Fisheries Research 214 (2019) 65–75

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Immediate physiological and behavioural response from catch-and-release of wild white sturgeon (*Acipenser transmontanus* Richardson, 1836)

M.F. McLean[a,*], M.K. Litvak[b], S.J. Cooke[c], K.C. Hanson[d], D.A. Patterson[e], S.G. Hinch[f], G.T. Crossin[a]

[a] Evolutionary Physiology and Animal Ecology Laboratory, Department of Biology, Dalhousie University, Halifax, B3H 1J8, Nova Scotia, Canada
[b] Fish Ecology and Aquaculture Laboratory, Department of Biology, Mount Allison University, Sackville, E4L 1E4, New Brunswick, Canada
[c] Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Sciences, Carleton University, Ottawa, Ontario, Canada
[d] US Fish and Wildlife Service, Abernathy Fish Technology Center, Longview, 98632, WA, USA
[e] Fisheries and Oceans Canada, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Vancouver, V5A 1S6, British Columbia, Canada
[f] Pacific Salmon Ecology and Conservation Laboratory, Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, V6T 1Z4, British Columbia, Canada

ARTICLE INFO

Handled by Bent Herrmann

Keywords:
White sturgeon
Exercise
Angling
Stress
Acoustic telemetry
Accelerometry

ABSTRACT

White sturgeon (*Acipenser transmontanus*) are anadromous and the largest fish occurring in fresh-water habitats in North America. The largest population is found in the lower Fraser River (LFR), British Columbia, Canada where anglers target the species in a catch-and-release (C&R) recreational fishery. Yet, little is known about the consequences of C&R on these wild fish. Sixty-three angled sturgeon had blood samples taken to assess the physiological stress response relative to fight times. Seven sturgeon were also fitted with acoustic transmitters equipped with accelerometer sensors to assess immediate post-release locomotor behaviour. To understand the relationship between accelerometry and fish behaviour, we calibrated the tags in a lab before deploying them in the field. A physiological stress response was apparent (i.e., increased whole-blood lactate and reduced plasma potassium) and was influenced by fight time. Post-release activity profiles showed a general decrease in activity over time. Post-release displacement was 2–75 m from the release site and all 7 sturgeon were relocated closer to shore. The possible preference we identified for nearshore areas after release should be examined in greater detail in the future as this may lend insight into optimal release locations for white sturgeon. Although C&R mortality rates are low for this species, there is some evidence of transient sub-lethal effects emphasizing the need to refine C&R practices to further improve fish welfare.

1. Introduction

Recreational angling is a common activity with many fish being subject to catch-and-release (C&R) whereby angled fish are subsequently released to comply with regulations or voluntarily as a result of conservation ethic (Arlinghaus et al., 2007). Although the premise of C&R fishing is high levels of survival and negligible sublethal effects (e.g., physiological alterations, behavioural impairments), that is not always the case (Cooke and Schramm, 2007). Over the past several decades much has been learned about the factors that influence C&R mortality (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Arlinghaus et al., 2007), yet comparatively less is known about sublethal consequences of C&R. The severity of the sublethal response varies with type and duration of the capture stressor, and on species-specific responses to stress (Cooke and Suski, 2005). Physiological changes occur as a result of anaerobic respiration that is activated during exhaustive exercise experienced by captured fish. These changes include a consumption of energy stores, lactate production, and osmotic/ionic disruptions (Kieffer, 2000; Wood, 1991). The stress of capture can be exacerbated by post-capture air exposure (Cook et al., 2015) and is mediated by water temperature (Gale et al., 2013). Capture and handling practices have also been demonstrated to disrupt upstream migration behaviour of salmonid fishes (Thorstad, 2003), impact post-release behaviour of bonefish (*Albula vulpes*) and influence their susceptibility to predation (Danylchuk et al., 2007). C&R has even changed behaviour of nest-guarding male black bass (*Micropterus* spp.)

* Corresponding author.
E-mail address: montana.mclean@dal.ca (M.F. McLean).

https://doi.org/10.1016/j.fishres.2019.02.002
Received 20 July 2018; Received in revised form 31 January 2019; Accepted 3 February 2019
0165-7836/ © 2019 Elsevier B.V. All rights reserved.

– potentially increasing risk of nest abandonment in the presence of nest predators (Hanson et al., 2007). Recently, duration and severity of post-release impairments of three angled reef fishes (common coral trout *Plectropomus leopardus*, emperor *Lethrinus* spp., and the Spanish flag snapper *Lutjanus carponotatus*) were studied under natural conditions using diver-recorded visual surveys (Raby et al., 2018). They found differences among the three species responses to simulated C&R with Spanish flag snapper spending significantly more time immobile when exposed to high stress treatment (Raby et al., 2018).

Understanding how individuals respond to fisheries-related stressors is the first step in understanding what effects, if any, this activity will have on wild populations (Patterson et al., 2017). However, not all environments allow for visual surveys of post-release behaviour. An alternate and effective way of studying effects of fisheries related activities on fish populations is through a combination of physiological assessments and surveillance of post-release behaviours and survival via electronic tracking (Cook et al., 2018; Cooke et al., 2002; Crossin et al., 2014, 2017; Donaldson et al., 2008; Patterson et al., 2017; Wilson et al., 2014).

Where angling is still permitted, sport fisheries for white sturgeon, *Acipenser transmontanus,* have grown in popularity throughout the species range along the west coast of North America (Columbia and Snake Rivers, Washington, U.S.A; Sacramento-San Joaquin Bay-Delta, California, U.S.A.; middle and lower Fraser River, British Columbia (B.C.), Canada; Hildebrand et al., 2016). In Canada, the lower Fraser River (LFR) population of white sturgeon is currently assessed as Threatened (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2012) and is the primary Canadian population exposed to an established recreational C&R fishery. Despite fishing pressures on white sturgeon, the physiological stress response and recovery behaviour have not been studied in the wild. In a study examining the post-release behaviour in relation to tagging and handling stressors on shortnose sturgeon (*Acipenser brevirostrum*), the authors suggested that the short-term behavioural adjustments made by fish post-release should be combined with physiological measurements as well as control animals to allow for behavioural comparisons that could be used to assess responses in the context of the physiological response to a fishery (Broell et al., 2016). The primary literature is sparse with respect to fisheries impact assessments on sturgeon species in the wild. Physiological changes (e.g., increased lactate) associated with longer handling times were observed in trawl-captured Atlantic sturgeon (*Acipenser oxyrinchus*; Beardsall et al., 2013) and recreational fishing for shortnose sturgeon (Struthers et al., 2018). Our previous lab study on white sturgeon showed that simulated stressors can elicit a physiological stress response that is directly related to the duration of combined exercise and air exposure (McLean et al., 2016). Species- and context-specific studies of fisheries interactions in the wild are especially important, as there may be opportunities to refine fisheries and handling practices to improve welfare outcomes for released fish.

Tri-axial accelerometers are being used with increasing frequency to provide insights on the biomechanics of fish swimming behaviour. Tri-axial accelerometers measure body movements along lateral, longitudinal, and vertical axes, at predetermined sampling frequencies. Estimating fine-scale behaviours such as activity levels has important implication for understanding energy dynamics, which is fundamental to the fitness of wild fish (Brownscombe et al., 2014a). This approach allows researchers to assess fine-scale locomotor behavioural changes (e.g., hyperactivity, hypoactivity) that occur as a result of fisheries capture and handling (e.g., Broell et al., 2016; Moser et al., 2017). Accelerometer transmitters have been used to determine the activity patterns for a number of free-swimming aquatic species (barracuda, *Sphyraena barracuda*, O'Toole et al., 2010; bonefish, *Albula vulpes*, Murchie et al., 2011; giant cuttlefish, *Sepia apama*, Payne et al., 2011; sockeye salmon, *Oncorhynchus nerka*, Wilson et al., 2013; dusky flathead, *Platycephalus fuscus*, Gannon et al., 2014; striped bass, *Morone saxatilis*, Tyrrell, 2014; muskellunge, *Esox masquinongy*, Landsman et al., 2015; sand flathead, *Platycephalus bassensis*, Stehfest et al., 2015), but only recently has the technology been used to address questions about changes in activity following an anthropogenic disturbance like a fisheries encounter. Tyrrell (2014) used accelerometer transmitters to characterize the post-release locomotor activity of striped bass following a C&R event and a recent pilot study suggested that accelerometer transmitters are potentially useful for monitoring the behaviour of green sturgeon (*Acipenser medirostris*) after gillnet capture and handling (Moser et al., 2017).

Here, we report on the first study to investigate the physiological stress response and recovery behaviour of wild white sturgeon. We had three objectives: 1) to determine the physiological stress response associated with increased fight times in the wild; 2) to describe post-release locomotor activity of white sturgeon after angling-induced exercise using acoustic tri-axial accelerometers; and 3) to identify any links between stress physiology and post-release locomotor activity. This is the first study on white sturgeon response to C&R angling. The results from our research have the potential to aid managers in the development of best-handling and release practices for sturgeon from wild fisheries.

2. Methods

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 Ministry of Forests, Lands, and Natural Resource Operations ([MFLNRO], Scientific Fish Collection Permit SU14-94586).

2.1. Field study site

The field component of this study took place between 08–21 May 2014, in the lower Fraser River (LFR), B.C., Canada (Fig. 1). The LFR spans ~200 km upstream, from where the river mouth drains into the Pacific Ocean, 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). 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 (~8800 $m^3 s^{-1}$, McLean et al., 1999). During intense snowfall years peak discharge can reach values up to 12 000 $m^3 s^{-1}$ (DFO, 2017). River discharge diminishes by late August and by late February the levels are at their lowest. The lower portion of the Fraser River is tidally influenced, with the location of the salt-wedge depending on the level of discharge. The LFR currently supports a large seasonal salmon fishery and a year-round world-renowned C&R fishery for white sturgeon.

