# MOVEMENT ECOLOGY OF WHITE STURGEON IN THE REGULATED UPPER COLUMBIA RIVER

by

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#### ABSTRACT

Advancements in animal tracking technology and analytical techniques have expanded the disciple of movement ecology. An improved understanding of where, when, and why an animal moves can greatly assist in the management and recovery of endangered species. White sturgeon (Acipenser transmontanus) in the Upper Columbia River (UCR) are listed as Endangered due to their considerable decline over the last century. Habitat fragmentation, caused by the construction of dams for hydroelectric generation and river regulation, has greatly impacted white sturgeon populations by preventing access to critical habitat, impacting water quality, and modifying natural flow regimes. The goal of this study was to apply more advanced analytical techniques to white sturgeon movement datasets from a regulated and transboundary reach of the UCR, so as to further understand white sturgeon movement and behaviour in relation to river regulation. Using hidden Markov models (HMMs) and generalized linear mixed models (GLMMs), this study investigated the fine-scale movements of wild adult white sturgeon residing immediately downstream of a hydroelectric operation and the coarse-scale movements of hatchery-origin white sturgeon residing throughout the Transboundary Reach of the UCR. In my fine-scale dataset, two behaviour states were identified: a "residential" behaviour representing short movements with persistent direction, and a "transitory" behaviour representing longer movements with frequent turns. Results revealed that white sturgeon were very likely to remain in a behaviour state, with environmental covariates influencing the probability of a behaviour state only when there was less certainty of the state in the previous timestep (i.e. probability of 50%). Overall, water temperature appeared to influence what behaviour state was more predominantly expressed while discharge appeared to influence where each behaviour state was expressed. Warming water temperatures related to decreased probabilities of residential behaviour and changes in discharge shifted the location of residential behaviour within eddy and tailrace habitats. In my coarse-scale dataset, two behaviour states were also identified: a similar "residential" behaviour state representing localized movement at a single receiver station, and a "transitory" state representing movements between receiver stations. Overall, hatchery-origin white sturgeon moved very little and demonstrated strong site fidelity. When fish did move, location (i.e. country, river zone), discharge, and water temperature had the greatest influence on maximum displacement and behaviour probability. Increases in discharge related to faster declines in maximum displacement in Canada compared to the United States, as well as fish in more channelized river zones having increased probabilities of residential behaviour when previously in a transitory state. Warming water temperatures related to increases in maximum displacement and decreases in the probability of residential behaviour (when previously in a transitory state). In both fine-scale and coarse-scale datasets, trends could be observed seasonally, with increased movement in the summer and fall compared to the winter and spring. Results from this study better described white sturgeon interactions with dams, help describe the effectiveness of recovery measures like conservation aquaculture, and inform management decisions related to river regulation.

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### **CHAPTER ONE**

## INTRODUCTION

White sturgeon (Acipenser transmontanus) are the largest and longest lived freshwater species in North America (Scott & Crossman 1973). They occupy large river systems and have been identified in the Sacramento, San Joaquin, Columbia, and Fraser river basins (Hildebrand et al. 2016). The unique life history characteristics of white sturgeon have allowed the species to persist over millions of years through major geologic and climatic events. They are slowgrowing and reach sexual maturity later in life, spawn intermittently with high fecundity, and can migrate great distances to take advantage of favorable feeding and spawning conditions (Hildebrand et al. 2016; Haxton & Cano 2016). While these life history traits allowed white sturgeon to adapt to environmental stochasticity over thousands of years, these same traits now make the species highly susceptible to anthropogenic impacts which have occurred within a single generation (Bemis et al. 1997). Over the last century, historical overharvesting, alterations in habitat quality and connectivity from damming and river regulation, and other industrial uses of rivers have led to the decline of white sturgeon across much of their range (Hildebrand et al. 2016). White sturgeon, as well as many other sturgeon and paddlefish species in the order of Acipenseriformes, are now among the most threatened species globally (Cooke et al. 2012).

In the Upper Columbia River (UCR), the construction of dams for river regulation and power generation has resulted in the reduction and fragmentation of white sturgeon populations. White sturgeon in the Transboundary Reach of the UCR, located between the Grand Coulee Dam (1941) in Washington and Hugh L. Keenleyside Dam (1968) in British Columbia, have demonstrated population declines and demographic shifts since post-dam assessments began in the 1980s (Hildebrand et al. 1999). A population once dominated by juveniles to one presently dominated by adults has been attributed to approximately 50 years of low recruitment (i.e. survival of juveniles into adulthood). In 2006, the population was listed as Endangered under the Canadian Species at Risk Act (Fisheries and Oceans 2014). Dams can prevent access to critical habitats required to complete life processes (e.g. spawning or feeding), impact water quality (e.g. temperature), and modify natural flow regimes (Cooke et al. 2016). Due to a combination of river regulation and climate change, the Transboundary Reach currently experiences spring and summer water temperatures 2 to 3 °C warmer than historical averages (McAdam 2001) and significant reductions in flooding and spring freshet flows (Hildebrand & Parsley 2013). Changes in water temperature and flow have been thought to influence the biological and ecological processes of white sturgeon, such as metabolic rates (Volkoff et al. 2020), migration cues and habitat suitability related to spawning (Hildebrand & Parsley 2013; Beamesderfer & Farr 1997), and resource demands and distributions related to feeding (Taylor et al. 2012; Turschwell et al. 2019). Better understanding how white sturgeon behave in response to changing conditions in this regulated and transboundary river reach could assist in species recovery through the development of improved mitigative measures related to river regulation and hydroelectric operations.

The study of animal movement has become a critical component of fisheries management and recovery (Crossin et al. 2017; Allen et al. 2016). Movement is fundamental to animal ecology, influencing growth, survival, and reproductive success (Shaw 2020). Advancements in acoustic telemetry over the past few decades, such as tag miniaturization, improved battery life, and software development, now allow for greater tracking of fish movement at different spatial and temporal scales (Hussey et al. 2015). Additionally, the development of advanced analytical techniques (Joo et al. 2019; Whoriskey et al. 2019) has improved the ability of researchers to answer fundamental questions in movement ecology, such as 'why move?', 'how to move?', 'when to move?', and 'where to move?' (Mueller et al. 2008; Nathan et al. 2008). Movement behaviour analyses, for example, deconstruct animal movement into distinct underlying behaviour states (e.g. assumed to represent resting, foraging, spawning) and offer researchers a new way of understanding how biological and environmental factors influence the movements of individuals and populations (Patterson et al. 2017). Such analyses have been utilized in fine-scale and coarse-scale acoustic telemetry studies of sturgeon (McLean et al. 2014; Dorazio & Price 2018) as well as other fish species (Bacheler et al. 2019; Cote et al. 2020) to identify interactions and responses to human activities and environmental conditions. Applying similar methods to threatened populations, such as white sturgeon affected by river regulation and hydroelectric operations, could provide important insight into the management and recovery of a species.

The goal of this study was to describe and quantify white sturgeon movement behaviour in relation to river regulation. To accomplish this, acoustic telemetry was utilized to collect data on white sturgeon movement at two different spatial scales. Chapter 2 used an overlapping acoustic telemetry array covering 2 river kilometers (rkm) to track the fine-scale movements of wild adult white sturgeon occupying critical habitat immediately downstream of a hydroelectric operation. In Chapter 3, a large acoustic telemetry array covering around 300 rkm was used to track the coarse-scale movements of hatchery-origin white sturgeon residing throughout the Transboundary Reach of the UCR. Hidden Markov models (HMMs) and generalized linear mixed models (GLMMs) were then applied to my fine-scale and coarse-scale movement datasets to identify ecologically meaningful movement behaviours and determine how movement behaviour is influenced by biological factors and environmental conditions (e.g. water temperature and discharge) that are frequently altered by river regulation. The results from this study elucidate how white sturgeon interact with dams and river regulation and will inform recovery measures and management decisions for the threatened population in the UCR.

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# CHAPTER TWO

# FINE-SCALE MOVEMENT ECOLOGY AND BEHAVIOUR PATTERNS OF WHITE STURGEON ON THE REGULATED UPPER COLUMBIA RIVER

## Introduction

Movement ecology has become a rapidly expanding discipline in recent decades, with large strides towards investigating the relationship between movement patterns and behaviour. This growth of the discipline can be attributed to significant advancements in animal tracking technology (Hussey et al. 2015; Lennox et al. 2017), analytical tools (Joo et al. 2019; Whoriskey et al. 2019), and movement theory (Mueller et al. 2008; Nathan et al. 2008). With a majority of studies in the field being empirical and focused on different components of movement ecology (Holyoak et al. 2008), there has been a push to implement a unifying conceptual framework which compels researchers to evaluate movement in a more comprehensive and broader context. Such frameworks seek to integrate the basic questions of movement ecology: 'why move?', 'how to move?', 'when to move?', and 'where to move?' (Mueller et al. 2008; Nathan et al. 2008).

Novel analytical techniques have begun to allow for the integration of these questions in movement ecology, with a focus on investigating the intrinsic (e.g. biological) and extrinsic (e.g. environmental) factors that influence how animals move across space and time (Patterson et al. 2017). Methods increasingly applied are those popularized by Morales et al. (2004) and Jonsen et al. (2005), which deconstruct animal movement track data into underlying behaviours. These methods center on the idea that animal movement is driven by switches in behaviour, and these switches can be influenced by biological and environmental variables (Nathan et al. 2008). Assessing movement in terms of behaviour (e.g. resting, foraging, migration) and the factors that influence switches in behaviour can help conceptualize and infer what drives growth, survival, and reproductive success of an animal (Shaw 2020). Such inferences are important when it comes to recovery and conservation of threatened species, particularly for fish populations that reside in regulated rivers.

