SECRETS OF THE ULTIMATE TROPHY FISH: THE PHYSIOLOGICAL ECOLOGY AND BEHAVIOUR OF WHITE STURGEON (*ACIPENSER TRANSMONTANUS* RICHARDSON, 1836) AFTER ANGLING

By

Montana F. McLean

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As the rare, endangered white rhino draws the avid hunter, a rare or endangered fish can hold the same allure to recreational anglers.

This thesis is dedicated to my husband, Tom, for nearly a decade of unconditional love and support and without whom I could not have finished this incredible journey. Also, to my parents for a lifetime of guidance and encouragement and for fostering my love for all creatures below the surface. Lastly, to my angel daughter, Vienna, and my earth daughter, Evelyn, for teaching me about life in ways I could never have dreamed.

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ABSTRACT

Around the world, human activities and climate change are altering ecosystems at unprecedented rates, which in many cases is outpacing our capacity to understand and predict the potential impacts on biodiversity. Fishing is one of the most pervasive anthropogenic stressors to fish populations worldwide, and so examination of fishing stressors is needed, especially in a changing climate. This thesis aimed to understand the physiological and behavioural consequences of catch-and-release (C&R) angling to white sturgeon, *Acipenser transmontanus,* in the lower Fraser River (LFR), British Columbia, Canada, with consideration of capture under different, seasonal river temperatures. White sturgeon are prized as a trophy species, with the largest individual sturgeon measuring more than 3 metres in length and putting up angling fight times of more than an hour. Currently, white sturgeon in the LFR are considered Threatened by the Committee on the Status of Endangered Wildlife in Canada. Despite conservation concerns, there are few regulations for the C&R fishery. Given the lack of restrictions, and knowledge that the Fraser River is warming due to climate change, I assessed the short- and long-term effects of C&R angling on white sturgeon in the LFR using physiological sampling of stress metabolites, a refined reflex impairment index, and acoustic telemetry. After angling wild sturgeon on the river, lactate concentrations were consistently higher in fish enduring long fight times, indicating anaerobic exhaustion. Here and in complimentary lab studies with captive sturgeon, reflex indicators of impairment were predicted by angling fight times and plasma lactate levels, and this effect was exacerbated in summer when temperatures are higher. Ultimately, recovery time from physical exhaustion increased with the duration of angling stress. Using tri-axial accelerometer acoustic transmitters, a snap-shot into the immediate post-release recovery behaviour of wild sturgeon revealed high inter-individual variability. Sturgeon required a recovery period after angling, which occurred consistently in nearshore environments. Long-term monitoring revealed high post-release survival (100%), indicating some resilience of sturgeon to angling, but there was some evidence of transient sublethal effects, and the fitness implications are still unknown. This is the most comprehensive examination of the impacts of recreational angling on a wild population of sturgeon. The results from this research revealed intriguing variance in the physiological and behavioural response of individual white sturgeon to C&R recreational angling, with some degree of environmental temperature dependence, and highlights the importance of understanding the drivers of such variation when managing fisheries.

LIST OF ABBREVIATIONS USED

ACTH	Adrenocorticotropin
ANOVA	Analysis of variance
C&R	Catch-and-release
COSEWIC	Convention on the Status of Endangered Wildlife in Canada
CRF	Corticotropin-releasing-factor
FL	Fork length (cm)
GLM	Generalized linear model
GnRH	Gonadotropin-releasing hormone
HPG	Hypothalamic-pituitary-gonadal
HPI	Hypothalmic-pituitary-interrenal
IUCN	International Union for the Conservation of Nature
LFR	Lower Fraser River
$m \cdot s^{-2}$	Metres per second squared
$mmol \cdot L^{-1}$	Millimoles per litre
$ng \cdot L^{-1}$	Nanograms per litre
PIT	Passive integrated transponder
RAMP	Reflex action mortality predictor
RMS	Root mean squared
rpm	Rotations per minute
USFWS	United States Fish and Wildlife Service

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CHAPTER 1

Introduction

Catch-and-Release (C&R) Recreational Angling

Recreational angling is both a favourite pastime for many, and a lucrative industry that has been estimated to be worth billions of dollars in North America alone (DFO, 2010). In 2010, a Fisheries and Oceans Canada survey revealed that 3.3 million adults participated in a variety of recreational fishing activities in Canada that year, generating revenue in excess of $8.3 billion to local economies (DFO, 2010). For many years, the importance and impacts of recreational fisheries have been overlooked, despite clear indications that they can contribute to reductions in fish abundance and size, alter food webs through selective harvest of predators, cause fishery-induced evolution, and disturb wildlife and habitats (Arlinghaus et al., 2019). The process of releasing a fish in angling is known as catch-and-release (C&R) and is analogous to the release of live bycatch from commercial or subsistence fisheries (Cooke and Wilde, 2007). C&R is regarded as an effective tool for the conservation of exploited fish populations, as each year an estimated 60% of all recreationally angled fish are released worldwide (Cooke and Cowx, 2004). In fact, in 2010, anglers in Canada caught over 193 million fish of all species but retained only 63 million (DFO, 2010) – translating to a 67% release rate. The release of fish as a conservation strategy may seem intuitive, but the underlying assumption is that the fish survives (Wydoski, 1977). There are a number of biological effects associated with C&R that have the potential to impact survival, reproduction, and/or fitness, and wide-ranging responses to C&R angling have been recognized in a number of recreationally targeted species (Cooke and Suski, 2005). For example, barotrauma was recognized in 76% tournament-caught smallmouth bass (*Micropterus dolomieu*) in Rainy Lake, Ontario, and individuals with less severe barotrauma had higher survival and evacuated the release site faster (Gravel & Cooke, 2008).

C&R angling has also been associated with evolutionary consequences, whereby fishing pressures exert selection for certain traits. To test this, Philip et al., (2009) conducted a long-term selection experiment on largemouth bass (*Micropterus salmoides*). Three successive generations of artificially selected bass from Ridge Lake, Illinois (an experimental reservoir) were produced from a single experimental population and individuals from each generation were identified as having either high- or low-vulnerability to angling. Interestingly, researchers found the response to selection for angling increased with each generation and that the calculated realized heritability (0.146, $r^2 = 0.995$) indicated that vulnerability to angling was indeed heritable (Philipp et al., 2009). Further, vulnerability to capture has been shown to be positively correlated with aggression, intensity of parental care, and reproductive fitness (i.e., angling-selectivity for fish with the highest fitness potential; Sutter et al., 2012). Direct physical injury (Cooke and Philipp, 2004) and physiological changes (Arlinghaus et al., 2009; Cooke et al., 2002b; Kieffer, 2000) have also been associated with C&R. As stated above, for C&R to be an effective conservation and management tool, fish must incur only negligible injuries or sub-lethal alterations in behaviour or physiology (Cooke and Schramm, 2007), but studies show that the sub-lethality of angling varies widely among species (Cooke and Suski, 2005). Researchers are thus attempting to quantify sublethal effects in multiple species so that species-specific recommendations can be made for minimizing risks.

The Stress Response

The theory of adaptation by natural selection proposed by Charles Darwin (1859) involved a discussion about the value of heritable, individual variation in various organismal traits which provide the raw materials upon which selection can act, thus driving evolution. His argument was that some individuals will adapt to changes in their environment, ultimately giving them a fitness advantage over others – favouring reproductive success and resulting in local adaptation. The ‘grandfather of stress’ Hans Selye (1935) was greatly influenced by Darwin, and he formalized his own ideas about the adaptiveness of the organismal stress response (Selye, 1950, 1946). Eventually, the concept of “stress” came to be regarded as the general, adaptive response of an organism to any “stressor” that upsets its homeostasis (Selye, 1973), such that when a stressor is experienced, an adaptive response activates various molecular, cellular, hormonal, metabolic, and behavioural systems to facilitate a return to homeostasis (Korte et al., 2005; Romero, 2004). The complex interplay between physiology, behaviour and life-history makes the stress response important not only to individuals but also populations (Ricklefs and Wikelski, 2002). Stressors persisting beyond an acute state and into a chronic state can push physiological systems beyond their limits, resulting in maladaptive rather than adaptive states.

To put stress into context, it is helpful to consider life-history theory. At some point in their lifetimes, most animals are faced with resource limitations, and trade-offs emerge to allow partitioning of limited resources to different functions (Stearns, 1989). Stress is central to the “survival versus reproduction” trade-off – a topic that is well studied and empirically supported (Stearns, 1989). Although the physiological mechanisms that help guide investment decisions are not fully understood, the endocrine stress response is a strong candidate mechanism because it is thought to promote survival-oriented functions (Bókony et al., 2009). Glucocorticoids are a class of “stress” hormones with two discrete functions. When expressed at baseline levels, glucocorticoids play a key role in the regulation of daily energy metabolism and activity (Romero, 2004; Sapolsky et al., 2000), and baseline levels can shift seasonally depending on the life-history demands of the animal (e.g., Love et al., 2004). When expressed at stress-induced levels, glucocorticoids are secreted in response to any number of environmental (e.g. temperature, salinity, oxygen levels), physical (e.g. capture, confinement, injury), or perceived (e.g. predator presence) stressors, thus providing a reliable measure of the non-specific, physiological response common to most vertebrates (Barton, 2002).

For fish, a common stressor is fisheries capture, which may result in direct mortality or sublethal stress effects via commercial discards or recreational C&R angling. Depending on the severity and duration of the stressor experienced, fish will elicit a well described and documented stress response, involving primary, secondary, and tertiary responses (Barton, 2002). During the primary response, the threat is perceived by the central nervous system and sympathetic nerve fibres stimulate chromaffin tissue in the teleost head kidney to rapidly release catecholamines into circulation (e.g., epinephrine). At the same time the hypothalamic-pituitary-interrenal (HPI; HPA or hypothalamic-pituitary-adrenal homolog in mammals) axis is activated. In short, the hypothalamus in the brain releases corticotropin-releasing factor (CRF) which stimulates the anterior pituitary to secrete adrenocorticotropin (ACTH). ACTH then stimulates the interrenal cells in the kidney to synthesize and release glucocorticoids into circulation to target other tissues and organs (Barton, 2002). Cortisol is the principle glucocorticoid synthesized in fishes and circulating levels of cortisol are commonly examined to investigate primary physiological stress responses of fish (Barton, 2002). One of the secondary components of the stress response includes the up-regulation of glucose synthesis, a cortisol-dependent process during the acute phase of stress which ultimately helps to maintain metabolic resources during prolonged or chronic stress states (Barton et al., 1987; Haddy and Pankhurst, 1999). In addition to cortisol and glucose, increased blood lactate levels can also be associated with acute stress, especially when this involves anaerobic metabolism. The increase in lactate post-stress is likely associated with anaerobiosis occurring in the white muscle fibres during “burst” swimming (Driedzic et al., 1981). Thus, lactate levels are also commonly sampled in studies investigating the physiological stress response in fish. The secondary responses also include changes in plasma and tissue ion levels, and hematological features (i.e., hematocrit and hemoglobin; Barton, 2002). The tertiary stress response involves changes affecting whole-animal performance, such as growth, condition, disease resistance, behaviour, and survival (Barton, 2002; Wedemeyer and McLeay, 1981). Depending on the magnitude and duration of a stressor, fish may be affected at one or all levels, and the process of the stress-response at each of these levels of organization, from molecular and biochemical, to population and community, varies across taxa.

It is well understood that stress impacts reproductive performance. Glucocorticoid effects on functioning of the hypothalamus-pituitary-gonadal (HPG) axis are thought to be significant to stress-mediated reproductive dysfunction (Alsop et al., 2009). Although glucocorticoids like cortisol are necessary for recovery from a stressor, they also impact the HPG axis, thus affecting reproduction (Alsop et al., 2009). As briefly mentioned above, during a stressful situation CRF activates the HPA signaling cascades while concurrently supressing the release of hypothalamic gonadotropin-releasing hormone (GnRH) (Alsop et al., 2009). In fish, activation of the HPI axis, specifically CRF and cortisol, have been shown to impact reproductive performance by targeting multiple sites along the HPG axis. Therefore, a stressed state is generally incompatible with reproduction. Effects of a stressor depend on when during reproductive development and maturation the stressor is applied and its duration and severity (Schreck et al., 2001). For this reason, the stress response is expected to be suppressed in individuals with high current reproductive values relative to the value of future reproduction and survival in an effort to ensure critical resources are not diverted away from reproduction (Wingfield and Sapolsky, 2003). For example, in species where breeding opportunities are limited, during the breeding season itself, and even in the sex that contributes more to parental care, the stress response is attenuated (Astheimer et al., 1994; Wingfield et al., 1995, 1992). Nonetheless, the degree of the stressor has the potential to elicit whole-animal changes such as changes in behaviour (Barton, 2002) and these behavioural impairments, translated by reduced locomotory capabilities, can reduce reproductive potential as the animal tries to recover from the stressor (Cooke et al., 2000). Reproductive migratory behaviour can be energetically costly, therefore the more energy resources an individual requires for stress resistance, the less that individual has to conduct other functions (Schreck, 2010) like finishing the migration to spawning grounds, mating, or courtship.

Sturgeon Biology

At present, our understanding of stress in fish stems mostly from studies on teleosts. There is very little information on stress processes in non-teleost fish, with most information deriving from laboratory studies on chondrosteans. From the work that has been done on sturgeon, the glucocorticoid response to stressors follows a similar pattern to that found in teleosts (Barton, 2002; Pankhurst, 2011). Plasma cortisol, glucose, and lactate have been shown to increase following subsequent exposure to a number of stressors in captivity; however, cortisol has been identified as the principle glucocorticoid in sturgeon (Barton, 2002; Pankhurst, 2011) despite the variability in its response. There is high variation between sturgeon species with respect to the level of increase in circulating glucocorticoids following stress but the general consensus is that Acipenseridae demonstrate resilience to common stressors like air exposure, confinement, handling, chasing, and water reduction compared to teleosts (e.g., Barton et al., 2000; Zuccarelli et al., 2008). Understanding the short- to long-term effects of stress in non-teleosts like sturgeon is important.

Sturgeon are a prehistoric, enigmatic group of fishes that have long been the center of conservation issues (Berstein, 1993). From a management standpoint, most sturgeon are protected to some extent, and are currently the most critically endangered taxa in the world (IUCN, 2010). Of 27 extant species, 2 are listed as endangered, and 17 as critically endangered, by the International Union for the Conservation of Nature [IUCN; iucn.org, accessed January 1, 2019]. Many species are listed due to the value of their roe, which sustains a lucrative caviar industry. The Caspian Sea has historically been well known as a major hot spot for illegal harvesting of critically endangered sturgeon (e.g., Beluga, *Huso huso*, Russian, *Acipenser gueldenstaedtii*, and stellate, *Acipenser stellatus*, sturgeon, Speer et al., 2000), with poaching activity estimated as 6-10 times the legal catch quotas that were set for the Volga-Caspian basin prior to its closure to commercial fishing (TRAFFIC, 2000). Presently, few sturgeon fisheries exist in North America, as most were closed after population collapses at the turn of the 19th century (Boreman, 1997). Because of their slow life-history, including long lifespan (>100 years), late onset of maturity (as late as 20-25 years) and intermittent or infrequent spawning (can be as long as 10 years between spawning events) (Billard and Lecointre, 2000), sturgeon population growth rates are slow (Secor and Waldman, 1999). This makes them susceptible to exploitation-induced population declines and low recovery capacity (Nelson et al., 2013b; Secor and Waldman, 1999).

Overall, sturgeon are understudied when compared to other major taxa, and knowledge gaps concerning fundamental aspects of their ecology (spatial distribution, abundance, stress response) exist – information that is critical for the conservation of populations and habitats (Nelson et al., 2013b).

Other threats to sturgeon worldwide include: river obstruction and habitat fragmentation, river flow regulation, dredging, and pollution, which have affected access to some spawning sites, as well as decreased the general quality of spawning habitat and juvenile rearing habitats (Hildebrand et al., 2016). The imperiled conservation status of sturgeon overall justifies the need for more research focused on understanding the effects of these activities on both an individual and population level.

Study Species – White Sturgeon (*Acipenser transmontanus* Richardson, 1836)

The white sturgeon is a fish species that experiences widespread and somewhat unregulated fisheries threats, despite being endangered in parts of its range (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2012). White sturgeon are the largest freshwater species (6.1 m and 816 kg; Scott and Crossman, 1973) in North America and are restricted to the west coast in three main watersheds: the Sacramento-San Joaquin Bay-Delta, Columbia, and Fraser Rivers. Like most sturgeon, white sturgeon populations were overharvested at the turn of the 19th century (Billard and Lecointre, 2000). Character traits such as long lifespan and delayed age of maturity make sturgeon especially susceptible to overexploitation and populations have likely failed to recover due to continued by-catch and habitat alterations (Hildebrand et al., 2016). In Canada, white sturgeon were initially listed as a species of special concern in 1990, but by 2003 all Canadian populations were designated endangered (COSEWIC, 2003). Reassessment in 2012, however, changed the conservation status to threatened for the lower and middle Fraser River populations, with the upper Fraser population retaining the endangered status (COSEWIC, 2012). Upper Columbia River white sturgeon populations in Canada are also considered endangered. In the United States, the same population of upper Columbia River white sturgeon cannot be harvested and the Kootenai River population (also part of the Kootenay River and Lake populations in BC, Canada) is listed as endangered under the U.S. Endangered Species Act (US Fish and Wildlife Service [USFWS], 1994). White sturgeon populations in the lower Columbia and Sacramento Rivers are not currently protected. Hildebrand et al. (2016) outlined the most prominent current and future threats facing white sturgeon populations in an extensive review on the status of white sturgeon throughout their range. Threats identified included: habitat fragmentation, alteration and loss; predation on eggs and age-0 by a number of species as well as on adults by sharks and sea lions; challenges associated with invasive species, including a reduction in prey value (non-native replacement of native prey), loss of benthic prey and productive prey areas, competition, disease introduction, habitat alteration and direct predation; water quality degradation and contaminants; climate change; and fishing activity. They also identified fishing activity as an area of future research requirements, especially since the biological and population-level effects of repeated C&R angling on white sturgeon populations are largely unknown (Hildebrand et al., 2016).

Interest in a sport fishery for white sturgeon has dramatically increased in recent years. In the Fraser River, B.C., the number of recreational sturgeon fishing permits increased from 69 to 1104 from 1969 - 1985 (Echols, 1995) and in 2013, 13,000 licenses were sold (English and Jesson, 2013). Similarly, sport fisheries for white sturgeon exist in the lower and middle Columbia, Sacramento-San Joaquin Bay-Delta, the Snake, and middle Fraser Rivers. What likely attracts many anglers to white sturgeon fishing is their size. White sturgeon have historically attained sizes up to 6.1 m and 816 kg (Scott and Crossman, 1973). Despite growing popularity of the recreational fishery there has been little work to date focusing on how acute angling stress affects white sturgeon. The key assumption of C&R is that individual fitness is not affected and that the released individual will survive to contribute their genes to subsequent generations (Cooke et al., 2002a). However, we now understand that the practice can result in immediate or delayed mortality and sublethal consequences (Donaldson et al., 2008). In fact, angling has been suggested as being one of the most severe forms of exhaustive exercise that fish experience (Booth et al., 1995). Knowledge of species-specific stress and mortality as it relates to acute angling stress from C&R is important because if left unmanaged it can cause significant losses of resources and productivity (Davis, 2010). Even low levels of fishing related mortality could effect population size structure and abundance (Idaho Department of Fish and Game [IDFG], 2008) and it has been suggested that >0.10 exploitation of some wild self-sustaining white sturgeon populations risks stock collapse (Rieman and Beamesderfer, 1990).

C&R Angling Science

Many recreational fisheries have adopted catch-and-release practices to reduce fisheries-related mortality pressures on sensitive populations, while still allowing for monetary gain through this form of eco-tourism. What dictates the success of a C&R fishery, however, is that there are minimal effects of the practice on the exploited fish populations. For years' C&R science has focused on individuals and hooking mortality as an endpoint, but Cooke et al. (2002a) were the first to propose that in order for fisheries scientists to apply C&R science to the management and conservation of populations, they must also begin looking beyond the endpoint of mortality. The authors suggested that this should include a comprehensive examination of real-time information collected on sublethal physiological effects, disruptions in behaviour, and long-term fitness consequences – or lifetime reproductive success – of released fish (Cooke et al., 2002a). These effects include direct acute or delayed mortality, as well as sublethal effects like physiological disturbances, behavioural impairments and fitness impairments. By identifying the potential effects a C&R angling event can have on a species, research supported guidelines can be developed that seek to minimize those effects (Cooke and Schramm, 2007; Cooke and Suski, 2005; Donaldson et al., 2008).

Before entering the field, a basic understanding of the physiological stress response of the study species needs to be addressed. These studies tell us how an animal's physiology or behaviour may alter in response to a change in one or a set of stressors (Metcalfe et al., 2012). Indeed captive studies investigating the role

C&R angling plays in stress physiology, delayed mortality, and behavioural impairments are becoming increasingly common in the literature. Sometimes, however, enclosures used in captive studies can exacerbate stress and mortality which can lead to overestimations (Donaldson et al., 2008; Pollock and Pine, 2007), which is why it is also important to validate with field studies whenever possible.

Arlinghaus et al. (2009) provided a good example of how an initial lab study can provide a basis for the underlying physiological processes, which can then be used to explain behaviours that are later observed in the wild. The authors first conducted a laboratory experiment to investigate the recovery dynamics of physiological indicators of stress in northern pike (*Esox lucius*) following a C&R event, coupled with or without air exposure. The results indicated that exhaustive exercise led to changes in physiology, including increased muscle lactate, decreased tissue energy stores (and resulting increased blood glucose), and alterations in plasma ionic status but that recovery was rapid for most variables except glucose. Recovery was also not affected by an additional 300 s air exposure. A field study combining physiological and behavioural assessment was performed to verify the lab results and to investigate long-term consequences of exhaustive exercise and air exposure. Their results corroborated the lab study indicating exhaustive exercise caused an increase in blood lactate values. Interestingly, although air exposure did not show a significant effect on the physiology of pike, exposure of the maximum 300 s did result in behavioural impairment for the first hr post-release. The combination of lab and field studies allowed the researchers to investigate whole-organism changes as a result of exhaustive exercise.

Post-release mortality can also be estimated using mark-recapture. Although this method allows for large numbers of fish to be tagged, survival estimates are sensitive to under-reporting of recaptures and natural mortality events (Donaldson et al., 2008). Additionally, if a closed population is assumed and fish migrate outside of the study system, then the validity of the abundance estimates are compromised (Robichaud et al., 2017). Because basic and applied animal ecology requires a fundamental understanding of multiple organismal processes and interactions with the natural environment (Wong and Candolin, 2015), multiple tools are required to effectively study them (Cooke et al., 2004). In order to address some of the issues associated with survival estimations and post-release physiology and behaviour, researchers are using electronic tags which allow for the remote monitoring of free-swimming fish post-release (Donaldson et al., 2008), and integrating their use with other disciplines.

Physiology has much to offer policy makers (Cooke and O'Connor, 2010), especially when coupled with other methods such as electronic tracking. When physiological sampling and electronic tracking are coupled, the two methods provide a powerful means for discerning the mechanisms mediating animal-environment interactions, which can directly inform conservation and management planning (Crossin et al., 2014, 2017; Hussey et al., 2015). Research surrounding Pacific salmon (*Oncorhynchus spp.*) is a great example of how integrated tools have improved our ability to sustainably manage populations exposed to a number of anthropogenic activities. In a review, Cooke et al. (2012) identified how their cross-cutting studies on up-river migrating Pacific salmon, including the use of physiology, have effectively informed management decisions for these ecologically and economically important species. In particular, physiological tools provided insights into the effects of fisheries capture and helped to enhance techniques for facilitating recovery before being released (Cooke et al., 2012).

Beardsall et al. (2013) were the first to incorporate physiology into a field study examining the stress response and post-release survival of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) caught as bycatch in two gear types and then released. Blood samples were taken from sturgeon captured in bottom trawls and intertidal weirs and constituents commonly associated with a stress response – plasma cortisol, lactate, glucose – were quantified to determine the degree of physiological stress. Since weir systems are designed to minimize stress on retained animals, values obtained from weir-caught sturgeon were used as control values to compare with samples obtained from sturgeon captured in trawls that varied in tow-length. Results demonstrated that the magnitude of blood lactate in trawl-captured fish relative to control fish (weir-captured) increased with longer handling times. This study was the first to attempt to address the question of how drivers of physiological responses at the level of the individual alter requirements for successful conservation and management of wild sturgeon populations. However, to effectively scale the physiological effects on the individual to impacts on population dynamics, ecology must be considered (Metcalfe et al., 2012). In their review of conservation physiology for the applied management of marine fish, Metcalfe et al. (2012) proposed that telemetry can strengthen our incorporation of physiology into ecology, since telemetry technology offers the capability to record an animal’s behaviour and it can be done over seasonal and multi-annual time scales.