2.2. Capture, sampling and surgery

White sturgeon were captured by rod-and-reel angling using a recreational fishing charter vessel in the non-tidal region of the LFR throughout May 2014 (Fig. 1; daily average water temperature = 8.9 °C). Angling was conducted by three research staff with a high-level of angling experience with the aid of two highly experienced professional fishing guides. Fight time was recorded as the time from when a fish was hooked until landing in a stern-mounted sling, a blood sample was taken from the caudal vasculature using a lithium heparin coated barrel syringe (4 mL Vacutainer, and 18 G, 1 ½ inch needle; Becton-Dickinson, Franklin Lakes, NJ, USA) and placed on an ice-water slurry for < 15 min before processing. Sturgeon were then measured (fork length [FL]) to the nearest centimeter. The overall condition of each captured fish was assessed upon landing and notes were made regarding any hook damage (foul-hooking, bleeding), net scarring, fresh wounds, or other visible signs of distress (e.g., bite marks). The weights of our captured sturgeon were estimated from the logarithmic transformation of the

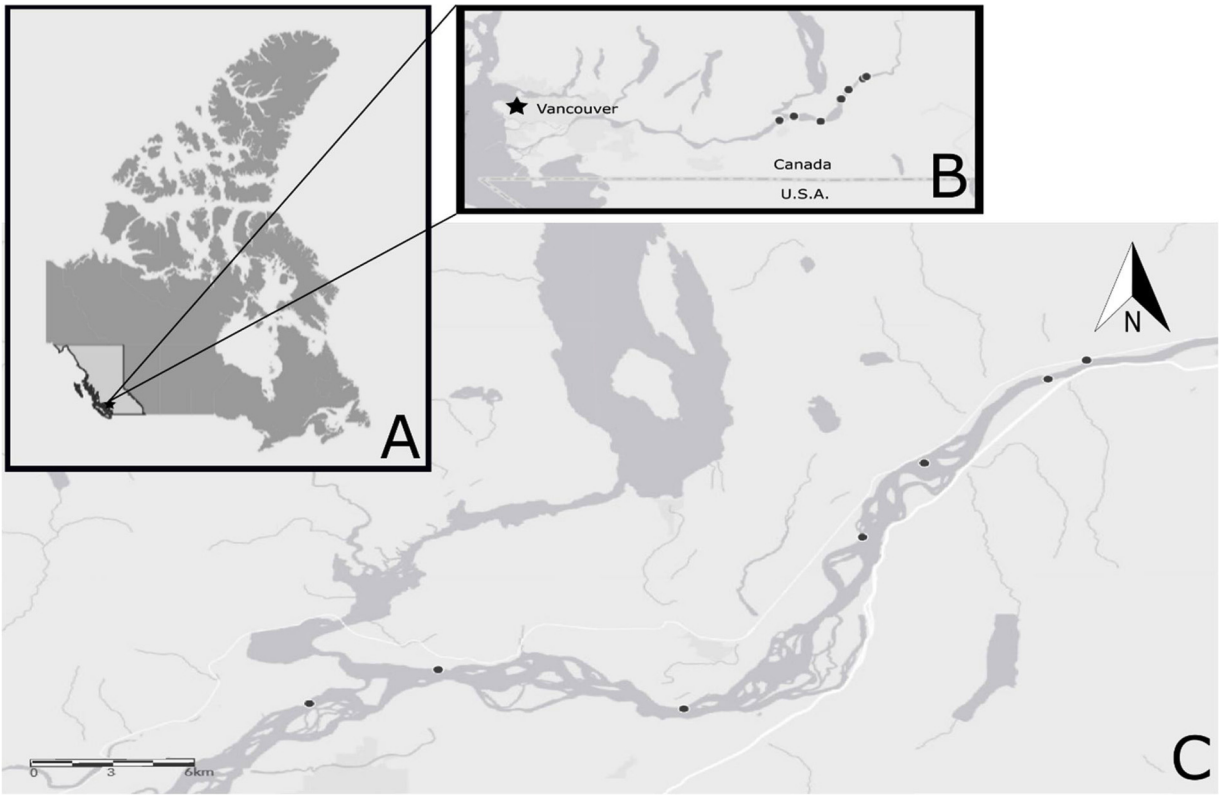

Fig. 1. A. Map of Canada highlighting the province of British Columbia (B.C.). B. and C. Capture and release locations for 7 white sturgeon, *Acipenser transmontanus*, in the non-tidal region of the lower Fraser River, B.C., Canada, which flows westerly through the province exiting south of Vancouver into the Strait of Georgia, Pacific Ocean. Sturgeon were angled, biopsied for physiological indices of stress, implanted with acoustic transmitters equipped with accelerometer sensors (V13A, Vemco), and manually tracked to assess post-release recovery behaviour.

linear regression equation: $\log(W) = -5.13 + 3.07\log(L)$ (or on the original scale, $W = 0.0059L^{3.07}$), where W is mass in kg and L is the fish length in cm. This equation was generated using publicly available historical catch information on average size/weight ratios for white sturgeon.

Following the blood sample, seven sturgeon were surgically implanted with an acoustic accelerometer transmitter (Vemco, Halifax, N.S., Model V13A, 69 kHz, 42 mm length × 13 mm diameter). All surgeries were performed by a single researcher and each occurred in < 3 min. A small incision (3 cm) was made to the ventral surface, anterior to the pelvic girdle, a transmitter was inserted into the body cavity, and the incision was closed with two interrupted absorbable sutures (Ethicon #Y267H Monocryl suture, precision point – reverse cutting, CP-1, 27-inch, size 0). Anesthetic was not used to decrease handling time and minimize behavioural changes associated with recovery from anesthesia.

2.3. Tracking

Sturgeon were immediately released, and individually manually tracked for up to 52 min using a VR100 portable acoustic hydrophone and receiver unit. Sturgeon locations were identified using a manual triangulation method (detailed in Taylor and Litvak, 2015) and one post-release location was calculated for each sturgeon within 30 min of release. A minimum of two researchers were required; one operated the directional hydrophone (Vemco model VH110) connected to the VR100 unit at the stern of the vessel, while the other followed the output of detections on the VR100 and directed the hydrophone operator on where to position the hydrophone. A compass was attached to a swivel to the top of the directional hydrophone and a combination of bearing and detection intensity was used to create a waypoint at that particular geographic location. The vessel was then moved to another location on an intersecting trajectory. A number of bearings and detection intensities were measured at the second location and the bearing with the strongest detection was recorded for that geographic location. The vessel was then moved the third and final location along another intercepting trajectory so the final detections could be recorded. Geographical coordinates were converted to Universal Transverse Mercator (UTM) to provide distance measures in metres. The three waypoints were used to triangulate a post-release position of the sturgeon by calculating the centroid coordinates of the triangle, with the equation: Centroid = $((N_1 + N_2 + N_3)/3, (E_1, E_2, E_3)/3)$, where N is the northing coordinate of each waypoint and E is the easting coordinate of each waypoint. The linear distance between release site and the triangulated position was calculated using the Pythagorean theorem, with the equation: Distance (m) = $((N_1 - N_2)^2 + (E_1 - E_2)^2)^{0.5}$. Positions were visualized using Google Earth Pro to determine whether post-release positions were upstream or downstream of the release site.

2.4. Physiology

Within 15 min of sampling, ~250 µL of whole blood was analyzed for lactate (Lactate Pro LT-1710 portable lactate analyser; Arkray Inc., Kyoto, Japan) and glucose (ACCU-CHEK glucose meter; Roche Diagnostics, Basel, Switzerland) – point of care devices previously validated for use in fish (Stoot et al., 2014). To determine hematocrit, ~70 µL of whole blood was then spun in a microhematocrit centrifuge (LW Scientific, Lawrenceville, GA, USA) for 5 min at 11 500 revolutions per minute (r.p.m.). The remainder of the blood sample was centrifuged (Portifuge; LW Scientific, Lawrenceville, USA) for 5 min at 3300 r.p.m. to separate red cells from plasma. Plasma was transferred to cryovial tubes and frozen on dry ice until it could be stored in a −80 °C freezer. Plasma was assayed for cortisol, chloride, sodium, potassium, and osmolality at the Department of Fisheries and Oceans West Vancouver