Riverine fishes are some of the most threatened species globally (Ricciardi et al. 1999; Darwall et al. 2016; Cooke et al. 2012). This is in part a result of anthropogenic impacts that include habitat fragmentation from the construction of dams for hydroelectric generation and river regulation (Dudgeon et al. 2006; Nilsson et al. 2005; Grill et al. 2015, 2019). Dams have modified natural flow regimes, impacted water quality (e.g. temperature), and can prevent access to critical habitats required to complete life processes (e.g. spawning or feeding) (Cooke et al. 2016). These changes can impact fish movement and behaviour. Water temperature, as a main driver of fish metabolism and physiology, can influence movement by altering metabolic demands for resource (e.g. prey) consumption (Volkoff et al. 2020). Flow influences movement by altering the energetic demands of fish to maintain position and move (Shepard et al. 2013). Flow can also change the resource abundance and distribution within a habitat (Taylor et al. 2012; Turschwell et al. 2019). Switches in foraging behaviour in response to changing prev availability has been observed in fish. Multiple species appear to adopt low-energy sit-and-wait strategies when prey is abundant and high-energy search strategies when prey is scarce (Killen et al. 2007; Higginson et al. 2015; Grant et al. 1987; Fausch et al. 1997; O'Brien et al. 1989). Threatened fish adjusting their movements to changing conditions, such as those caused by river regulation, could have serious implications for a species (Tuomainen et al. 2011). This is because fish must manage finite energy budgets, and there will be trade-offs between expending energy on movement or other physiological functions such as growth and reproduction (Rennie et al. 2005).

In this study, I examined the movement behaviours of white sturgeon residing below a dam on the regulated Upper Columbia River (UCR). White sturgeon are a species at risk almost everywhere they occur (Hildebrand et al. 2016), with a majority of their historical range being

altered by river regulation and fragmented by dams (Haxton & Cano 2016; Dynesius et al. 1994). In the UCR, white sturgeon were listed as Endangered under the Canadian Species at Risk Act after continuous recruitment failure and population declines over the last century (Fisheries and Oceans 2014). The population has critical habitat associated with feeding, overwintering, and spawning located below, or influenced by, multiple hydroelectric operations (Hildebrand et al. 1999). This is not uncommon for sturgeon (Haxton & Cano 2016) and has been observed in other populations (Gillespie et al. 2020; Cooke et al. 2012). The release of fast-flowing waters over coarse substrate can create habitat typically selected by sturgeon for spawning, and these fast-flowing waters can also form adjacent eddies which create both productive feeding and overwintering areas (Hildebrand et al. 1999; Hildebrand et al. 2016). This occupance of white sturgeon in critical habitat below hydroelectric facilities makes understanding their interactions with operations and river regulation imperative.

The objective of this study was to describe and quantify fine-scale movement behaviour of white sturgeon occupying critical habitat immediately downstream of a dam on the UCR in relation to hydroelectric operations and river regulation. An overlapping array of acoustic telemetry receivers was used to collect fine-scale positions of acoustically tagged wild adult white sturgeon. I then applied hidden Markov models (HMMs) and generalized linear mixed models (GLMMs) to investigate the relationship between white sturgeon movement behaviour and its possible driving factors. This was accomplished by 1) identifying ecologically meaningful movement behaviours within the fine-scale dataset and 2) assessing the influence of biological (e.g. sex) and environmental (e.g. water temperature, discharge, season, photoperiod) factors on movement behaviour. The results reveal how white sturgeon interact with dams and will inform recovery measures, such as discharge management and optimization of operations to reduce the possibility of negative impacts to white sturgeon.

### Methods

### Study area

This study was conducted in the Transboundary Reach of the UCR, an impounded section of river between the Hugh L. Keenleyside Dam in British Columbia and the Grand Coulee Dam in Washington. Movements were tracked in the 2 rkm section immediately downstream of the Hugh L. Keenleyside Dam (HLK) and Arrow Lakes Generating Station (ALH). HLK is a storage-only facility (i.e. no power generation) and was constructed in 1968 under the Columbia River Treaty. ALH, located adjacent to HLK, is a power-generation facility constructed in 2001 and operated by Columbia Power Corporation. Water supply for both facilities comes from the upstream Arrow Lakes Reservoir. Combined HLK and ALH discharge is coordinated weekly with the United States under Columbia River Treaty agreements (BC Hydro 2021). While discharge volume is held consistent through the week, hourly or daily adjustments are sometimes required for maintenance activities or other demands around power generation. Fluctuations in discharge marginally alter water surface elevation and do not affect the habitat availability of white sturgeon anywhere in the study area.

The study area was divided into four habitat zones based on river structure and environmental parameters: HLK Eddy, HLK Tailrace, ALH Tailrace, and Downstream (Figure 2.1). HLK Eddy is a large circulating eddy caused by the inflows from both tailraces. High use of the HLK Eddy for feeding and overwintering has been identified for white sturgeon (Fisheries and Oceans 2014; BC Hydro 2016). The HLK Tailrace consists of inflows from HLK and is a deep pool that shallows where it joins the ALH Tailrace. Use of the HLK Tailrace for feeding has been observed seasonally. The ALH Tailrace consists of inflows from ALH and is a shallow section of the study area. Prior research has identified spawning in the ALH Tailrace (Terraquatic Resources 2011). Lastly, Downstream consists of more riverine (i.e. channelized) habitat from combined HLK and ALH inflows. It is a transitional area in which fish move in and out of the study area.

## Fish sampling and tagging

Wild adult white sturgeon were captured and tagged with acoustic tags in the Canadian portion of the Transboundary Reach (rkm 1261 – 1204) between the years of 2007 and 2013 for projects outside of this study related to movement and habitat use research and broodstock collection for conservation aquaculture. Fish capture abided by capture protocols and set line configurations commonly used for white sturgeon throughout the Columbia River (Golder Associates 2006; Nigro et al. 1988). Set lines were deployed at both random and preselected sampling locations determined by the physical parameters (e.g. depth and velocity) of the site in relation to efficiency and safety of fish capture (BC Hydro 2015).

A total of 132 wild adult white sturgeon captured over this period were implanted with VEMCO V16-4x acoustic tags (69 kHz, 120-180 sec ping rate). Surgical procedures were used to tag and determine the sex of fish. A 1.5 - 2.0 cm long incision was made through the ventral body wall and adjacent to the sturgeon's mid-line. Using an otoscope, the gonad tissue was visually assessed for sex (Webb et al. 2019). Afterwards, fish were implanted with a uniquely-coded VEMCO V16-4x acoustic tag through the surgical incision. Incisions were then closed using half circle CP-2 reverse cutting-edge needles wedged to 2-0 polydioxanone violet

monofilament sutures (Ethicon, Z969H). Fish selected for broodstock (n = 106) experienced transportation and holding at the Kootenay Sturgeon Hatchery in Wardner, BC for induced spawning prior to being acoustically tagged (FFSBC 2014). After processing, sturgeon were returned to the water near their location of capture (BC Hydro 2015).

### Acoustic array

The fine-scale movement dataset of tagged white sturgeon was acquired from a VEMCO Positioning System (VPS) study conducted between December 1, 2013 and November 15, 2014. VPS studies consist of an array of fixed submersible acoustic receivers that record a timestamp of the arrival of transmissions from acoustic tags. The collected time-of-arrival data of at least three separate receivers are then processed using a hyperbolic positioning technique to achieve fine-scale tracking of acoustically tagged fish (Smith 2013). This technique has been widely used to investigate the movement of species within marine and freshwater environments (Espinoza et al. 2011a,b; Farrugia et al. 2011; Coates et al. 2013; McLean et al. 2014; Bacheler et al. 2019; Cote et al. 2020). The VPS study consisted of an array of 29 acoustic receivers (VEMCO VR2W) in the 2 rkm study area (Figure 2.1). The number of receivers deployed in the VPS array did fluctuate through time (range: 18 - 29). Fluctuations were due to dislocation of receivers by seasonal discharge or entanglement with commercial tugboat operations. Maintaining these types of arrays in fast-flowing and working rivers can be challenging (Bergé et al. 2012). To account for receiver clock drift, horizontal position error (HPE), and detection efficiency over time, each receiver was equipped with a synchronization tag and four separately anchored sentinel tags were placed within the array (Golder Associates 2015).

## Data filtering

Fine-scale acoustic telemetry can result in a significant amount of location data that are not accurate and requires filtering before analysis. Factors such as the spatial configuration of acoustic receivers (e.g. density) and surrounding environment (e.g. water velocity) can affect both detection efficiency and positional error in an array (Bergé et al. 2012; Roy et al. 2014). Prior analysis of the VPS found that the number of receivers in the array did influence overall detection efficiency and the number of tags positioned, resulting in fewer positions being resolved with a reduction in array size (Golder Associates 2015). For positional error, assessments were performed using HPE. HPE is a relative and unitless estimate of how sensitive a calculated position is to error. This estimate is derived by applying known measurement error (e.g. synchronization and sentinel tags) to the sensitivity of the system (Smith 2013). Higher HPE values represent less accurate positioning than lower HPE values. Prior analysis of the VPS determined an HPE value of 16 to be the optimal threshold for positional accuracy without reducing too much of the dataset via filtering (Golder Associates 2015). This value lies within the typical 10 to 20 HPE threshold range of other VPS studies (Roy et al. 2014). Positions with HPE >16 were considered inaccurate and excluded from the final dataset I used in the analysis.