Acoustic Telemetry to Study Sturgeon

Electronic tracking of aquatic species has greatly improved our ability to not only locate them, but also to assess their physiology and behaviour within the context of their own environment (Crossin et al., 2014, 2017; Hussey et al., 2015). Tools used for the remote monitoring of fish include passive integrated transponder (PIT) tags, satellite and archival tags, radio, and acoustic telemetry, and biologging devices (Lucas and Baras, 2001). Acoustic transmitters and biologgers are often equipped with sensors for monitoring internal and/or external conditions (i.e., heart rate, body temperature, water temperature, swim depth, acceleration, etc.). Hussey et al. (2015) provided a comprehensive review of recent advances in the electronic tracking of animal populations, with a specific focus on the complexities of animal movements and interactions and the structuring of aquatic ecosystems. This review covered all forms of electronic tracking (e.g., acoustic and radio telemetry, archival satellite or data storage tags, etc.). Remarkably, they found a sixfold increase in aquatic telemetry studies over the past decade, across a range of taxa including crustaceans, seabirds, fishes, marine mammals, and more, which have provided important information about ecosystem health and how animals respond to the ever-changing ocean conditions. Historically, most telemetry studies have focused on teleost fishes, and nearly 500 studies have been dedicated to the use of acoustic telemetry alone (Hussey et al., 2015).

Kessel et al. (2014) reviewed the history and development of acoustic telemetry. Active/mobile tracking dominated telemetry studies in the 1970s, which involved fitting a target animal with an acoustic transmitter and monitoring it with a directional hydrophone and above-water acoustic receiver. More commonly, passive telemetry is now the preferred method of detection, and involves the use of stand-alone archival battery powered hydrophone/receiver units that can relay the information collected in real-time – if attached to cables – or can store it for download (Kessel et al., 2014). As with all technologies there are limitations to passive acoustic monitoring, such as interference from biofoul (Heupel et al., 2008), environmental noise (see review in Cooke et al., 2013b), or even depth and orientation (Huveneers et al., 2016). But overall it allows for the simultaneous monitoring of multiple individuals from a population over long-periods of time and can be used effectively in most environments (Heupel et al., 2006). When compared to archival tags, acoustic tags are less likely to provide information on open-ocean migrations since detection locations are limited by the ability for passive receiver placement, however they are cost-effective (~$350 CAD + tax/acoustic tag, vs >$5284 CAD + tax/archival tag, in 2016) and monitoring arrays established by organizations (e.g., the Ocean Tracking Network, http://oceantrackingnetwork.org/; the Florida Atlantic Coast Telemetry Network, https://secoora.org/fact/; the University of Maine Ocean Observing System, Goulette et al., 2014), are extending open-ocean receiver coverage (Hussey et al., 2015). These receiving networks are extremely advantageous as researchers can make use of pre-existing infrastructure in areas that they may not have been able to cover on their own, freeing up personal infrastructure for site-specific coverage, like at potential spawning grounds, etc. Although radio and/or acoustic telemetry were historically favoured for studying sturgeon habitat and behaviours, more recently there has been a shift towards the primary use of acoustic telemetry, sometimes in conjunction with other data-storing tags. The ability for the acoustic signal to transmit through all media (fresh, brackish, salt) with the same signal strength is especially important for the study of anadromous fish. Additionally, for highly migratory, long-lived fish like sturgeon, acoustic telemetry provides a unique opportunity to monitor multiple individuals of a population over long periods of time (>10 year lifespan tags).

Nelson et al., (2013a) briefly reviewed the use of tracking technologies on wild sturgeon and identified 55 studies that had used electronic tags (radio, acoustic telemetry, and/or satellite archival) to answer questions primarily about habitat use and general ecology. Given its increasing pervasiveness in sturgeon research, I focus solely on acoustic telemetry use for the remainder of this chapter where I provide an updated review of research articles using the technology to study sturgeon. Using the key terms “acoustic”, “telemetry”, “ultrasonic”, and “sturgeon,” I found 148 peer-reviewed journal articles to be published (in-print or first appearance online) on *Web of Science* before January 1, 2018.

Fifteen species of sturgeon ranging in conservation status from critically endangered to least concern (IUCN listing) have been studied using acoustic telemetry (Table 1). Given the range of tag sizes available to researchers, all ontogenetic stages have been studied, from fingerling to adult (Table 2), with sample sizes ranging from one to 429. Most studies were conducted on North American species (86%, or 127/148 studies; Table 1), with only a handful occurring in other parts of the world (China – 8, France – 6, Italy – 1, Poland – 1, Romania – 5).

Table 1.1. Fifteen species of sturgeon have been studied using acoustic telemetry ranging in conservation status from Least Concern to Critically Endangered (International Union for the Conservation of Nature [IUCN]). Associated references can be found in the Appendix A.

Common name	Species name	IUCN conservation status	# of studies
Adriatic sturgeon	*Acipenser naccarii*	Critically Endangered	1
Atlantic sturgeon	*Acipenser oxyrinchus oxyrinchus*	Near Threatened	26
Atlantic/shortnose sturgeon	*Acipenser oxyrinchus oxyrinchus/Acipenser brevirostrum*	Near Threatened/Vulnerable	3
Beluga/Russian/Stellate/ Sterlet sturgeon	*Huso huso/Acipenser gueldenstaedtii/Acipenser stellatus/Acipenser ruthenus*	Criticaly Endangered; Sterlet -Vulnerable	5
Chinese sturgeon	*Acipenser sinensis*	Endangered	8
European sturgeon	*Acipenser sturio*	Endangered	5
Green sturgeon	*Acipenser medirostris*	Near Threatened	16
Gulf sturgeon	*Acipenser oxyrinchus desotoi*	Near Threatened	18
Lake sturgeon	*Acipenser fulvescens*	Least Concern	26
Pallid sturgeon	*Scaphirhynchus albus*	Endangered	5
Shortnose sturgeon	*Acipenser brevirostrum*	Vulnerable	17
Shovelnose sturgeon	*Scaphirhynchus platorynchus*	Vulnerable	2
Siberian sturgeon	*Acipenser baerii*	Endangered	2
White sturgeon	*Acipenser transmontanus*	Least Concern	14

Table 1.2. Acoustic telemetry studies involving sturgeon have covered a range of topics, ontogenetic life-stages, and habitats. Articles that branched across study topics (e.g., were investigating both habitat use and anthropogenic influences) are included in all appropriate rows (i.e., the reference will appear under Study Topic Habitat Use **and** Anthropogenic Influences). Associated references can be found in the Appendix A.

Study topic	Total no. studies	Ontogenetic stages studied	Water body
Anthropogenic influences (e.g., hydroelectric facilities, dredging, catch-and-release)	15	juvenile, subadult, adult	river, estuary
Capture probability	1	Juvenile	river
Habitat use/movement/migration/ swimming behaviour	106	juvenile, subadult, adult	river, estuary, coastal/marine
Population structure/Abundance	4	juvenile, subadult, adult	river, estuary
Restocking/hatchery fish	14	YOY/juvenile/subadult	river, estuary
Spawning	24	adult	lake, river, estuary, coastal/marine
Survival/natural mortality	9	juvenile, subadult, adult	lake, river, estuary, coastal/marine
Tagging/handling effects	13	fingerling, juvenile, subadult, adult	lab, lake, river

It is unclear why most studies are centralized in North America, but given that 3 of 4 Danube River sturgeon species (Beluga, Russian, and stellate), the Adriatic sturgeon (*Acipenser naccarii*), and the Chinese sturgeon (*Acipenser sinensis)* are listed by the IUCN as critically endangered, conservation status in addition to local and external governance, likely play a role in which species can be tagged for research purposes. Varying access to research funds is also likely an important factor. For example, historically Turkey had substantial sturgeon stocks but the lack of effective management and overfishing has led to their decline and a subsequent absence in data collection and monitoring has made it difficult to provide accurate figures for current population sizes for sturgeon in Turkish waters of the Black Sea (Ustaoglu and Okumus, 2004). Additionally, 8 of the acoustic studies we found focused on the post-release behaviours and habitat use of hatchery-raised individuals for the purpose of restocking due to the imperiled status of the wild populations (Adriatic sturgeon, Bronzi et al., 2006; European sturgeon, *Acipenser sturio*, Acolas et al., 2012, 2017, Carrera-García et al., 2017; Du et al., 2013, Chinese sturgeon, Wang et al., 2014, Wu et al., 2018; Eastern Atlantic sturgeon, *Acipenser oxyrinchus*, Kapusta et al., 2016).

The first study to use acoustic telemetry to understand sturgeon biology used 14 primarily prototype acoustic tags to examine the movements of shortnose sturgeon (*Acipenser brevirostrum*, McCleave et al., 1977). The primary objectives of that study were to identify summer movements in relation to tidal and diel cycles, and to variation in salinity. Results indicated an affinity for movement in water less than 1-2 m in depth. Sturgeon were also found to be well oriented to tidal currents and moved widely through different salinities. Indeed, habitat use and/or general movement in relation to biotic and abiotic factors comprise the majority of research articles in the sturgeon-acoustic telemetry database (Table 2). Many of these studies were undertaken solely in river systems to answer questions about riverine movements and migrations (e.g., shortnose sturgeon, O'Herron et al., 1993; green sturgeon, *Acipenser medirostris*, Benson et al., 2007) or differential size-class habitat selection (e.g., juvenile white sturgeon, Young and Scarnecchia, 2005).

Since many species of sturgeon are anadromous, inclusion of estuarine habitat is key to understanding seasonal movements to and from river systems (e.g., Fernandes et al. 2010) and spawning migrations (e.g., Wippelhauser et al., 2015; Taylor & Litvak, 2017), and to the study of estuarine habitat importance to specific age-classes (e.g., Hatin et al., 2002). Over time, advances in receiver technology and/or placement of receiver infrastructure in unsheltered waters has expanded the scope to sturgeon studies to include coastal and marine movements. The marine migration patterns of green sturgeon were assessed using a network of automated hydrophone arrays deployed along the west coast of North America, from southeast Alaska to Monterey Bay, California (Lindley et al., 2008). Results showed that green sturgeon exhibited annual migrations along the continental shelf from south Pacific USA to Canada and parts of Alaska indicating important overwintering habitat. Aggregations were also located off Vancouver Island, Canada, from May-June which may represent an important feeding area. The results also suggested that the rapid and frequent migrations along the coastal shelf make green sturgeon susceptible to bycatch in bottom-trawl fisheries operated by both countries (Lindley et al., 2008). This study represented the first large-scale sturgeon telemetry study to document important seasonal coastal habitat use of two countries and highlighted the importance of understanding habitat needs of trans-boundary species. Habitat connectivity at a more local scale has been identified using acoustic telemetry in a sturgeon species assumed to be less migratory than some of its anadromous cousins. Zydlewski et al., (2011) first identified long-range coastal migrations of shortnose sturgeon to tributaries and non-natal river systems. These findings highlighted the importance of habitat connectivity and identified a migratory behaviour that was previously unknown for this species.

Like the partnership between Canadian and USA researchers in the study by Lindley et al., (2008), the sharing of acoustic telemetry detection data has allowed for large-scale marine migrations to be identified. Welch et al., (2006) were the first to document the >1,000 km migration of an adult white sturgeon originating from the Klamouth River, California, USA, to the Fraser River, British Columbia, Canada using acoustic detections made in each system. Although they did not have coastal receiver coverage, the dates of riverine detections in each system provided information about the seasonal importance of these habitats during the migration. Trans-boundary migrations are also common for Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) on the east coast of North America, where mixed stock aggregations have been detected at important foraging grounds (Stokesbury et al., 2016; Wippelhauser et al., 2017) and overwintering sites (Taylor et al., 2016). These trans-boundary movements and lengthy visits to areas outside of local protection jurisdictions complicates the conservation of these species – a topic of concern for quite some time (Apostle et al., 2013).

Acoustic telemetry has also been used to directly measure how anthropogenic stressors affect sturgeon behaviour. Studies examining the interactions between sturgeon and physical barriers and other man-made infrastructure such as dikes, tidal turbines, dams, etc., were common in my literature search, for acoustic telemetry helps researchers determine whether the addition or removal of infrastructure might affect fish passage and thus have potential population level consequences. For example, the movements and habitat use of lake sturgeon (*Acipenser fulvescens*) was studied in a small reservoir near a hydroelectric facility to assess the risk of entrainment based on movement patterns. The results indicated that residents within the small impoundments were indeed susceptible and the smaller size-classes (subadults) whose movements were more restricted were entrained more frequently than adults that had fewer habitat restrictions (McDougall et al., 2013a). Similarly, in the same system, researchers identified a potential solution for downstream migration success. Most lake sturgeon used bottom-draw regulating sluice gates, with passage survival at 91% when migrating downstream through the hydroelectric facility, suggesting that the implementation of these gates caters to the bottom-dwelling behaviour of these fish and is effective for conservation (McDougall et al., 2014a). In the Columbia River, a fine-scale acoustic monitoring system was deployed to identify changes in habitat use by white sturgeon during and after dredge dumping operations. Results indicated a very short-term effect of dredge dumping on behaviour, where sturgeon showed only a short-term and short distance displacement from their core area of habitat-use, but returning within 24 hr. Behaviours characterized by rates of movement, depth use, and diel patterns, showed little change, suggesting that natural behaviours were not altered (Parsley et al., 2011). More recently, results from studies examining spatial and temporal habitat use of sturgeon in areas slated for development are identifying areas of potential importance for various life-history phases, which can then feedback to management plans before development begins. For example, Atlantic sturgeon in the Bay of Fundy (Canada) were equipped with depth sensing acoustic transmitters, which revealed a predictable, recurring pattern of occupancy in a pelagic area known as an important migratory corridor but which is also scheduled for the development of tidal energy extraction (Stokesbury et al., 2016).

Despite the number of studies examining sturgeon behaviour reviewed here, none have incorporated physiological tools as a means for understanding the sublethal consequences of anthropogenic stressors. For example, following a mass stranding event in the Sacramento River, researchers tagged and rescued 24 threatened green sturgeon and then monitored their movements post-release. Telemetry data revealed that 17 of the tagged sturgeon continued their upstream migration to spawn grounds (Thomas et al., 2013). Blood samples from these fish before release could have provided insight into individual-level physiological changes (i.e., sublethal) that were associated with the stranding event and it may have helped to explain future spawning success or failure. These sublethal consequences are arguably just as important as modelling survivability, and yet they are vastly understudied in wild sturgeon populations. Conservation and management planning for sturgeon populations would, therefore, benefit from the incorporation of the cross-disciplinary approaches via the coupling of physiological techniques with electronic tracking (Crossin et al., 2014; Hussey et al., 2015).

Research Objectives and Expectations

My overall objective of this thesis is to further our understanding of sturgeon biology in the context of C&R angling and behavioural ecology. Most emphasis on sturgeon stress research has been placed on aquaculture with little understanding of physiology and behaviour in wild populations. Relatively little is known about the effects of C&R angling practices on sturgeon physiology and behaviour and knowledge gaps still exist pertaining to their movement ecology in the wild. My overarching hypothesis for this thesis was that i) the severity of capture stressors influences the magnitude of the response (e.g., reflex impairment and measured changes in blood chemistry), ii) the response would predict post-release outcomes (e.g., recovery and movements), and iii) the effects would be exacerbated at higher water temperatures and during periods of high discharge (i.e., peak freshet). Three separate studies were conducted to address this.

In chapter 2 I evaluated the physiological stress response in captive white sturgeon exposed to a capture-handling stressor at two temperatures (i.e., summer vs winter water temperatures). In addition to examining the stress physiology, Reflex Action Mortality Predictors (RAMP) were used to assess fish vitality (i.e., the capacity to survive) following the capture-handling event. In short, the presence or absence of specific organismal reflexes (e.g., ventilation, reorientation ability, body and tail responses to touch stimulus, etc.) that are normally expressed in unstressed individuals are assessed to predict the likelihood for post-release mortality. Therefore, RAMP is functionally useful as a quantitative link between the stress response and a fitness outcome (Davis, 2010, 2007, 2005). I expected that longer exposure to capture-and-handling would produce a measurable stress response in white sturgeon and that this response would be exacerbated in warm temperatures. Additionally, RAMP scores were expected to be positively related to the length of the stressor, to the physiological stress response, as well as to an increased potential for post-release mortality (i.e., longer treatment = exacerbated physiological stress response = greater level of impairment (higher ramp score) = increased risk of mortality). Immediate (<30 min) recovery behaviour was monitored with the expectation that more stressed individuals would take longer to recover.

In chapter 3 I evaluated the fine-scale (i.e., immediate <1 hr) post-release recovery behaviour of white sturgeon using novel tri-axial acceleration acoustic transmitters, active tracking, and tested triangulation methods. Because this was the first study to use these transmitters on white sturgeon in the wild, the transmitters had to be calibrated to sturgeon swim behaviours. First, using captive sturgeon, I used the accelerometer transmitters to describe various swimming behaviours of white sturgeon in a controlled, carefully monitored swimming raceway. From these observations I was able to construct an ethogram of acceleration values that we could use to characterize specific high, low, and moderate swimming activities. In addition, this chapter acted as a pilot study (i.e., low sample size and one sampling season) to collect information on the physiological stress response of wild white sturgeon exposed to C&R angling in the lower Fraser River, B.C. I expected that activity level and physiology would be affected by angling time. Specifically, the physiological stress response would be more pronounced (i.e., higher levels of circulating glucocorticoids) and activity level would be reduced in fish angled for longer periods of time.

In chapter 4 I linked environmental factors with reflex action mortality predictors, physiological stress, and acoustic telemetry to evaluate the response of white sturgeon to catch and release angling. Using a combination of acoustic telemetry data, and mark-recapture information provided by the FRSCS Passive Integrated Transponder (PIT) volunteer tagging program, I determined the survival of white sturgeon that were captured by angling and then released in the LFR. I then investigated factors underlying the physiological stress response and reflex response of white sturgeon, captured over a range of river temperatures (~2 – 21 °C) and discharge rates (1270 to 9430 $m^3 \cdot s^{-1}$). Based on previous work revealing correlations between RAMP scores and physiological stress measures in captive sturgeon (McLean et al., 2016), I 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. I also predicted variation in post-release movement metrics would be directly related to fight metrics, stress physiology, and environmental condition at capture.

In Chapter 5 I summarized the findings of these studies and placed the results of this thesis in the context of our overall understanding of sturgeon biology.

In addition, I provided suggestions for fisheries managers and future research initiatives.

Ultimately, my goals were to contribute to an increased appreciation of the impact of recreational fisheries on white sturgeon and to develop a novel physiological and tracking approach that can be used to inform regulation and protection of aquatic animals.

Statement of Co-Authorship

This dissertation contains three data chapters and one literature review and meta-analysis (embedded in introduction). Each chapter corresponds to a manuscript written for publication in a scientific journal and largely follows the regular structure of scientific papers consisting of an abstract, introduction, materials and methods, results, discussion, and conclusion.

All co-authors contributed to these manuscripts through comments, advice, support in research design and method development, as well as interpretation. The publication status of each chapter at the time of submission of this thesis is as follows:

Chapter 1: McLean, M.F., Litvak, M.K., Crossin, G.T. Acoustic telemetry and physiology can inform our understanding of sturgeon interactions with anthropogenic stressors (unpublished).

Chapter 2: 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. Conservation Physiology 4: cow031.

Chapter 3: McLean, M.F.**,** Litvak, M.K., Cooke, S.J., Hanson, K.C., Patterson, D.A., Hinch, S.G., Crossin, G.T. 2019. Immediate physiological and behavioural response from catch-and-release of wild white sturgeon (*Acipenser transmontanus* Richardson, 1836). Fisheries Research. 214: 65 – 75.

Chapter 4: McLean, M.F.**,** Litvak, M.K., Cooke, S.J., Stoddard, E.A, Welch, D.W., Patterson, D.A., Hinch, S.G., Crossin, G.T. 2019. Linking environmental factors with reflex action mortality predictors, physiological stress, and post-release behaviour to evaluate the response of white sturgeon to catch and release angling. Comparative Biochemistry and Physiology – Part A: Molecular & Integrative Physiology. Pending minor revision.

Three of these chapters (2, 3, and 4) have either been published or are pending minor revision. Details are provided on the last page of each chapter. Chapter 2 and 3 have been published under an open-access license and special permission for duplication in this thesis was not required by the publisher.

Data Accessibility

Telemetry data is freely available through oceantrackingnetwork.org and upon request to montana.mclean@dal.ca.

CHAPTER 2

Physiological Stress Response, Reflex Impairment, and Delayed Mortality of White Sturgeon Exposed to Simulated Fisheries Stressors

Abstract

White sturgeon *Acipenser transmontanus* are the largest freshwater fish in North America and a species exposed to widespread fishing pressure. Despite the growing interest in recreational fishing for white sturgeon, little is known about the sub-lethal and lethal impacts of angling on released sturgeon. In summer (July 2014, mean water temperature = 15.3°C) and winter (February 2015, mean water temperature = 6.6°C), captive white sturgeon (N = 48) were exposed to a combination of exercise and air exposure as a method of simulating an angling event. Following the stressor, sturgeon were assessed for a physiological stress response and reflex impairments were quantified to determine overall fish vitality (i.e., capacity for survival). A physiological stress response occurred in all sturgeon exposed to a fishing-related stressor with the magnitude of the response correlated with the duration of the stressor. Moreover, the stress from exercise was more pronounced in summer, leading to higher reflex impairment scores (mean +/- SEM, 0.44 +/- 0.07 and 0.25 +/- 0.05, in summer and winter, respectively). Reflex impairment also correlated with lactate levels (e.g. physiological stress measures related to exhaustive exercise; r=0.53) and recovery time (r=0.76). Two mortalities occurred >24 hr following the cessation of treatment in the summer. Given natural habitats for white sturgeon can reach much higher temperatures than presented in

our study, we caution the use of this mortality estimate for a summer season as latent mortality could be much higher when temperatures exceed 16°C. This is the first experiment investigating the physiological disturbance and reflex impairment of capture and release at two temperatures on sub-adult/adult white sturgeon, and the results suggest that future research needs to examine the longer term and fitness consequences of extended play and air exposure times, as these are largely unknown for wild populations.

Introduction

Many recreational fisheries have adopted catch-and-release (C&R) practices as a means for reducing fisheries-related mortality and conserving fish populations (Arlinghaus et al., 2007). The long-term success of a C&R fishery hinges on an assumption of high post-release survival (Cooke and Schramm, 2007). Research has shown that not all fish survive (reviewed in Bartholomew & Bohnsack, 2005) and that for fish that survive, significant sub-lethal physiological disturbances and behavioural impairments can occur (Arlinghaus et al., 2009). These effects may vary among species, life-history stages, sexes, environment (i.e., seasonal changes in water temperature), and by gear types (Arlinghaus et al., 2007; Cooke and Suski, 2005). For this reason, it is important not to generalize the results of C&R studies across multiple species (Cooke and Suski, 2005). The development of fisheries management plans and best practices for a target species would benefit from a better understanding of the physiological, behavioural, and survival aspects of C&R impacts in different contexts, such as at different temperatures.

Reflex action mortality predictors (RAMP) have become a popular tool among researchers for the rapid assessment of fish vitality (i.e., the capacity for survival) after fisheries capture by quantitatively linking the stress response to fitness outcomes (Davis, 2010, 2007, 2005), although this technique has not yet been broadly adopted by fisheries managers. From a functional perspective, RAMP is a way of measuring the impairment of normal reflexes that provide a measure of vitality. The premise behind the reflex impairment method is that stress state and the likelihood for post-release mortality can be predicted by scoring the absence or presence of specific organismal reflexes that are normally expressed in unstressed individuals. Reflexes are defined as involuntary movements induced by a peripheral stimulus, and the suite of specific reflexes used in RAMP assessments will vary among species. Once an assessment is made, a final RAMP score is calculated and assigned to an angled fish, which serves as proxy for compromised physiological state and whole-animal well-being (Davis, 2010; Raby et al., 2013). Among fishes, observable reflex impairment assessments have successfully predicted the post-release mortality of migrating coho salmon *Oncorhynchus kisutch* (Raby et al., 2014, 2012), sockeye salmon *Oncorhynchus nerka* (Gale et al., 2014, 2011), bonefish *Albula* spp. (Brownscombe et al., 2013), and a number of elasmobranch species (Danylchuk et al., 2014; Gallagher et al., 2014). Further, reflex impairment assessments have also predicted post-release behaviour and impaired swimming performance (Brownscombe et al., 2013; J.W. Brownscombe et al., 2014; Cooke et al., 2014; Szekeres et al., 2014). Of note, RAMP scores have also been unsuccessful in predicting post-release mortality following fisheries encounters (i.e., sockeye salmon; Robinson et al., 2015), further supporting the need for species- and context-specific assessments of the technique.