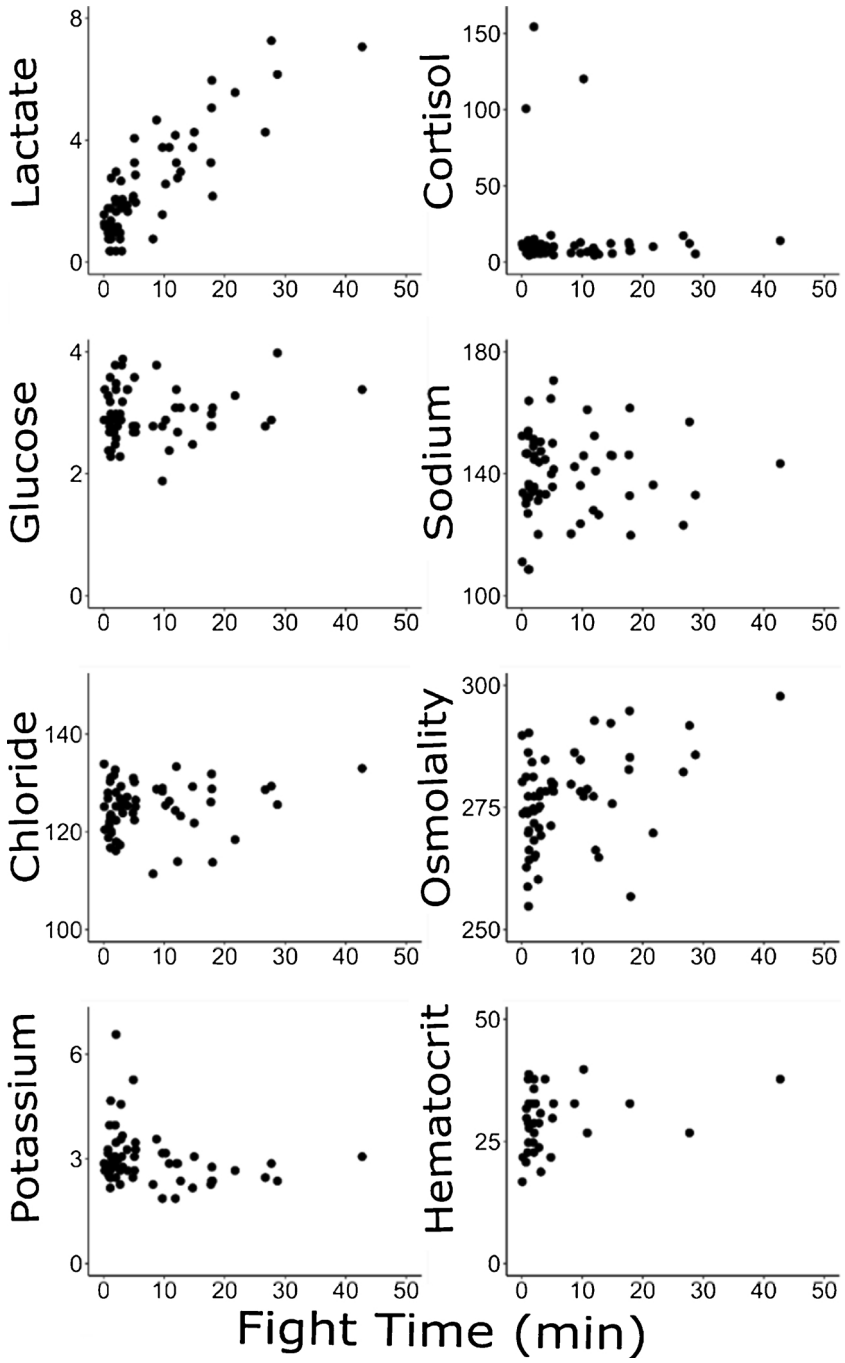

Fig. 2. Blood constituents from white sturgeon (n = 64) angled in the lower Fraser River, B.C. They are presented in raw form for various fight durations. Lactate, glucose, sodium, chloride, and potassium are presented in units mmol L^{-1}, cortisol in ng mL^{-1}, and osmolality in mOsmol kg^{-1}.

Laboratory, as detailed in McLean et al. (2016).

2.5. Accelerometer calibration in captivity

Accelerometer calibration trials were performed using tri-axial accelerometer acoustic transmitters, which have not been previously used in white sturgeon. Transmitters were surgically implanted into two captive white sturgeon (141.0 and 144.8 cm fork length) held at the US Fish and Wildlife Abernathy Fish Technology Center, WA, U.S.A. (latitude 46.2, longitude −123.1) ~450 km south of Vancouver, Canada, on February 25th, 2015. Sturgeon were housed in a long outdoor raceway (24.4 m in length × 2.4 m in width × 0.8 m in depth) with water provided at ~0.01 $m^3 s^{-1}$ from the adjacent Abernathy Creek, a tributary to the Columbia River. Average daily water temperature during swim trials was 8 °C (similar to wild releases). Each sturgeon was corralled into a modified sling and measured before surgery. Internal implantation of the tag was done using the surgical methods outlined above. All accelerometer transmitters used in this study were programmed to transmit every 25–35-s, with an acceleration sampling period of 22-s. The transmitters provided the mean acceleration in three axes over 22-s, at a rate of 5 Hz, with the root mean square (RMS) acceleration being calculated using the equation; $RMS = (X^2 + Y^2 + Z^2)^{0.5}$. The RMS had a range of 0.00–3.47 m s^{-2}.

Following surgery, sturgeon behaviour was monitored for ~2 h before they were forced to burst-swim. Sturgeon were physically chased around the raceway for 30-s, followed by 120-s rest period and then

another 30-s burst period. Acceleration transmissions were recorded using an acoustic receiver with an omnidirectional hydrophone. The burst trials were repeated until at least three burst-style accelerometer readings were obtained for each tagged sturgeon. A mean "burst swimming" activity value was calculated from all values obtained from both fish combined. When sturgeon were at rest the hydrophone was used to monitor "sedentary" activity and to obtain resting acceleration values. Further trials were run opportunistically to obtain acceleration values for cruising behaviour – swimming at a constant velocity. These accelerometer transmitter behaviours were classified as "sustained swimming" activity.

2.6. Analysis

Linear regression was used to test whether fish size (fork length, FL) was a predictor of fight time duration. Because this was the first study to physiologically sample wild white sturgeon, we wanted to explore the influence of fight time duration independent of size on all physiological indicators of stress. Since we found a significant relationship between fight time and body size we decided to control for the effect of body size on physiological dependent response variables by using the residuals from the fight time x fork length regressions (fork length corrected fight time) as the predictors, which by definition would now be fight time independent of fork length. Linear regressions were used to test the relationships of fight time with physiological response variables cortisol, glucose, lactate, sodium, potassium, chloride, osmolality, and hematocrit. Model residuals were tested for normality (Shapiro–Wilk test). Where log transformation was not successful in normalizing, a Theil-Sen nonparametric regression was used. As all measurements of stress could not be acquired from all fish, sample sizes differ among some statistical analyses. Immediate (within 5 min) accelerations were compared to fork length and fight time using Pearson correlation tests. The estimated amount of force exerted by each fish was calculated using the equation $F = ma$, where F is force in N, m is the fish mass in kg, and a is the average acceleration in m s^{-2}. All statistical analyses were conducted using RStudio (RStudio Team, version 1.1.447, 2018) and R (R Core Team, version 3.5.1, 2018). Significance was assessed with $\alpha = 0.05$. In cases where multiple independent statistical tests were run, a Bonferonni correction was applied and the adjusted critical p-value was used to assess significance.

3. Results

3.1. Capture and stress physiology

Sixty-three white sturgeon were angled (mean ± SE, 148.1 ± 6.3 cm FL) and 7 (195.4 ± 12.1 cm FL) were surgically implanted with accelerometer transmitters. Fight times averaged 7.4 ± 1.1 min for all angled sturgeon and 17.4 ± 5.2 min for tagged individuals. All fish showed a high level of condition upon capture with very few hook wounds, scarring, or other noticeable markings. One individual did present with a "bite mark" wound that appeared to be healed. Overall, fight time increased significantly with sturgeon body length (FL; $F_{[1,61]} = 353.6$, $p < 0.001$, $R^2 = 0.85$, log(y) = 2.9log (x) – 5.8). The relationships between fight time duration and physiology are presented as raw data in Fig. 2. However, due to the significant influence of body size on fight time duration, the residuals from the fight time x fork length linear regression (fork length corrected fight time) were used as the predictors for the linear models (Table 1). The Bonferonni corrected α used to assess significance was 0.006 ($p = 0.05$/8 independent tests). Fork length corrected (FLC) fight times were only significantly predictive of increasing blood lactate ($F_{[1,61]} = 11.2$, $p = 0.001$, $R^2 = 0.16$, y = 1.5x + 2.4; Fig. 3). There was also a noticeable trend, though not significant after correction, in decreasing plasma potassium ($F_{[1,59]} = 6.6$, $p = 0.01$, $R^2 = 0.10$, y = 0.2log (x) + 0.5; Fig. 3).

3.2. Acceleration calibration

Both tagged sturgeon exhibited typical behaviours immediately following surgery – including burst swimming away from the release site and cruising around the raceway. These were the same behaviours we observed in other captive sturgeon that were not part of the surgical trials. Calibration trials (n = 3/activity type) with the V13A transmitters revealed that "sedentary" sturgeon had acceleration readings ranging from 0.05 to 0.11 m s^{-2}. "Sedentary" activity typically corresponded with resting behaviour, with small fin movements to adjust position while the fish remained in a single location on the bottom of the raceway. "Sustained swimming" activity ranged from 0.12 to 1.59 m s^{-2} and typically corresponded with cruising behaviour, where the fish was swimming in the raceway at a relatively constant velocity. "Burst swimming" activity was measured while the sturgeon was burst swimming for 22 s and these values ranged from 1.54 to 3.47 m s^{-2}. The maximum capacity of the accelerometer transmitters in this study was 3.47 m s^{-2}.

3.3. Post-release activity in the Fraser River

Sturgeon tagged with accelerometer transmitters were tracked for 10–52 min which was dependent on the river conditions since it was difficult to manually track during peak freshet and high flows. Post release behaviour varied among individuals (Fig. 4). For example, four of seven sturgeon reached high accelerations upon release, followed by a period of low to moderate activity. Total track average accelerations were higher during the immediate 10 min post-release period (0.9 m s^{-2}) versus those collected after 10 min of tracking (0.5 m s^{-2}). All tagged sturgeon spent > 60% of their total tracking time in moderate sustained swimming speeds (Table 2) but there was some variability in the percent of the track spent burst swimming. For example, two sturgeon (Fish 100 and 101) spent considerably more time burst swimming (high accelerations) than the other five individuals (Table 2). There was no correlation between acceleration and sturgeon fork length (r = 0.1, n = 7, $p = 0.9$).