## Movement behaviour

I used hidden Markov models (HMMs; R package momentuHMM) to conduct the analyses of movement behaviour (McClintock et al. 2018). HMMs are statistical models which describe sequences of observable events that depend on unobservable or "hidden" discrete states (McClintock et al. 2020). HMMs use the probability distribution of movement metrics, computed from sequential animal locations, to decompose movement tracks into distinct hidden states (assumed to represent different behaviour states of an animal) (Jonsen et al. 2005). For this study, I used step length (meters; Gamma distribution with zero-inflation) and turning angle ([ $-\pi$ ,  $\pi$ ]; Von Mises distribution) as the movement metrics for a two-state HMM. Selecting the appropriate number of states for a HMM can be challenging (Pohle et al. 2017). Based on the movement tendencies described for white sturgeon as a species and in the Transboundary Reach (Hildebrand et al. 2016; BC Hydro 2018a), a two-state model was determined to be the best fit for the dataset. The two behaviour states identified by the HMM fit to the white sturgeon dataset were characterized by 1) short step length with infrequent changes in direction (hereafter, residential behaviour) and 2) longer step lengths with frequent changes in direction (hereafter, transitory behaviour).

HMMs are well suited to analyze movement datasets that are 1) recorded at regular time intervals and 2) recorded with negligible positional error (Patterson et al. 2017). Fish detections in my study often occurred on an irregular time interval due to fluctuations in imperfect detection efficiency. To regularize the data, fish movement tracks were first split into unique bouts if time between consecutive positions was greater than 2 hours. Utilizing bouts in this way helps define large gaps in detection as periods in which fish location cannot be determined or fish temporarily left the array (Cote et al. 2020). Furthermore, bouts with less than 100 positions were removed to avoid problems with model convergence (Bacheler et al. 2019). Remaining bouts were then interpolated at a regular 15-minute time interval using the crawlWrap function in momentuHMM, which implements a continuous-time correlated random walk model to predict locations at the selected time interval (McClintock et al. 2018). Positional error associated with intervals of HPE (e.g. (14,15]) was accounted for in the crawlWrap function by including an error ellipse model. Parameters for the error ellipse model (log standard deviation, correlation) were calculated using the argosDiag2Cov function in the R package crawl (Johnson et al. 2008) from positional error data acquired by the study's sentinel tags (i.e. difference between true and estimated sentinel tag positions).

After movement interpolation, HMMs were fit in momentuHMM using multiple imputation. Multiple imputation is a method which allows pooled parameter estimates to reflect uncertainty from factors such as positional error (McClintock et al. 2018). Instead of a definite behaviour state estimated for each observation, the probability of a behaviour state was determined for each interpolated location by calculating the proportion of times the state was estimated over 100 imputations. Before fitting any imputation, HMMs must be provided starting parameters to estimate behaviour states. These starting parameters describe the distribution of movement metrics in each state, which in my case would be represented by mean step length with a zero mass parameter (i.e. proportion of step length values at 0) and turning angle concentration (Michelot et al. 2016). Turning angle concentration is a positive number which measures how concentrated turning angles are around their mean, with larger values representing smaller variance (Michelot et al. 2019). Mean turning angle is usually 0, as is the case for my dataset, and represents a persistence in direction of movement. Starting parameters for this study were determined using the getPar function in momentuHMM. This function helps estimate the best starting parameters for different behaviour states when fitting HMMs to a dataset.

### Model predictions

Once the probability of a behaviour state was estimated for each position using hidden Markov modelling, the influence of biological and environmental covariates on movement behaviour was assessed. As some environmental covariates changed on a coarser timescale than the 15-minute interval in my HMM (e.g. HLK and ALH discharge adjusted on a weekly basis), I assessed movement behaviour using two methods: 1) the probability of fish expressing residential behaviour given the probability of residential behaviour at time *t-1* (i.e. 15-min before), and 2) the mean weekly probability of residential behaviour given the mean weekly probability of residential behaviour given the mean weekly probability of residential behaviour given the mean weekly generalized linear mixed models (GLMMs) with a beta distribution and logit link function. Template Model Builder (TMB, Kristensen et al. 2016) via the package glmmTMB (Brooks et al. 2017) was used to perform all GLMMs. Analyses of movement behaviour in this study will focus on reporting the probability of residential behaviour, however it is important to note that the probability of transitory behaviour would be the complement of these results.

For GLMMs assessing the probability of residential behaviour given the probability at time *t-1*, candidate models included combinations of one individual (sex) and seven environmental (water temperature, combined discharge, ALH discharge, HLK discharge, photoperiod, habitat zone, season) covariates. Discharge was assessed in two formats: a single parameter representing combined ALH and HLK discharge, and two separate parameters each representing ALH or HLK discharge. Due to correlation, combined discharge was not included in any candidate models with ALH or HLK discharge, and season was not included in any candidate models with water temperature or discharge covariates. A random intercept by bout nested within individual was included in all models. For GLMMs assessing mean weekly probability of residential behaviour given the mean weekly probability at time *t-1*, candidate models included the same covariates with the exclusion of photoperiod. Mean weekly probabilities were calculated for each fish and habitat zone in which a fish was positioned. Water

temperature and discharge covariates represented mean values for a given week. A random intercept for individual was included in all models.

Temperature and discharge data were measured at 1-hour increments and values were interpolated across 15-minute time intervals to match the locations estimated at a 15-minute interval. Temperature data were acquired from BC Hydro's Birchbank gauging station (rkm 1,290) and discharge data were obtained from the ALH and HLK facilities. A 6-hour lag effect was applied to the discharge data to ensure that all flow changes had stabilized in the downstream environment, given that flows were only changed on a weekly basis. Photoperiod was categorized as day, night, or twilight. Sunrise and sunset times for each day of the study period were obtained from the National Research Council Canada website (http://www.nrc-cnrc.gc.ca). Season was categorized as winter (December – February), spring (March – May), summer (June – August), and fall (September – November).

### Model selection

I used bias-corrected Akaike Information Criterion (AIC<sub>c</sub>) scores to rank and select candidate models. AIC is useful in model selection in that it estimates the relative quality of a model within the candidate set for explaining the given data (McElreath 2020), with the lowest AIC representing the best or top model. Top models were compared against the null model (intercept and state probability at time *t-1* variable) for validation. Due to model selection uncertainty (Burnham et al. 2004), models included in a set defined by a cumulative weight AIC<sub>c</sub> residing just at or below 0.95 were used for model averaged predictions. Model averaging was performed using the R package MuMIn (Bartoń et al. 2020), and all analyses in this study were performed in R (R Core Team 2021).

## Results

## Data filtering

A total of 818,577 positions from 51 acoustically tagged white sturgeon (16,050  $\pm$  14,777 positions per fish; range: 14 – 67,176) were determined from the VPS. HPE filtering resulted in a total of 459,569 positions for the 51 fish (9,011  $\pm$  8,223 positions per fish; range: 11 – 28,432). Six fish did not meet the minimum requirements I identified for the HMM (bouts of at least 100 positions), resulting in a sample of 45 fish. The final dataset resulted in a total of 596 bouts, with an average of 13 bouts per fish (range: 1 – 53) and five days per bout (range: 0.4 - 89.6 days).

### Movement behaviour

Movement parameters of the residential and transitory behaviour states resulted in mean step lengths of 1.9 ( $\pm$  2.0) and 27.4 ( $\pm$  28.5) meters respectively (Figure 2.2). Both behaviour states had zero mass parameters close to 0, representing few instances of no movement between consecutive positions. For turning angle, residential behaviour had an angle concentration of 0.8 and transitory behaviour had a concentration of 0.3. These concentrations describe residential behaviour as having more directed movement than transitory behaviour. This is seen in turning angle distributions, with residential behaviour having 46% of turning angles concentrated between -0.5 and 0.5 radians and transitory behaviour being more homogeneously distributed between - $\pi$  and  $\pi$  radians (Figure 2.2). Residential behaviour was therefore characterized as movements with short step lengths and more persistent direction, and transitory behaviour by movements with longer step lengths and more frequent turns (Figure 2.3).

White sturgeon were detected for an average of 65 days (range: 1 - 193 days), or 19% (range: 0.3% - 55.8%) of the study period. During that time, sturgeon spent 50% of it with

residential probabilities greater than 75% (likely residential) and 36% with residential probabilities less than 25% (likely transitory). A total of 14% of time was spent with residential probabilities between 25% and 75%, representing instances with less certainty of behaviour state. Using these intervals of certainty, patterns in what behaviour state fish exhibited changed across season and habitat zone (Figure 2.4). When broken down by season, time in residential behaviour was highest in the winter (48%) and spring (68%), and lowest in the summer (24%) and fall (12%). When broken down by habitat zone, the HLK eddy had the greatest proportion of time in residential behaviour (58%), followed by the ALH tailrace (32%), Downstream (23%), and HLK tailrace (15%). Seasonal trends outlined above were observed in all habitat zones except the HLK tailrace, which had a larger proportion of time as residential during the fall (36%) compared to other seasons. Among individual fish, variance for time spent in a behaviour state was observed within seasons (Figure 2.5). Around 18% of fish had bouts in all four seasons.

When examined spatially, residential behaviour and movement during the winter and spring was concentrated in large patches (>100 m diameter) of the ALH tailrace and HLK eddy (Figure 2.6 and 2.7). In the summer and fall, however, movement was more dispersed, with higher rates of transitory behaviour exhibited across all habitat zones and residential behaviour concentrated in smaller patches of the ALH tailrace, HLK tailrace, and HLK eddy. Downstream had the least fish presence and demonstrated seasonal shifts from residential behaviour in the winter and spring to transitory behaviour in the summer and fall.

