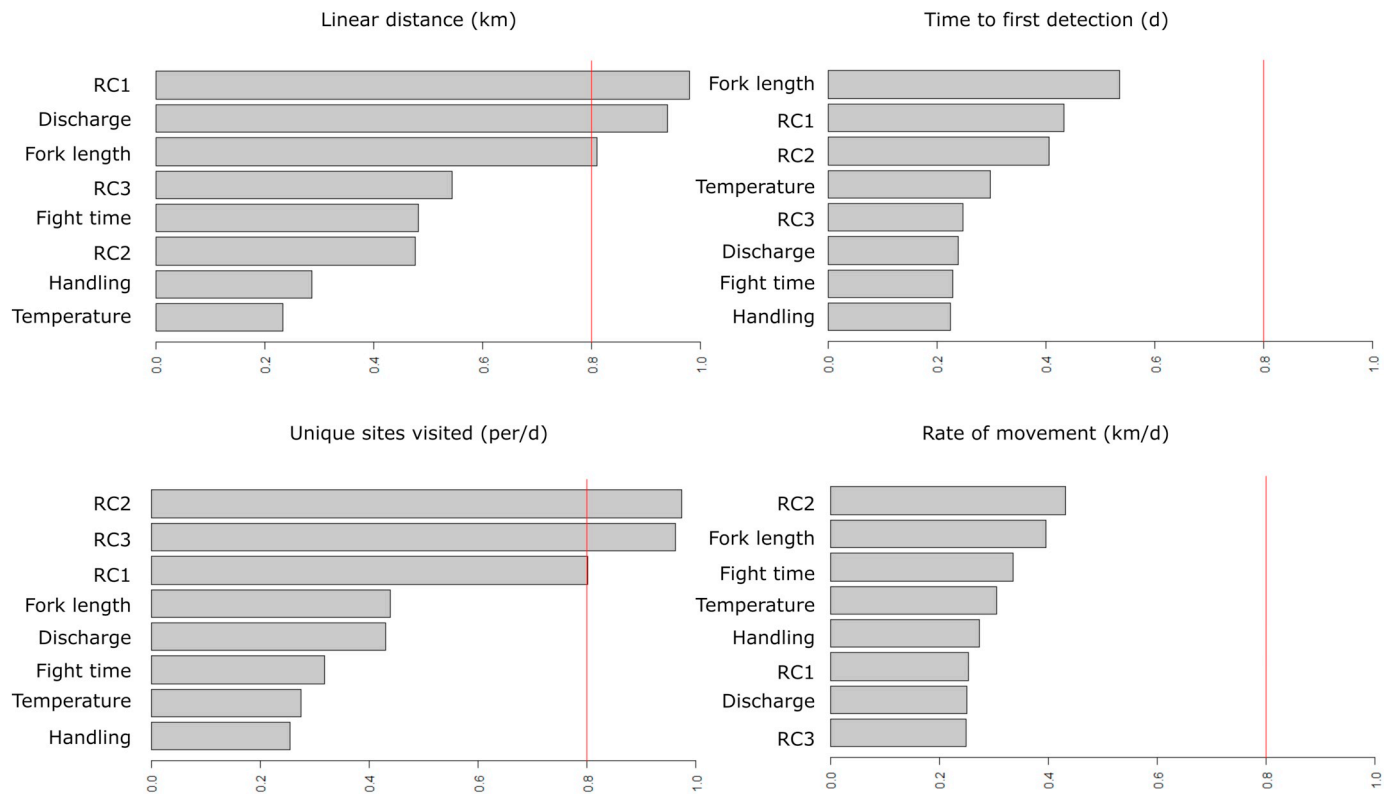


Fig. A2. The model-averaged importance of terms (predictor variables) for each movement metric (dependent variables). Ordinated blood axes RC1 (lactate + chloride), RC2 (glucose + potassium), and RC3 (cortisol) are unitless. Surface temperature was measured at the time of capture, and river discharge rates were reported as a daily average on the date of capture. The importance value for each term is equal to the sum of the weights/probabilities for the models in which the variable appears. A variable appearing in many models with large weights receives a high importance value. The vertical red line at 0.80 is sometimes used to visually identify “very” important variables. Plot was developed using the R package *gmulti*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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