Triangulated positions for white sturgeon were made within 30 min of release. Distance from release site to triangulated positions ranged from ˜2 to 75 m with 3 out of 7 sturgeon located downstream from their release location, 2 upstream, and 2 laterally across the river (Table 3). Distance was not significantly correlated with fight time (r = −0.1, n = 7, $p = 0.8$), or body size (r = 0.2, n = 7, $p = 0.4$). However, there was a notable negative correlation between distance and max and mean acceleration (r = −0.7, n = 7, $p = 0.1$ and r = −0.7, n = 7, $p = 0.1$, respectively). Post-release distance from release site was significantly positively correlated with higher levels of glucose (r = 0.5, n = 7, $p = 0.03$) and negatively correlated with lactate concentration (r = −0.8, n = 7, $p = 0.05$). An estimate of force ranged from 22.7 to 192.8 N (Table 3).

4. Discussion

This is the first study to use physiological sampling and accelerometry to characterize the activity and behaviour of wild, freely ranging white sturgeon after recreational C&R angling. Indeed, such studies are rare among Acipenseridae. Consistent with the literature on a wide range of fish species, our analysis showed that longer fight times elicited greater physiological stress responses in white sturgeon relative to short fight times characterized by increases in blood lactate and decreases in plasma potassium. Calibration of the accelerometer transmitters in a lab setting allowed us to link specific swim behaviours to acceleration profiles, which were compared to values recorded from sturgeon in the wild. Upon release, acoustic accelerometry provided a snap-shot of the short-term post-release locomotor behaviour of seven individuals. Triangulation data revealed white sturgeon displacement distance was < 75 m from the release site with all seven sturgeon

Table 1
General linear regression models (or Theil-Sen nonparametric regressions in the case of cortisol) were used to test whether fight time duration was predictive of a physiological stress response. To correct for the significant effect of body size (fork length, cm) on fight time duration, the residuals from that linear model were used as the new predictors for the models presented in this table. Descriptive statistics for the physiological indicators of stress measured in blood collected from white sturgeon following angling are also shown.

Tested linear relationship w fight time (min) as predictor	*df*	F	R^2	*p*	Mean ± SEM	Range	Unit
x Lactate	61	11.5	0.16	< 0.001*	2.4 ± 0.2	0.4–7.3	mmol L^{-1}
x Cortisol	53	–	–	0.8	15.6 ± 3.5	5.1–155.1	ng mL^{-1}
x Glucose	61	0.0	< 0.001	0.9	3.0 ± 0.1	1.9–4.2	mmol L^{-1}
x Osmolality	60	1.7	0.02	0.2	276.8 ± 119.6	255.0–298.0	mOsmol kg^{-1}
x Sodium	58	0.2	< 0.001	0.7	140.3 ± 174.1	109.0–171.0	mmol L^{-1}
x Chloride	60	1.2	0.02	0.3	125.0 ± 0.7	111.7–134.2	mmol L^{-1}
x Potassium	60	6.6	0.10	0.01	3.0 ± 0.1	1.9–6.6	mmol L^{-1}
x Hematocrit	34	0.8	0.02	0.4	29.6 ± 1.0	17.0–40.0	% percent

* Denotes statistical significance at the level of Bonferonni adjusted P ≤ 0.006.

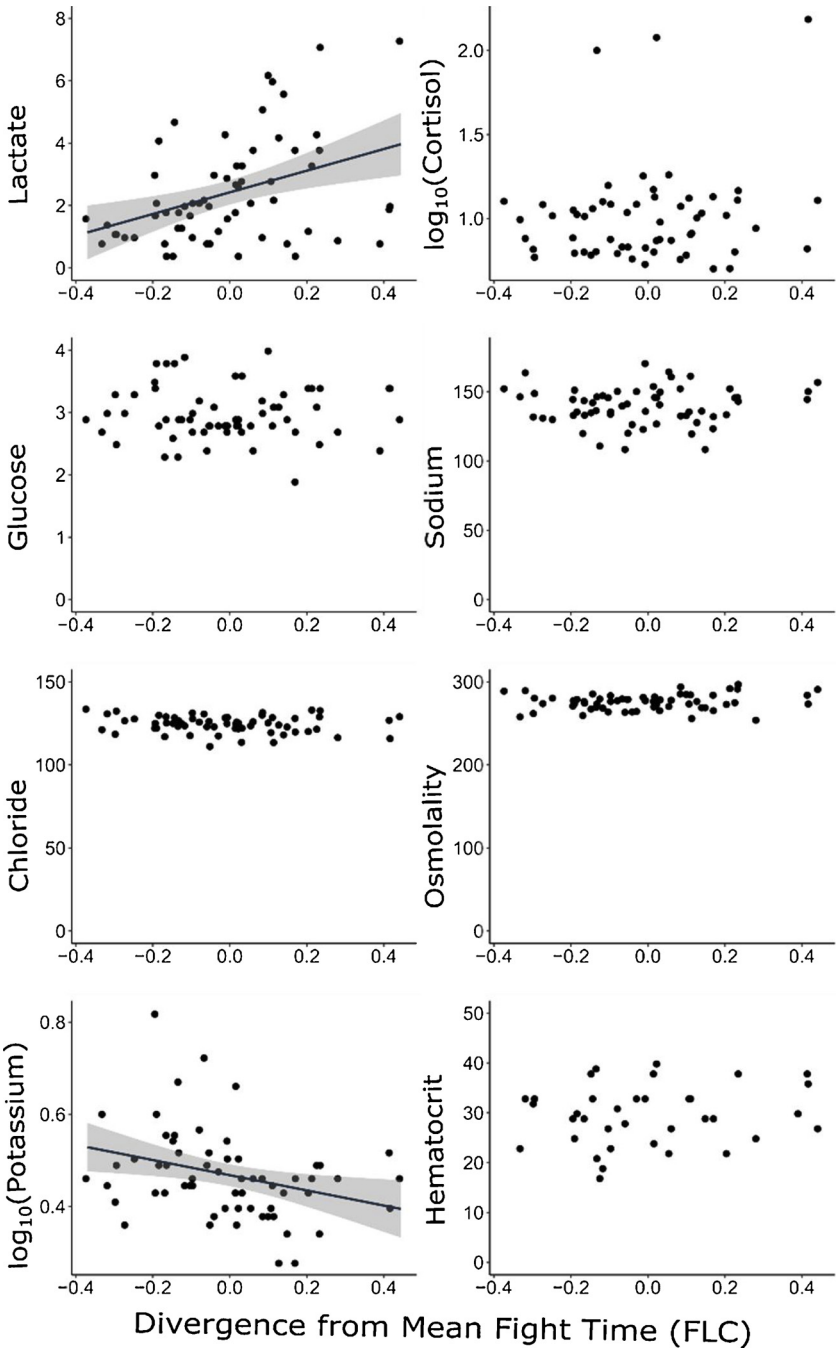

Fig. 3. Linear regressions were used to test the predictive relationship between fight time (min) and physiological indicators of stress sampled from white sturgeon (N = 63) after angling. Lactate, glucose, sodium, chloride, and potassium are presented in units mmol L^{-1}, cortisol in ng mL^{-1}, and osmolality in mOsmol kg^{-1}. To correct for the effect of fork length (cm) on fight time, the residuals of the linear model fight time ~ fork length were used in the subsequent predictive models (fork length corrected, FLC). Fight time was only significantly predictive of lactate concentration ($p < 0.001$). There was a trend in decreasing potassium with longer fight times, but it was not significant with respect to the Bonferonni adjusted *p*-value ($p > 0.006$). Individual black dots represent sample observations, the solid black line is the regression line for the linear model after correcting for fight time. Upper and lower 95% confidence limits are shown as grey bands.