Understanding the physiological mechanisms that lead to reflex impairment is important for linking the sublethal effects of stress to fitness. For example, Raby et al., (2013) were the first to quantitatively link reflex impairment scores to physiological measures of stress and homeostasis, thereby establishing a relationship between RAMP and physiological condition. Of particular note was a significant relationship between plasma lactate (a measure of anaerobic metabolism) and RAMP score after exhaustive fisheries capture in pink salmon *O. gorbuscha*. The authors cautioned, however, that lactate is not a causative agent impairing the suite of reflexes, but is instead a correlated by-product of the complex physiological pathways more directly responsible for inducing impairment. Gallagher et al., (2014) also identified a correlation between lactate level and mortality of some shark species. However, given that clearance rates for lactate are highly variable, it is possible that the impact of high lactate levels on reflex impairment varies among species, and likely depends on when post-capture samples are collected. Although useful as an indicator of post-capture condition and reflex impairment, lactate is but one of several relevant physiological measures involved in the stress response. Each of the reflexes selected for a RAMP protocol are likely modulated by several different physiological pathways and these may vary among species. It is therefore important to assess other measures of exhaustion and stress (e.g., cortisol, glucose, ions), when attempting to understand the mechanisms underlying fish vitality.

In this study, we build upon the growing body of research on reflex impairment as a potential conservation and management tool applied to important recreational fish species, and focus our efforts on the white sturgeon *Acipenser transmontanus*. White sturgeon are exposed to fishing stressors throughout their range from California, U.S., to Canada's Fraser River. Currently, white sturgeon populations exposed to fisheries in the U.S. are considered of least concern by the International Union for the Conservation of Nature (IUCN; Duke et al., 2004), however the absence of information about pre-release stress on white sturgeon has become increasingly important for managers in the context of recreational fisheries (Z. Jackson, U.S. Fish and Wildlife Service, Lodi, CA, pers. comm.). Indeed, globally there is little known about how imperiled fishes respond to different C&R practices making it difficult to determine if C&R angling is compatible with recovery strategies (Cooke et al., 2016). Until 2012, all Canadian populations of white sturgeon were considered endangered, however reassessment in 2012 resulted in the separation of populations into Designatable Units (DU), to be subsequently assessed separately. The upper Columbia, Kootenay, and Upper Fraser River DUs were assessed as being endangered. The Lower Fraser River (LFR) DU was assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as being threatened, however it is not officially recognized by the Species at Risk Act due to its socioeconomic importance to the province of British Columbia (COSEWIC, 2012). Despite the growing popularity of recreational fishing for white sturgeon, there has been limited published work focusing on the potential impacts of acute angling stressors. Recent mark-recapture data indicates that the LFR white sturgeon population is not growing to the extent expected, and that juvenile recruitment may be an issue (Nelson et al., 2013b). Since adult white sturgeon are critical to juvenile recruitment and recovery of the population, it is essential that the effects of angling on post-release behaviour, physiology, and mortality are quantified so that it can be closely monitored.

There are few to no seasonal restrictions on the recreational fishing of white sturgeon and in Canada's Fraser River, BC, that includes angling in water temperatures ranging from below 0 to > 20°C in parts of their range. Therefore, this research is crucial to the understanding of the combined effects of river temperature and fishing-related stressors and how they influence the physiological status, vitality, and recovery potential of recreationally angled sturgeons. Using a population of wild white sturgeon held at the U.S. Fish and Wildlife Service, Abernathy Fish Technology Center in Longview, Washington (USA), our aim was to develop, refine, and validate a reflex impairment protocol by exposing sturgeon to controlled simulated fisheries capture events. We then linked the resulting reflex impairment indices (RAMP score) to stress physiology and recovery times. By doing so, we predicted that the magnitude of the physiological disturbance and reflex impairment would be correlated with treatment time, and that physiological disturbance and reflex impairment would be further modulated by water temperature. Results from these experiments allow us to not only quantify the sublethal impacts of recreational C&R stressors, but also how these might change seasonally with respect to water temperature.

Materials and Methods

A wild origin, now captive population of white sturgeon housed at the U.S. Fish and Wildlife Service, Abernathy Fish Technology Center, WA, USA were used for our experiments. Sturgeon were maintained in two outdoor raceways (24.4 m in length x 2.4 m in width x 0.8 m in depth) with water provided at ~0.01 $m^3 \cdot s^{-1}$ from the adjacent Abernathy Creek, a tributary to the Columbia River. Experiments ran from 25-29 July 2014 at an average water temperature of ~15.3 °C, and from 23-27 February 2015 at ~ 6.6°C.

Experimental Treatments

Forty-eight white sturgeon (24 per season; mean ± SD 109.20 ± 22.17 and 112.55 ± 18.72 cm fork length, FL; in July and February, respectively) were corralled into a sling, and allowed to thrash for a specified period of time to mimic forced exercise. Sturgeon were also partially exposed to air during this period of exercise by maintaining the sling out of water and only providing enough water to half cover the gills. These treatments were used to elicit a stress response and push the sturgeon to their physiological limits by using a combination of stress and air exposure to simulate a fisheries interaction. Often chasing is considered a suitable proxy for a fisheries stressor (S. J. Cooke et al., 2013), but given the size of our study fish and the layout of the raceway (i.e., all untreated fish in one raceway), forced thrashing in the sling provided a means of inducing a stress response while at the same time reducing the exposure of untreated fish to additional stress. In the LFR, white sturgeon angling events can last anywhere from 30 s to > 2 hr (median time = 5.78 min; McLean, 2015; unpub. data). In brief, the rectangular sling (1.84 m in length x 0.55 m in width) was constructed of tarpaulin and supported by two poles threaded through either side. To assist in capture, the sling was reinforced with a nylon hood at one end so that when corralled head first, the hood would help support the head of the sturgeon while the sides of the sling were pulled together. The poles of the sling were extended using four pieces of PVC piping so that during treatments the sling could rest across the raceway and help support the sturgeon. Individual white sturgeon were selected at random to receive a specific treatment of exercise and partial air exposure for either 0 (control), 5, 10, or 15 mins, for a total of 6 sturgeon per treatment/season. Although we did the best to obtain immediate samples from time = 0 fish, some thrashing occurred during capture and thus our controls should be regarded as “handled controls.” As mentioned above, the exercise occurred in a sling with the gills partially covered in water to obtain the combined effect of partial air exposure and exercise for set periods of time. In each treatment, fish were corralled, treated, bled from the caudal vasculature, and immediately checked for reflexes before being transferred to a recovery raceway.

Reflex Assessments

A modified reflex impairment index was developed for white sturgeon based on the RAMP method previously described for other taxa (see Raby et al., 2013). Immediately following treatment, all sturgeon were tested for five reflexes determined to be present/absent in untreated control individuals. All reaction times were chosen based on testing these reflexes on control sturgeon. Ventilation, mouth extension, orientation, tail grab and body flex were the reflexes tested on treated white sturgeon (Figure 2.1). Using a categorical assessment, 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 while half-submerged in the sling, as observed by watching the number of opercular movements. Mouth extension was considered unimpaired if the mouth of the sturgeon did not fully extend during a 10 s period out of water, since mouth extensions have been associated with stress events in other sturgeon species (M. McLean, pers. obs. of Atlantic sturgeon, *Acipenser oxyrinchus*). To test orientation, upon release in the recovery raceway 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 holding the sturgeon partially out of water using two hands wrapped under the pectoral fins. If the sturgeon actively struggled free it was characterized as an unimpaired response. All RAMP assessments were completed in <30 s. RAMP assessments and recovery were recorded on a GoPro for each sturgeon. Some sturgeon were too vigorous to allow for complete testing of reflexes and were assigned an overall unimpaired status. This was the case for all control fish. From the reflex results for each sturgeon, a

RAMP score was calculated as a simple proportion of the five measured reflexes that were impaired in an individual fish (0 = no reflexes impaired, 1 = all reflexes impaired).

Figure 2.1. Body flex (top) and orientation (bottom) were two of five reflexes tested on white sturgeon following a combined treatment of exercise and air exposure for 0, 5, 10, or 15 mins. From the reflex results for each sturgeon, a RAMP score was calculated as a simple proportion of the five measured reflexes that were impaired in an individual fish (0 = no reflexes impaired, 1 = all reflexes impaired).

Physiology

A non-lethal blood sample was taken from the caudal vasculature of white sturgeon immediately following treatment cessation using a 10 ml lithium heparin coated barrel (Braun) and a 3.8 cm (1.5 in) 18 gauge needle (Becton-Dickinson, Franklin Lakes, New Jersey). The time to bleed was recorded to the nearest second as “bleed time” and samples were immediately placed in a 50:50 ice-water slurry and processed within 30 mins of collection. Glucose and lactate levels were measured on whole blood (10 µl) using hand-held glucose (ACCU-CHECK glucose meter; Roche Diagnostics, Basel, Switzerland) and lactate meters (Lactate Pro LT-1710 portable lactate analyzer; Arkray Inc., Kyoto, Japan). These portable readers have been validated for use on fish (see Cooke et al., 2008) and have been used for analysis on whole blood of other sturgeon species (Atlantic sturgeon *A. oxyrinchus*, (Beardsall et al., 2013). To determine hematocrit, a small sample of whole blood was then spun in a micro-haematocrit centrifuge (LW Scientific, Lawrenceville, GA) for 5 mins at 10 000 g (11 500 rpm) to determine packed cell volume as a proportion of red cells to the total volume of the sample. The remainder of the blood sample was centrifuged (Portifuge; LW Scientific, Lawrenceville, USA) for 5 mins at 3,300 g to separate red cells from plasma. Plasma was transferred to cryovial tubes and then frozen and stored in a -80 freezer at the U.S. Fish and Wildlife Service facility until it could be analyzed further.

Laboratory assays were run at the Department of Fisheries and Oceans facility in West Vancouver, British Columbia. Plasma cortisol, osmolality, and Cl^-

were quantified following the detailed instructions on the assay kits or the associated instrument instructions. In brief, hormone ELISAs (enzyme-linked immunosorbent assays) were run on plasma samples to quantitatively identify cortisol titers. As per directions on the Neogen Corporation ELISA kit, samples and standards were run in duplicates. Inter- and intra-assay variation for cortisol were 10 and 1.8%, respectively. Osmolality was measured in plasma samples inserted into a freezing-point osmometer (model 3320, Advanced Instruments, Inc., Norwood, USA). Once again, samples were run in duplicate falling within 5 units of one another. Chloride was measured from plasma samples using a chloridometer (Haake Buchler Digital, Saddle Brook, USA). Samples were run in duplicates and fell within 3 units of one another.

Recovery

A holistic (whole-animal assessment) approach was used to characterize recovery since all five reflexes could not be re-tested following the recovery period due to limited staffing. Anecdotally we were interested in determining whether we could predict fate based on observational recovery, or lack thereof. Thus, sturgeon were considered fully recovered when they resumed “normal” behaviours as predetermined by control fish. Any unusual post-release behaviour was recorded up to 30 mins post-release. As such, fish were considered unrecovered if normal behaviour did not ensue after the 30 min recovery period. This behaviour typically consisted of sedentary-solitary confinement to one side of the tank, and was often associated with a loss of buoyancy control in all or parts of their body. The 30 min observation period was chosen solely because of limited staffing and time, and we recognize that continued monitoring of post-release behaviour would allow us to better estimate potential sub-lethal effects and/or delayed mortality. However, given most wild caught sturgeon are released immediately, we believe this observation period still offers insight to potential post-release behavioural changes.

Analysis

Physiological variables, RAMP scores, bleed and recovery times were related to sturgeon size (FL) via general linear models. To evaluate the status (i.e., vitality) of sturgeon prior to release into the recovery raceways, a series of two-way (season and treatment) ANOVAs were used to assess how treatment affects the physiological response and RAMP impairment scores in two seasons. A series of one-way ANOVAs were used to evaluate the relationship between blood parameters and reflex impairment. Recovery time was compared to blood physiology parameters via generalized linear regressions. One-way ANOVA was used to assess whether treatment time and/or RAMP score had an effect on recovery time. Because mortality was low in our study, we tested the power of RAMP as an indicator of post-release vitality on the individuals that were observationally "recovered" and "unrecovered" by the end of the 30 min recovery period. Using the assumption that fish vitality is lower – and suggestive of an increased risk of delayed mortality – among individuals that did not present as fully "recovered" by the end of the 30 min observational period, a Student's t-test was used to compare mean RAMP scores of "recovered" and "unrecovered" sturgeon.

In cases of deviation from the underlying assumptions of parametric tests (normality, variance homogeneity, $p < 0.05$), continuous data were loge –

transformed. In all cases transformations successfully normalized the data ($p > 0.05$). For all comparisons the significance was assessed at α – 0.05. *Post hoc* Tukey HSD multiple comparison tests were used to determine significant differences ($P \leq 0.05$). All analyses were conducted using R statistical software (R version 3.1.3, February 2015). All data are presented as means ± SEM unless otherwise indicated.

Results

Reflex Impairment Indices

With the exception of controls, all treatments resulted in some loss of reflexes in all individuals. Ventilation was the first reflex to be affected across individuals, followed by orientation, mouth extension, tail grab, and lastly, body flex (Table 2.1). A proportion of sturgeon experienced reflex impairment at five mins, except tail grab and body flex responses remained intact. The 10 and 15 min treatments resulted in a proportion of sturgeon experiencing a loss of all five tested reflexes. All sturgeon experienced ventilation impairment (fewer opercular beats) after the maximum treatment time of 15 min, and 90% were unable to reorient themselves (i.e., impaired orientation).

Table 2.1. Impairment of individual reflexes with increasing overall reflex impairment (RAMP score). Values represent the proportion of white sturgeon with a particular reflex impaired within each level of overall impairment. For example, of the white sturgeon with overall RAMP scores of 0.4, all of them had impaired ventilation, but only 0.50 (50%) had impaired orientation.

RAMP score (proportion)	Ventilation	Orientation	Mouth extension	Tail grab	Body flex
0.0 N = 10	0.00	0.00	0.00	0.00	0.00
0.2 N = 13	0.46	0.31	0.23	0.00	0.00
0.4 N = 12	1.00	0.50	0.42	0.08	0.00
0.6 N = 4	1.00	0.75	0.50	0.25	0.50
0.8 N = 6	1.00	1.00	0.17	1.00	0.86
1.00 N = 3	1.00	1.00	1.00	1.00	1.00

Treatment and Season Effects on RAMP Score and Physiology

There was no relationship between sturgeon size and indices of physiological stress, RAMP scores, handling or recovery times ($p > 0.05$). The clearest evidence of a treatment effect was seen with RAMP impairment and lactate. White sturgeon reflex impairment increased consistently with the degree of the stressor or treatment ($F_{3,40} = 46.07$, $p < 0.001$; Figure 2.2). Mean RAMP score was significantly different between all treatment groups, with the exception of the RAMP scores of the 10 and 15 min groups (Figure 2.2). RAMP scores were significantly higher in summer treated fish ($F_{1,40} = 19.307$, $p < 0.001$), but there was not a significant interaction between season and treatment group ($F_{3,40} = 2.762$, $p = 0.054$). Lactate concentrations were significantly different between treatment groups ($F_{3,40} = 10.37$, $p < 0.001$) and season ($F_{1,40} = 42.29$; $p < 0.001$), but again there was no significant interaction between treatment group and season ($F_{3,40} = 2.04$, $p = 0.12$). Specifically, a post hoc test revealed that the control and 5 min groups had significantly lower levels of plasma lactate than the 15 min treatment group (Figure 2.2), and lactate was significantly higher in summer-sampled fish than winter.

Plasma cortisol was also significantly higher in the 15 min treatment group than in controls ($F_{3,40} = 2.93$, $p = 0.04$; Figure 2.2), and was significantly higher in the summer sampling period ($F_{1,40} = 4.83$, $p = 0.03$). There was no significant interaction between treatment and season ($F_{3,40} = 0.57$, $p = 0.64$). Fifteen min groups had higher glucose levels, but these differences were not significant ($F_{3,40} = 2.79$, $p = 0.05$; Figure 2.2). Similarly, there was no significant difference in glucose concentrations between seasons ($F_{1,40}$ = 0.40, p = 0.53) and there was no significant interaction between treatment and season ($F_{3,40}$= 0.52, p = 0.67). White sturgeon hematocrit ranged from 6 to 56% (mean = 33%), but treatment time did not have a significant effect on the percent red blood cells ($F_{3,40}$ = 0.50, p = 0.69; Figure 2.3). Hematocrit was also similar between seasons ($F_{1,40}$ = 0.02, p = 0.89) and no interaction was seen ($F_{3,40}$ = 0.42, p = 0.74). Plasma osmolality was significantly different among treatments ($F_{3,40}$ = 5.09, p < 0.01; Figure 2.2), with a post hoc test revealing that individuals in the 15 min treatment groups had significantly higher osmolality than the controls. Osmolality was also significantly higher in winter-sampled fish ($F_{1,40}$= 2.93, p < 0.01), but there was not a significant interaction between treatment and season ($F_{3,40}$= 0.46, p = 0.71). Plasma Cl^- was also significantly different among treatment groups ($F_{3,40}$ = 4.58, p < 0.01; Figure 2) and between seasons, with winter fish having significantly higher plasma Cl^- ($F_{1,40}$ = 48.80, p < 0.01). Once again, there was not a significant interaction between treatment and season ($F_{3,40}$ = 0.33, p = 0.80).

White sturgeon recovery time was measured up to 30 mins for each individual. On average, sturgeon took 10.42 mins to recover across all treatments (n = 46). Recovery time increased significantly with treatment time ($F_{3,42}$ = 52.45, p < 0.01; Figure 2.2), with all groups having significantly different recovery times with the exception of the control and 5 min treatments. Recovery time did not differ between seasons ($F_{1,42}$ = 0.56, p = 0.46; Figure 2.2), nor was there a significant interaction identified between treatment and season ($F_{3,42}$ = 0.28, p = 0.84). Individuals with longer recovery times had higher levels of circulating lactate ($F_{1,46}$

= 11.35, $p < 0.01$), higher osmolality ($F_{1,46} = 6.85$, $p = 0.01$) and higher concentrations of Cl^- ($F_{1,46} = 4.18$, $p = 0.04$). Recovery time was not, however, significantly related to plasma cortisol ($F_{1,46} = 1.96$, $p = 0.17$), glucose ($F_{1,46} = 0.50$, $p = 0.48$), or hematocrit ($F_{1,46} = 0.24$, $p = 0.62$).

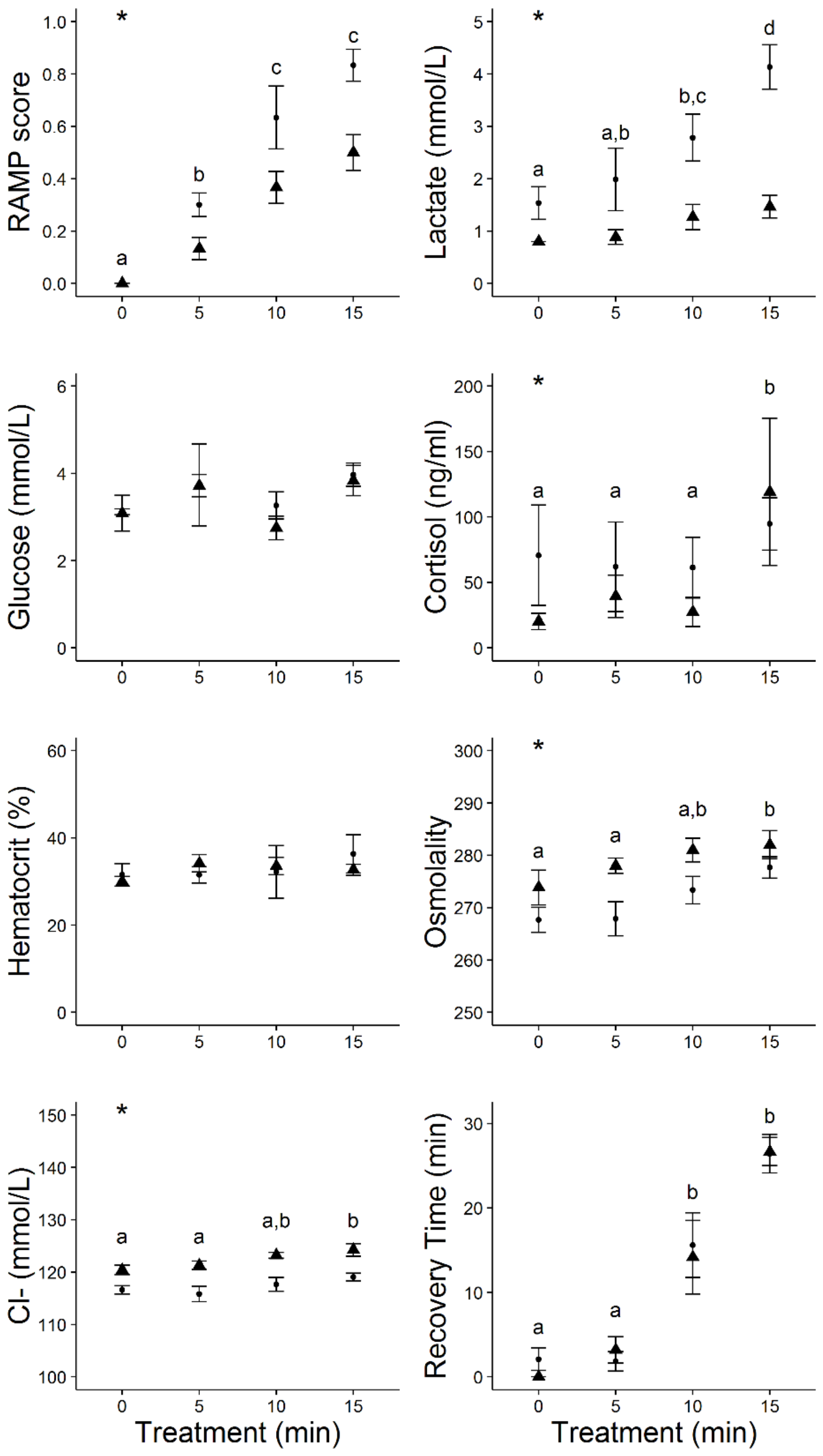
RAMP score
1.0
0.8
0.6
0.4
0.2
0.0
*
a
b
c
c
Lactate (mmol/L)
5
4
3
2
1
0
*
a
a,b
b,c
d
Glucose (mmol/L)
6
4
2
0
Cortisol (ng/ml)
200
150
100
50
0
*
a
a
a
b
Hematocrit (%)
60
40
20
0
Osmolality
300
290
280
270
260
250
*
a
a
a,b
b
Cl- (mmol/L)
150
140
130
120
110
100
*
a
a
a,b
b
Recovery Time (min)
30
20
10
0
a
a
b
b
0
5
10
15
Treatment (min)
Treatment (min)

Figure 2.2. Mean ± SEM RAMP scores and physiological variables measured in white sturgeon for each of the four treatments (*n* = 12 sturgeon per treatment) in July 2014 (●) and February 2015 (▲). In each group, fish were corralled, treated, had a blood sample taken from the caudal vasculature, were measured to the nearest centimeter for FL and girth, and immediately checked for reflexes before being transferred to a recovery raceway. Treated sturgeon were corralled into a sling, and allowed to thrash for a specified period of time to mimic forced exercise. Sturgeon were also partially exposed to air during this period of exercise by maintaining the sling out of water and only providing enough water to half cover the gills. Control sturgeon were sampled immediately. Among-group differences were assessed using a series of two-way ANOVA (treatment and season). *Post hoc* differences among groups are indicated by dissimilar letters. An asterisk (*) denotes a significant difference between seasons (summer & fall) for a particular parameter.

Relationship Between RAMP Impairment, Physiology, and Recovery

White sturgeon with higher RAMP scores (approaching 1) had higher concentrations of lactate ($F_{5,42} = 3.69$, $p < 0.05$; Figure 2.3), specifically between control groups and sturgeon with RAMP scores of 0.8 and 1. Loge transformed plasma cortisol and blood glucose concentrations were not significantly different among RAMP scores ($F_{5,42} = 0.59$ and $F_{5,42} = 1.18$, $p > 0.05$, respectively; Figure 2.3). Similarly, hematocrit, osmolality and Cl^- were not significantly different among RAMP scores ($F_{5,42} = 2.37$, $F_{5,42} = 0.84$ and $F_{5,42} = 1.66$, $p > 0.05$, respectively; Figure 2.3). Individuals with higher RAMP scores did take significantly longer to recover ($F_{5,42} = 11.90$, $p < 0.01$; Figure 2.3). Specifically, there were significant differences in recovery time between individuals with impairments scores of 0 and 0.4, 0.6, 0.8 and 1, as well as between 0.2, 0.8, and 1.0.