### Model selection and predictions

The top model ranked by AIC<sub>c</sub> predicting the probability of fish expressing residential behaviour given the probability at time t-1 (i.e. 15-min before) included photoperiod and a

season and habitat zone interaction as covariates (Table 2.1). One other candidate model including sex as a covariate also closely explained the dataset and met criteria for inclusion in a 95% confidence set for the best model. Consequently, this candidate model in addition to the top model was included in model averaged predictions. Overall, white sturgeon exhibited a strong persistence in expressing a behaviour state. When a fish expressed a given state at time t-1 (e.g. residential probability of 0% or 100%), it was very likely to remain in that state at time t. When fluctuations did occur, it was when there was less certainty about residential behaviour in the previous timestep (e.g. residential probability of 50%). The season and habitat zone interaction was the most influential predictor in these instances (Figures 2.8 and 2.9). Fish in the HLK Eddy demonstrated increased probabilities of residential behaviour in the winter and spring when probabilities at time t-1 were 50%. In the Downstream habitat zone, fish demonstrated decreased residential probabilities during the winter and increased residential probabilities in the spring. For the ALH and HLK tailraces, season had less of an influence on residential behaviour when probabilities at time *t-1* were 50%. Photoperiod and sex were the least influential covariates. There were minimal differences between photoperiods and sexes when probabilities at time t-1were 50% (Figures 2.10 and 2.11).

The top model ranked by AIC<sub>c</sub> predicting the mean weekly probability of residential behaviour given the probability at time t-1 (i.e. 1 week before) included the covariates of water temperature, ALH discharge, and habitat zone (Table 2.2). Three other candidate models including HLK discharge and sex as covariates also closely explained the dataset and met criteria for inclusion in a 95% confidence set for the best model. Consequently, these three candidate models in addition to the top model were included in model averaged predictions. Averaged model predictions again demonstrated that white sturgeon were very likely to remain in the same state at time *t-1* that they expressed at time *t*. Fluctuations in mean weekly residential probability did occur when probabilities at time *t-1* were less certain (e.g. residential probability of 50%). Habitat zone and water temperature were the most influential predictors in these instances (Figure 2.12). Fish in the HLK Tailrace and Downstream habitat zones demonstrated decreased mean weekly probabilities of residential behaviour when probabilities at *t-1* were 50% (Figure 2.13), while the ALH Tailrace and HLK Eddy had less of an influence on mean weekly fish behaviour. Warming water temperature resulted in decreased mean weekly probabilities of residential behaviour at *t-1* were 50% (Figure 2.14). Discharge from the ALH facility was the next strongest predictor. Increased flow from ALH resulted in increased mean weekly residential probabilities given probabilities of 50% at time *t-1* (Figure 2.15). The covariates of sex and HLK discharge had the least influence on mean weekly residential probability. There were minimal differences in mean weekly residential probability between sexes and across HLK discharge when probabilities at time *t-1* were 50% (Figures 2.16 and 2.17).

### Discussion

Analyzing movement in terms of behaviour, compared to other conventional approaches, enables researchers to identify emergent patterns in movement, evaluate relationships with internal and external mechanisms, and conceptualize results in terms of ecologically meaningful processes (Nathan et al 2008). I used fine-scale positioning of wild adult white sturgeon located below a hydroelectric facility to identify distinct residential and transitory patterns in movement behaviour, with the former representing short movements with more persistent direction and the latter representing longer movements with more frequent turns. In my analyses, sturgeon demonstrated strong persistence in a behaviour state (i.e. high probability of expressing the same behaviour state at time *t-1*). Environmental covariates influenced behaviour only when there was less certainty of a behaviour state in the previous timestep (i.e. behaviour probability of 50%). At a 15-minute timescale, the interaction of season and habitat zone was the strongest predictor of behaviour probability given probabilities at time *t-1* were 50%. The HLK Eddy and Downstream habitat zones were the most sensitive to change, with probabilities of residential behaviour fluctuating differently in each habitat zone depending on season. At a coarser timescale, the environmental covariates of habitat zone, water temperature, and discharge were strong predictors of mean weekly behaviour probability given probabilities at time *t-1* were 50%. Fish located in the HLK Tailrace and Downstream habitat zones, as well as warming water temperatures, related to decreased mean weekly probabilities of residential behaviour. For discharge, increased flows from the ALH facility were related to increased mean weekly probabilities of residential behaviour.

While analyses of movement behaviour can broaden our understanding of an animal's movement ecology, interpreting behaviour states in terms of ecological functions (e.g. resting, foraging, migrating) can be challenging (McClintock et al. 2020). In fact, recognizing uncertainty when interpreting behaviour states is critical for ecologists using HMMs. These models simply decipher the strongest patterns in movement data regardless of the ecological meaningfulness behind those patterns (Patterson et al. 2017). Identified patterns are also inherently guided by the number of states and movement metrics specified by the researcher (Buderman et al. 2021). To highlight this, Patterson et al (2017) offers the hypothetical example of identifying resting, feeding, and travelling behaviour from a movement dataset. That three-state model could be unsuccessful, especially when there are subtle differences in movement

metric distributions. Patterson et al (2017) explains how the model may lump resting and feeding into one behaviour state due to distance and turn rates being of similar magnitude, and then split travelling into two behaviour states based on distances traveled. While the incorporation of more states into a model may be tempting to remedy such an issue, often the temporal resolution of data (e.g. 15-min time steps) limits our ability to appropriately capture subtle differences in movement (Patterson et al. 2017). Additionally, incorporating a larger number of states can lead to more difficulty distinguishing ecological meaningfulness between behaviours (Pohle et al. 2017). Understanding the challenges and limitations of HMMs should not deter researchers from their use. Rather, researchers should recognize the uncertainty in the data and modelling process, and use their own intuition and knowledge when interpreting the ecological meaningfulness of movement behaviours.

While the exact biological and ecological processes that dictate behaviour cannot be known for certain, an understanding of a species' life functions can offer relevant insight. In the case of sturgeon, movement and habitat use are often driven by the biological functions of feeding, overwintering, and spawning (Hildebrand et al. 2016; Kynard et al. 2016). Interpreting foraging behaviours from fine-scale telemetry is not new to sturgeon research. A VPS study of Atlantic sturgeon within an intertidal summer feeding area identified three types of movement which they related to foraging strategies and prey availability (McLean et al. 2014). These movements were described as Type 1) slow and winding (i.e. less intense turn angles), Type 2) fast and tortuous (i.e. more intense turn angles), and Type 3) fast and linear. While Type 3 was more indicative of larger migratory movements in and out of the feeding area, McLean et al (2014) interpreted the decreased distance and turn angles of Type 1 as representing active feeding within a suitable prey patch; and the increased distance and turn angles of Type 2 as
representing a searching strategy which can cover large areas. These two types of foraging strategies have also been identified in lab studies of sturgeon (Kasumyan 1999) and other fish species (Killen et al. 2007; Grant et al. 1987; Fausch et al. 1997; O'Brien et al. 1989), and changes in strategy are often explained by changes in prey abundance and distribution (Higginson et al. 2015). With descriptions of Type 1 and Type 2 movements from McLean et al (2014) aligning closely with the residential and transitory behaviours identified in my study, the mechanisms for these behaviour states might reflect the feeding ecology of white sturgeon and offer insight into how sturgeon are influenced by hydroelectric operations.

Overall, my results reflected that environmental covariates did not have a strong effect on fish changing from one behaviour state to another (e.g. 100% residential probability to 100% transitory probability). Analyses at both a fine and coarse timescale revealed that white sturgeon often remain in the same state, with the probability at time t-1 having high autocorrelation to the probability at time t (Figures 2.8 and 2.12). However, trends were observed seasonally and spatially (Figure 2.4). The proportion of time fish expressed residential behaviour (>75% probability) was greatest in the winter and spring, and lowest in the summer and fall. Across habitat zones, the HLK Eddy followed by the ALH Tailrace had the greatest proportion of time as residential. Fish spent less time overall in the HLK Tailrace and Downstream, as well as having a lower proportion of time expressing residential behaviour. It is possible the habitat zones in my analyses do not appropriately capture the more subtle spatial distribution of behaviour across time. Patches of residential behaviour (>75% probability), for example, were observed to shift seasonally even within a single habitat zone (Figure 2.6). These seasonal and spatial trends are likely influenced by environmental variables related to hydroelectric operations (e.g. water temperature, discharge). In cases where there was less certainty of a behaviour state

in the previous timestep (50% probability), the influence of environmental covariates on behaviour was reflected in my results.

My results demonstrated that water temperature had a strong influence on behaviour state when there was uncertainty of the state in the prior time step. Warming temperature led to decreased mean weekly probabilities of residential behaviour given probabilities at time t-1 were 50% (Figure 2.14). These results align with seasonal trends described earlier, with sturgeon during warmer seasons (i.e. summer and fall; Figure 2.18) spending the lowest proportion of time as residential (Figure 2.4). Observing changes in movement activity in response to water temperature is not uncommon for white sturgeon (Hildebrand et al. 2016; Robichaud & English 2017), as water temperature is a driver of fish metabolism and alters demands for prey consumption (Volkoff et al. 2020). In terms of feeding ecology, it would be reasonable to assume that sturgeon are adopting transitory behaviour, a more high-energy search strategy, as metabolic demands for energy increase with warming water temperatures. Transitory behaviour also allows for the coverage of larger areas in the pursuit of prey, and in the summer and fall I observed not only more frequent but also more dispersed transitory behaviour across the study area (Figure 2.7). While water temperature appeared to influence what behaviour state was more predominantly expressed, discharge appeared to influence where each behaviour state was expressed.