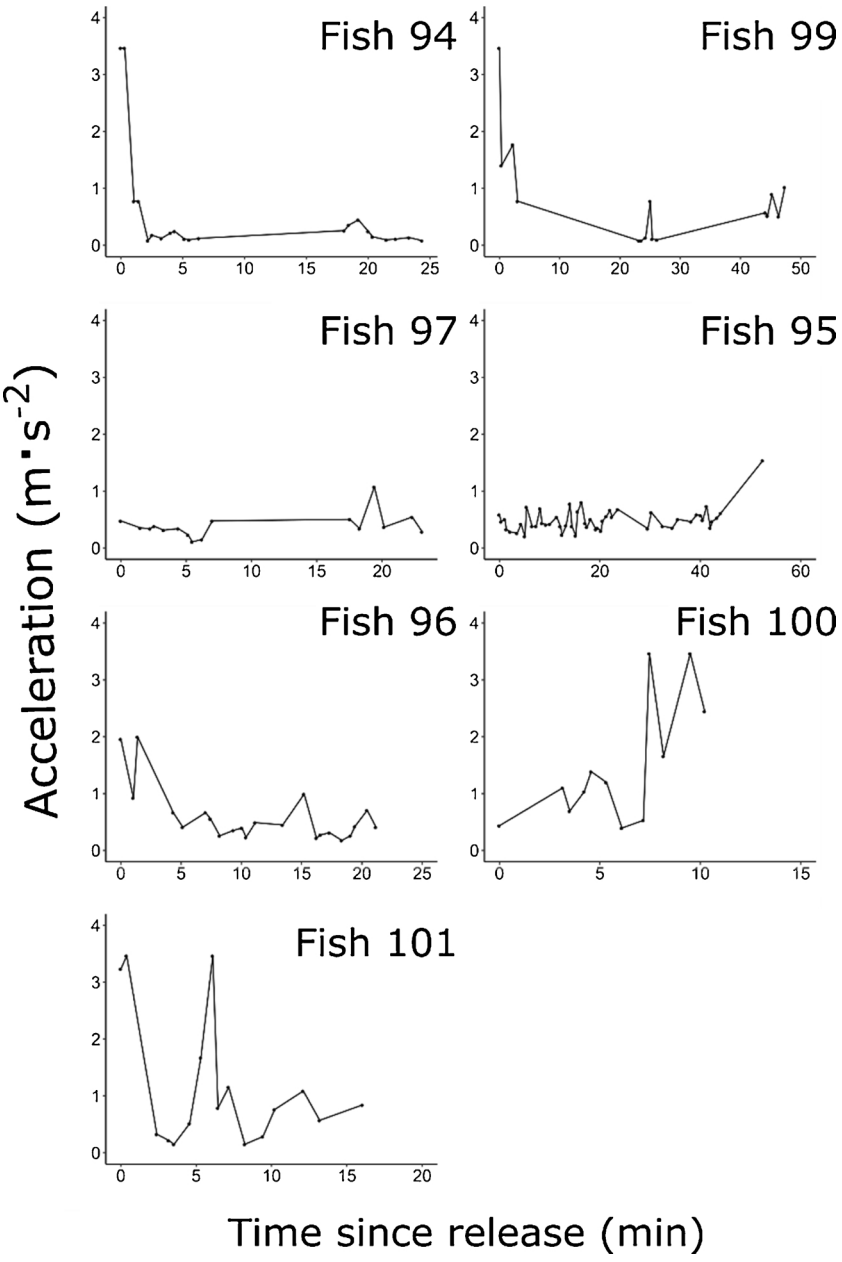

Fig. 4. Acceleration (m s^{-2}) profiles for acoustically tagged white sturgeon (n = 7) manually tracked for 10–52 min after release. The points represent individual acoustic detections and are connected by lines for visualization. Plots are ordered based on sturgeon size, from smallest (156 cm FL – Fish 94) to largest (257 cm FL – Fish 101).

Table 2
White sturgeon (n = 7), were captured in the lower Fraser River, British Columbia, Canada by rod-and-reel, surgically implanted with acoustic transmitters equipped with accelerometer sensors (V13A, Vemco) and manually tracked post-release. The percentage of total track time spent in each level of activity (burst, sustained, or sedentary – based on calibrated activities) is also presented.

Acoustic ID	Fork length (cm)	Fight time (min)	Total time tracked (min)	No. accelerometer readings	% Total track activity		
					Burst	Sustained	Sedentary
Fish 94	156	6	24	21	9	67	24
Fish 99	177	5	48	15	13	60	27
Fish 97	187	11	23	16	0	100	0
Fish 95	189	11	52	50	2	98	0
Fish 96	190	28	21	23	9	91	0
Fish 100	212	18	10	12	33	67	0
Fish 101	257	43	16	16	25	75	0

Table 3
Accelerations ($m\,s^{-2}$) obtained from acoustic transmitters equipped with accelerometer sensors (V13A, Vemco) were used to calculate the force exerted by white sturgeon (n = 7) after a capture-tag-release event. Force was estimated using the equation $F = ma$, where F is force in Newtons (N), m is mass in kg, and a is the mean acceleration in $m\,s^{-2}$. Manual tracking and triangulation of post-release locations for each fish were made. Sturgeon are presented based on the triangulated relocation position post-release (U = upstream, D = downstream, or L = laterally across the river).

Acoustic ID	Mass (kg)	Mean acceleration ($m\,s^{-2}$)	Mean force (N)	Distance from release site (m)
Fish 96	58.4	0.9 ± 0.3	51.3 ± 16.0	12 (U)
Fish 99	47.0	1.7 ± 0.5	77.9 ± 22.6	17 (U)
Fish 94	31.9	0.9 ± 0.6	29.2 ± 20.4	25 (D)
Fish 97	55.6	0.4 ± 0.1	22.7 ± 3.8	40 (D)
Fish 95	57.5	0.4 ± 0.0	24.9 ± 1.6	75 (D)
Fish 100	81.8	1.1 ± 0.4	89.2 ± 31.9	2 (L)
Fish 101	147.7	1.3 ± 0.7	192.8 ± 105.8	4 (L)

relocated closer to shore. Burst swimming activity was common immediately upon release, and higher accelerations were recorded in the first 10 min of tracking followed by lower accelerations indicative of sustained swimming or sedentary behaviour. These results could indicate escape and refuge-seeking behaviour for recovery and/or predator-avoidance that has also been documented in other released fish (Brownscombe et al., 2014b). Sea lion predation on white sturgeon is common. In fact, white sturgeon was found to be the principle prey species for California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) throughout the winter in the Columbia River (Keefer et al., 2012). Stellar sea lion occurrence and predation events on white sturgeon have also increased in the LFR in recent years (E. Stoddard, person. obs., Ecosystem Biologist, Forests, Lands and Natural Resource Operations, B.C., Canada). The collection of capture stress physiology immediate post-release movement data provided us with a unique opportunity to discuss potential recovery behaviour strategies for these large and ancient fish in the wild.

Exhaustive exercise typical of angling, results in metabolic, acid-base, and endocrine disturbances to fish that are measurable in the blood (Milligan, 1996; Kieffer, 2000) – some of which were observed in our study. Our data show that white sturgeon were metabolically challenged after angling. This was measured especially in increased blood lactate that was also dependent on the duration of the fight. The physiological alterations observed here compare reasonably well with values reported for various sturgeon species in the literature. For example, plasma lactate concentrations observed in this study (mean 2.42 $mmol\,L^{-1}$, range 0.4–7.3) were higher than for several domesticated sturgeon species subjected to forced exercise (1.0–4.5 $mmol\,L^{-1}$, Baker et al., 2005a; Kieffer et al., 2001; McKenzie et al., 2001; McLean et al., 2016), but were comparable to other wild sturgeon captured through recreational fishing (0–4 $mmol\,L^{-1}$; shortnose sturgeon; Struthers et al., 2018) and commercial fishing gear in the wild (Atlantic sturgeon in otter-trawl, 3.2 $mmol\,L^{-1}$, Beardsall et al., 2013; lake sturgeon, *Acipenser fulvescens*, in gill net, 6.5 $mmol\,L^{-1}$, Baker et al., 2008). Mean plasma cortisol was moderate (15.6 ng ml) for angled white sturgeon. Resting cortisol measures for sturgeon species are typically around 1 to 5 ng ml (Baker et al., 2005a, 2008; Barton et al., 2000; Lankford et al., 2003) but have been shown to increase substantially when exposed to certain stressors. For example, plasma cortisol in *Scaphirhynchus* spp. sturgeon increased four-to-seven-fold following 1–4 h of confinement (Barton et al., 2000) and shortnose sturgeon plasma cortisol raised from a resting concentration of ˜2 to > 120 $ng\,mL^{-1}$ post-exercise (Baker et al., 2005a). Three of our fish experienced much higher concentrations (100–155 ng ml) that were similar to captive white sturgeon exposed to longer periods of combined exercise and air exposure (˜100 ng ml; McLean et al., 2016). Cortisol has many effects in teleosts but its most widely discussed function is in response to stress to enhance metabolic capacity and mobilize energy stores to restore homeostasis (Mommsen et al., 1999). Although cortisol is the primary corticosteroid released during the sturgeon stress response (Barton, 2002), the peak response can be slow and not typically seen in fish for 1–2 h following the cessation of the stressor (Milligan, 1996), or at least 30 min as measured in white sturgeon (Zuccarelli et al., 2008). Most of our sturgeon were angled and sampled in under 30 min so it is possible that maximum cortisol concentrations were not achieved for most of our samples as a result of blood sampling immediately after the relatively short duration of angling. Similarly, glucose was not related to fight time, although this is likely correlated with the low cortisol levels since the process of liver gluconeogenesis and glycogenolysis to create and mobilize glucose to cope for the energy demands of the stressor is a partially cortisol-dependent pathway (Iwama et al., 1999).

During glycolysis, lactate production decreases muscle and blood pH (Wang et al., 1994). As water shifts from blood to muscle tissue, there can be a disruption of ion osmoregulatory balance that can lead to temporary increases in concentrations of some plasma ions in freshwater, followed by depressed ion concentrations over the longer term (Wood, 1991). The trend of decreasing potassium in white sturgeon from the present study demonstrates that solute redistribution occurred with increasing fight time, although sodium, chloride and osmolality were not significantly altered by fight time. Fight time did not significantly change hematocrit levels – a common indicator of physiological adaptations to increased oxygen demand (Kieffer, 2000), but this was likely a factor of sampling time. At rest, hematocrit values are highly variable across fish species (10 to > 50%, reviewed in Gallaugher and Farrell, 1998), with sturgeon hematocrit typically falling somewhere in the middle of this range (Baker et al., 2005b). Hematocrit levels for the wild caught white sturgeon in this study were ˜29%, similar to white sturgeon from both the control and maximum treatment groups of our previous captive study (31% and 35%, respectively, McLean et al., 2016). Overall, blood lactate and potassium were useful indicators of physiological stress in wild white sturgeon captured via angling. On the other hand, the function and stress response of other parameters, such as cortisol, glucose, hematocrit, and other ions, require further investigation as our non-significant findings could have been a function of natural individual or seasonal variability, representative of a reduced cortisol-dependent physiological stress response in wild white sturgeon, or sampling time. The time-course of these different physiological parameters when sturgeon are exposed to different stressors is poorly understood. As such, there will always be a trade-off in selecting the best time to blood sample fish to determine peak response (Cooke et al., 2013). The results from our study contribute to the knowledge of wild sturgeon exercise physiology and overall, the physiological responses we measured in wild fish were very similar to the samples we previously collected from captive fish exposed to longer treatment periods (McLean et al., 2016). This unique opportunity to validate our prior lab results bodes well for research on exercise physiology via fishing studies that are performed in captivity.