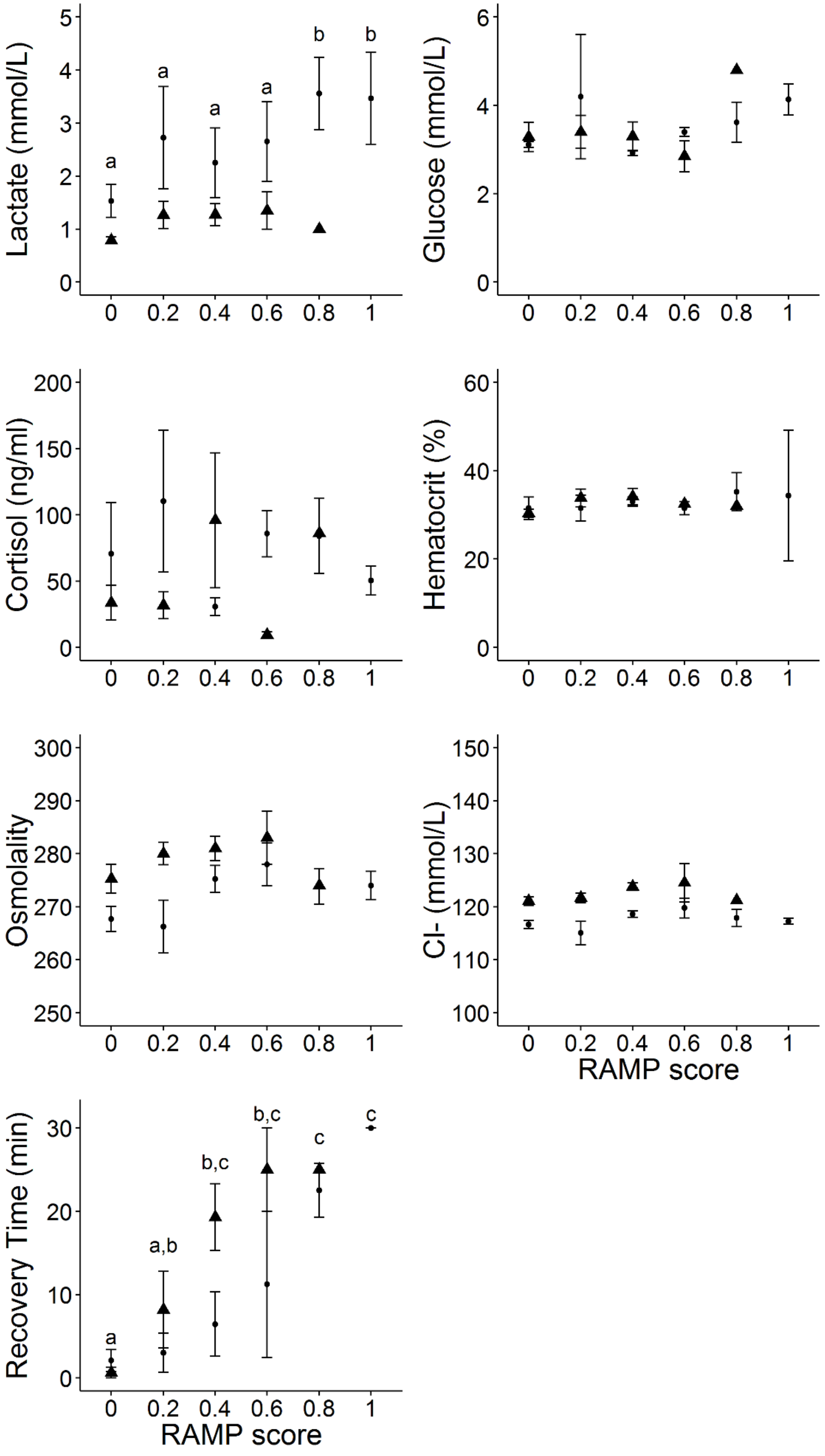
Lactate (mmol/L)
0
1
2
3
4
5
a
a
a
a
b
b
Glucose (mmol/L)
0
2
4
6
Cortisol (ng/ml)
0
50
100
150
200
Hematocrit (%)
0
20
40
60
Osmolality
250
260
270
280
290
300
Cl- (mmol/L)
100
110
120
130
140
150
Recovery Time (min)
0
10
20
30
a
a,b
b,c
b,c
c
c
0
0.2
0.4
0.6
0.8
1
RAMP score

Figure 2.3. Mean ± SEM plasma lactate, cortisol, glucose and hematocrit values for white sturgeon assessed at five different RAMP scores of overall reflex impairment in July 2014 (●) and February 2015 (▲). Higher scores indicate a greater proportion of impaired reflexes of the five reflexes tested (see Figure 2): ventilation, mouth extension, orientation, body flex, and tail grab. Among-group differences were assessed via one-way ANOVA and *post hoc* differences among groups are indicated by dissimilar letters.

Prediction of Fate and Delayed Mortality

Of 48 treated individuals, 9 were considered "unrecovered" by the end of the 30 min observational period (n = 5 summer and 4 winter). All unrecovered fish were from the longer treatment groups (n = 7 from 15 min. and 2 from 10 min.) and had significantly higher reflex impairment scores (M =0.69, SD = 0.30) than recovered fish (M = 0.27, SD = 0.26; t(11.02) = 3.87, $p < 0.01$).

Of the 9 unrecovered fish, only two mortalities occurred following 10 and 15 min treatments in the summer sampling period (July 2014). One mortality occurred 48 hr following cessation of the treatment and the other, < 72 hr after treatment. RAMP scores for both fish were 1, indicating all reflexes were impaired at the time of release (Table 2.2). Both mortalities revealed opposing but extreme hematocrit profiles of 6 and 56%, along with upper-range levels of circulating lactate, and mid-range cortisol, glucose and osmolality (Table 2.2). One individual presented with a number of skin lesions suggestive of a potential pre-treatment illness.

Table 2.2. Size, capture and handling times, physiological parameters and reflex action mortality predictor (RAMP) scores for white sturgeon following simulated capture treatments in captivity in July 2014 (summer) and February 2015 (winter). Both mortalities occurred in July 2014.

Measurement	No Mortality (N = 46)				Mortality (N = 2)	
	Summer		Winter		Summer only	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Fork length (cm)	106.8 (21.7)	63.5 – 170.2	112.6 (18.7)	72.5 – 149.9	117.1(32.0)	94.5 – 139.7
Girth (cm)	42.0 (7.6)	30.5 – 61.0	46.4 (8.3)	33.0 – 62.2	56.4 (2.2)	54.9 – 57.9
Treatment (min)	------	0.0 – 15.0	------	0.0 – 15.0	------	10.0 -15.0
Bleed time (min)	2.6 (1.3)	1.2 – 6.9	1.9 (0.7)	1.0 – 3.3	3.0 (1.4)	2.0 – 4.0
Lactate (mmol·L^{-1})	2.5 (1.5)	0.8 – 5.3	1.1 (0.5)	0.8 – 2.4	3.9 (1.8)	2.6 – 5.2
Glucose (mmol·L^{-1})	3.4 (1.2)	2.4 – 8.4	3.3 (0.9)	1.6 – 4.8	4.5 (0.4)	4.2 – 4.7

Cortisol (ng·ml^{-1})	73.2 (72.8)	13.47 – 261.4	51.5 (79.4)	7.2 – 383.5	61.2 (4.4)	58.1 – 64.3
Hematocrit (%)	33.0 (6.2)	22.0 – 52.0	32.6 (4.1)	25.0 – 43.0	31.0 (35.4)	6.0 – 56.0
Osmolality	271.2 (7.5)	256.0 – 283.0	278.7 (6.6)	261.0 – 289.0	276.5 (2.1)	275.0 – 278.0
Chloride (mmol·L^{-1})	118.0 (3.0)	110.1 – 121.6	122.3 (2.6)	117.9 – 128.1	117.2 (1.3)	116.2 – 118.1
RAMP score (proportion)	0.4 (0.3)	0.0 – 1.0	0.3 (0.2)	0.0 – 0.8	1.0 (0.0)	-----
Recovery time (min)	9.8 (10.8)	0.0 – 30.0	11.0 (12.1)	0.0 – 30.0	-----	-----

Discussion

Reflex Impairment Indices

Our study demonstrates that reflex impairment (RAMP) indices are a promising tool to predict post-release vitality in white sturgeon exposed to acute fisheries encounters, like an angling event. The reflexes used in our RAMP protocol were chosen so that multiple neurological and/or muscle pathways underlying the overall stress response were tested. What we found was that sturgeon exposed to fishing-related stressors had higher RAMP scores and took significantly longer to recover than control fish. The relationship between reflex impairment and stressor intensity (i.e., fishery-related treatment) indicates sturgeon are undergoing whole-animal – or tertiary – responses to varying degrees of capture stress.

Reflex impairment indicators were surprisingly sensitive to fisheries stressors. Control fish had all reflexes intact, whereas multiple reflexes were absent after fish were treated. For white sturgeon, ventilation, mouth extension, and orientation were typically the first reflexes affected by treatment, followed by body flex and tail grab. Indeed, ventilation and orientation are commonly affected fairly quickly following exposure to a stressor across fish taxa (Gale et al., 2014, 2011; Raby et al., 2013). Body flex and tail grab reflexes were absent in most white sturgeon exposed to the longer treatments (10 and 15 min). This lack in body tone and/or ability to respond to a physical stimulus is likely a result of white muscle exhaustion (i.e., increased lactate; (Raby et al., 2013), and has been identified in other stressed fishes (Brownscombe et al., 2013; J.W. Brownscombe et al., 2014;

Raby et al., 2013; Szekeres et al., 2014). Interestingly, a number of salmon species subjected to fisheries stressors lost their ability to respond to physical stimulus almost immediately (coho, Raby et al., 2013; sockeye, Gale et al., 2011, 2014), whereas white sturgeon were fairly resilient to the loss of those reflexes until they were exposed to the longer treatments. This difference in reflex responsiveness is likely due to the reduced anaerobic stress response in sturgeon when compared to teleosts (Kieffer et al., 2001). Anterior positive buoyancy was also recognized in stressed white sturgeon. Sturgeon have open (physostomous) swim bladders that connect directly to the oesophagus. Swim bladder volume (i.e., buoyancy) is therefore regulated by gulping or expelling gas (Brown et al., 2013). The loss of equilibrium in white sturgeon could be explained in part by the loss of controlled regulation of the swim bladder, subsequently causing the swim bladder to inflate and create positive buoyancy. Indeed, neutral buoyancy was regained following the expulsion of air – a process that took longer for individuals which experienced longer treatments.

Physiological Findings and Reflex Impairment

The underlying assumption of reflex impairment is that it has a basis in the physiological stress response (Davis, 2010). Greater reflex impairment (i.e., higher RAMP scores) was indeed associated with physiological exhaustion (i.e., increased lactate), suggesting RAMP scores can indicate or predict an alteration in physiological condition in angled sturgeon. This movement away from homeostasis is subsequently a predictor of overall vitality – or the capacity for survival. The direct measurement of reflex impairment following the stressor suggests that physiological disturbances which manifest quickly are likely causes of impairment, further supporting the tight association between lactate concentrations and reflex impairment indices in this study and a number of others (i.e., Brownscombe et al., 2013; Raby et al., 2013; Gale et al., 2014; McArley & Herbert, 2014). Latent physiological changes, such as increases in circulating plasma cortisol, are therefore unlikely to be direct causes of reflex impairment (McArley and Herbert, 2014) and may explain why we did not find a relationship between other tested indices of physiological stress and RAMP scores.

In addition to examining the relationship between RAMP score and physiology, the individual physiological parameters were compared to treatment time. As expected, sturgeon demonstrated a stress response that was related to the magnitude of the applied stressor. In particular, circulating lactate, glucose, plasma osmolality and Cl^- were significantly higher in longer treated individuals (Fig. 2.2). Similar physiology profiles have been demonstrated in sturgeons exposed to varying degrees of stressors (D. W. Baker et al., 2005; Bayunova et al., 2002; Beardsall et al., 2013; Kieffer et al., 2001; Semenkova et al., 1999). There was not a significant difference in cortisol between treatments, but given cortisol has been shown to peak in white sturgeon ~30 min. after exposure to air (Zuccarelli et al., 2008), it is likely that maximal cortisol levels were not achieved due to blood sampling immediately following the stressor. Similarly, a secondary stress response was elicited in sturgeon exposed to longer treatments, as indicated by elevated levels of circulating glucose, lactate, hematocrit, plasma osmolality, and Cl^-. Glucose was higher in 15 min. treatment groups than controls, however the difference was not significant. The effects of acute stressors on blood glucose varies between sturgeon species from moderate to completely absent. It is possible that low glucose levels coincide with a lower metabolic rate in sturgeon, an advantageous characteristic that may be used to compensate for periods of hypoxia in their natural environment (D. W. Baker et al., 2005). It is also possible that glucose changes were delayed given the cortisol response was also not evident. Increased cortisol should stimulate higher glucose levels (Wendelaar Bonga, 1997), potentially indicating an issue with sampling time immediately following the cessation of treatment.

Anaerobic metabolism was activated in sturgeon, as demonstrated by the increase in circulating lactate. Similarly, an increase in hematocrit is a common response to higher oxygen demands and increases in hematocrit have been noted in other sturgeon exposed to acute stressors (Kieffer et al., 2011). Although hematocrit was not significantly different among treatment groups, longer treated sturgeon showed markedly higher hematocrit than controls. Lastly, the increase in osmolality and Cl^- demonstrates that osmotic and ionic redistribution occurred during the stress response. Taken together, these results suggest that anaerobic metabolism does contribute to the energy budget of white sturgeon exposed to fisheries-related stressors.

Allometric differences in physiological and reflex responses to stress were not explored in this study but should be considered in future studies. Larger body size has been connected to greater physiological disturbance in other fish species. For example, following exposure to exhaustive exercise, large largemouth bass

(*Micropterus salmoides*) exhibited elevated concentrations of plasma glucose and sodium relative to small fish and they required additional time to clear the metabolites (Gingerich and Suski, 2012). These results indicate smaller fish have an improved ability to recover from disturbances, suggesting more work needs to be done on larger white sturgeon as our results could be underestimating the potential effects on those size classes. Between 2013 and 2016, McLean et al. angled and tagged white sturgeon in the Lower Fraser River at a mean size of 192 cm FL (McLean, unpub. data). Therefore, although much larger fish (>3 m, McLean, unpub. data) can be caught, the size class from the present study (110 cm FL) is comparable to the mean sizes of white sturgeon caught in the wild C&R fishery, suggesting the results presented in this study are representative of the majority of fish caught.

Proximate Causes of Delayed Mortality

Reflex impairment indices are commonly used to predict delayed mortality in aquatic organisms where post-release monitoring is difficult (Cooke et al., 2014; Davis, 2010, 2007, 2005; Raby et al., 2013). Indeed, the two mortalities in our study occurred > 24 hr following cessation of the stressor, both individuals showed impairment across all reflexes at the time of release into recovery raceways, and both failed to “recover” during the 30 min post-release recovery observation period. The proximate cause of delayed mortality in this study is unknown. One prediction is that lower levels of physiological disturbance and subsequently lower reflex impairment during the capture and handling of individuals can promote better survival upon release, particularly during warm temperatures. Indeed, the two mortalities occurred in fish exposed to longer treatment times (10 and 15 min.) in the summer sampling period (July – mean temp. 15.6°C), and both fish had upper-range levels of physiological indicators of stress (i.e., lactate) as well as overall RAMP impairment scores of 1 (all reflexes impaired). In fact, reflex impairment had a stronger association with delayed mortality than the physiological metrics, as other surviving fish had similar physiological profiles to the deceased fish but lower reflex impairment scores. One exception was the extreme hematocrit profile of the two dead individuals (6% and 56%; Table 2.2). During the stress response, there is an increased oxygen demand for the tissues that can result in the rapid release of stored red blood cells into circulation. This results in a measure of increased percentage of red blood cells, or hematocrit; a hematological profile that is common in stressed fishes (Barton, 2002). Baseline hematocrit values for white sturgeon have been reported ~30% (Baker and Brauner, 2012), which suggests the individual with hematocrit of 6% was in an anemic state prior to the treatment stressor and likely predisposed to an increase risk of delayed mortality. Given that there were so few mortalities in our study, it is difficult to identify the lethal thresholds for white sturgeon using indicators of excess stress metabolites or anaerobic acid-base/ionic imbalances. However, the significant relationship we found between lactate concentration and reflex impairment suggests excess stress metabolites may contribute to delayed mortality, as has been shown in studies on other species (Gale et al., 2014).

It is important to note that it was not the aim of this study to produce accurate mortality estimates for use in C&R fisheries, but rather to explore the use of RAMP on a sturgeon species frequently angled in the wild. We recognize the subjectivity of a whole-animal assessment and categorization, however, given the statistically significant difference in RAMP scores of observationally “recovered” and “unrecovered” sturgeon, we suggest RAMP is an effective tool for predicting a lowered state of vitality post-release and that this suggests a continuum to an increased risk of delayed mortality.

Effects of Temperature

Warmer water temperatures affected the stress response of white sturgeon, as evidenced by some of the plasma variables and reflex impairment indices. In particular, cortisol and lactate were significantly higher in summer-treated sturgeon, while chloride and osmolality were significantly lower after each treatment. Previous studies have demonstrated that water temperature modifies the physiological stress response in green sturgeon *A. medirostris* (Lankford et al., 2003), and Atlantic sturgeon *A. oxyrinchus* (Kieffer et al., 2011), which may explain some of the variation between seasonal physiology values. For example, Atlantic sturgeon exposed to severe (<10 mm Hg) hypoxia for one hr at 5 or 15°C had increased lactate concentrations compared to individuals under normoxic conditions, indicating an increase in anaerobic metabolism (Kieffer et al., 2011). Additionally, there was a significant increase in plasma glucose concentrations solely at the cooler temperature (5°C), suggesting fuel demands differ for Atlantic sturgeon under different temperatures (Kieffer et al., 2011). Lankford *et al.* (2003) noted that the rate of synthesis of cortisol was delayed in green sturgeon acclimated to 11°C compared with those acclimated to 19°C; likely due to temperature dependent reduction in enzymatic activity resulting in decreased synthesis rates of cortisol. This is important because although we saw a dampened cortisol response in winter-treated fish, it is possible peak levels were overlooked due to the slower rate of synthesis. Interestingly, they also found a slower rate of plasma cortisol clearance at cooler water temperatures, an important finding when considering post-release recovery of white sturgeon in wild populations.

Higher resting plasma lactate was also noted in green sturgeon acclimated to higher water temperatures (Lankford et al., 2003). Sturgeon occupy a range of thermal regimes so the impact of water temperature on fish performance is expected to differ from stenothermal species, of which many temperature effects studies are based on. Upper thermal tolerances of green sturgeon have been identified ~33 °C, after which normal ventilatory function is inhibited. Exposure to near-lethal temperatures caused an increase in hematocrit and plasma osmolality in green sturgeon, likely due to the elevated metabolic demands of temperature increase and the subsequent increase in the osmotic gradient across the gill (Lankford et al., 2003). Higher water temperatures (19°C) have also been linked to elevated plasma chloride and lactate in Pacific salmon, suggesting a disturbance in osmoregulatory homeostasis (Jeffries et al., 2012). In fact, ~70% of studies examining the effects of fisheries capture-and-release stress at different temperatures have found a positive relationship between water temperature, indices of stress, and mortality (See Gale et al., 2013 for full review; Gale et al., 2011, 2014; Robinson et al., 2013; Raby et al., 2015). It is unknown as to why Cl^- and osmolality were significantly lower in summer-treated fish, but one hypothesis is that osmoregulatory impairment may be related to the higher impact of the stressor on particular reflexes, like ventilation at warmer temperatures. Sturgeon reflex impairment was indeed dependent on temperature, with higher temperatures causing higher reflex impairment at each level of treatment. Higher temperatures generally coincide with higher resting metabolic rates and higher oxygen demands. Our control sturgeon did indeed have higher resting ventilation rates in the summer sampling period. Although ventilation was impaired in both seasons, it became impaired faster in summer-treated sturgeon. The impaired ventilation likely translates to reduced gas exchange and oxygen uptake, resulting in an inability to recover oxygen debt from anaerobic exercise quickly, one potential explanation for the summer mortalities.

Conclusions and Management Implications

Our study highlights the importance of examining whole-animal changes when characterizing sturgeon stress responses to fisheries-related stressors. Further, the relationship between stress physiology and reflex impairment in white sturgeon suggests that RAMP could provide a simple and inexpensive evaluation of fish vitality after exposure to fisheries-related stressors and could be used without the use of more invasive research methods on sturgeon (e.g., blood physiology). The difference in physiology and reflex impairment in winter and summer-sampled sturgeon highlights the importance of considering management plans for wild fisheries as the same stressor intensity can have varying impacts at different temperatures. Since the water temperatures from our study were mild in comparison to summer temperatures white sturgeon often experience in the wild (i.e., max LFR temperature mid-July 2015 = 21.20 °C; data provided by the Ministry of Forests Lands and Natural Resource Operations of British Columbia), we suggest future work investigate the physiological stress response, reflex impairment, and recovery, in wild fish at extremely high temperatures. Additionally, the strong correlation between reflex impairment and recovery time suggests that reducing play-time and handling could benefit wild sturgeon by reducing the time it takes them to recover.

The combination of exercise stress and partial air exposure typical of angling were physiologically demanding for white sturgeon in our study, but it is not likely to be a direct cause of mortality if the duration is <15 min at temperatures between 6 – 16°C. Our mortality estimates should be interpreted carefully in relation to wild C&R fisheries as angling events often last much longer than what was explored in this study, and the events are often coupled with angler experience, gear type, temperature, and species (Arlinghaus et al., 2007). The individual roles of air exposure and exercise were not parsed out in this study; however, this is a topic that requires further attention as each stressor may not have an equal impact on the stress physiology and impairment of white sturgeon.

RAMP proved to be an effective measure of sub-lethal stress and is therefore a potentially useful tool for assessing the release condition of angled white sturgeon. In particular, our RAMP methodology should be applied in future studies where the impacts of extended angling events and strenuous exercise in wild white sturgeon are evaluated in situ, e.g., the Fraser River recreational sturgeon fishery. The changes in stress physiology and reflex impairment suggest to us that future work needs to examine the longer-term fitness consequences (i.e., growth impairment, reproductive impacts) of extended play and air exposure times, as these are largely unknown for wild populations. In particular, future research should examine the impacts of extended periods of strenuous exercise in wild white sturgeon as the methods used in our study do not fully reproduce the intensity and/or duration of an actual angling event. Further, allometric and sex differences in the physiological stress response of white sturgeon requires attention.

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CHAPTER 3

Immediate Physiological and Behavioural Response from Catch-and-Release of Wild White Sturgeon

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.

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 (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Muoneke and Childress, 1994), 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.) – 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), 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 (M. L. 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.

Materials and 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).

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 (Figure 3.1). 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. Snow-melt constitutes 75% of the total runoff, beginning in April and increasing to a maximum in late May and early June (~8 800 $m^3 \cdot s^{-1}$, McLean et al., 1999). During intense snowfall years peak discharge can reach values up to 12 000 $m^3 \cdot s^{-1}$ (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.

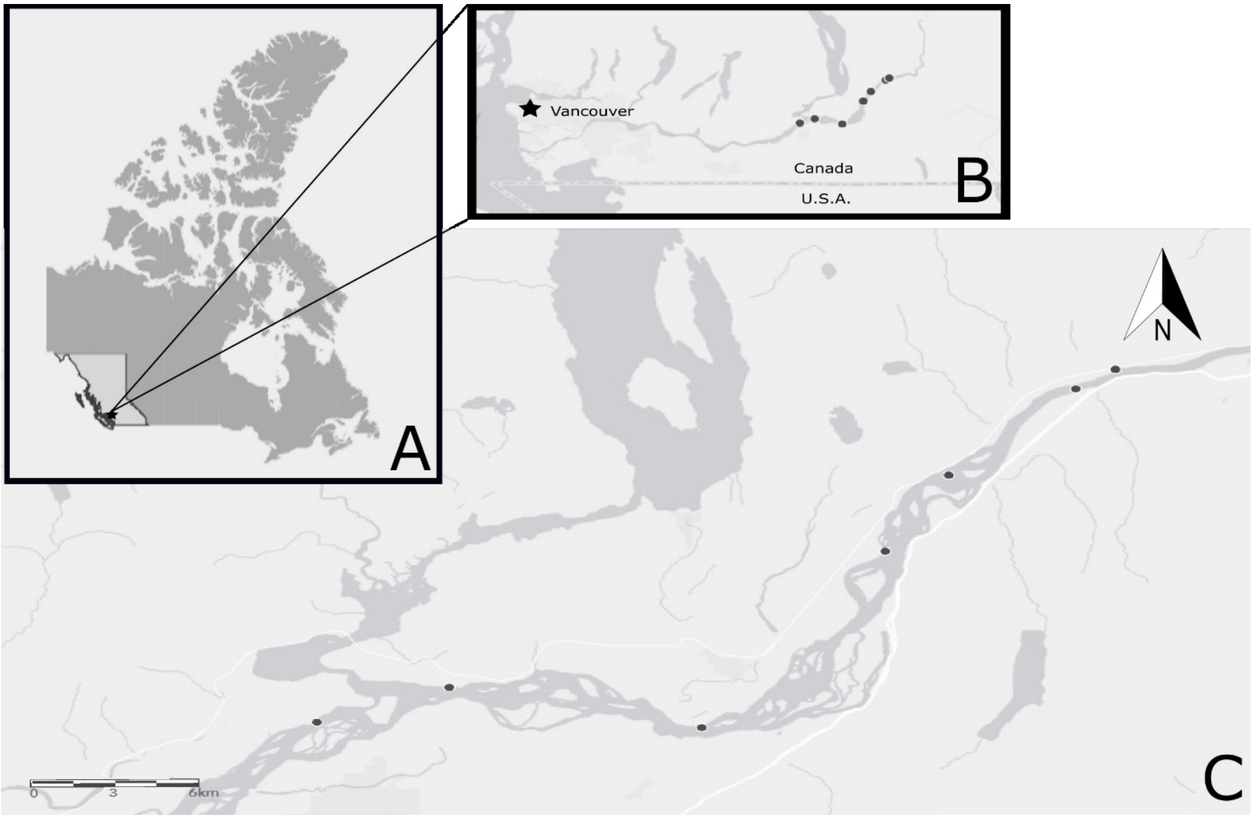

Figure 3.1. A. Map of Canada highlighting the province of British Columbia (B.C.). B. and C. Capture and release locations for white sturgeon, *Acipenser transmontanus*, in the non-tidal region of the lower Fraser River, B.C., Canada, which flows westerly through the province exiting south of Vancouver into the Strait of Georgia, Pacific Ocean. Sixty-three sturgeon were angled and biopsied for physiological indices of stress. Seven individuals were also implanted with acoustic transmitters equipped with accelerometer sensors (V13A, VEMCO Ltd.) and manually tracked to assess post-release recovery behaviour.