The influence of discharge on behaviour was observed in relation to individual facilities and the spatial distribution of behaviour across seasons. Discharge has been shown to influence fish movement by altering the energetic demands of fish to maintain position and move, with greater energy required in higher flows (Shepard et al. 2013). In my mean weekly analysis of behaviour, increased discharge from the ALH facility was related to increased mean weekly probabilities of residential behaviour given probabilities at time *t-1* were 50% (Figure 2.15). This result may reflect the increased likelihood of sturgeon to adopt low-energy residential behaviour in high flows, as well as the importance of ALH discharge on the flow environment (e.g. most consistent source of inflow throughout a given year). The spatial distribution of where fish expressed residential behaviour also appeared to be influenced by discharge. For example, in the summer and winter when ALH and HLK are both discharging water (Figure 2.19), patches of residential behaviour are observed in the center of the HLK Eddy where circulation is strengthened by discharge from both facilities (Figure 2.6 and 2.20). Patches of residential behaviour can also be seen in areas adjacent to inflows and behind environmental structures (e.g. peninsulas) providing relief from water velocities. In the fall and spring however, when discharge from the HLK facility is greatly reduced (Figure 2.19), residential patches either disappear or shift away from the eddy's center as flow dynamics change and circulation is reduced (Figures 2.6 and 2.21). Residential behaviour, in terms of feeding ecology, represents a movement strategy adopted when an area of suitable prey abundance has been identified. Discharge has been shown to alter prey abundance and distribution within habitats (Taylor et al. 2012; Turschwell et al. 2019). For sturgeon, research has suggested that low velocity habitats adjacent to fast-flowing waters can foster productive feeding areas due to the continuous deposition of resources from upstream inflows and minimal energy required for movement (Hildebrand & Parsley 2013). Adjustments in facility discharge, therefore, may be causing the relocation of these productive feeding areas and changing spatial distribution of residential behaviour through time.

While feeding ecology is a relevant and insightful lens in which to interpret the behaviour states identified in this study, other biological functions and activities may be important. The

movement metrics of residential behaviour, specifically, could possibly reflect functions such as overwintering or spawning. Overwintering is a state in which fish activity levels and metabolic rates decline in response to cooling water temperatures. In sturgeon, feeding does still occur in river systems that do not freeze-over, however, high-energy movements and foraging in general is greatly reduced (Hildebrand et al. 2016). The decreased probability of transitory behaviour and low proportion of time as transitory observed in the cooler winter and spring seasons is likely a reflection of the overwintering biology of these fish. Visually, one can even observe transitory behaviour behaviour being less dispersed across habitat zones when it does occur in cooler water temperatures (Figure 2.7). For residential behaviour, feeding and overwintering biology may be overlapping. Metabolic demands and movement are greatly reduced due to overwintering, however, seasonal shifts in the location of residential patches between the winter and spring suggest white sturgeon are still making spatial selections in response to discharge dynamics and possible changing prey availability.

In this study, I could not differentiate spawning activity from residential or transitory behaviour. White sturgeon in the UCR typically spawn during the summer from June to July, and spawning habitat in the ALH tailrace has been confirmed via passive embryo and larvae collection (Terraquatic 2011). While sturgeon did express residential and transitory behaviour in the known spawning area of the ALH tailrace during the spawning period, there is little supporting knowledge of fine-scale spawning movements that would relate either behaviour state to that activity. Sturgeon spawning is rarely observed because it often takes place in deep and fast-flowing waters (Hildebrand et al. 2016). The few descriptions of white sturgeon movement in known spawning areas include surface breaching and rolling (Parsley et al. 1993), as well as video of a presumed gamete release from a spawning pair after rapid body undulations and unison upstream movement (Liebe et al. 2004). Even with more easily observable species, mateinteraction can be hard to identify in HMMs. It is suggested models incorporate more independent data to reduce assumptions about spawning behaviour inferred from location data (Buderman et al. 2021). In my case, this could include timestamped embryo collection, reproductive stage, or mate availability. An embryo and larvae collection program in the ALH Tailrace did take place concurrently with this study, however no embryos or larvae were collected and spawning activity could therefore not be confirmed (BC Hydro 2016).

While the interpretation of movement behaviour is not without uncertainty, analyzing telemetry data in this way is an insightful and effective method for understanding fish movement. Due to their conservation status, telemetry arrays tracking the movements of white sturgeon, as well as other riverine species, are plentiful. However, very little of this research becomes published (Fraser et al. 2018) or assesses movement beyond basic detection summaries (Holyoak et al. 2008; Katzner & Arlettaz 2020). While detection summaries do provide useful information such as habitat occupation and population densities, they lack the ability to deconstruct the complexities of movement and analyze movement in a more ecologically meaningful way. Using movement behaviour analyses, I was able to identify and relate states of movement to critical ecological functions such as feeding, and determine the effects of environmental variables on such states. Discharge, an environmental variable controlled directly by hydroelectric operations, demonstrated a strong spatial correlation to movement patterns suggestive of a low-energy feeding strategy and likely changing prey availability. Knowledge like this can help inform recovery measures for species impacted by dam operations, such as the optimization of discharge management to reduce the impacts of river regulation during periods of critical feeding activity. Overall, analyses of movement behaviour proved a useful tool in

understanding white sturgeon movement below a hydroelectric facility and I would recommend the application of similar comprehensive frameworks in fish movement ecology and telemetry. Table 2.1. Models predicting the probability of residential behaviour given the probability of residential behaviour at time *t*-1 ranked by increasing order of the bias-corrected Akaike Information Criterion (AIC<sub>c</sub>). Differences in AIC<sub>c</sub> relative to the top model ( $\Delta$ AIC<sub>c</sub>), weighted AIC<sub>c</sub> (wAIC<sub>c</sub>), cumulative weighted AIC<sub>c</sub> (cwAIC<sub>c</sub>), log-likelihood (log(*L*)), and the number of parameters in a model (K) are shown. The top two models were selected for averaged predictions.

| Model                                  | K | AICc     | $\Delta AIC_{c}$ | wAICc | cwAICc | log(L)  |
|--|---|----------|------------------|-------|--------|---------|
| $seas \times zone + light + tm1$       | 4 | -2717204 | 0.00             | 0.71  | 0.71   | 1358624 |
| $seas \times zone + light + sex + tm1$ | 5 | -2717202 | 1.84             | 0.29  | 1.00   | 1358625 |
| zone + tm1                             | 2 | -2716597 | 607.08           | 0.00  | 1.00   | 1358307 |
| light + tm 1                           | 2 | -2716316 | 888.15           | 0.00  | 1.00   | 1358165 |
| zhlk + tm1                             | 2 | -2716227 | 977.68           | 0.00  | 1.00   | 1358119 |
| seas + tm1                             | 2 | -2716217 | 987.24           | 0.00  | 1.00   | 1358114 |
| zdisc + tm1                            | 2 | -2716217 | 987.58           | 0.00  | 1.00   | 1358116 |
| zalh + tm 1                            | 2 | -2716215 | 989.06           | 0.00  | 1.00   | 1358114 |
| ztemp + tm1                            | 2 | -2716212 | 991.97           | 0.00  | 1.00   | 1358112 |
| sex + tm1                              | 2 | -2716210 | 993.82           | 0.00  | 1.00   | 1358110 |
| tm1                                    | 1 | -2716210 | 994.70           | 0.00  | 1.00   | 1358112 |

zdisc, Combined discharge from ALH and HLK facilities; zalh, Discharge from ALH facility; zhlk, Discharge from HLK facility; zone, Habitat zone; tm1, Probability of residential behaviour at time *t*-*1*; seas, Season; sex, Sex of fish; ztemp, Water temperature. All models include bout nested within individual as a random effect.

Table 2.2. Models predicting the mean weekly probability of residential behaviour given the mean probability of residential behaviour at time *t*-1 ranked by increasing order of the bias-corrected Akaike Information Criterion (AIC<sub>c</sub>). Differences in AIC<sub>c</sub> relative to the top model ( $\Delta$ AIC<sub>c</sub>), weighted AIC<sub>c</sub> (wAIC<sub>c</sub>), cumulative weighted AIC<sub>c</sub> (cwAIC<sub>c</sub>), log-likelihood (log(*L*)), and the number of parameters in a model (K) are shown. The top four models were selected for averaged predictions.

| Model                                  | K | AICc     | $\Delta AICc$ | wAICc | cwAICc | log(L)  |
|--|---|----------|---------------|-------|--------|---------|
| ztemp + zalh + zone + tm1              | 4 | -5860.61 | 0.00          | 0.35  | 0.35   | 2939.37 |
| ztemp + zalh + zone + sex + tm1        | 5 | -5860.29 | 0.32          | 0.29  | 0.64   | 2941.25 |
| ztemp + zalh + zhlk + zone + tm1       | 5 | -5859.51 | 1.10          | 0.20  | 0.84   | 2939.84 |
| ztemp + zalh + zhlk + zone + sex + tm1 | 6 | -5859.10 | 1.51          | 0.16  | 1.00   | 2941.67 |
| ztemp + tm1                            | 2 | -5848.88 | 11.73         | 0.00  | 1.00   | 2929.46 |
| zone + tm1                             | 2 | -5843.39 | 17.22         | 0.00  | 1.00   | 2928.74 |
| seas + tm1                             | 2 | -5841.58 | 19.03         | 0.00  | 1.00   | 2927.83 |
| tml                                    | 1 | -5836.31 | 24.30         | 0.00  | 1.00   | 2922.17 |
| zalh + tm l                            | 2 | -5835.66 | 24.95         | 0.00  | 1.00   | 2922.85 |
| zdisc + tm 1                           | 2 | -5835.41 | 25.20         | 0.00  | 1.00   | 2922.73 |
| sex + tm1                              | 2 | -5835.19 | 25.42         | 0.00  | 1.00   | 2923.63 |
| zhlk + tm1                             | 2 | -5834.39 | 26.22         | 0.00  | 1.00   | 2922.22 |

zdisc, Combined discharge from ALH and HLK facilities; zalh, Discharge from ALH facility; zhlk, Discharge from HLK facility; zone, Habitat zone; tm1, Mean weekly probability of residential behaviour at time *t*-*1*; seas, Season; sex, Sex of fish; ztemp, Water temperature. All models include individual as a random effect.