Our lab calibration work suggested that we can discriminate activity/behaviours of white sturgeon with accelerometer transmitters which can provide an insight on activity patterns/behaviours of free-swimming white sturgeon after a capture-tag-release event. All seven tagged sturgeon spent > 60% of their time post-release in a low acceleration sustained swimming activity with very little time spent burst swimming or sedentary (Table 2). We did observe high (often the maximum capacity of the tag) accelerations immediately upon release that were characteristic of the startle response (or fast-start) in fish. This response is described as the large amplitude non-repeated movement comprising the first tail-beat following a startle stimulus where rates of acceleration typically peak (Webb, 1976). Interestingly, the acceleration averages and maximums reached by each fish were independent of the size of the fish. Although theoretically acceleration should change with fish length, empirical work on other fish species has suggested that

acceleration (at least fast-start) is independent of body size (Domenici and Blake, 1997; Webb, 1976).

Sturgeon accelerometer profiles showed a general trend toward lower activity 10+ min post-release (Fig. 4). Extended resting periods have been demonstrated in accelerometer-tagged shortnose sturgeon, where the authors suggested the fish were likely holding station on the river bed as an energy saving strategy or as a compensatory mechanism for recovering from post-handling stressors (Broell et al., 2016). During the resting phase, the authors measured short time-scale burst accelerations, but these events occurred most frequently immediately post-release followed by low accelerations for 2–5 h (Broell et al., 2016). It is well documented in the literature that the energy required for maximum burst swimming are derived from the enzymes of the glycolytic pathway that converts glycogen stored in the white muscle cells to lactic acid (Wardle and Videler, 1993). The maximum swimming speed is available to the fish for a short period of time and then long rest periods are required for repeat bouts of fast swimming (Wardle and Videler, 1993). In our study, individuals with the longest fight times and highest concentrations of lactate (Fish 100 and 101) spent a considerable amount of time undergoing high burst swimming activities (~28% of total track spent burst swimming) compared to the other five individuals (~7% burst swimming); however, they were both tracked for < 20 min and may not have entered the resting phase described by Broell et al. (2016). The longer tracked individuals (Fish 94–99) also had elevated lactate levels (2.9–7.3 mmol L) when compared to control fish (< 2 mmol L; McLean et al., 2016) from our previous lab study, and subsequent burst swimming behaviour did not occur for these fish ~5+ min after release (Fig. 4).

As the muscle glycogen is depleted, fish are more reluctant to swim and instead seek shelter where they remain until the muscle regains its full potential (Black et al., 1961). In our study, sturgeon remained within 75 m of the release site and all seven moved closer to the shoreline with none relocating into the middle of the river. The displacement direction of tagged sturgeon appears to be related to immediate post-release acceleration and calculated force. For instance, three sturgeon had a displacement downstream of their original release site and had the lowest accelerations and exerted less force (Table 3). Steady flows – like those found in the lower Fraser River – can displace the location of the fish relative to the environment without a change in the fishes swimming kinematics (Liao, 2007). In this case, the body of the swimming sturgeon may have drifted downstream because the force exerted was less than the current it was swimming in. This contrasts the two sturgeon that moved upstream and had moderate levels of acceleration and force; while the two that moved laterally across the river had the highest force estimates (Table 3). Interestingly, the two fish that moved laterally were the largest fish, they had the longest fight times, and they were the most physiologically exhausted (e.g., highest lactate). Moving upstream against the current is easier than traversing across it as most fish have evolved to minimize drag forces (Webb, 2004), however the benefits of a fusiform design are lost when they attempt to laterally traverse a flow field. So, moving laterally, even though it may require the most energy to do so, could be functionally important post-release recovery behaviour to these fish. It is also possible that released fish, especially the larger ones, are taking advantage of the increase in velocity that can come from laterally crossing a current. In which case, energy expenditure would be lower. Studies have shown that chaotic and wide fluctuations in velocity will repel fishes, while flows with components of predictability can attract them (Liao, 2007). The fact that all seven sturgeon were located closer to shore, could be indicative of an active refuge-seeking behaviour for recovery in areas where flow velocity may be predictable – especially during periods of extreme velocity currents during the freshet. It has been hypothesized that fish, including white sturgeon, inhabit deep, low-current areas to recover metabolic energy that was spent during migration or by spawning (Apperson and Anders, 1991; Robichaud et al., 2017). So, it is possible that captured and released white sturgeon are seeking calmer habitat like they often do during overwintering (Apperson and Anders, 1991).

Accelerometer transmitters revealed that most sturgeon maintained moderate activity immediately post-release that could be indicative of active recovery during which time sustained swimming would support increased oxygen uptake, lactate clearance rates, and the subsequent restoration of glycogen stores (Milligan et al., 2000). The increasing trend to higher activity at the end of some of the tracking sessions may indicate a trend towards recovery, although the time to full metabolic recovery in wild sturgeon remains unknown. There was individual variability in the time before increased activity was observed, with one individual (Fig. 2, Fish 100) showing trends toward increased activity within 10 min of release, whereas others, like the longest tracked individual (Fig. 2, Fish 99), only increased activity at the very end (52 min). The high variability in the seven post-release acceleration profiles suggests we should interpret results from this with caution. However, it does provide a window to potential patterns in post-release activity and has highlighted important areas for future research.

Although it would have been interesting to estimate the amount of mechanical work done by each sturgeon across the entire tracking period it would be somewhat rudimentary given our dataset. There was a strong relationship between post-release distance and time tracked, which results in higher estimates of work for fish tracked longer ($W = fd$). It was not possible to properly standardize our force estimates across all seven fish because we did not have triangulated positions or direction (upstream/downstream/lateral) that would have allowed for comparisons of work across individuals. In this scenario, we do not feel as though integrated estimates of work are more informative than simply force itself. Additionally, sturgeon swim depth was unknown in our study. Swim depth and body size can affect the amount of flow experienced by an individual and in turn, affect estimates of work. For example, it has been observed that larger species of salmon (e.g. chinook *Oncorhynchus tshawytscha*) swim further from the bank than smaller species (e.g., sockeye salmon); despite the obvious energetic costs of encountering higher currents further from the bank (Hughes, 2004). One way sturgeon have been observed reducing energetic costs is through station-holding, whereby they take advantage of their flattened body morphology by pressing both body and pectoral fins against the substrate as a means of flow-refuging (Geist et al., 2005; Kieffer et al., 2009). Although station-holding behaviour has been considered a mechanism for refuge from high velocity, it has been suggested by others that it may also function as a compensatory mechanism for recovery from post-handling stress (Broell et al., 2016). Future efforts should be made to investigate the mechanical work exerted by sturgeon post-release into varying flows and the effect of depth on work, since it likely plays a significant role in displacement and the downstream-upstream escape response.

Although our work focused solely on understanding the stress physiology that is associated with exhaustive exercise during angling and the behaviour of a capture-tag-release event, we acknowledge there are many additional factors that can contribute to the variation in fish stress physiology and recovery behaviour. Handling time and air exposure were not specifically examined in our current study but the literature is replete with information on the negative impact of increased air exposure on fish recovery (Cook et al., 2015). Environmental temperature has also been shown to influence the stress physiology, recovery behaviour, and risk for mortality in many fish species after C&R (reviewed in Gale et al., 2013). We suggest future work examine these factors for sturgeon under different thermal conditions following capture since water temperatures can sometimes reach > 20 °C in the lower Fraser River. Angler experience is another important factor when comparing our results to the wild fishery since it will likely affect how the fish is played – less experienced anglers may create more exhausted fish or cause greater injury (e.g., Meka and McCormick, 2005). Sturgeon from this study were brought in by experienced anglers with fight times averaging 7 min. We suggest that reduced fight times

can encourage faster recovery and suggest that times longer than employed in this study may lead to reduced recovery given that these fish were likely not fished to exhaustion. The limited number of burst swimming events for the duration of the tracking suggests that swimming performance may be limited during the recovery period of a capture-tag-release event, as has been shown in other sturgeon exposed to exhaustive exercise (Cai et al., 2015). The increase in lactate concentration and measured solute changes demonstrated by angled white sturgeon in our study means that some form of metabolic recovery is necessary and regardless of the time it takes to recover, it has been shown that performance may be limited while high energy stores (e.g., glycogen) are restored (Milligan, 1996). Lastly, the possible preference we identified for nearshore areas following the release of should be examined in greater detail in the future as this may lend insight into optimal release locations for white sturgeon. Overall, this work contributes to the growing body of literature that suggests that acipenserids are rather robust to the stressors associated with C&R angling. More research is needed, however, since there appears to be high individual variability in some of the responses (e.g., physiology and behaviour) and certain individuals may be affected more than others.