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 (Figure 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 linear regression equation: $\log(W) = -5.13 + 3.07\log(L)$ ($R^2 = 0.91$; 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 (http://www.riverfishingbc.com/WhiteStrugeonWeightandAgeChart.pdf).

Following the blood sample, seven sturgeon were surgically implanted with an acoustic accelerometer transmitter (VEMCO Ltd., Halifax, N.S., Model V13A, 69 kHz, 42 mm length x 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.

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 was required; one operated the directional hydrophone (VEMCO Ltd. 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.

Physiology

Within 15 min of sampling, ~250 µL 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) – 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 min (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 Laboratory, as detailed in McLean et al. (2016).

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 $m^3 \cdot s^{-1}$ 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 to 3.47 $m \cdot s^{-2}$.

Following surgery, sturgeon behaviour was monitored for ~2 hr 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.

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 $m \cdot s^{-2}$. 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.

Results

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; $F_{[1,61]} = 353.6$, $p < 0.001$, $R^2 = 0.85$, $\log(y) = 2.9\log(x) - 5.8$). The relationships between fight time duration and physiology are presented as raw data in Figure 3.2. 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 3.1). 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 ($F_{[1,61]} = 11.2$, $p = 0.001$, $R^2 = 0.16$, $y = 1.5x + 2.4$; Figure 3.3). There was also a noticeable trend, though not significant after correction, in decreasing plasma potassium ($F_{[1,59]} = 6.6$, $p = 0.01$, $R^2 = 0.10$, $y = 0.2\log(x) + 0.5$; Figure 3.3).

Table 3.1. 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

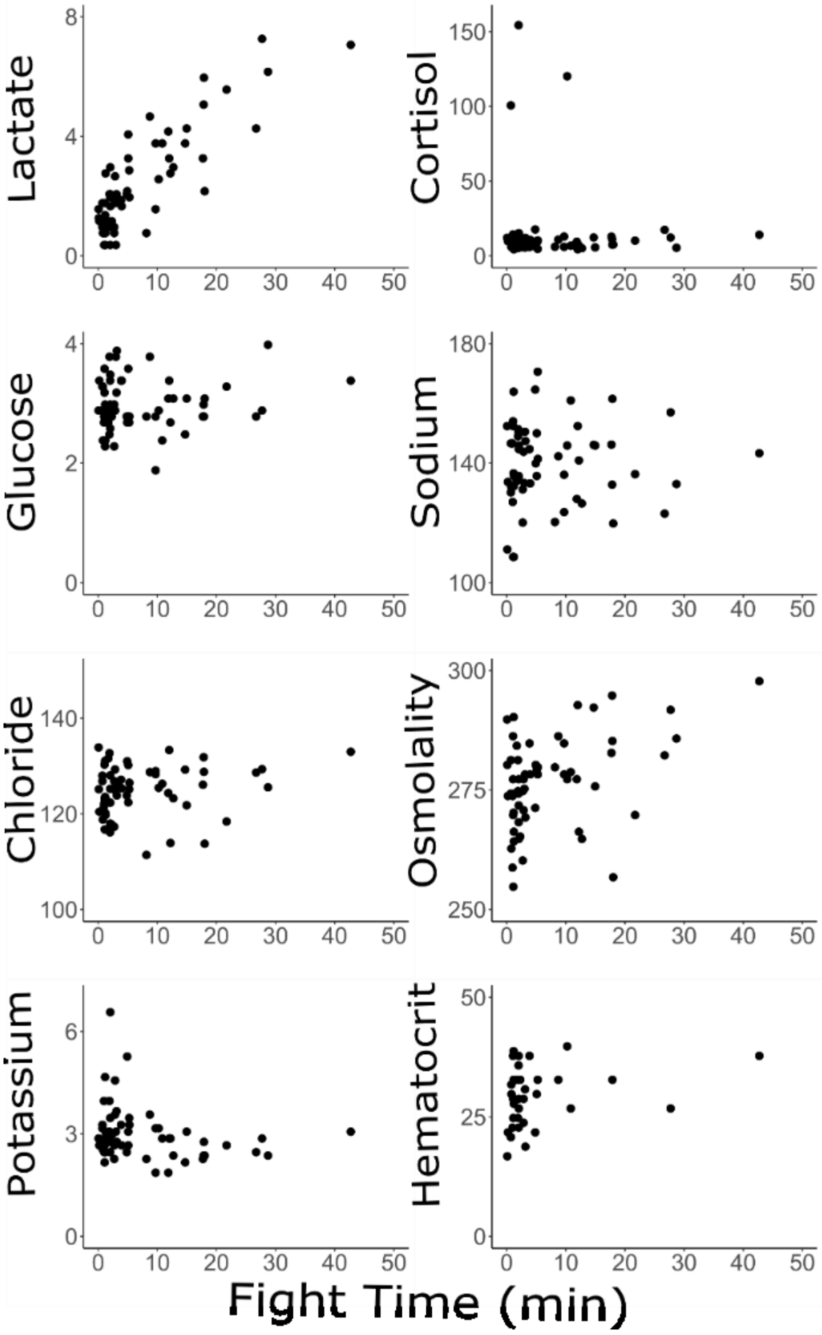

Figure 3.2. Blood constituents from white sturgeon (n = 63) angled in the lower Fraser River, B.C. They are presented in raw form for various fight durations. Lactate, glucose, sodium, chloride, and potassium are presented in units mmol·L^{-1}, cortisol in ng·mL^{-1}, and osmolality in mOsmol·kg^{-1}.

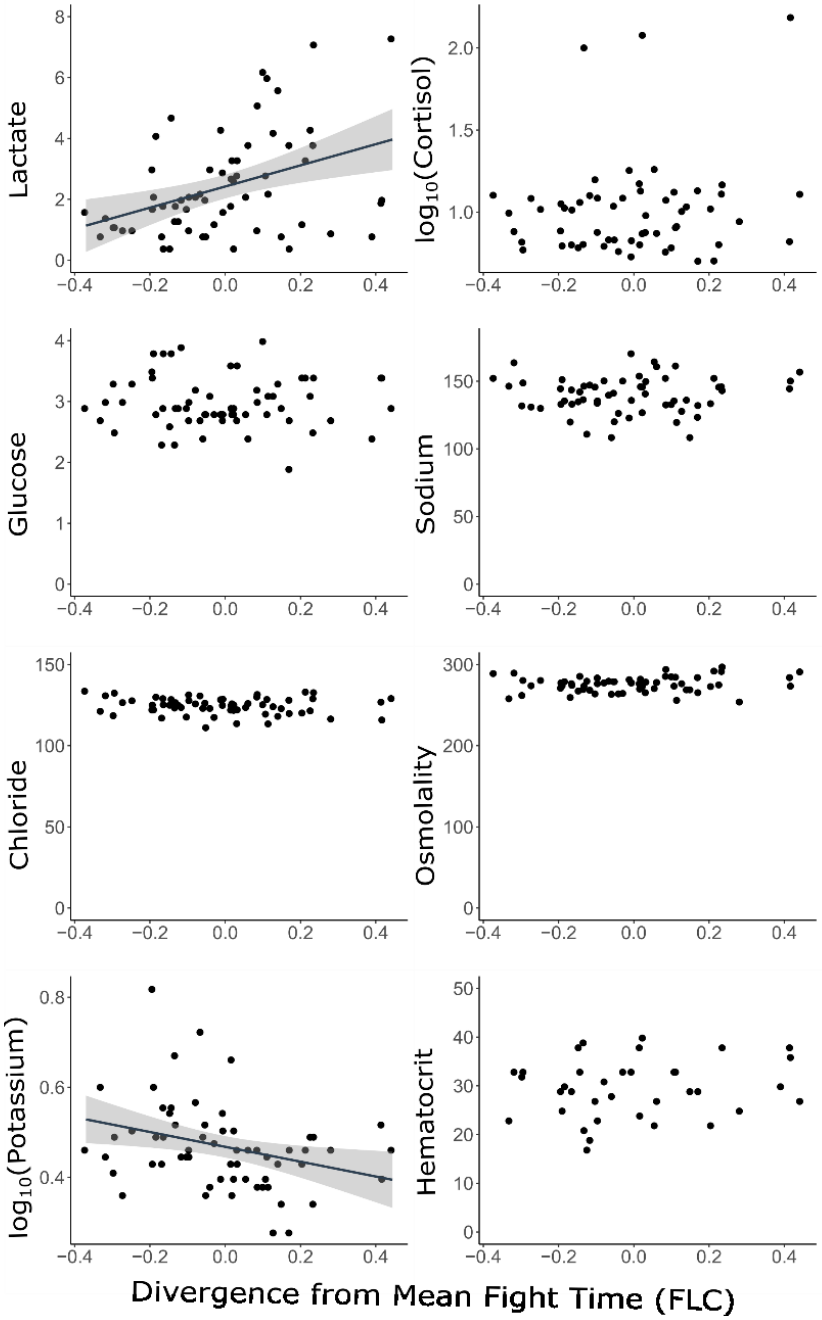

Figure 3.3. Linear regressions were used to test the predictive relationship between fight time (min) and physiological indicators of stress sampled from white sturgeon (N = 63) after angling. Lactate, glucose, sodium, chloride, and potassium are presented in units mmol·L^{-1}, cortisol in ng·mL^{-1}, 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.

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 – 0.11 $m \cdot s^{-2}$. "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 – 1.59 $m \cdot s^{-2}$ 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 - 3.47 $m \cdot s^{-2}$. The maximum capacity of the accelerometer transmitters in this study was 3.47 $m \cdot s^{-2}$.

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 (Figure 3.4). 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 $m \cdot s^{-2}$) versus those collected after 10 min of tracking (0.5 $m \cdot s^{-2}$). All tagged sturgeon spent >60% of their total tracking time in moderate sustained swimming speeds (Table 3.2) 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 3.2). There was no correlation between acceleration and sturgeon fork length ($r=0.1$, $n=7$, $p=0.9$).

Table 3.2. 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 Ltd.) 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. accel. 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

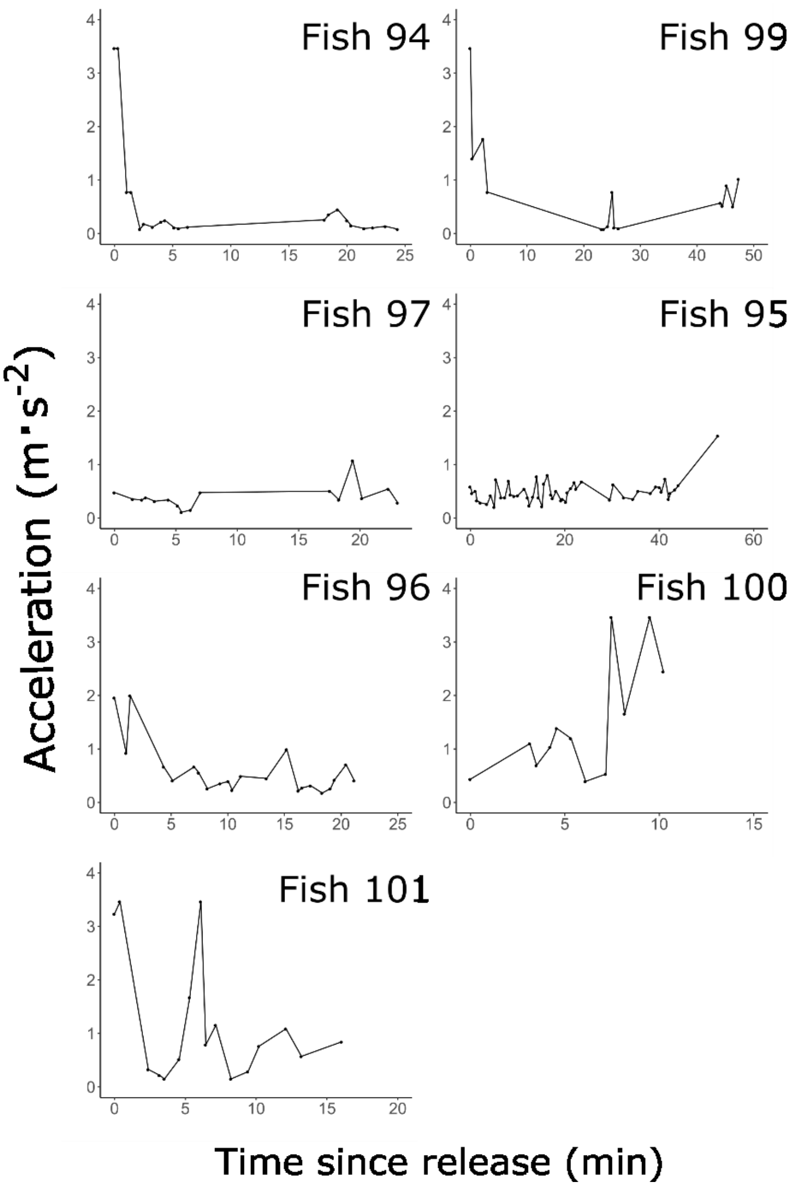

Figure 3.4. Acceleration (m·s^{-2}) profiles for acoustically tagged white sturgeon (n = 7) manually tracked for 10 – 52 mins after release. The points represent individual acoustic detections and are connected by lines for visualization. Plots are ordered based on sturgeon size, from smallest (156 cm FL – Fish 94) to largest (257 cm FL – Fish 101).

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 3.3). 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 3.3).

Table 3.3. Accelerations ($m \cdot s^{-2}$) obtained from acoustic transmitters equipped with accelerometer sensors (V13A, VEMCO Ltd.) 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 $m \cdot s^{-2}$. 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 ($m \cdot s^{-2}$)	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)

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 response 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 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 compared reasonably well with 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; Baker et al., 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 hr 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^{-1}) that were similar to captive white sturgeon exposed to longer periods of combined exercise and air exposure (~100 ng·ml^{-1}; 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 glucocorticoid released during the sturgeon stress response (Barton, 2002), the peak response can be slow and not typically seen in fish for 1-2 hr following the cessation of the stressor (Milligan, 1996), or at least 30 mins as measured in white sturgeon (Zuccarelli et al., 2008). Most of our sturgeon were angled and sampled in under 30 mins 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 (S. J. 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 3.2). 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 (Figure 3.4). 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 $\text{mmol}\cdot\text{L}^{-1}$) when compared to control fish (<2 $\text{mmol}\cdot\text{L}^{-1}$; McLean et al., 2016) from our previous lab study, and subsequent burst swimming behaviour did not occur for these fish ~5+ min after release (Figure 3.4).

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 3.3). 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 3.3). 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 (Figure 3.2, Fish 100) showing trends toward increased activity within 10 min of release, whereas others, like the longest tracked individual (Figure 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℃ 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, 2004). 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.

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CHAPTER 4

Linking Environmental Factors with Reflex Action Mortality Predictors, Physiological Stress, and Acoustic Telemetry to Evaluate the Response of White Sturgeon to Catch and Release Angling

Abstract

White sturgeon (*Acipenser transmontanus* Richardson, 1836) are the largest freshwater fish in North America and are readily captured and released (C&R) by anglers at high rates. The effects of C&R to white sturgeon are relatively 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 also tagged with acoustic transmitters to assess survival and post-release behaviour. Survival was high with 100% of individuals detected or subsequently recaptured in the C&R fishery within an average of 98 ± 32 (± SEM) days after release. Water temperature and discharge at capture ranged from ~2 to >20°C, and 1270 to 9430 $m^3 \cdot s^{-1}$, respectively, and influenced post-capture blood physiology. Specifically, lactate, chloride, and cortisol concentrations were higher in individuals captured at higher water temperatures, during periods of higher river discharge, in addition to being elevated with longer capture times. Cortisol was affected by fish size, with lower concentrations found in larger individuals. Only lactate and chloride were positively related to higher 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 larger distances. When time to first detection was incorporated to assess movement rates, however, only higher levels of glucose and potassium were significant predictors of increased rates of movement. Sturgeon tended to move smaller distances and at slower rates when reflex impairment was high, although reflex impairment scores in general did not explain a significant proportion of the variation of any movement metric. Our results show intriguing variance in the physiological and behavioural response of individual white sturgeon to C&R recreational angling, with some degree of environmental dependence, and highlights the importance of understanding the drivers of such variation when managing fisheries.

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; 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, 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* L. 1758) – 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* L. 1758) 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* Richardson, 1836) are an economically important species for recreational freshwater fisheries throughout their native North American spawning range from the Sacramento-San Joaquin (California, USA) watershed, north to the Fraser River (British Columbia, Canada) watershed (Hildebrand et al., 2016). Some white sturgeon populations are anadromous, while others are primarily freshwater but occasionally migrate to marine environments when accessible (Welch et al., 2006). Sexual maturity is reached between the ages of 12 (125 cm) to 32, with males reaching sexual maturity before females (PSMFC, 1992). White sturgeon are iteroparous broadcast spawners that experience varying periods of intermittent spawning that has been documented to range from 3 – 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 located in the lower Fraser River, British Columbia (LFR, B.C.). The most recent mean abundance estimate for LFR white sturgeon from 60-279 cm FL was 34, 870, with evidence to suggest a decline in the total abundance by 38.2% compared to the highest abundance estimate in 2003 (Nelson et al., 2019). Despite concerns about the species' conservation status, white sturgeon are highly prized game fish and many populations sustain important recreational fisheries throughout parts of their range along the Pacific coast of North America.

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 recent SARA review for the status of white sturgeon in the LFR began in 2015, and highlighted a significant information gap in terms of sources of mortality and other effects from various fisheries (CSAS 2015, unpublished). 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” are 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., 2019, 2017; Crossin et al., 2017; Donaldson et al., 2008). 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, 2010, 2007, 2005). 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* [Walbaum 1792]*,* Raby et al., 2012, 2014; sockeye salmon *Oncorhynchus nerka* [Walbaum 1792], Gale et al., 2011, 2014; bonefish *Albula* spp. Scopoli 1777, Brownscombe et al., 2013, 2015; black sea bream *Spondyliosoma cantharus* [L. 1758], Pinder et al., 2017), and white (McLean et al., 2016) and shortnose sturgeon *Acipenser brevirostrum* Lesueur 1818 (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, 2010, 2007, 2005). 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* (Mitchill 1818) and sauger *S. canadensis* (Griffith and Smith 1834) 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).

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 experience a range of environmental conditions, with 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 ~1.8°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°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 latent mortality (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 changed in response to high levels of lactate after exercise (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;2014). 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.

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 for this study: 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 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 river temperatures

(~2 – 21°C) and river discharge rates (1270 to 9430 $m^3 \cdot s^{-1}$). 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.

Materials and Methods

Study Site

The study took place between 05 May 2014 and 16 September 2016 in the LFR, B.C., Canada (Figure 1). The LFR spans ~200 km from the delta, where the river mouth drains into the Pacific Ocean (Georgia Strait), 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; Figure 1). Freshwater discharge varies yearly and seasonally with marked fluctuations noticeable over periods of a few days. Snow-melt constitutes 75% of the total runoff, beginning in April and increasing to a maximum in late May and early June (~8 800 $m^3 \cdot s^{-1}$; McLean et al., 1999). River discharge diminishes throughout the summer and fall and by mid-February the levels are at their lowest (~880 $m^3 \cdot s^{-1}$). 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 ~80 – 94 near the small town of Mission, B.C. (Figure 1) is tidally influenced, with the maximum intrusion of the salt-wedge being km 20. Surface water temperature was measured at the time of capture and daily average river discharge levels 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 (Figure 1; available at https://wateroffice.ec.gc.ca).

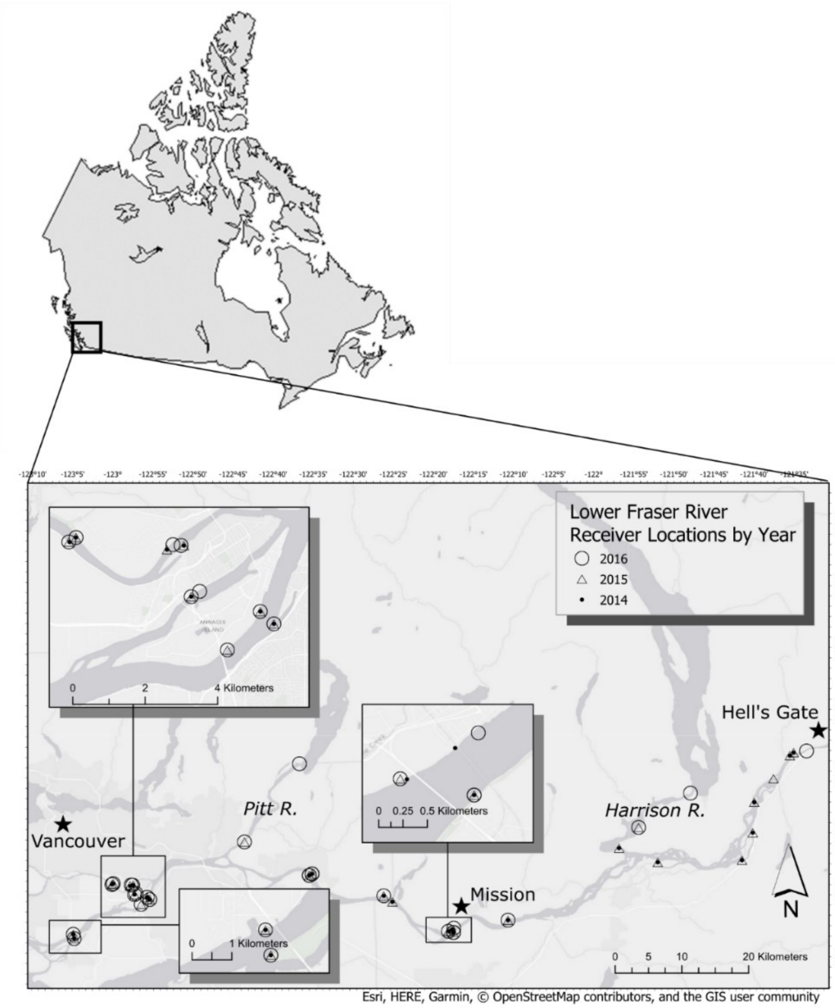

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Figure 4.1. Map of Canada highlighting the province of British Columbia (B.C.) and VR2W passive acoustic receiver locations for 2014, 2015 and 2016 in the lower Fraser River, B.C., Canada. White Sturgeon, *Acipenser transmontanus*, were angled, biopsied for physiological and reflex impairment indices of stress, implanted with passive integrated technology tags and acoustic transmitters (V16 series, VEMCO, Ltd.), and passively tracked to assess post-release survival and behaviour.

Capture and Sampling

To ensure relevance of our research, we partnered with the recreational fishing community (e.g., Cooke et al., 2013b). 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 (± 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). Within 15 min of sampling, ~250 µL 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 3,300 revolutions per minute. 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).

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 Ltd., Bedford, N.S. Model V16, 69 kHz, mm length x 16 mm diameter) was inserted into the body cavity of 60 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 (V16-3x and 4x series, VEMCO, Ltd.). 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. 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 (Figure 1) when tags were within the detection range (~545 m; Appendix), 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.

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 B, Table 1). 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, sturgeon were 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 characterized 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.

Post-Release Survival and Movements

Post-release survival and movement metrics were determined by using fixed-place receivers (Figure 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 were deployed and maintained by FLNRORD and Kintama Research Services. Receiver station coverage was designed for multispecies tracking studies in the system. Receiver stations covered the LFR mainstem, the North Arm, and two primary tributaries, the Harrison and Pitt Rivers and the associated lake mouths (Figure 1). Stations were considered unique if they were separated by >1 km, and receivers <1 km were grouped together. In the LFR, there appears to be high intraspecific variability in the movement patterns of white sturgeon (Robichaud et al. 2017; E. Stoddard, FLNRORD, unpublished data), 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). If acoustic tracking data was not available for a fish, we assessed survival by checking the FRSCS PIT recapture 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., 2013b). 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 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.