Figure 2.1. Map of study area below Hugh L. Keenleyside Dam (HLK) and Arrow Lakes Generating Station (ALH) (black dots), British Columbia, Canada. Habitat zones are highlighted by colour, acoustic receivers are represented by white circles, and anchored sentinel tags are represented by yellow circles.



Figure 2.2. State-dependent distributions for step length (meters) and turning angle (radians).



Figure 2.3. Individual bouts from two white sturgeon in the study area with behaviour state estimated by the hidden Markov model represented by colour. Ovals represent the error ellipse associated with a position.



Figure 2.4. Proportion of time white sturgeon spent having an upper (>75%), middle (25-75%), or lower (<25%) probability of being in residential behaviour. Results are separated by season and habitat zone.



Figure 2.5. Proportion of time individual white sturgeon spent having an upper (>75%), middle (25-75%), or lower (<25%) probability of being in residential behaviour. Results are separated by season and empty columns indicate a fish was not detected in a season.



Figure 2.6. White sturgeon positions having greater than 75% probability of being in a residential behaviour state. Positions are shown by season with black lines distinguishing habitat zones.



Figure 2.7. White sturgeon positions having greater than 75% probability of being in a transitory behaviour state. Positions are shown by season with black lines distinguishing habitat zones.



Figure 2.8. Model averaged coefficients and standard errors (SE) of the beta generalized linear mixed model parameters predicting the probability of residential behaviour given the probability of residential behaviour at time *t*-1. Model averaged intercept estimate of -3.76 ( $\pm$  0.06 SE).



Figure 2.9. Model averaged predictions of the probability of being in the residential behaviour state by season, habitat zone, and probability of residential behaviour at time *t*-*1*. Whiskers denote 95% confidence interval. Categorical covariates sex and photoperiod were set to Female and Day respectively.



Figure 2.10. Model averaged predictions of the probability of being in the residential behaviour state by photoperiod and probability of residential behaviour at time t-1. Whiskers denote 95% confidence interval. Categorical covariates sex, season, and habitat zone were set to Female, Summer, and HLK Eddy respectively.



Figure 2.11. Model averaged predictions of the probability of being in the residential behaviour state by sex and probability of residential behaviour at time *t-1*. Whiskers denote 95% confidence interval. Categorical covariates photoperiod, season, and habitat zone were set to Day, Summer, and HLK Eddy respectively.



Figure 2.12. Model averaged coefficients and standard errors (SE) of the beta generalized linear mixed model parameters predicting the mean weekly probability of residential behaviour given the mean weekly probability of residential behaviour at time *t*-1. Model averaged intercept estimate of -3.30 ( $\pm$  0.07 SE).



Figure 2.13. Model averaged predictions of the mean weekly probability of being in the residential behaviour state by habitat zone and mean weekly probability of residential behaviour at time t-1. Whiskers denote 95% confidence interval. To isolate effects, other numeric model covariates were fixed at their mean and the categorical covariate sex was set to Female.



Figure 2.14. Model averaged predictions of the mean weekly probability of being in the residential behaviour state by water temperature and mean weekly probability of residential behaviour at time t-1. Shaded areas denote 95% confidence interval. To isolate effects, other numeric model covariates were fixed at their mean and the categorical covariates sex and habitat zone were set to Female and HLK Eddy respectively.



Figure 2.15. Model averaged predictions of the mean weekly probability of being in the residential behaviour state by ALH discharge and mean weekly probability of residential behaviour at time *t*-1. Shaded areas denote 95% confidence interval. To isolate effects, other numeric model covariates were fixed at their mean and the categorical covariates sex and habitat zone were set to Female and HLK Eddy respectively.



Figure 2.16. Model averaged predictions of the mean weekly probability of being in the residential behaviour state by HLK discharge and mean weekly probability of residential behaviour at time *t*-1. Shaded areas denote 95% confidence interval. To isolate effects, other numeric model covariates were fixed at their mean and the categorical covariates sex and habitat zone were set to Female and HLK Eddy respectively.



Figure 2.17. Model averaged predictions of the mean weekly probability of being in the residential behaviour state by sex and mean weekly probability of residential behaviour at time *t*-*1*. Whiskers denote 95% confidence interval. To isolate effects, other numeric model covariates were fixed at their mean and the categorical covariate habitat zone was set to HLK Eddy.



Figure 2.18. Water temperature in the study area from December 2013 – November 2014. Blue line represents LOESS smoothed data and grey points represent raw data.



Figure 2.19. Discharge from Hugh L. Keenleyside Dam (HLK) and Arrow Lakes Generating Station (ALH) from December 2013 – November 2014. Total discharge is the combination of HLK and ALH. Blue lines represent LOESS smoothed data and grey points represent raw data.



Figure 2.20. Modeled velocity conditions during peak summer discharge below Hugh L. Keenleyside Dam (HLK) and Arrow Lakes Generating Station (ALH), British Columbia, Canada. Velocity and direction of discharge represented by coloured arrows. Figure pulled from West et al. (2020) unpublished data.



Generating Station (ALH), British Columbia, Canada. Velocity and direction of discharge represented by coloured arrows. Figure Figure 2.21. Modeled velocity conditions during low fall discharge below Hugh L. Keenleyside Dam (HLK) and Arrow Lakes pulled from West et al. (2020) unpublished data.

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# **CHAPTER 3**

# COARSE-SCALE MOVEMENT ECOLOGY AND BEHAVIOUR PATTERNS OF HATCHERY-ORIGIN WHITE STURGEON IN THE REGULATED UPPER COLUMBIA

RIVER

#### Introduction

Movement ecology has become a powerful tool in informing management and recovery measures for threatened species (Allen et al. 2016). Movement is essential to most animals, and can be linked to the growth, survival, and reproductive success of individuals and populationlevel processes (Shaw 2020). Some species, however, face greater challenges to movement than others. Migratory fish that cross international boundaries can be subject to compounding threats when transboundary management and cooperation is absent or ineffective (Cooke et al. 2012; Runge et al. 2014). Such threats can include overfishing, habitat degradation, loss of connectivity between critical habitats (e.g. spawning, feeding), and alterations in water quality (e.g. water temperature) and natural flow regimes (Dudgeon et al. 2006). Trends showing population declines of many transboundary fish highlight this issue (Valbo-Jørgensen et al. 2008; Limburg & Waldman 2009; Palacios-Abrantes et al. 2020). In response, the formation of international conventions (e.g. Convention on Migratory Species) and regional river basin collectives (e.g. Great Lakes Fishery Commission) has become a common strategy in facilitating cooperation and species recovery between nations (Cooke et al. 2012). These groups, however, are only as effective as the knowledge informing their management decisions. Research on the movement ecology of migratory species would offer valuable insight for improving and developing international mitigative measures, as it allows for a better understanding of how animals move spatially, temporally, and in response to human activities (e.g. river regulation).

In this study, I examined the movements of hatchery-origin white sturgeon in the Canada – United States Transboundary Reach of the Upper Columbia River (UCR). White sturgeon are a species at risk almost everywhere they occur due to issues such as habitat fragmentation, habitat degradation, and historical fisheries (Hildebrand et al. 2016). In the UCR, white sturgeon have

been experiencing recruitment failure and population declines over the last century. They were listed as Endangered under the Canadian Species at Risk Act in 2006 (Fisheries and Oceans 2014), but remain a species of Least Concern under the Endangered Species Act in the United States. Due to current recruitment estimates suggesting an inability to support a self-sustaining population (Hildebrand & Parsley 2013), Canada and the United States implemented a joint recovery effort and conservation aquaculture program in 2001. From its inception to 2018, the conservation aquaculture program has released around 150,000 hatchery-origin juveniles (6 – 9 months of age) with an estimated survival of 15,000 in the Transboundary Reach (BC Hydro 2018b). While the program has been an overall success in delaying the extirpation of the species, information is limited on how this new population of hatchery-origin sturgeon move within the regulated and transboundary river section of the UCR. Better understanding movement and its drivers for hatchery-origin sturgeon could offer more insights into their growth, survival, and reproduction. Such insights would assist recovery programs in setting long-term population targets and making decisions related to stocking, fishing, and discharge management.