Acknowledgements

This work was supported by the Ocean Tracking Network via funding from the Canada Foundation for Innovation, and the Natural Sciences and Engineering Research Council of Canada (NSERC). Additional support was provided by an NSERC Discovery Grant to G.T.C. and an NSERC Alexander Graham Bell Canadian Graduate Scholarship to M.F.M. S.J.C. is supported by NSERC and the Canada Research Chairs program. We would like to thank E. Stoddard from the Ministry of Forests, Lands and Natural Resource Operations, B.C., for sharing his extensive knowledge of the study system and species, and for lending logistical and hands-on help in the field. We thank J. Beardsall, and N. Fowler for assisting with the calibration trials at the US Fish and Wildlife Abernathy Fish Technology Center. We also thank research assistants P. Szekeres and E. Lotto, as well as a number of volunteers, for their help in the field. Thanks to A. Taylor for helping with post-release triangulation, as well as T. Nettles, J. Hills and M. Shimomura for running the plasma assays. A special thanks to T. Nootebos and Y. Bisson of B.C. Sportfishing for field assistance, their expertise navigating the Fraser River watershed, and their dedication to the conservation of white sturgeon. Thank you to E. Stoddard and T. Nelson for reviewing our manuscript before submission. Lastly, we thank two anonymous reviewers and the editor for providing critical feedback to improve our manuscript.

References

Apperson, K.A., Anders, P.J., 1991. Kootenai River White Sturgeon Investigations and Experimental Culture. Annual Report for the Bonneville Power Administration, Portland, Oregon.

Arlinghaus, R., Cooke, S.J., Schwab, A., Cowx, I.G., 2007. Fish welfare: a challenge to the feelings-based approach, with implications for recreational fishing. Fish Fish. 8, 57–71. https://doi.org/10.1111/j.1467-2979.2007.00233.x.

Baker, D.W., Wood, A., Litvak, M.K., Kieffer, J.D., 2005a. Haematology of juvenile Acipenser oxyrinchus and Acipenser brevirostrum at rest and following forced activity. J. Fish Biol. 66, 208–221. https://doi.org/10.1111/j.1095-8649.2004.00595.x.

Baker, D.W., Wood, A.M., Kieffer, J.D., 2005b. Juvenile Atlantic and shortnose sturgeons (Family: Acipenseridae) have different hematological responses to acute environmental hypoxia. Physiol. Biochem. Zool. 78, 916–925. https://doi.org/10.1086/432860.

Baker, D.W., Peake, S.J., Kieffer, J.D., 2008. The effect of capture, handling, and tagging on hematological variables in wild adult lake sturgeon. North Am. J. Fish. Manag. 28, 296–300. https://doi.org/10.1577/M06-255.1.

Bartholomew, A., Bohnsack, J.A., 2005. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Rev. Fish Biol. Fish. https://doi.org/10.1007/s11160-005-2175-1.

Barton, B.A., 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integr. Comp. Biol. 42, 517–525. https://doi.org/10.1093/icb/42.3.517.

Barton, B., Bollig, H., Hauskins, B., Jansen, C., 2000. Juvenile pallid (*Scaphirhynchus albus*) and hybrid pallid x shovelnose (*S. albus* × *platorynchus*) sturgeons exhibit low physiological responses to acute handling and severe confinement. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 126, 125–134. https://doi.org/10.1016/S1095-6433(00)00192-6.

Beardsall, J.W., Mclean, M.F., Cooke, S.J., Wilson, B.C., Dadswell, M.J., Redden, A.M., Stokesbury, M.J.W., 2013. Consequences of incidental otter trawl capture on survival and physiological condition of threatened Atlantic sturgeon. Trans. Am. Fish. Soc. 142. https://doi.org/10.1080/00028487.2013.806347.

Black, E.C., Robertson, A.C., Parker, R.R., 1961. Some aspects of carbohydrate metabolism in fish. In: Martin, A.W. (Ed.), Comparative Physiology of Carbohydrate Metabolism in Heterothermic Animals. University of Washington Press, Seattle, pp. 89–122.

Broell, F., Taylor, A.D., Litvak, M.K., Taggart, C.T., 2016. Post-tagging behaviour and habitat use in shortnose sturgeon measured with high-frequency accelerometer and PSATs. Anim. Biotelemetry 4, 2–13. https://doi.org/10.1186/s40317-016-0103-x.

Brownscombe, J.W., Gutowsky, L.F.G., Danylchuk, A.J., Cooke, S.J., 2014a. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. Mar. Ecol. Prog. Ser. 505, 241–251. https://doi.org/10.3354/meps10786.

Brownscombe, J.W., Nowell, L., Samson, E., Danylchuk, A., Steven, J., 2014b. Fishing-related stressors inhibit refuge-seeking behavior in released subadult. Great Barracuda 143, 613–617. https://doi.org/10.1080/00028487.2014.880744.

Cai, L., Johnson, D., Mandal, P., Gan, M., Yuan, X., Tu, Z., Huang, Y., 2015. Effect of exhaustive exercise on the swimming capability and metabolism of juvenile Siberian sturgeon. Trans. Am. Fish. Soc. 144, 532–538. https://doi.org/10.1080/00028487.2015.1007163.

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. https://doi.org/10.1080/03632415.2015.1074570.

Cook, K.V., Reid, A.J., Patterson, D.A., Robinson, K.A., Chapman, J.M., Hinch, S.G., Cooke, S.J., 2018. A synthesis to understand responses to capture stressors among fish discarded from commercial fisheries and options for mitigating their severity. Fish Fish. 1–9. https://doi.org/10.1111/faf.12322.

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. https://doi.org/10.1007/s10531-004-7845-0.

Cooke, S.J., Schramm, H.L., 2007. Catch-and-release science and its application to conservation and management of recreational fisheries RID F-4193-2010. Fish. Manag. Ecol. 14, 73–79. https://doi.org/10.1111/j.1365-2400.2007.00527.x.

Cooke, S.J., Schreer, J.F., Dunmall, K.M., Philipp, D.P., 2002. Strategies for quantifying sublethal effects of marine catch-and-release angling: insights from novel freshwater applications. Am. Fish. Soc. Symp. 30, 121–134.

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. https://doi.org/10.1111/j.1365-2400.2012.00867.x.

COSEWIC, 2012. Assessment and Status Report on the White Sturgeon *Acipenser transmontanus*. Ottawa. .

Crossin, G., Cooke, S., Goldbogen, J., Phillips, R., 2014. Tracking fitness in marine vertebrates: current knowledge and opportunities for future research. Mar. Ecol. Prog. Ser. 496, 1–17. https://doi.org/10.3354/meps10691.

Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D., Cooke, S.J., 2017. Acoustic telemetry and fisheries management. Ecol. Appl. 27, 1031–1049. https://doi.org/10.1002/eap.1533.

Danylchuk, S.E., Danylchuk, A.J., Cooke, S.J., Goldberg, T.L., Koppelman, J., Philipp, D.P., 2007. Effects of recreational angling on the post-release behavior and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. J. Exp. Mar. Bio. Ecol. 346, 127–133. https://doi.org/10.1016/j.jembe.2007.03.008.

DFO, 2017. Monitoring Southern BC Coastal Waters. [WWW Document]. URL. (Accessed 2 January 2018). http://www.dfo-mpo.gc.ca/science/data-donnees/cotesud-southcoast/index-eng.html.

Domenici, P., Blake, R.W., 1997. The kinematics and performance of fish fast-start swimming. J. Exp. Biol. 200, 1165–1178.

Donaldson, M.R., Arlinghaus, R., Hanson, K.C., Cooke, S.J., 2008. Enhancing catch-and-release science with biotelemetry. Fish Fish. 9, 79–105. https://doi.org/10.1111/j.1467-2979.2007.00265.x.

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. https://doi.org/10.1111/j.1467-2979.2011.00441.x.

Gallaugher, P., Farrell, A.P., 1998. Hematocrit and blood oxygen-carrying capacity. In: Perry, S.E., Tufts, B.L. (Eds.), Fish Physiology. Academic Press, San Diego, pp. 185–227. https://doi.org/10.1016/S1546-5098(08)60262-9.

Gannon, R., Taylor, M.D., Suthers, I.M., Gray, C.A., van der Meulen, D.E., Smith, J.A., Payne, N.L., 2014. Thermal limitation of performance and biogeography in a free-ranging ectotherm: insights from accelerometry. J. Exp. Biol. 217, 3033–3037. https://doi.org/10.1242/jeb.104455.

Geist, D.R., Brown, R.S., Cullinan, V., Brink, S.R., Lepla, K., Bates, P., Chandler, J.A., 2005. Movement, swimming speed, and oxygen consumption of juvenile white sturgeon in response to changing flow, water temperature, and light level in the Snake River. Idaho. Trans. Am. Fish. Soc. 134, 803–816. https://doi.org/10.1577/T04-108.1.

Hanson, K.C., Cooke, S.J., Suski, C.D., Philipp, D.P., 2007. Effects of different angling practices on post-release behaviour of nest-guarding male black bass, *Micropterus* spp. Fish. Manag. Ecol. 14, 141–148. https://doi.org/10.1111/j.1365-2400.2007.