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 (Jollife and Cadima, 2016). 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 4.1). There were some missing values in the blood physiology that we chose to impute (‘imputePCA’, package = “missMDA”) rather than remove these fish from the dataset.

Table 4.1. 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

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 Breush-Pagan test ('ncvTest', package = "car"), respectively.

Post-Release Movement Behaviour

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). 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 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 model with the overall highest support (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 2012).

Results

Linking Angling, 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 ± SEM; Appendix B, Table 1) were angled at water temperatures ranging from 1.7 to 20.4ºC (8.7 ± 0.4ºC) with daily average water discharge ranging from 1270 to 9430 $m^3 \cdot s^{-1}$. The mean fight duration was

9.8 ± 1.3 minutes (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 4.1). Fight time, water temperature at the time of capture, and daily average water discharge on the date of capture were all significant explanatory variables of the first ordinated blood physiology dependent variable (Figure 4.2; RC1; t = 2.26, P = 0.03; t = 4.45, P < 0.001; t = -2.51, P = 0.01, respectively; see Table 4.2 for full model). There were no significant individual explanatory variables of the second axis, RC2 (full model in Table 4.2). For the third ordinated blood physiology dependent variable, RC3, both fish size and fight time were significant explanatory variables (Figure 4.2; t = -2.35, P = 0.02 and t = 2.12, P = 0.04, respectively; Table 4.2).

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 B, Table 1). Orientation was the most prevalent reflex lost in impaired sturgeon, with 95% of tested fish unable to reorient 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 (Figure 4.3; t = 2.54, P = 0.02; full model is presented in Table 4.3).

Table 4.2. Multiple regression outputs of wild white sturgeon blood physiology (n = 121), ordinated axes RC1 (lactate + chloride), RC2 (glucose + potassium), and RC3 (cortisol). 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℃ and the daily average water discharge on the day of capture ranged from 1270 to 9430 $m^3 \cdot s^{-1}$. Significance at $P \leq 0.05$ is denoted by an asterisk (*).

Dependent variable	Fixed effect	Value ± SEM	*t*-value	P-value
RC1	(Intercept)	-1.82 ± 0.38	-4.84	<0.001*
	Fork length	0.005 ± 0.003	1.38	0.17
	Log(Fight time)	0.35 ± 0.16	2.17	0.03*
	Capture temperature	0.01 ± 0.002	5.17	<0.001*
	Average daily water discharge	$-9.21e^{-05}$ ± $3.67e^{-05}$	-2.51	0.01*
RC2	(Intercept)	0.03 ± 1.02	0.03	0.93
	Fork length	-0.01 ± 0.01	-0.67	0.51
	Log(Fight time)	0.35 ± 0.37	0.94	0.35
	Capture temperature	-0.02 ± 0.03	-0.50	0.62
	Daily average water discharge	$7.87e^{-05}$ ± $4.84e^{-05}$	-0.40	0.70
RC3	(Intercept)	0.98 ± 0.27	3.57	<0.001*
	Fork length	-0.02 ± 0.01	-2.35	0.02*
	Log(Fight time)	0.95 ± 0.45	2.12	0.04*
	Capture temperature	0.01 ± 0.06	0.16	0.87
	Daily average water discharge	$4.87e^{-05}$ ± $2.91e^{-05}$	1.62	0.11

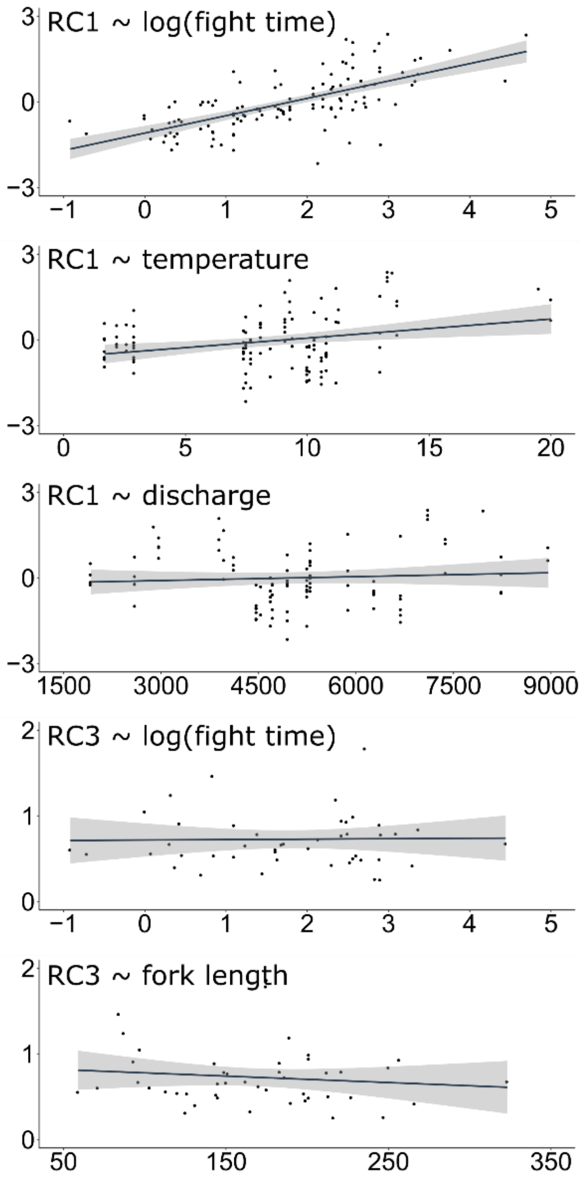
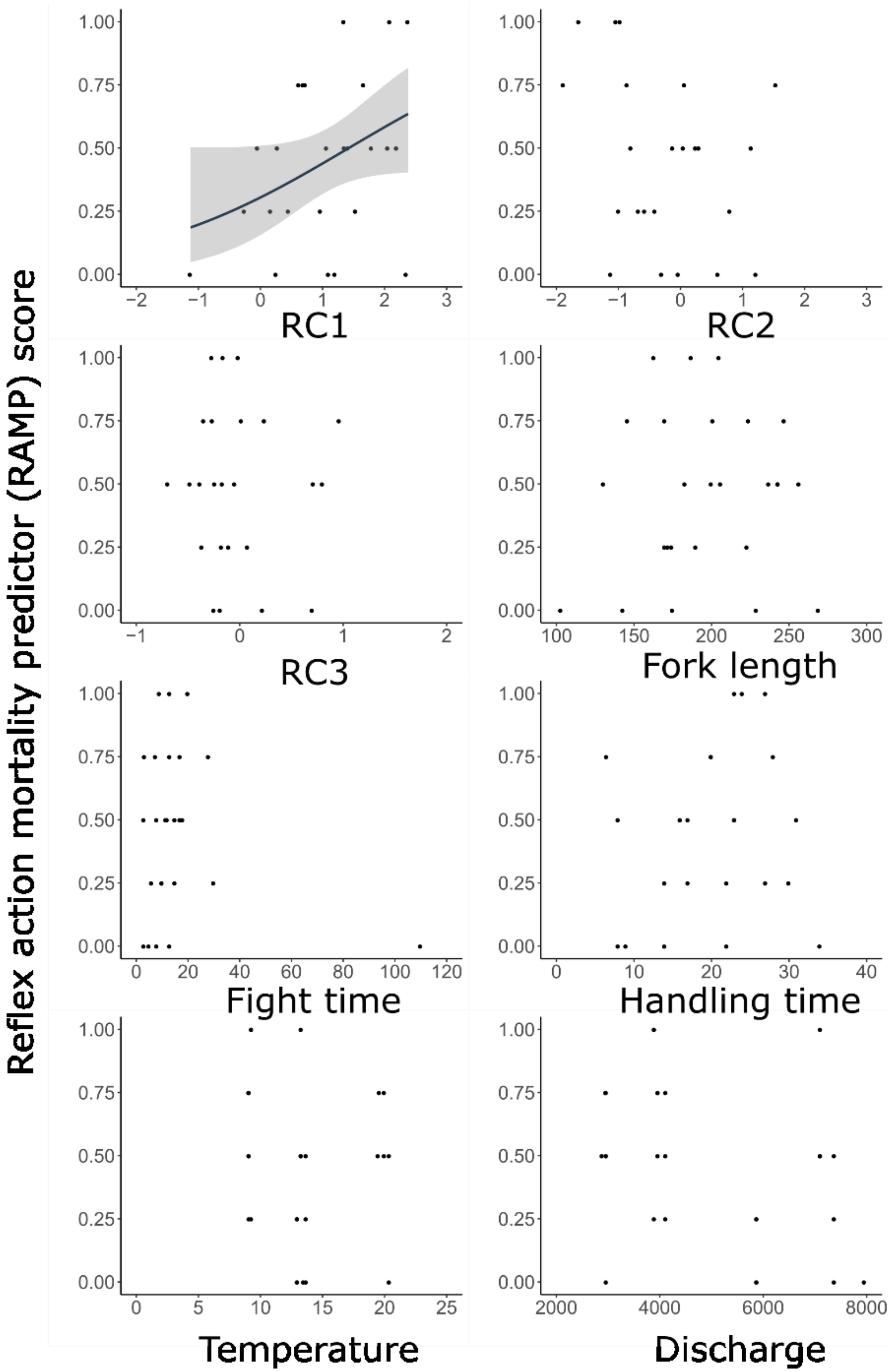


Figure 4.2. Significant explanatory variables for ordinated blood axes RC1 and RC3 are shown. All variables were assessed for predictability of stress physiology via linear models. Ordinated blood axes RC1 (lactate + chloride) and RC3 (cortisol) are unitless. Fork length was measured in centimeters, fight times were rounded to min, temperature was measured in degrees Celsius at the time of capture, and river discharge rates were measured in cubic metres per second 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.

Table 4.3. 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). 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℃ 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 (*).

Dependent variable	Fixed effect	Value ± SEM	t-value	P-value
RAMP score	(Intercept)	1.60 ± 2.22	0.72	0.48
	RC1	1.13 ± 0.43	2.65	0.02*
	RC2	-0.21 ± 0.31	-0.69	0.50
	RC3	-0.07 ± 0.25	-0.29	0.78
	Fork length	0.002 ± 0.01	0.21	0.83
	Fight time	-0.04 ± 0.08	-1.12	0.28
	Capture temperature	-0.12 ± 0.08	-1.46	0.16
	Daily average water discharge	-0.0003 ± 0.0002	-1.48	0.16
	Handling time	0.01 ± 0.05	0.14	0.89



Reflex action mortality predictor (RAMP) score
RC1
RC2
RC3
Fork length
Fight time
Handling time
Temperature
Discharge
0.00
0.25
0.50
0.75
1.00
−2
−1
0
1
2
3
100
150
200
250
300
20
40
60
80
100
120
10
30
40
5
15
25
2000
4000
6000
8000

Figure 4.3. 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. Fork length was measured in centimeters, fight and handling times were rounded to min, temperature was measured in degrees Celsius at the time of capture, and river discharge rates were measured in cubic metres per second and reported as a daily average on the date of capture. Only RC1 was a significant explanatory variable ($t = 2.65$, $P = 0.02$). The solid line represents the fitted GLM and shaded areas are the 95% confidence limits.

Post-Release Survival and Movements

In total, 60 (mean ± 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 B, Table 1). 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. One fish (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. (Figure 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 B, Table 1). 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 B, Table 1), 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 (± SEM) of 98 ± 32 days, ranging from 0.7 to 1641 days (Appendix B, Table 1).

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 B,

Table 1). The remaining 57 tagged fish were first detected within an average (± SEM) of 47 d (± 5.9) after their initial release. Average (± 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 (±SEM) 0.7 (± 0.1) km/d. The model with the most support to predict post-release linear distance included the ordinated blood parameters, RC1, RC2, fight time, fish size, and daily average water discharge (Table 4.4). Specifically, higher RC1 and longer fight times resulted in reduced linear distances (t = -4.83, P = <0.001, and t = -2.76, P = 0.01, respectively). Contrastingly, higher RC2 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 B, Figure 2).

The null model provided greatest support for days to first detection (~ 1), although handling time, fork length, RC1, RC2 and RC3 appeared in lower order models (Table 4.4). Model-averaging revealed that fish size was the most important term for predicting the days to first detection (Appendix B, Figure 2) but no variable was significant.

The model with the greatest support for predicting the number of unique sites visited/day (activity metric) included ordinated blood parameters RC1, RC2, and RC3 (Table 4.4). All variables explained a large proportion of the variance when model-averaging was used to assess the importance of terms across all models (Appendix B, Figure 2). RC1, RC2, and RC3 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 4.4).

RC2 was the only explanatory variable included in the model with the best support 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 4.4; Appendix B, Figure 2).

Reflex Action Mortality Predictor (RAMP) scores (four tested reflexes represented as a proportion ranging from 0 – 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. 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 ± 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 4.5) and sturgeon that experienced reflex impairment (RAMP score > 0) did have rates of movement that were the same as the population average of 0.7 km/d.

Table 4.4. 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). 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 model with the greatest support had the highest normalized evidence weight (AICw) and is indicated in boldface.

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
Time to first detection (d)	**NULL**	**586.022**	**0.051**
	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
	RC1 + RC2 + RC3 + Capture temp.	-41.229	0.074
	RC1 + RC2 + RC3 + Handling	-41.168	0.072
Rate of movement (km/d)	**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 + Capture temp.	159.412	0.021
	RC2 + Handling	159.443	0.021
	FT	159.498	0.020

Table 4.5. Reflex Action Mortality Predictor (RAMP) scores (four tested reflexes represented as a proportion ranging from 0 – 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. 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 $P \leq 0.05$.

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

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, 2000). For example, Wilkie et al. (1996) found that angling at temperatures above 20°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. These results corroborate our previous findings in a lab study that found higher levels of lactate and chloride 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 tagged fish survived the initial C&R event but only three were captured in high water temperatures (~20°C) so survival at extremely high temperatures is unknown. The positive significant relationship we found between temperature and stress physiology is important, however, since extreme biochemical alterations at high water temperatures have been proposed to be important factors to consider in latent mortality (Wilkie et al., 1996). Our results are important in the context of fisheries management since during the warmest months (e.g.,>20°C in summer) and during the highest levels of river discharge (e.g., up to 9 430 $m^3 \cdot s^{-1}$ in May 2014 during our study), fish are exposed to faster currents and may already have higher levels of circulating metabolites, especially lactate, that could be compounded by a C&R event.

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 lack of potential mortalities left us unable to assess the efficacy of RAMP scores as predictors of post-release mortality rates in the wild. The significant positive relationship between RC1 (lactate + chloride) and RAMP score 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). The relationship we found between stress physiology and post-release movement patterns, as well as RC1 and RAMP, suggests RAMP may be useful in providing a connection between stress physiology after capture and post-release behaviour if sample sizes were large enough to account for individual and seasonal variations. 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.

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 (depth) 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 (Ferter 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 displayed a characteristic final spurt of energy at the end of the fight that was visibly recognized by the release of air bubbles – presumably from the swim bladder – followed by a “belly-up” position as they were towed toward the boat or shoreline (Figure 4.4). 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 summer sample size (>15°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 has been identified as ~33°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 (~15°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 minutes, 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 (7 960 $m^3 \cdot s^{-1}$), 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 (8 240

$m^3 \cdot s^{-1}$). 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 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 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). The relationships between fish size, stress physiology, and post-release movement behaviour is a relationship that warrants further consideration in future work.

Figure 4.4. 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, 7 110 $m^3 \cdot s^{-1}$ river discharge, 13.3 °C surface 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.

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). 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. Although our results suggest there could be reduced locomotor activity that extends beyond the 30 min. observation period from previous work (see McLean et al. 2019), the results are someone equivocal since higher physiological disturbance in some cases actually resulted in higher overall activity and rates of movement, suggesting the model selection lent insight into some of the drivers of white sturgeon movement in general, but not as it relates to the angling event. In the LFR, there appears to be high intraspecific variability in the movement patterns of white sturgeon (Robichaud et al. 2017; E. Stoddard, FLNRORD, unpublished data), 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 post-release 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.

Understanding 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 for which there is need to ensure that fishing activities do not impede population recovery and where optimal fishing and fish handling practices are needed. 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.

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˚C during summer low flows. 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.

How the individual was fought (i.e., angler skill and experience) and how the fish fought back are likely two important factors that should 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 in the physiological responses to the angling event highlighted in the current study and may be influenced by fish age. 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. 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.

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CHAPTER 5

Conclusion

The evolution of sturgeon (order Acipensiformes) dates back to the Triassic era, to the age of the dinosaurs nearly 300 million years ago, and they have proved incredibly resilient, remaining relatively unchanged in time. Yet in a comparatively short period of time, within the last ~ 200 years in the age of the 'Anthropocene' (Crutzen and Stoermer, 2000), most extant sturgeon species have been pushed to the brink of extinction, and currently 19 of 25 species are listed as endangered or critically endangered by the IUCN. Only three species hold the status of 'least concern', the lowest IUCN listing. Among these, my study species, the white sturgeon from the lower Fraser River (LFR), has maintained a considerably healthy population but their behaviour is complex and poorly understood. Additionally, low recruitment of the population in recent years (Nelson et al., 2018) has prompted the need for research concerning their basic biology as well as an understanding of how anthropogenic activities affect individuals and populations.

There is a conceived, and well documented, idea that sturgeon are rather resilient to common stressors such as hypoxia, thermal stress, and typical aquaculture stressors (i.e. crowding, handling) under captive conditions (Barton, 2002). Sturgeon stress responses in the wild are considerably less studied but overall the consensus is that their responses are tempered in comparison to teleosts exposed to similar stressors. It is perhaps the unique evolution and physiology of sturgeon that may explain these differences. Since their divergence from the ancient lineage leading to teleosts (Hurley et al., 2007), sturgeon have changed very little morphologically. Their slow evolution rate (Krieger and Fuerst, 2002) may have translated to a more conserved or ancestral physiological stress response compared to teleosts, which are more derived and diverse. Further, life-history traits such as large body size, long lifespan, and lack of natural predators may have negated the necessity to develop a capacity for a sensitive stress response (Barton et al., 2000).

There is the potential for anthropogenic stressors to have large evolutionary consequences by inducing greater selection pressures than would occur naturally (Reznick, 2001). Traditionally, Darwinian theory suggested evolutionary responses would take thousands of years to occur (Darwin, 1859), however, more recently it has been shown that evolution can occur over a much shorter timescale. For many fish species, fishing pressures are a common anthropogenic stressor that have even been connected to evolutionary change to traits including body size, migration timing, and age of maturation in ten or fewer generations in anadromous salmonids (Hard et al., 2008). Although take fisheries for acipenserids are rare, there are some instances of by-catch and recreational catch-and-release (C&R) fisheries, including for white sturgeon in the LFR. 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, 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). 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).

Taken together, my research aimed to better understand the physiological ecology and behaviour of an ancient acipenserid after an anthropogenic stressor (C&R angling) and to attempt to tease apart any environmental effects. My overarching hypothesis for this thesis was that i) the severity of capture stressors influences the magnitude of the response (e.g., RAMP impairment and measured changes in blood chemistry), ii) the response would predict post-release outcomes (e.g., recovery and movements), and iii) the effects would be exacerbated at higher water temperatures and during periods of high discharge (i.e., peak freshet). The first part of my hypothesis (i - the severity of capture stressors influences the magnitude of the response) was supported by each chapter of this thesis. In chapter 2, I characterized a fisheries-like encounter as a combination of forced thrashing exercise and partial air-exposure and applied groups of captive white sturgeon to varying treatments. The level of the disturbance (i.e., longer treatments) affected reflex impairment and physiological measures of stress in the blood. In chapters 3 and 4, longer fight times via recreational angling led to higher physiological measures in the blood, and in chapter 4 higher measures of lactate + chloride resulted in higher reflex impairment. Interestingly, lactate was the most consistently affected physiological marker that was measured and increased linearly with treatment and fight time in each research chapter. This was unsurprising given white sturgeon experienced anaerobic exercise, which was induced via thrashing in chapter 2, and occurred during the angling events in chapters 3 and 4. During burst performance swimming, there is a depletion of glycogen reserves and associated build-up of lactate in white muscles from anaerobic glycolysis. Some of this lactate is measurable in the blood, although the levels in the white muscle would be much higher (Wood, 1991). The range of whole blood lactate in our studies (0.2 to 10.0 $\text{mmol}\cdot\text{L}^{-1}$) could reflect the fact that not all sturgeon fight as aggressively or use burst performance swimming as often during the fight as others and was the first indication of high interindividual variability in the stress response of white sturgeon to angling.

Results from reflex impairment assessments in chapters 2 and 4 were interesting. Although the results provide good evidence that reflex impairment is likely a result of some physiological process (i.e., lactate accumulation and changes in plasma ion concentrations), there was considerable individual variation in the impairment responses that warrant future consideration. For example, longer fight times were often associated with full reflex impairment, however, one individual fought for 110 minutes, 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 (7 960 $\text{m}^3\cdot\text{s}^{-1}$), 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 (8 240 $\text{m}^3\cdot\text{s}^{-1}$). 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. Several species have shown a reduction in stress responsiveness with increasing age (Andrews et al., 2017), so biological age may explain some of the individual variation seen in the white sturgeon stress response. Sex, stage-of-maturity and size are likely also important life-stage drivers behind some of the variation, and although I was unable to collect information on sex and stage-of-maturity for most of the individuals I sampled, there was a negative relationship between the ordinated blood axis RC3 (cortisol) and fish size in chapter 4 – a relationship that warrants further consideration in future work.

The second part of my hypothesis (ii – the response would predict post-release outcomes (e.g., recovery and movements)) was generally supported in all chapters, but evaluation of fitness outcomes proved difficult in the wild and the supporting evidence was resultingly equivocal (chapters 3 and 4). RAMP scores would likely have been effective predictors of post-release fate in chapter 2, however, our sample size of two mortalities made it difficult to show a predictive relationship. Additionally, we experienced no mortality in wild white sturgeon that were assessed for reflex impairment in chapter 4. The proximate cause of delayed mortality in chapter 2 is unknown. One prediction is that lower levels of physiological disturbance and, subsequently, lower reflex impairment during the capture and handling of individuals can promote better survival upon release. Indeed, the two mortalities occurred in fish exposed to longer treatment times (10 and 15 min) and both fish had upper-range levels of physiological indicators of stress (i.e., lactate) as well as overall RAMP impairment scores of 1 (all reflexes impaired). In fact, reflex impairment had a stronger association with delayed mortality than the physiological metrics, as other surviving fish had similar physiological profiles to the deceased fish but lower reflex impairment scores. Given that there were so few mortalities in any study, it is difficult to identify the lethal thresholds for white sturgeon using indicators of excess stress metabolites or anaerobic acid–base/ionic imbalances. However, the significant relationship we found between lactate concentration and reflex impairment in chapters 2 and 4 suggests that excess stress metabolites may contribute to delayed mortality, as has been shown in studies on other species (Gale et al., 2013). The effect of higher reflex impairment and stress physiology on recovery was obvious in chapter 2 where recovery time was significantly longer in sturgeon subjected to longer treatments and that had subsequently higher reflex impairment (RAMP scores) and higher concentrations of circulating stress metabolites. Although I was unable to identify the clearance rates of the various metabolites, the literature suggests that it can take upwards of 10 hrs for lactate concentrations to return to baseline (e.g., Wood et al., 1983) during which time other functions can not be carried out (e.g., foraging, feeding, breeding, etc.). Reflexes are typically recovered faster than stress metabolites (e.g., 15-30 min., Raby et al., 2013). This finding is what led Raby et al. (2013) to conclude that although there is a basis for physiology in reflex impairment studies, the drivers behind the impairment of various reflexes (i.e., tail grab vs equilibrium) likely differ and may be by-products of some of the common measured variables (e.g., lactate) that recover faster. Interestingly, a number of salmon species subjected to fisheries stressors lost their ability to respond to physical stimulus almost immediately (e.g., sockeye, Gale et al., 2011, 2013; e.g., coho, Raby et al., 2013), whereas white sturgeon were fairly resilient to the loss of those reflexes until they were exposed to the longer treatments. This difference in reflex responsiveness is likely to be a result of the reduced anaerobic stress response in sturgeon when compared with teleosts (Kieffer et al., 2001).

In the introduction of my dissertation I argued for a need to integrate physiological sampling with other tools like acoustic telemetry to better understand the drivers of behaviour and potential fitness outcomes in the wild. Although the literature is replete with examples of integrative sampling in other fish species, its use is underrepresented in research focused on acipenserids. In chapters 3 and 4, I attempted to fill this knowledge gap by combining acoustic telemetry with measures of stress and reflex impairment (chapter 4). In chapter 3, the transmitters I used were equipped with accelerometer sensors that allowed me to assess fine-scale post-release activity in the short-term. By manually tracking the individuals I was able to recreate recovery profiles that revealed patterns of recovery that were like tagged shortnose sturgeon (Broell et al., 2016) following a capture-tag-release event, and included low periods of activity for much of the <50 min. tracking period. Interestingly, the recovery of all tracked individuals appeared to take place in nearshore habitats, with all individuals moving closer to shore after release. 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. Although the small sample size in chapter 3 made it difficult to draw useful connections between stress physiology and post-release movement patterns, in chapter 4 I tied it all together with the results showing a clear connection between stress physiology, reflex impairment, and post-release behaviour. Specifically, higher lactate and chloride were associated with reduced movement. Additionally, survival of the initial capture event was high (100% released fish were recaptured or detected). 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 was associated with a lower post-release movement distance (km) to first detection as well as a reduction in the number of unique stations visited by the individual over the entire tracking period. Combined, I suggest these results translate to reduced locomotor activity that extends beyond the 30 min. observation period in chapter 3. This is particularly important for understanding fitness implications since during the recovery process, there is a deficit of oxygen available for normal behaviour and movements such as startle reactions and anti-predation behaviours (i.e., flight response), potentially increasing their susceptibility to predation or recapture via angling or as by-catch in other fisheries.