Long-distance movements in sturgeon are often to locate feeding, overwintering, and spawning habitat (Hildebrand et al. 2016; Kynard et al. 2016). Direct capture studies performed annually in the spring and fall have shown that hatchery-origin white sturgeon have high site fidelity and occur throughout the Transboundary Reach, with preferences for habitats characterized by small substrate (e.g. sand, small gravel) and deep (>10 m), slow-moving water (<1 m/s) (BC Hydro 2018a,b). Sturgeon presence in such habitats have been linked to their ability to support productive feeding and overwintering areas (Hildebrand & Parsley 2013). The greatest amount of movement observed from hatchery-origin sturgeon in the Transboundary Reach has been immediately after hatchery release, with higher numbers of fish released in

Canada moving downstream and being first recaptured in the United States compared to fish released in the United States being first recaptured in Canada (BC Hydro 2020). Similar movement trends have also been observed in Kootenay River hatchery-origin sturgeon, with post-hatchery dispersal linked to the availability of habitat with small substrate and slow-moving water (Neufeld et al. 2009). Such habitat preferences may be the reasoning for dispersal trends in the Transboundary Reach, as slow-moving (i.e. low-velocity) habitat is more abundant in the United States compared to Canada. Information is lacking on how hatchery-origin sturgeon are moving after this initial dispersal. Implementing movement analyses beyond direct captures could offer a more detailed understanding of hatchery-origin sturgeon movement year-round and in response to changing environmental conditions by river regulation.

Direct capture studies, due to their occurrence outside of the spawning period, have not been able to provide detailed information on the presence or movement of hatchery-origin sturgeon to spawning areas in the UCR. This is significant because hatchery-origin sturgeon are beginning to reach sexual maturity. Males specifically are of interest as they typically mature at smaller sizes and ages (~15 years) than females (~25 years), and they are able to spawn most years following maturation while females require 3 – 5 year intervals between spawning events (Hildebrand & Parsley 2013). Sexually mature sturgeon migrate to spawning areas in the UCR typically between late June – July when water temperatures reach around 14 °C. However, unlike river systems where sturgeon spawning movements can be defined by clear one-directional (e.g. upstream or downstream) migrations (Balazik et al. 2020; Forsythe et al. 2012), sturgeon in the UCR have access to multiple spawning areas both within and across international borders. Assessing the movement of hatchery-origin sturgeon to spawning areas would help inform recovery programs of the reproductive potential and possible genetic distribution of future populations. Additionally, movement of hatchery-origin sturgeon from Canada to the United States, whether to spawn or feed, could have direct implications for survival. Due to different endangered species listings and management practices between countries, hatchery-origin white sturgeon in the United States have been subject to fishing mortality since 2017 while remaining protected from fishing in Canada. Better understanding movement between countries would also assist in determining survival estimates and maintaining population targets in future hatchery releases.

The objective of this study was to describe and quantify the coarse-scale movement behaviour of hatchery-origin sturgeon residing throughout the Transboundary Reach of the UCR. I applied hidden Markov models (HMMs) and generalized linear mixed models (GLMMs) to acoustic telemetry data to investigate how movement behaviour varied spatially (between habitats and countries), temporally (between seasons), and by biological factors (e.g. age, size, sex) and river regulation (e.g. water temperature, discharge). Results will help inform management decisions related to river regulation, hatchery release strategies, and the overall cross-border recovery of this threatened species.

#### Methods

# Study area

The study area resides on the Upper Columbia River between the Hugh L. Keenleyside Dam (HLK) in British Columbia (443705 E, 5465875 N) and the Grand Coulee Dam in Washington (352493 E, 5314347 N). This regulated 296 river kilometer (rkm) section is called the Transboundary Reach due to it being divided at the Canada – United States international border (rkm 1204.2) (Figure 3.1).

The Transboundary Reach is subdivided into 15 river zones, 11 of which were utilized by my study population of hatchery-origin white sturgeon and will be the focus of this study (Figure 3.2). Zones 1 - 5 comprise the Canadian section of the Transboundary Reach, with Zone 2B representing a tributary and regulated segment of the Kootenay River. Zones 6 - 10 comprise the United States section of the Transboundary Reach. The range of these river zones are evenly dispersed by country (~10 rkm in Canada and ~30 rkm in USA). Each river zone begins at the termination of the previous zone. River zones are characterized by stream morphology and water velocity. Zone 1 is predominantly deep (~20 m in the thalweg) and slow-moving (<1 m/s). Zones 2 - 6 are characterized by shallower depths (<10 m in the thalweg) and swifter flows (>1 m/s) with occasional large, deep eddies (Crossman et al. 2016). In Zones 7 - 10, the UCR transitions into a more reservoir-like environment, with wider reaches (~2,500 m) and slow-moving flows (Hildebrand et al. 1999).

There are three main discharge sources and five known spawning areas in the Transboundary Reach (Figures 3.1 and 3.2). In Zone 1, the most upstream impoundment is HLK which regulates discharge of the UCR from the Arrow Lakes Reservoir. Discharge from HLK is coordinated weekly between Canada and the United States under Columbia River Treaty agreements (BC Hydro 2021). A known spawning area is located in Zone 1 immediately below HLK (Fisheries and Oceans Canada 2014). Zone 2 contains a discharge input from the Kootenay River which is regulated by Brilliant Dam in Zone 2B. A known spawning area in Zone 2 is located around 4 rkm downstream of this confluence near Kinnaird, BC. Zone 5 contains a discharge input from the Pend d'Oreille River which is regulated by Waneta Dam. A known spawning area in Zone 5 is located 0.5 rkm downstream of this confluence near the international border. The United States section of the Transboundary Reach (Zones 6 – 10) contains no main discharge sources. However, known spawning areas have been identified near Northport, WA in Zone 6 and China Bend, WA in Zone 7 (Fisheries and Oceans Canada 2014).

This study defined six environmental monitoring zones based on the locations of temperature and discharge monitoring stations (Figure 3.2). Discharge records were obtained from four gauge stations in Canada operated by BC Hydro and one gauge station in the United States operated by USGS. Water temperature was monitored using underwater loggers (VEMCO Minilog-II-T Temp Logger) at seven locations in Canada operated by BC Hydro and one location in the United States operated by USGS. The distribution of environmental monitoring zones was skewed, with the Canadian section of the Transboundary Reach containing the majority of monitored zones and the United States section consisting mainly of one. While not ideal, Canada does contain more input sources (e.g. tributaries), which would cause greater fluctuations in temperature and discharge along this section of river.

#### Fish sampling and tagging

A total of 75 hatchery-origin white sturgeon were acoustically tagged for this study. Fish were captured in the spring and fall of 2019. The sampling area extended from HLK in British Columbia to Gifford in Washington (Zones 1 - 9). Sturgeon in the Canadian section of the Transboundary Reach were captured by BC Hydro in the spring (May 20 – June 11) and sturgeon in the United States section were captured by Colville Confederated Tribes in the fall (September 4 - 11). Fish capture abided by capture protocols and set line configurations commonly used for white sturgeon throughout the Columbia River (Golder 2006; Nigro et al. 1988). Four different hook sizes were used on each set line to facilitate the capture of various sizes of white sturgeon (14/0, 16/0, 18/0, 20/0). Set lines were deployed at preselected sampling

locations across the sampling area. Sampling locations were determined by the physical parameters (e.g. depth and velocity) of the site in relation to efficiency and safety of fish capture (BC Hydro 2018a).

Juvenile white sturgeon from the conservation aquaculture program have been marked with Passive Integrated Transponder (PIT) tags and released annually since 2001. Therefore, the PIT tag number of captured sturgeon allowed us to confirm their hatchery-origin and the age of each fish prior to acoustic tagging. Acoustic tags were distributed across age, size, and river zone (Figure 3.5). We balanced acoustic tag application within the age range of 9 – 18 years, as older hatchery-origin sturgeon are reliably captured in the highest numbers during sampling (Crossman et al. 2021). We attempted to distribute 100 tags evenly among river zones and countries, however, only 25 of a possible 50 fish were tagged in the United States section of the Transboundary Reach. The United States experienced lower collection efforts which focused on the upper and lower river zones (i.e. Zones 6 and 9).

Sturgeon were measured for fork length (nearest 0.5 cm) and weight (nearest 0.02 kg). The relative condition of each fish was calculated by dividing the observed weight of fish by the expected weight given its measured fork length (Neff & Cargnelli 2004; Yard et al. 2015). Expected weights were determined from a weight-length regression of all hatchery-origin sturgeon collected during 2013 - 2019 stock assessments. Expected weights and relative condition calculations were separated by country of capture, as sturgeon in the United States are around 50% larger on average (Crossman et al. 2021). The sex of study fish was determined during the surgical implantation of the acoustic tag. A 1.5 - 2.0 cm long incision was made through the ventral body wall and adjacent to the sturgeon's mid-line. An otoscope was inserted to visually determine sex based on gonad tissue (Webb et al. 2019) and a biopsy of gonad tissue

was collected for histology to confirm sex and stage of maturity. Study fish were then implanted with a uniquely-coded VEMCO V16-4x (69 kHz, 120-180 sec ping rate) acoustic tag. Incisions were closed using half circle CP-2 reverse cutting-edge needles wedged to 2-0 polydioxanone violet monofilament sutures (Ethicon, Z969H). After processing, sturgeon were returned to the water at their location of capture. Procedures for capture, handling, and tagging of white sturgeon were approved under a Species at Risk Act permit (permit number: 19-PPAC-00013) and by the Animal Care and Use Committee of the University of Northern British Columbia (protocol number: 2019-02).