00534.x.
Hildebrand, L.R., Drauch Schreier, A., Lepla, K., McAdam, S.O., McLellan, J., Parsley, M.J., Paragamian, V.L., Young, S.P., 2016. Status of white sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. J. Appl. Ichthyol. 32, 261–312. https://doi.org/10.1111/jai.13243.
Hughes, N.F., 2004. The wave-drag hypothesis: an explanation for size-based lateral segregation during the upstream migration of salmonids. Can. J. Fish. Aquat. Sci. 61, 103–109. https://doi.org/10.1139/f03-144.
Iwama, G.K., Vijayan, M.M., Forsyth, R.B., Ackerman, P.A., 1999. Heat shock proteins and physiological stress in fish. Am. Zool. 39, 901–909. https://doi.org/10.1093/icb/39.6.901.
Keefer, M.L., Stansell, R.J., Tackley, S.C., Nagy, W.T., Gibbons, K.M., Peery, C.A., Caudill, C.C., 2012. Use of radiotelemetry and direct observations to evaluate sea lion predation on adult pacific salmonids at Bonneville Dam. Trans. Am. Fish. Soc. 141, 1236–1251. https://doi.org/10.1080/00028487.2012.688918.
Kieffer, J.D., 2000. Limits to exhaustive exercise in fish. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 126, 161–179. https://doi.org/10.1016/S1095-6433(00)00202-6.
Kieffer, J.D., Wakefield, A.M., Litvak, M.K., 2001. Juvenile sturgeon exhibit reduced physiological responses to exercise. J. Exp. Biol. 204, 4281–4289.
Kieffer, J.D., Arsenault, L.M., Litvak, M.K., 2009. Behaviour and performance of juvenile shortnose sturgeon *Acipenser brevirostrum* at different water velocities. J. Fish Biol. 74, 674–682. https://doi.org/10.1111/j.1095-8649.2008.02139.x.
Landsman, S.J., Martins, E.G., Gutowsky, L.F.G., Suski, C.D., Arlinghaus, R., Cooke, S.J., 2015. Locomotor activity patterns of muskellunge (*Esox masquinongy*) assessed using tri-axial acceleration sensing acoustic transmitters. Environ. Biol. Fishes 98, 2109–2121. https://doi.org/10.1007/s10641-015-0433-1.
Lankford, S.E., Adams, T.E., Cech, J.J., 2003. Time of day and water temperature modify the physiological stress response in green sturgeon, *Acipenser medirostris*. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 135, 291–302. https://doi.org/10.1016/S1095-6433(03)00075-8.
Liao, J.C., 2007. A review of fish swimming mechanics and behaviour in altered flows. Philos. Trans. R. Soc. B Biol. Sci. 362, 1973–1993. https://doi.org/10.1098/rstb.2007.2082.
McKenzie, D.J., Cataldi, E., Romano, P., Taylor, E.W., Cataudella, S., Bronzi, P., 2001. Effects of acclimation to brackish water on tolerance of salinity challenge by young-of-the-year Adriatic sturgeon (*Acipenser naccarii*). Can. J. Fish. Aquat. Sci. 58, 1113–1121. https://doi.org/10.1139/cjfas-58-6-1113.
McLean, D.G., Church, M., Tassone, B., 1999. Sediment transport along lower Fraser River. Measurements and hydraulic computations. Water Resour. Res. 35, 2533–2548.
McLean, M.F., Hanson, K.C., Cooke, S.J., Hinch, S.G., Patterson, D.A., Nettles, T.L., Litvak, M.K., Crossin, G.T., 2016. Physiological stress response, reflex impairment and delayed mortality of white sturgeon *Acipenser transmontanus* exposed to simulated fisheries stressors. Conserv. Physiol. 4https://doi.org/10.1093/conphys/cow031. cow031.
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. https://doi.org/10.1016/j.fishres.2004.10.006.
Milligan, C.L., 1996. Metabolic recovery from exhaustive exercise in rainbow trout. Comp. Biochem. Physiol. A Physiol. 113, 51–60. https://doi.org/10.1016/0300-9629(95)02060-8.
Milligan, C.L., Hooke, G.B., Johnson, C., 2000. Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in rainbow trout. J. Exp. Biol. 203, 921–926. https://doi.org/10.1016/0300-9629(93)90373-c.
Mommsen, T.P., Vijayan, M.M., Moon, T.W., 1999. Cortisol in teleosts: dynamics, mechanisms of action, and metabolic regulation. Rev. Fish Biol. Fish. 9, 211–268. https://doi.org/10.1023/A:1008924418720.
Moser, M.L., Corbett, S.C., Burke, B.J., Langness, O.P., 2017. Potential for use of accelerometers to monitor green sturgeon *Acipenser medirostris* (Ayres, 1854) behavior after handling. J. Appl. Ichthyol. 34, 1–7. https://doi.org/10.1111/jai.13571.
Muoneke, M.I., Childress, W.M., 1994. Hooking mortality: a review for recreational fisheries. Rev. Fish. Sci. 2, 123–156.
Murchie, K.J., Cooke, S.J., Danylchuk, A.J., Suski, C.D., 2011. Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. J. Exp. Mar. Biol. Ecol. 396, 147–155. https://doi.org/10.1016/j.jembe.2010.10.019.
O'Toole, A.C., Murchie, K.J., Pullen, C., Hanson, K.C., Suski, C.D., Danylchuk, A.J., Cooke, S.J., 2010. Locomotory activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. Mar. Freshw. Res. 61, 1446–1456. https://doi.org/10.1071/MF10046.
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. Secr. Res. Doc. 2017/010, ix + 155 p.
Payne, N.L., Gillanders, B.M., Seymour, R.S., Webber, D.M., Snelling, E.P., Semmens, J.M., 2011. Accelerometry estimates field metabolic rate in giant Australian cuttlefish *Sepia apama* during breeding. J. Anim. Ecol. 80, 422–430. https://doi.org/10.1111/j.1365-2656.2010.01758.x.
Raby, G.D., Messmer, V., Tobin, A.J., Hoey, A.S., Jutfelt, F., Sundin, J., Cooke, S.J., Clark, T.D., 2018. Swim for it: effects of simulated fisheries capture on the post-release behaviour of four Great Barrier Reef fishes. Fish. Res. 206, 129–137. https://doi.org/10.1016/j.fishres.2018.05.012.
R Development Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (version 3.5.1).
Robichaud, D., English, K.K., Nelson, T.C., 2017. Annual movements of acoustic-tagged white sturgeon in the lower reaches of the Fraser river and its tributaries. Trans. Am. Fish. Soc. 146, 611–625. https://doi.org/10.1080/00028487.2017.1294542.
Stehfest, K.M., Lyle, J.M., Semmens, J.M., 2015. The use of acoustic accelerometer tags to determine seasonal changes in activity and catchability of a recreationally caught marine teleost. ICES J. Mar. Sci. 72, 2512–2520. https://doi.org/10.1093/icesjms/fsv115.
Stoot, L.J., Cairns, N.A., Cull, F., Taylor, J.J., Jeffrey, J.D., Morin, F., Mandelman, J.W., Clark, 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. 2https://doi.org/10.1093/conphys/cou011. cou011.
Struthers, D.P., Bower, S.D., Lennox, R.J., Gilroy, C.E., Macdonald, E.C., Cooke, S.J., Litvak, M.K., 2018. Short-term physiological disruption and reflex impairment in shortnose sturgeon exposed to catch-and-release angling. N. Am. J. Fish. Manage. 38, 1075–1084. https://doi.org/10.1002/nafm.10212.
Taylor, A.D., Litvak, M.K., 2015. Quantifying a manual triangulation technique for aquatic ultrasonic telemetry. North Am. J. Fish. Manag. 35, 865–870. https://doi.org/10.1080/02755947.2015.1059909.
Thorstad, E., 2003. Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. Fish. Res. 60, 293–307. https://doi.org/10.1016/S0165-7836(02)00176-5.
Tyrrell, H.M., 2014. Movement Patterns and Catch-and-release Impacts of Striped Bass in a Tidal Coastal Embayment in Massachusetts. University of Massachusetts, Amherst.
Wang, Y., Heigenhauser, G.J.F., Wood, C.M., 1994. Integrated responses to exhaustive exercise and recovery in rainbow trout white muscle: acid-base, phosphogen, carbohydrate, lipid, ammonia, fluid volume and electrolyte metabolism. J. Exp. Biol. 258, 227–258.
Wardle, C.S., Videler, J., 1993. Fish swimming. In: Elder, H.Y., Trueman, E.R. (Eds.), Aspects of Animal Movement. Cambridge University Press, Great Britain, pp. 125–147. https://doi.org/10.1007/978-94-011-1580-3.
Webb, P.W., 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator–prey interactions. J. Exp. Biol. 65, 157–177. https://doi.org/10.1016/S1546-5098(05)23009-1.
Webb, P.W., 2004. Response latencies to postural disturbances in three species of teleostean fishes. J. Exp. Biol. 207, 955–961. https://doi.org/10.1242/jeb.00854.
Wilson, S.M., Hinch, S.G., Eliason, E.J., Farrell, A.P., Cooke, S.J., 2013. Calibrating acoustic acceleration transmitters for estimating energy use by wild adult Pacific salmon. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 164, 491–498. https://doi.org/10.1016/j.cbpa.2012.12.002.
Wilson, S.M., Raby, G.D., Burnett, N.J., Hinch, S.G., Cooke, S.J., 2014. Looking beyond the mortality of bycatch: sublethal effects of incidental capture on marine animals. Biol. Conserv. 171, 61–72. https://doi.org/10.1016/j.biocon.2014.01.020.
Wood, B.Y.C.M., 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise. J. Exp. Biol. 160, 285–308.
Zuccarelli, M.D., Kusakabe, M., Nakamura, I., Prentice, E.F., Young, G., Ingermann, R.L., 2008. Acute stress response of Kootenai River white sturgeon *Acipenser transmontanus* Richardson reflected in peritoneal fluid and blood plasma. J. Fish Biol. 72, 1831–1840. https://doi.org/10.1111/j.1095-8649.2008.01840.x.