The final part of my hypothesis (iii – the effects would be exacerbated at higher water temperatures and during periods of high discharge) was integrated into and generally supported in chapters 2 and 4. It is well documented that the environment of which the fish is caught can affect its fate post-release (Cooke and Wilde, 2007). Abiotic factors like water temperature and discharge (e.g., flow) are known to act as cumulative stressors during events that would already be stressful, like an angling event. I found this to be the case in chapter 2 when I compared the stress response, reflex impairment, and recovery of summer and winter-treated fish and found a clear exacerbation in the responses during warmer water temperatures. Similarly, in chapter 4, higher surface water temperatures and higher discharge rates of the LFR were associated with a higher physiological disturbance. In fact, ~70% of studies examining the effects of fisheries C&R stress at different temperatures have found a positive relationship between water temperature, indices of stress and mortality (see Gale et al., 2013 for full review; Gale et al., 2011, 2014; Robinson et al., 2013; Raby et al., 2015). My research findings on the difference in physiology and reflex impairment under different environmental conditions is supported by the general literature and highlights the importance of considering flexible management plans for wild fisheries, because the same stressor intensity can have varying impacts that can be dependent on the external environmental conditions.

Bridging Physiological Studies to Ecology

In 1987, Bennet proposed the idea of the “tyranny of the Golden Mean”, suggesting that the fields of comparative and ecological physiology suffer from an almost complete focus on central tendencies in physiological studies, and that instead we should be shifting focus to the interindividual variability (Bennett, 1987). His thesis argued that the analysis of interindividual variability could bridge the gap between physiology and other fields of biology (i.e., ecology, behaviour, evolution; (Bennett, 1987; Williams, 2008). In 2008, Tony Williams built further on this idea and provided a conceptual framework for how to best “capitalize on the central role that hormones play in adaptation”. Spicer and Gaston (1999) previously presented a comprehensive collection of studies showcasing interindividual diversity, but it has historically been more common in fisheries research to focus on averages. The work I conducted on white sturgeon examined population averages (“the Golden Mean”) but I also looked at individual variation. In chapter 2, average values provided insight into the relationship between stress physiology, reflex impairment and recovery and allowed me to compare between two seasons. This analysis identified a treatment effect on the physiology and impairment reactions of white sturgeon that was also influenced by temperature, but it also revealed high interindividual variability in the responses. In chapter 3, my small sample size meant that the variability in the recovery behaviour profiles could not be compared to the post-capture stress physiology values but once again, the physiological diversity was prominent. In chapter 4, I had collected enough blood samples and deployed additional acoustic transmitters, so I was able to incorporate the variability into my analysis via model selection. This analysis revealed some interesting trends, including that life-stage may help explain some of the interindividual variability in the responses to angling. Typically, larger body size has been connected to greater physiological disturbance in other fish species. For example, after exposure to exhaustive exercise, largemouth bass (*Micropterus salmoides*) exhibited elevated concentrations of plasma glucose and sodium relative to small fish, and they required additional time to clear the metabolites (Gingerich and Suski, 2012). Contrarily, several species have also shown a reduction in stress responsiveness with increasing biological age (Andrews et al., 2017). In chapter 4, there was a negative relationship between the ordinated blood axis RC3 (cortisol) and fish size. Although life-stage may explain some of the variability in the cortisol response, more research is required to understand the unexplained variability. For example, our largest captured fish (323 cm FL) was angled for 83 minutes and demonstrated complete visible exhaustion when pulled to shore. The physiology profile revealed this fish was the population average for all stress metabolites but had fully impaired reflexes. Because this individual was only carrying a short life-span transmitter, it was not included in the survival estimate in chapter 4 but it was never detected on any receiver and was not recaptured in the fishery again. This could suggest that aging may cause a failure to activate specific stress response pathways (i.e., diminished cortisol response) but it may also cause decreased resistance (i.e., sublethal mortality) that could negatively impact fitness. The variability in the response could also be associated with the individual’s previous encounters with similar stressors since the recapture rate for some areas of the LFR is >90% (E. Stoddard, personal communication) and exposure to multiple or cumulative acute stressors can impact individuals differently.

Tyranny of the Golden Hormone

Cortisol is the favoured glucocorticoid for behavioural ecologists. And, as Barton (2002) highlights in his review on the diversity of the stress response in fishes, cortisol is commonly used as an indicator of the degree of stress experienced by fish. Interestingly, across taxa, cortisol elevations following acute stressors are documented to range between ~30 to >300 ng·mL^{-1}, and many studies have successfully linked glucocorticoid concentration (mainly cortisol) to fitness outcomes in wild populations. For example, elevated pre-stress and stress-induced cortisol concentrations at arrival to the spawning grounds was associated with reduced survival in semelparous Pacific salmon (*Oncorhynchus* spp.; Cook et al., 2011). Similarly, higher cortisol concentrations were associated with migration failure in semelparous sockeye salmon (*Oncorhynchus nerka*; Cook et al., 2014). Acute angling stress duration has also been shown to correlate with increases in circulating concentrations of cortisol in other species. For example, plasma cortisol was elevated in wild rainbow trout that were angled for longer than 2 min (Meka and McCormick, 2005). Until recently, the peak levels of cortisol following an acute stressor in acipenserids was documented as being low but very few of these studies were on wild fish. For example, in scaphirhynchid sturgeon the peak was only 3 after an acute handling stressor in captivity (Barton et al., 2000) and peak concentrations were 40 ng·mL^{-1} in cultured white sturgeon (Belanger et al., 2001). My research, however, revealed even greater variability in the cortisol response to acute angling stress with post-capture cortisol concentrations ranging from to ~5 to 383 ng·mL^{-1} – as much variability as Barton (2002) observed across all fish taxa.

Although I did not find a treatment effect on cortisol concentration in Chapter 2, I did find a weak association between increased fight time and cortisol in Chapter 4. Given cortisol has been shown to peak in white sturgeon ~30 min. after exposure to air (Zuccarelli et al., 2008), it is possible that I was unable to capture peak cortisol levels due to my sampling procedure. Given the high variation in cortisol concentration in white sturgeon and its inability to predict with any confidence the impacts of angling stressors (e.g., RAMP score, recovery, behaviour), I suggest a renaming as the 'Golden Hormone' in homage to Bennet's original thesis and suggest other metrics are likely more appropriate for assessing acute angling stress in sturgeon in the wild. As previously mentioned, I suggest an integrative approach that incorporates the use of physiological indicators of stress that manifest quickly following angling and are likely to be measurable upon capture (e.g., lactate), an assessment of whole-animal response to the event such as an assessment of reflex impairment, and telemetry to assess post-release recovery behaviour and survival. My research supports the general notion that sturgeon are resilient to acute angling stress but also highlights how important it is to not solely rely on metrics that have been used to study responses in other species or systems. Since individual variation in stress hormones are thought to mediate life-history trade-offs (Ricklefs and Wikleski, 2002) and behaviour (Koolhaas et al., 1999) there is more work to be done investigating the extreme variability in cortisol expression in wild white sturgeon. Studying the inter individual variability of this Golden Hormone could help us to understand other fundamentals about the biology and evolution of these ancient fish.

Management Implications

The results from my dissertation have contributed to the overall understanding of acute angling stress on the physiological ecology of white sturgeon. My findings are applicable to conservation efforts and have partially been implemented in management guidelines for the C&R fishery in the lower Fraser River. Although post-release survival of angled white sturgeon is high (as confirmed in chapter 4 – 100% survival with our methods), other direct effects of angling on fitness, like reproductive output, remain unknown. Due to the life-history traits of sturgeon, including long lifespan and long periods of intermittent spawning (up to 10 years for female fish), the most direct link I could hypothesize between a C&R event and other sublethal fitness effects would be a reduced spawning capacity as a result of the capture event. This could include catching a spawn-ready adult resulting in potential fall-back from the event and subsequently an increased energy expenditure and abandonment of the spawn-run altogether. Or a capture event in the staging-year (prior to planned spawning) that results in a reduced energy budget that perhaps forces the individual to wait an additional year before they are spawn-ready. Female sturgeon are highly fecund, and produce up to 700,000 eggs at each spawning event (Scott & Crossman, 1973; BC Ministry of Environment, 1997), and only a handful of offspring need to survive to sexual maturity to maintain the population. The LFR population is experiencing recruitment failure so there may be an effect on the population where eggs, larvae, young-of-year, and juveniles are not surviving, and/or adults are not surviving to sexual maturity and/or are not spawning as often as they did historically.

Unfortunately, there remains a knowledge gap in our basic understanding of white sturgeon spawning movements and migrations within the LFR that need to be addressed before we can fully understand potential population-level impacts of acute stressors in the wild.

Interestingly throughout my research on sturgeon, including my MSc and PhD research, I have encountered a long-standing public opinion that sturgeon are extremely resilient animals. My results certainly support this general idea, but they also show that in some cases individuals can reach levels of distress (beyond their capacity to maintain homeostasis). It is well documented that the magnitude of the physiological alteration associated with angling affects recovery, and longer recovery times decrease the likelihood of survival (Lennox et al., 2016). As I argue in Chapters 2-4, longer periods of recovery also hinder an individual's ability to carry out normal functions (e.g., eating, foraging, breeding). My advice to management is to use the science from my dissertation to support guidelines that are intuitive but might require tangible evidence to convince anglers. Minimal fight and handling times can reduce: the physiological stress response (Chapters 2-4), recovery times (Chapter 2-3), reflex impairment (Chapters 2 and 4), risk of mortality (Chapters 2 and 4), and potential alterations to short- and long-distance movements (Chapters 3-4). Environmental conditions should also be considered since I have shown that higher water temperatures and changing river flows can affect the physiological stress response and reflex impairment (Chapters 2 and 4). This is especially important as river temperatures continue to rise as a result of climate change. In fact, recent models published in the journal *Nature* found that the average summer water temperatures have doubled the number of days exceeding 20˚C in the Fraser River watershed in the last 65 years (Islam et al., 2019). So - “play them fast, keep them wet” (KEEPEMWET® catch-and-release education program; www.keepemwet.org), reduce handling and air exposure, and consider warm water temperatures (>20˚C) and periods of peak flows as potentially harmful cumulative stressors that may negatively impact the health and survival of white sturgeon.

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APPENDIX A

Chapter 1 Supplementary Material

Table A.1. References for Table 1.1.

Common name	References
Adriatic sturgeon	(Bronzi et al., 2006)
Atlantic sturgeon	(Collins et al., 2000; Secor et al., 2000; Caron, Hatin, and Fortin, 2002; D. Hatin, Fortin, and Caron, 2002; Daniel Hatin et al., 2007; Balazik, Garman, et al., 2012; Balazik, Reine, et al., 2012; Beardsall et al., 2013; Breece et al., 2013, 2016; Kahn et al., 2014; McLean et al., 2014; Hightower et al., 2015; Smith, Flowers, and Hightower, 2015; Balazik, 2015; Balazik and Musick, 2015; Hale et al., 2016; Ingram and Peterson, 2016; Kapusta et al., 2016; Stokesbury et al., 2016; Taylor et al., 2016; Altenritter et al., 2017; Melnychuk et al., 2017; Novak et al., 2017; Taylor and Litvak, 2017; Wippelhauser et al., 2017)
Atlantic/shortnose sturgeon	(Crossman et al., 2013; Fernandes et al., 2010; Kieffer and Kynard, 1993)
Beluga/Russian/Stellate/ Sterlet sturgeon	(Contreras-Sanchez et al., 1998; Deak et al., 2014b, 2014a; Kynard et al., 2002; Raischi et al., 2017)
Chinese sturgeon	(Du et al., 2013; Kynard et al., 1995; Wang et al., 2014, 2012; Watanabe et al., 2008; Wu et al., 2018; Yang et al., 2006; Zhang et al., 2011)
European sturgeon	(Taverny et al. 2002; Lepage and Taverny 2005; Acolas et al. 2012, 2017; Carrera-García et al. 2017)
Green sturgeon	(Benson et al., 2007; Borin et al., 2017; Erickson and Webb, 2007; Heublein et al., 2009; Huff et al., 2011; Kelly et al., 2007; Klimley et al., 2017; Lindley et al., 2011, 2008; Miller et al., 2014; Mary L. Moser et al., 2017; M. L. Moser et al., 2017; Moser and Lindley, 2007; Thomas et al., 2014, 2013; Wyman et al., 2017)
Gulf sturgeon	(Carr et al., 1996; Chapman and Carr, 1995; Duncan et al., 2011; Edwards et al., 2007, 2003; Fox et al., 2002, 2000; Harris et al., 2005; Havrylkoff et al., 2012; Parauka et al., 2011; Parkyn et al., 2006; Peterson et al., 2016;

	Randall and Sulak, 2012; Rogillio et al., 2007; Ross et al., 2009; Rudd et al., 2014; Sulak et al., 2009; Wrege et al., 2011)
Lake sturgeon	(Adams et al., 2006; Altenritter et al., 2013; Barth et al., 2011; Boase et al., 2014, 2011; Caswell et al., 2004; Crossman et al., 2009; Damstra and Galarowicz, 2013; Donofrio et al., 2017; Ganus et al., 2017; Genz et al., 2014; Hondorp et al., 2017, 2015; Hrenchuk et al., 2017; Kessel et al., 2018; Knights et al., 2002; McDougall et al., 2014b, 2014a, 2013a, 2013b; Shaw et al., 2013; Smith and King, 2005; Snobl et al., 2015; Struthers et al., 2017; Thayer et al., 2017; Welsh and McLeod, 2010)
Pallid sturgeon	(Herrala et al., 2014; Jordan et al., 2006; Koch et al., 2012; Steffensen et al., 2015; Wanner et al., 2007)
Shortnose sturgeon	(McCleave et al., 1977; Hall et al., 1991; O'Herron et al., 1993; Kieffer & Kynard, 1996; Kynard et al., 2000, 2009; Collins et al., 2002; Li et al., 2007; Trested et al., 2011; Zydlewski et al., 2011; Kieffer et al., 2012; Dionne et al., 2013; Farrae et al., 2014; Wippelhauser & Squiers, 2015; Wippelhauser et al., 2015; Broell et al., 2016; Altenritter et al., 2017)
Shovelnose sturgeon	(DeLonay et al., 2007; Wildhaber et al., 2011)
Siberian sturgeon	(Boone et al. 2013; Carrera-García et al. 2017)
White sturgeon	(Ashton et al., 2017; Counihan and Frost, 1999; Geist et al., 2005; Hatten and Parsley, 2009; Liss et al., 2017; Nelson and McAdam, 2012; Neufeld and Rust, 2009; Paragamian and Kruse, 2001; Parsley et al., 2007, 2011, 2008; Robichaud et al., 2017; Welch et al., 2006; Young and Scarnecchia, 2005)

Table A.2. References for Table 1.2.

Study topic	References
Anthropogenic influences (e.g., hydroelectric facilities, dredging, catch-and-release)	(McCleave et al. 1977; Geist et al. 2005; Parkyn et al. 2006; Parsley et al. 2007; Parsley et al. 2011; Balazik et al. 2012a; Beardsall et al. 2013; McDougall et al. 2013a; McDougall et al. 2013b; McDougall et al. 2014b; McDougall et al. 2014a; Raischi et al. 2016; Stokesbury et al. 2016; Hondorp et al. 2017; Klimley et al. 2017; Moser et al. 2017a)
Capture probability	(Steffensen et al. 2015)
Habitat use/movement/ migration/swimming behaviour	(McCleave et al. 1977; Hall et al. 1991; Kieffer and Kynard 1993; O'Herron et al. 1993; Carr et al. 1996; Collins et al. 2000; Fox et al. 2000; Kynard et al. 2000; Paragamian and Kruse 2001; Caron et al. 2002; Collins et al. 2002; Fox et al. 2002; Hatin et al. 2002; Knights et al. 2002; Kynard et al. 2002; Taverny et al. 2002; Edwards et al. 2003; Caswell et al. 2004; Lapage et al. 2004; Geist et al. 2005; Harris et al. 2005; Smith and King 2005; Young and Scarnecchia 2005; Adams et al. 2006; Bronzi et al. 2006; Jordan et al. 2006; Parkyn et al. 2006; Welch et al. 2006; Yang et al. 2006; Benson et al. 2007; DeLonay et al. 2007; Edwards et al. 2007; Erickson and Webb 2007; Hatin et al. 2007; Kelly et al. 2007; Li et al. 2007; Moser et al. 2007; Parsley et al. 2007; Rogillio et al. 2007; Wanner et al. 2007; Lindley et al. 2008; Parsley et al. 2008; Watanabe et al. 2008; Hatten and Parsley 2009; Heublein et al. 2009; Kynard et al. 2009; Neufeld and Rust 2009; Ross et al. 2009; Sulak et al. 2009; Fernandes et al. 2010; Welsh and McLeod 2010; Barth et al. 2011; Boase et al. 2011; Duncan et al. 2011; Huff et al. 2011; Lindley et al. 2011; Parauka et al. 2011; Trested et al. 2011; Wildhaber et al. 2011; Wrege et al. 2011; Zydlewski et al. 2011; Balazik et al. 2012a; Havrylkoff et al. 2012; Kieffer et al. 2012; Koch et al. 2012; Nelson and McAdam 2012; Altenritter et al. 2013; Breece et al. 2013; Damstra and Galarowicz 2013; Dionne et al. 2013; Du et al. 2013; McDougall et al. 2013a; Shaw et al. 2013; Boase et al. 2014; Deak et al. 2014a; Deak et al. 2014b; Ferrae et al. 2014; Herrala et al. 2014; McDougall et al. 2014a;

	McDougall et al. 2014b; McLean et al. 2014; Rudd et al. 2014; Thomas et al. 2014; Wang et al. 2014; Wippelhauser et al. 2015a; Wippelhauser et al. 2015b; Breece et al. 2016; Broell et al. 2016; Hale et al. 2016; Peterson et al. 2016; Raischi et al. 2016; Stokesbury et al. 2016; Taylor et al. 2016; Altenritter et al. 2017a; Altenritter et al. 2017b; Borin et al. 2017; Donofrio et al. 2017; Ganus et al. 2017; Hansel et al. 2017; Hondorp et al. 2017; Hrenchuk et al. 2017; Kessel et al. 2017; Melnychuk et al. 2017; Moser et al. 2017b; Novak et al. 2017; Raischi et al. 2017; Robichaud et al. 2017; Struthers et al. 2017; Thayer et al. 2017; Wippelhauser et al. 2017; Wyman et al. 2017)
Population structure/ Abundance	(Kynard et al. 2009; Nelson and McAdam 2012; Hale et al. 2016; Peterson et al. 2016)
Restocking/ hatchery fish	(Secor et al. 2000; Bronzi et al. 2006; Jordan et al. 2006; Crossman et al. 2009; Neufeld et al. 2009; Trested et al. 2011; Acolas 2012; Du et al. 2013; Wang et al. 2014; Kapusta et al. 2016; Acolas et al. 2017; Carrera-Garcia et al. 2017a; Ganus et al. 2017; Wu et al. 2018)
Spawning	(Chapman and Carr 1995; Kynard et al. 1995; Kieffer and Kynard 1996; Fox et al. 2000; Paragamian and Kruse 2001; Caswell et al. 2004; Parkyn et al. 2006; DeLonay et al. 2007; Erickson and Webb 2007; Boase et al. 2011; Wildhaber et al. 2011; Zhang et al. 2011; Balazik et al. 2012b; Randall and Sulak 2012; Wang et al. 2012; Breece et al. 2013; McDougall et al. 2013b; Kahn et al. 2014; Balazik and Musiak 2015; Smith et al. 2015; Wippelhauser et al. 2015b; Ingram and Peterson 2016; Donofrio et al. 2017; Taylor and Litvak 2017)
Survival/natural mortality	(Crossman et al. 2009; Acolas et al. 2012; Beardsall et al. 2013; Thomas et al. 2013; Genz et al. 2014; McDougall et al. 2014b; Rudd et al. 2014; Hightower et al. 2015; Kapusta et al. 2016)
Tagging/handling effects	(Counihan et al. 1999; Beardsall et al. 2013; Boone et al. 2013; Crossman et al. 2013; Genz et al. 2014; Miller et al. 2014; Balazik 2015; Hondorp et al. 2015; Snobl et al. 2015; Broell et al. 2016; Ashton et al. 2017; Carrera-Garcia et al. 2017b; Liss et al. 2017)

APPENDIX B

Chapter 4 Supplementary Material

Table B.1. Summary of the original capture-tag-release event and subsequent detection/recapture information for 60 white sturgeon *Acipenser transmontanus* in the lower Fraser River, British Columbia, Canada. White sturgeon were angled, biopsied for physiological indicators of stress, internally implanted with acoustic transmitters (V16 series) and Passive Integrative 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)	Capture date	Season	Water temp. (ºC)	Discharge $(m^3 \cdot s^{-1})$	RAMP score	First detection or recapture	First detection/recapture (days)	Linear distance (km)	Last detection	(d) Tracked	# fixed VRWs detected on	# unique locations visited
1	25056	166	2014-05-05	Spring	8.1	5300	---	2014-05-05	0.7	0.1	2016-08-04	821.7	2	2
2	25057	227	2014-05-05	Spring	8.1	5300	---	2014-05-16	11.4	0.4	2016-11-13	912.5	11	5
3	25058	266	2014-05-05	Spring	8.1	5300	---	2018-11-01	1641	---	---	---	0	0

4	25059	181	2014-05-05	Spring	8.1	5300	---	2014-07-22	78.5	7.2	2014-07-26	4	1	1
5	25060	156	2014-05-05	Spring	8.1	5300	---	2014-07-13	69.8	33	2016-10-17	826.4	15	9
6	25061	216	2014-05-05	Spring	8.1	5300	---	2014-08-06	93.3	4.4	2015-09-06	395.9	2	2
7	25062	221	2014-05-06	Spring	7.4	5250	---	2014-05-15	9.9	16.3	2016-10-03	871.2	11	5
8	25063	162	2014-05-06	Spring	7.4	5250	---	2014-06-05	30.5	2	2016-09-16	834	4	4
9	25064	150	2014-05-06	Spring	7.4	5250	---	2014-06-19	45	20.1	2016-10-04	837.9	16	8
10	25065	183	2014-05-07	Spring	7.5	4950	---	2014-07-08	62.2	33.1	2016-10-05	820	13	7
11	25066	172	2014-05-07	Spring	7.5	4950	---	2016-08-08 (recap.); 2016-08-12 (detect)	828	7.2	2016-08-12	1	0	1
12	25067	186	2014-05-07	Spring	7.5	4950	---	2014-06-27	51.6	55.7	2016-10-24	850.3	9	4
13	25068	212	2014-05-07	Spring	7.5	4950	---	2014-06-02	26.9	41	2014-06-07	4.6	1	1
14	25069	213	2014-05-07	Spring	7.5	4950	---	2014-06-25	49.6	50	2016-11-09	867.5	7	3
15	25070	165	2014-05-08	Spring	7.7	4690	---	2014-09-09	124.2	5.1	2016-12-20	833.5	14	8
16	25071	160	2014-05-11	Spring	10	4470	---	2014-07-22	72.2	26.7	2016-10-18	819.3	18	11

17	25072	199	2014-05-11	Spring	10	4470	---	2016-06-02	753.3	20.3	2016-06-09	7	2	2
18	25073	190	2014-05-12	Spring	10.1	4720	---	2014-05-16	4.9	0.1	2016-10-31	898.5	22	12
19	25074	183	2014-05-14	Spring	10.3	5300	---	2014-06-08	25.4	14.3	2016-11-03	879	5	4
20	25075	250	2014-05-14	Spring	10.3	5300	---	2014-09-06	115.1	4	2016-11-29	815.1	4	4
21	25419	174	2014-10-31	Fall	9.4	2600	---	2015-03-23	143.8	4.9	2016-12-31	649.2	19	10
22	25420	168	2014-10-31	Fall	9.4	2600	---	2015-04-10	161.2	4.9	2016-10-14	552.8	15	8
23	25421	151	2014-10-31	Fall	9.4	2600	---	2015-02-06	98.1	4.9	2016-12-30	693.2	13	6
24	25422	201	2014-10-31	Fall	9.4	2600	---	2015-04-11	162.1	4	2016-08-26	503.2	8	4
25	25423	162	2014-12-02	Winter	2.6	1340	---	2014-12-03	1.1	0.5	2016-11-08	706.1	3	3
26	25424	194	2014-12-02	Winter	2.6	1340	---	2014-12-03	1.5	2	2016-09-09	646	3	3
27	25425	198	2014-12-03	Winter	1.7	1270	---	2014-12-22	19.2	0.5	2016-10-05	653	13	8
28	25426	201	2014-12-03	Winter	1.7	1270	---	2014-12-04	1.6	1.5	2016-07-08	581.8	2	2
29	25427	194	2014-12-03	Winter	1.7	1270	---	2014-12-09	6.6	1.5	2016-12-31	753.4	3	3
30	25433	192	2015-01-22	Winter	2.9	1270	---	2015-05-18	116.5	5.1	2016-12-01	562.7	15	9
31	25434	180	2015-01-22	Winter	2.9	1270	---	2015-05-30	128.3	19.2	2016-12-05	555.4	2	2

32	25435	211	2015-01-22	Winter	2.9	1270	---	2015-02-14	23.6	5.1	2016-11-19	644.2	3	2
33	25436	191	2015-01-22	Winter	2.9	1270	---	2015-01-24	2.2	5.1	2016-11-29	675.3	10	6
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

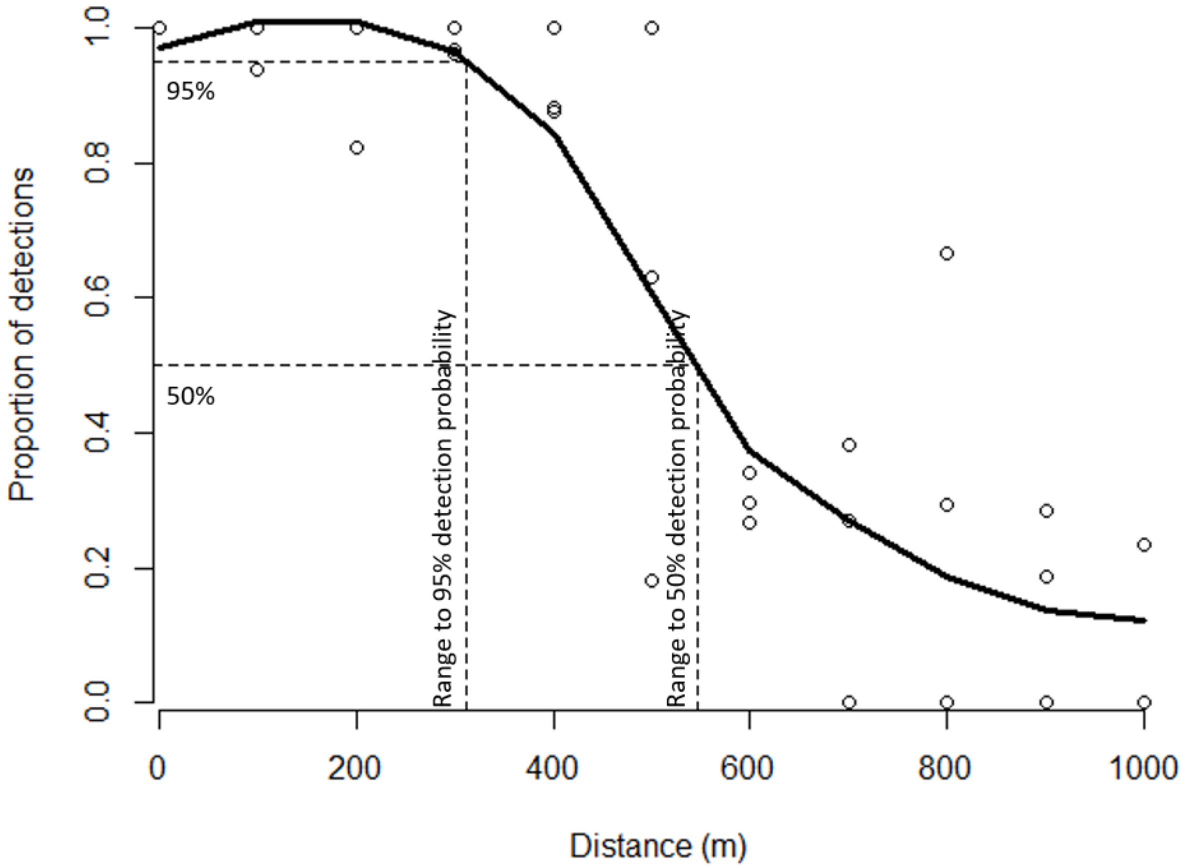

Figure B.1. Range metrics for acoustic receiver data. *Black circles* represent proportions of detections received on four VR2W passive acoustic receivers stationed throughout the mainstem channel of the Lower Fraser River in May 2015. The *solid black line* is the logistic regression through data points and the *dotted black lines* represent the range metrics, labelled accordingly.

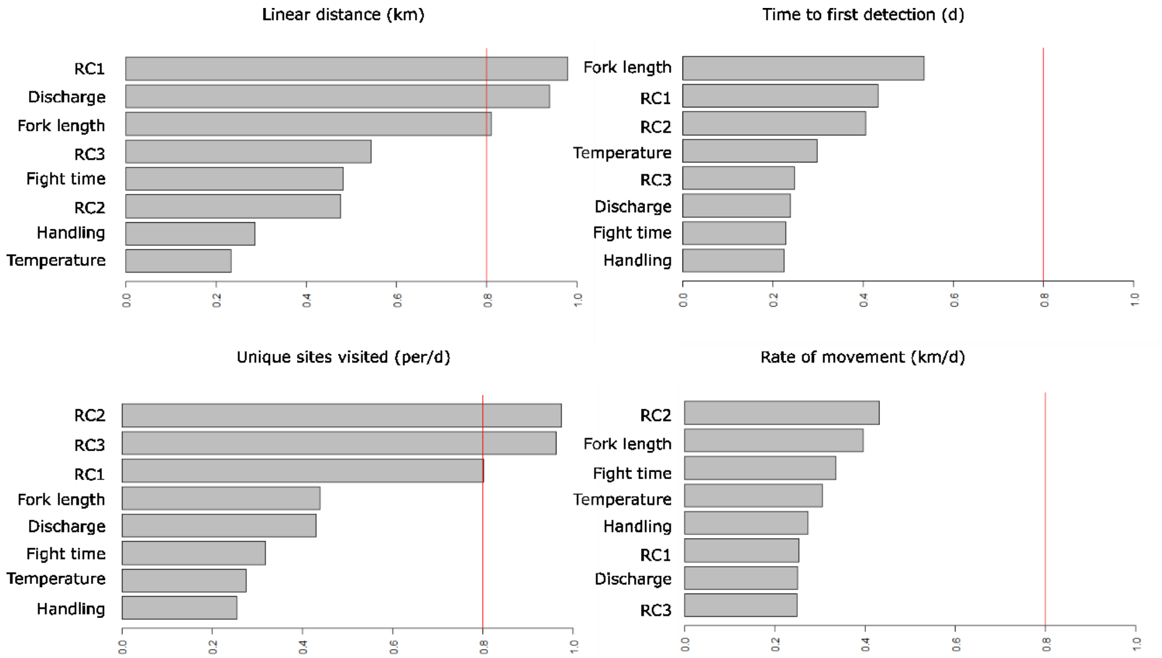

Figure B.2. The model-averaged importance of terms (predictor variables) for each movement metric (dependent variables). The importance value for each term is equal to the sum of the weights/probabilities for the models in which the variable appears. A variable appearing in many models with large weights 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 *glmulti*.

APPENDIX C

ABSTRACTS OF NON-THESIS PUBLICATIONS ARISING DURING DOCTORAL STUDIES

1. Landry, J., Kessel, S.T., **McLean, M.F.**, Ivanova, S.V., Hussey, N.E., O'Neill, C., Vagle, S., Dick, T.A., Fisk, A.T. 2018. Movement types of an Arctic benthic fish, Shorthorn Sculpin (*Myoxocephalus scorpius*), during open water periods in response to biotic and abiotic factors. Canadian Journal of Fisheries and Aquatic Sciences. 76(4): 626-635.

Shorthorn sculpin (*Myoxocephalus scorpius*) are among the most numerous consumers in the Arctic nearshore marine habitats. Despite this, little is known about their movement ecology or predator–prey interactions, particularly with Arctic cod (*Boreogadus saida*), an important forage fish in the Arctic. Using acoustic telemetry, the movements of tagged sculpin and cod were quantified based on specific locations using a Vemco positioning system during open water when both species were present in the near shore. Movement trajectories of sculpin distinguish three unique types: foraging and feeding behaviour and large transiting movements. The relative time of each of these movement types were correlated to biotic (presence of large numbers of acoustically tagged Arctic cod) and abiotic factors (percent ice coverage and temperature). This study provides unique data on the movement, feeding ecology, and behaviour of an abundant Arctic benthic fish that demonstrates similar movement types to temperate fish. However, further study is needed to quantify specifically the trophic interactions of these important fish and impact on food webs in the rapidly changing Arctic.

2. Ivanova, S.V., Kessel, S.T., Landry, J., O'Neill, C., **McLean, M.F.**, Espinoza, M., Vagle, S., Hussey, N.E., Fisk, A.T. 2018. Impact of vessel traffic on the

home ranges and movement of shorthorn sculpin (Myoxocephalus scorpius) in the nearshore environment of the high Arctic. Canadian Journal of Fisheries and Aquatic Sciences. 75(12): 2390-2400.

Sea ice reduction in the Arctic is allowing for increased vessel traffic and activity. Vessel noise is a known anthropogenic disturbance, but its effects on Arctic fish are largely unknown. Using acoustic telemetry — Vemco positioning system — we quantified the home ranges and fine-scale movement types (MT) of shorthorn sculpin (*Myoxocephalus scorpius*), a common benthic Arctic fish, in response to vessels and environmental drivers during open water over 3 years (2012–2014). Low overlap of core home ranges (50%) for all years and a change of overall MT proportions (significant in 2012 only) were observed when vessels were present compared with absent. However, changes in MTs associated with vessel presence were not consistent between years. Photoperiod was the only environmental driver that influenced (R^2 = 0.32) MTs of sculpin. This is the first study of vessel impacts on Arctic fish using acoustic telemetry and demonstrates that individuals alter their behavior and home ranges when vessels are present. Given increasing vessel traffic in the Arctic, additional study on the impact of vessels on these ecosystems is warranted.

3. Dadswell, M.J., Spares, A.D., **McLean, M.F.**, Harris, P.J., Rulifson, R. 2018. Long-term effect of a tidal, hydroelectric propeller turbine on the populations of three anadromous fish species. Journal of Fish Biology. 93(2): 192-206.

Tidal hydroelectric power has been proposed as one potential solution for sustainable energy sources. The first tidal turbine in North America began continuous operation in the Annapolis River estuary (44 °45′N; 65° 29′W) in June, 1985. The machine is an axial-flow, hydraulic-lift propeller turbine, a type known to cause fish mortality. Anadromous populations of American shad *Alosa sapidissima*, striped bass *Morone saxatilis* and Atlantic sturgeon *Acipenser oxyrinchus* utilize the Annapolis River for spawning and other life history phases. After power generation commenced obvious turbine mortalities of these fishes began appearing downstream of the turbine. Assessments of the *A. sapidissima* adult spawning runs during 1981–1982 (pre-operation) and 1989–1996 (operational) indicated significant changes in population characteristics after power generation began. Adult length, mass, age and per cent repeat spawners declined and total instantaneous mortality (*Z*) increased from 0.30 to 0.55. The pre-turbine spawning runs had older fish with numerous adult cohorts whereas by 12 years after operation began runs consisted of younger fish with fewer adult cohorts. During 1972–1987 numerous studies indicated the Annapolis River had an important angling fishery for *M. saxatilis*, but detailed annual records kept by a fishing contest during 1983–1987 and an elite angler family during the period 1976–2008 demonstrated a rapid decline in the number of fish >4.0 kg after turbine operation began. Pre-turbine catch by the angling family of fish >4.0 kg accounted for 84.1% of total catch, but declined significantly to 39.6% of total catch from 1986–1999, and to none from 2000–2008. The existence of an *A. oxyrinchus* stock in the Annapolis River was unknown before turbine operation, but during 1985–2017, 21 mortalities were recovered by chance seaward of the turbine. Mechanical strike and cavitation mortalities consisted of juveniles, mature males and gravid and spent females of ages 10 to 53 years found during June to October, the period when this anadromous species returns to its natal river to spawn. The results of the long-term studies at Annapolis indicate managers should realize substantial risks exist for the fish resources of the world's oceans from deployment of instream propeller turbines.

4. Dadswell, M.J., Wehrell, S.A., Spares, A.D., **Montana F. McLean**, Beardsall, J.W., Logan-Chesney, L.M., Nau, G.S., Redden, A.M., Stokesbury, M.J.W. 2016. The annual feeding aggregation of Atlantic sturgeon (*Acipenser oxyrinchus*) in the inner Bay of Fundy: population characteristics and movements. Journal of Fish Biology

Atlantic sturgeon *Acipenser oxyrinchus* aggregate to feed from May to October in Minas Basin (45◦ N;64◦ W), a large, cul-de-sac embayment of the inner Bay of Fundy. The aggregation consists mainly of migrants from the Saint John, NB and Kennebec Rivers, ME (99%). During 2004–2015, 4393 *A. oxyrinchus* were taken as by-catch by commercial fish trawlers or at intertidal fishing weirs, and 1453 were marked and/or sampled and released. Fork length (LF) ranged from 458 to 2670mm, but 72·5% were <1500mm. Mass (M) ranged from 0·5 to 58 ·0kg. The mass-length relationship for fish ≤50kg was log10M=3·32log10LF −5·71. Observed growth of unsexed *A. oxyrinchus* recaptured after 1–8 years indicated fish of 90–179cm LF grew c. 2–4cm a year. Ages obtained from pectoral spines were from 4 to 54 years. The Von Bertalanffy growth model predicted K = 0·01 and L∞ = 5209mm LF. Estimated annual mortality was 9·5–10·9%. Aggregation sizes in 2008 and 2013 were 8804 and 9244 individuals, respectively. Fish exhibited high fidelity for yearly return to Minas Basin and population estimates indicated the total at-sea number utilizing the Basin increased from c. 10700 in 2010 to c. 37500 in 2015. Abundance in the Basin was greatest along the north shore in spring and along the south shore in summer, suggesting clockwise movement following the residual current structure. Marked individuals were recaptured in other bays of the inner Bay of Fundy, north to Gaspé, Quebec, and south to New Jersey, U.S.A., with 26 recoveries from the Saint John River, NB, spawning run. Fish marked at other Canadian and U.S. sites were also recovered in Minas Basin. Since all *A. oxyrinchus* migrate into and out of the Basin annually they will be at risk of mortality if planned tidal power turbines are installed in Minas Passage.

5. Stokesbury, M.J.W., Logan-Chesney, L.M., **McLean, M.F.**, Buhariwalla, C.F., Redden, A.M., Beardsall, J.W., Broome, J.E., Dadswell, M.J. 2016. Atlantic sturgeon spatial and temporal distribution in Minas Passage, Nova Scotia, a region of future tidal energy extraction. PLOSone 11(7): e0158387.

In the Bay of Fundy, Atlantic sturgeon from endangered and threatened populations in the USA and Canada migrate through Minas Passage to enter and leave Minas Basin. A total of 132 sub-adult and adult Atlantic sturgeon were tagged in Minas Basin during the summers of 2010–2014 using pressure measuring, uniquely coded, acoustic transmitters with a four or eight year lifespan. The aim of this study was to examine spatial and seasonal distribution of sturgeon in Minas

Passage during 2010–2014 and test the hypothesis that, when present, Atlantic sturgeon were evenly distributed from north to south across Minas Passage. This information is important as tidal energy extraction using in-stream, hydrokinetic turbines is planned for only the northern portion of Minas Passage. Electronic tracking data from a total of 740 sturgeon days over four years demonstrated that Atlantic sturgeon used the southern portion of Minas Passage significantly more than the northern portion. Sturgeon moved through Minas Passage at depths mostly between 15 and 45 m (n = 10, 116; mean = 31.47 m; SD = 14.88). Sturgeon mean swimming depth was not significantly related to bottom depth and in deeper regions they swam pelagically. Sturgeon predominately migrated inward through Minas Passage during spring, and outward during late summer autumn. Sturgeon were not observed in Minas Passage during winter 2012–2013 when monitoring receivers were present. This information will enable the estimation of encounters of Atlantic sturgeon with in-stream hydrokinetic turbines.

6. Redden, A.M., Stokesbury, M.J.W., Broome, J.E., Keyser, F.M., Gibson, A.J.F., Halfyard, E.A., **McLean, M.F.**, Bradford, R., Dadswell, M.J., Sanderson, B., Karsten, R. 2014. Acoustic tracking of fish movements in the Minas Passage and FORCE demonstration area: pre-turbine baseline studies (2011-2013). Final Report to the Offshore Energy Research Association of Nova Scotia and Fundy Ocean Research Centre for Energy, Acadia Centre for Estuarine Research Technical Report No. 118, Acadia University, Wolfville, NS. 153 p.

The impact on fish of large tidal in-stream tidal energy converters (TISEC) deployed in very high flow environments (>2 m/s) is unknown. The issue is especially pertinent in areas where migratory fish, including transboundary species of special concern (endangered, threatened or commercial) are present. Direct contact with turbine blades and subsequent injury or mortality, and indirect effects on behaviour and use of natural migratory pathways, continue to be the primary concerns of regulators and many other stakeholders.

To address the potential risk of environmental effects on fish that utilize the FORCE test area as a migratory route and for other movements (e.g. foraging), a multi-year tracking study was conducted to assess the movements of four species of concern - Atlantic sturgeon (regionally threatened), Atlantic salmon (smolts; endangered inner Bay of Fundy population), American eel (silver stage; threatened) and striped bass (endangered Bay of Fundy population). They display broad characteristics of movement and depth preferences, and may provide insight on potential impacts on species with similar natural history characteristics.

The main objectives of the study were to: 1. Determine temporal (seasonal, diel) movements of tagged fishes within the Minas Passage and FORCE test area; 2. Identify broad distribution patterns in the Minas Passage (north to south, east to west); 3. Determine depth preferences and movements in relation to tidal stage (ebb/flood) and current speed; 4. Estimate maximum travel speeds through Minas Passage; and 5. Assess potential risks of fish-turbine interactions at the FORCE site.

VEMCO animal tracking technology was used to detect near year-round animal movements (path, velocity and depth) and behaviour of 386 tagged fish in Minas Passage during 2010-2013. VEMCO VR2w hydro-acoustic receivers provided autonomous, passive, single channel, omnidirectional detection of coded acoustic transmitters which entered the detection radius. Receivers were placed in lines ("listening gates") at 300-400 m intervals across both the Minas Passage (5 km wide) and the FORCE test site (1 km wide). The arrays were designed to detect the presence of transmitters surgically implanted in fish as they moved within the Minas Passage and during migrations into and out of the Minas Basin. Custom modified A2 Model SUB streamlined instrument floats were fitted with instrumentation (receiver and an acoustic release), and moored 2-3 m above the seafloor for periods up to 1 year.

Fish were implanted with V9, V13 or V16 electronic transmitters, depending on fish size. Most tags included pressure sensors for travel depth determination. Salmon were tagged in the Stewiacke and Gaspereau Rivers; eels were tagged in the

Gaspereau River; striped bass were tagged in the Stewiacke River and Minas Basin nearshore areas; and Atlantic sturgeon were tagged from Minas Basin intertidal weirs and an otter trawl fishing vessel.

Results show that the Minas Passage is used for fish migration purposes and other movements by fish tagged in this and other tracking projects. Detection of non-target species included white shark and spiny dogfish.

Atlantic salmon post-smolts traversed the passage in late May to mid-June en route to the Bay of Fundy and beyond. Of those smolts detected leaving the river mouths (N=20), nine were detected in Minas Passage as they quickly out-migrated; of these, five were detected by receivers at the FORCE test site.

Tagged American eels (silver stage) were shown to exit the Minas Basin via the Minas Passage during mid-September to mid-November, with movements occurring primarily in the southern half of the passage, over short time periods (1-6 days), and mostly at night during ebb tide. Maximum estimated travel rate was 3 m/s. At the FORCE test area, about 90% of eel detections occurred during ebb flow periods, with movements largely within the top 30 m of the water column.

Atlantic sturgeon sub-adults entered Minas Basin (summer feeding grounds) via Minas Passage in the spring. They made sporadic use of the Minas Passage throughout the summer, prior to exiting to the outer Bay in the fall. Sturgeon detections in the passage were more concentrated in the southern region of the passage. Although sturgeon were detected at all water depths, their movements in and near the FORCE site showed a preference for depths ranging from 15 to 40 m. The highest estimated travel speed (current assisted), between receiver lines, was 3.2 m/s.

Striped bass, especially large bass (>60 cm), spent more time in the Minas Passage and near the FORCE test area than any of the other fish species examined. Residency spanned summer, fall and winter. Of the 165 tagged striped bass, 52 swam through the FORCE tidal turbine test site in the Minas Passage, and many at depths of proposed turbine hub height. Striped bass were detected mostly in the top 40 m of the water column, and were located closer to the surface during the night. Maximum travel rate (tide assisted) across the Minas Passage was 4.0 m/s. Many tagged striped bass moved within Minas Passage throughout the winter months when water temperatures were in the range of 0-3°C. At these temperatures, striped bass are expected to have reduced metabolic rates (i.e. sluggish) and may have limited abilities to detect and avoid turbine infrastructure. This species makes near year-round use of the passage, including the FORCE test site during winter, and may be at considerable risk of interaction with turbines. Modelling of collision probability, based on available tracking data and associated environmental conditions (current speed and water temperature), is currently underway.

Although general trends in the movements of tagged fish were apparent, the tag transmission datasets for Minas Passage represent only a fraction (<40%) of the potential detections of tag transmissions, in large part because of high flow effects (i.e. elevated ambient noise levels) on the detection of complete transmission sequences (8-10 consecutive pings separated by unique spacing intervals). If the receiver does not detect a complete ping sequence, then the transmission is not logged. Detection range (distance) is known to decline as flow speed increases. These effects can result in tagged fish being able to pass through Minas Passage undetected during high flow periods.

The FORCE site represents a relatively small area within the Minas Passage (<20% of the passage width), with a single turbine of about 100 m2 occupying only 0.02% of the cross sectional area of Minas Passage. It is unknown how well migratory fish can control their movements and avoid structures within the passage when travelling at times of peak current speed. The likelihood of fish-turbine encounters may vary among species and may also increase with increasing numbers of tidal turbines. Risk is largely dependent on fish size, swimming depth, duration of occupancy at the site, sensory abilities, and water temperature (i.e. effects of metabolic rate and alertness). The hypothesis that fish avoid swimming in very fast currents in Minas Passage remains untested due to detection efficiency limitations of acoustic receivers operating in a tidal race.

Recommendations for further work at the FORCE test site include near-field studies using a range of acoustic technologies (e.g. multibeam sonar, acoustic cameras) and applications to examine fish-turbine interactions and fish behaviour (e.g. turbine avoidance) in close proximity to in-stream turbine devices. Species of commercial and conservation importance, and periods of high fish traffic in Minas Passage, should be considered for inclusion in the environmental effects monitoring program.

7. **McLean, M.F.,** Simpfendorfer, C.A., Heupel, M.R., Dadswell, M.J., Stokesbury, M.J.W. 2014. Diversity of behavioural patterns displayed by a summer feeding aggregation of Atlantic sturgeon in the intertidal region of Minas Basin, Bay of Fundy. Marine Ecological Progress Series. 496: 59-69.

Quantifying animal movements can reveal spatial and temporal patterns of habitat use and may improve our understanding of the foraging strategies of marine predators where direct observations of feeding behaviour are rare or impossible because of turbidity. Fine-scale movement data from 25 acoustically tagged Atlantic sturgeon *Acipenser oxyrinchus* (Mitchill, 1815) were gathered using a Vemco Positioning System array of hydroacoustic receivers in the intertidal zone of Minas Basin, Bay of Fundy, Canada, during summer 2011. From these data, sturgeon relocations and movement trajectories were determined. Sturgeon movement trajectories were categorized into 3 movement types by analyzing 4 calculated metric variables including (1) mean distance between successive relocations; (2) mean relative angle or ‘turning angle’; (3) mean rate of movement (ROM; m s−1); and (4) a linearity ratio. Movement Type 1 trajectories were characteristically slow and winding, with short steps between relocation, whereas Type 2 movements were fast and tortuous. Movement Type 3 trajectories were fast and linear, with large steps between relocations. Considerable variability in movement type was recognized with 11 individuals performing all 3 types of movement during the monitoring period. Movement Types 1 and 2 occurred primarily over the intertidal zone, where sediment type was comprised of larger sand and sandy/silt particles. This association with larger grain size may coincide with a diet preference for sand-tube dwelling polychaetes and indicates the importance of the intertidal zone to foraging Atlantic sturgeon. All movement types were equally likely to occur throughout a 24 h day and throughout all tidal stages; however, there was higher overall crepuscular activity which revealed a temporal pattern not previously recognized for Atlantic sturgeon.