#### Acoustic array

I used a pre-existing array of stationary VEMCO VR2W acoustic receivers managed by BC Hydro in Canada and Spokane Tribal Fisheries and Colville Confederated Tribes in the United States to detect the spatial and temporal movements of hatchery-origin white sturgeon between May 21, 2019 – August 31, 2020. The array is dispersed at 3 – 10 rkm intervals across the study area, covering all river zones and locations of interest (Figure 3.2). There were 31 acoustic receiver stations in Canada and 25 in the United States. Not all receivers were in operation simultaneously in Canada. There were a total of eight receiver stations in Zone 2B whose deployment was temporary and operated separately by Fortis BC and BC Hydro over the study period. Additionally, Canada had multiple locations of interest (e.g. spawning areas, international border, confluences) where more than one receiver was stationed within 0.5 rkm. On average, the Canadian section of the Transboundary Reach had three receiver stations every 10 rkm and the United States section had two receiver stations every 10 rkm. The United States likely has higher detection efficiency (DE) than Canada due to the prominence of slow-moving reservoir habitat. Range testing performed at all receiver stations in the United States during Summer 2015 and 2016 (~3,000 m<sup>3</sup>/s at the international border) demonstrated an average of 40% detection efficiency at distances of 165 – 330 m for receivers located upstream of Gifford, Washington (Witte 2017). Range testing at eight receiver stations across the Canadian section of the Transboundary Reach during Summer 2020 (~3,550 m<sup>3</sup>/s at the international border) achieved an average of 13% detection efficiency at similar distances.

Additionally, I used sentinel tags to assess detection efficiency in Canada over the entire study period. Individual sentinel tags (range: 1 - 2 per river zone) were deployed at a distance from 10 receiver stations across the reach to quantify temporal and spatial variation in detection efficiency caused by environmental conditions (Gjelland et al. 2013; Kessel et al. 2014). Deployment distances ranged from 140 - 360 m based on midpoint (50% detection efficiency) range testing (Brownscombe et al. 2020) performed in Spring 2019 and feasibility for long-term deployment. Sentinel tags were oriented at a horizontal angle near the river bottom (0.5 m) to simulate typical tag orientation within sturgeon and sturgeon use of benthic habitats. Detection efficiency was assessed by season and river zone (Figure 3.3). Mean detection efficiency for the study period ranged from 41% - 64% among river zones, with Zone 5 having the highest detection efficiency and Zone 3 having the lowest. Mean daily detection efficiency was highest during the fall (72%) and lowest during the summer in both 2019 (40%) and 2020 (14%). Very low detection efficiency during Summer 2020 was likely due to higher discharge during the study period (Figure 3.4). Zone 1 performed the best during Summer 2020, demonstrating higher mean daily detection efficiency (70%) than the other river zones (5%). This is likely due to Zone 1 discharge (HLK) being lower than river zones downstream with more water input sources.

# Data filtering

Acoustic systems often generate erroneous detections (i.e. false positives) due to environmental noise or acoustic tag collision (Simpfendorfer et al. 2015). Realism of movement (<3 m/s) and frequency of detection (at least 120 secs between detections) approaches were applied to identify potential erroneous detections and filter them from the dataset (Brownscombe et al. 2019). In addition to filtering erroneous detections, these approaches highlighted the issue of some receiver stations having overlapping ranges of detection in my dataset (i.e. fish being detected at more than one receiver at the same time). To remedy this issue, detections from receiver stations <1 rkm apart were aggregated to a single midpoint location. For receiver stations >1 rkm apart, the station with the most detections within a 6-hour time interval (described later) was determined the closest to the fish.

# Movement behaviour analysis

I used hidden Markov models (HMMs; R package momentuHMM) to conduct the analyses of movement behaviour (McClintock et al. 2018). HMMs are statistical models which describe sequences of observable events that depend on unobservable or "hidden" discrete states (McClintock et al. 2020). HMMs use the probability distribution of movement metrics, computed from sequential animal locations, to decompose movement tracks into distinct hidden states (assumed to represent different behaviour states of an animal) (Jonsen et al. 2005). This study used speed (m/h; Gamma distribution with zero-inflation) and direction (directed/undirected; Binomial distribution) as the movement metrics for a two-state HMM. Direction was determined by whether a fish continued movement in an upstream or dow nstream direction (directed) or exhibited a reversal or halt in movement direction (undirected). Speed was determined by dividing the distance traveled (meters) by the time between positions (hours). Selecting the appropriate number of behaviour states for a HMM can be challenging (Pohle et al. 2017). Based on the general movement tendencies described for white sturgeon as a species and in the Transboundary Reach (Hildebrand et al. 2016; BC Hydro 2018a), a two-state model was determined to be the best fit for the dataset. The two behaviour states identified by the HMM fit to the white sturgeon dataset were characterized by 1) low speeds with undirected movement (hereafter, residential behaviour) and 2) higher speeds with more directed movement (hereafter, transitory behaviour).

HMMs are well suited to analyze movement datasets that are 1) recorded at regular time intervals and 2) recorded with negligible positional error (Patterson et al. 2017). Fish detections in my study often occurred on an irregular time interval due to fluctuations in imperfect detection efficiency. To regularize our telemetry data, fish movement tracks were first split into unique bouts if time between consecutive positions was greater than 96 hours (four days). Utilizing bouts in this way helps define large gaps in detection as periods in which fish location cannot be determined (Cote et al. 2020). Furthermore, bouts with less than four positions were removed to avoid problems with model convergence (Bacheler et al. 2019). Remaining bouts were then interpolated at a regular 6-hour time interval using the crawlWrap function in the R package momentuHMM, which implements a continuous-time correlated random walk model to predict locations at the selected time interval (McClintock et al. 2018). Positional error was not accounted for in the crawlWrap function, as positions were determined from receiver stations with defined GPS coordinates and erroneous detections were removed in my data filtering process. Due to crawlWrap being unable to interpolate within the constraints of the river boundary, positions were predicted on a linear simulation of the Transboundary Reach and

snapped to the nearest 0.5 rkm. This simulation decreased distorted calculations of speed caused by natural bends in the river system.

After movement interpolation, HMMs were fit in momentuHMM. HMMs must be provided starting parameters to estimate behaviour states. These starting parameters describe the movement metrics of each state, which in my case would be represented by mean speed with a zero mass parameter (i.e. proportion of speed values at 0) and the proportion of movement being directed (Michelot et al. 2016). Starting parameters for this study were determined using the getPar function in momentuHMM. This function helps estimate the best starting parameters for the behaviour states when fitting an HMM to a dataset. Once a behaviour state was estimated for each position using hidden Markov modelling, I assessed the probability of fish expressing residential behaviour given the behaviour state at time *t-1* using generalized linear mixed models (GLMMs) with a binomial distribution and logit link function. Template Model Builder (TMB, Kristensen et al. 2016) via the R package glmmTMB (Brooks et al. 2017) was used to perform all GLMMs. Analyses in this study focused on the probability of residential behaviour, however, it is important to note that the probability of transitory behaviour would be the complement to these results.

Candidate models included combinations of three individual (relative condition, age, sex) and four environmental (water temperature, discharge, season, river zone) covariates. Due to its correlation with water temperature and discharge, season was not included in any candidate models with these covariates. A random intercept by bout nested within individual was included in all models. Relative condition was fixed at the value recorded during time of capture, age increased at 0.5 year increments over the study period, and water temperature and discharge represented mean values at the location (environmental monitoring zone) and time interval (6-

hour) of positioning. Season was divided into winter (December – February), spring (March – May), summer (June – August), and fall (September – November).

#### Maximum displacement analysis

Maximum displacement analyses were performed with generalized linear mixed models (GLMMs) using a gamma hurdle distribution with log link function. Template Model Builder (TMB, Kristensen et al. 2016) via the R package glmmTMB (Brooks et al. 2017) was used to perform all GLMMs. Maximum displacement was calculated as the distance (rkm) between the highest and lowest position of a fish by country and seasonal period of each year. The filtered dataset from the movement behaviour analysis was used to calculate these values. Candidate models included combinations of three individual (relative condition, age, sex) and four environmental (water temperature, discharge, season, country) covariates. Season was divided into four periods as described earlier, relative condition was fixed at the value recorded during time of capture, age increased to the nearest 0.5 year during a seasonal period, and water temperature and discharge represented mean values at the location (country) and time interval (season) of displacement. Due to its correlation with water temperature and discharge, season was not included in any candidate models with these covariates. A random intercept by individual was included in all models.

#### Model selection

I used bias-corrected Akaike Information Criterion  $(AIC_c)$  scores to rank and select candidate models. AIC is useful in model selection in that it estimates the relative quality of a model within the candidate set for explaining the given data (McElreath 2020), with the lowest AIC representing the best or top model. Top models were compared against the null model (intercept and state at time *t-1* variable) for validation. Due to model selection uncertainty (Burnham et al. 2004), models included in a set defined by a cumulative weight AIC<sub>c</sub> residing just at or below 0.95 were used for model averaged predictions. Model averaging was performed using the R package MuMIn (Bartoń et al. 2020), and all analyses in this study were performed in R (R Core Team 2021).

#### Results

Out of the 75 tagged hatchery-origin white sturgeon, 70 were included in my analyses. Three fish were never detected and two fish did not meet the minimum requirements I identified for the HMM (bouts of at least four positions). The final dataset resulted in a total of 250 bouts, with an average of four bouts per fish (range: 1 - 10) and 40 days per bout (range: 1 - 432 days). Fish were detected for an average of 144 days (range: 3 - 432 days), or 32% (range: 0.7% - 96%) of the study period.

Fish presence varied by season and river zone. More fish went undetected in the winter and spring than the summer and fall (Figure 3.6). When fish were detected, Zone 1 had the most fish presence on average, followed by Zone 2 and Zone 5 (Figure 3.7). Sturgeon spent an average of 82% of their time in a single river zone (range: 32 - 100%) and occupied an average of two river zones (range: 1 - 5) during the study period. Cross-zone movements occurred most frequently in the summer and fall between Zones 1 - 2 and 8 - 9 (Figure 3.8). A total of three fish moved across the Canada–United States international border, two of which were initially tagged in Zone 5 and the other in Zone 6 (border adjacent zones). A total of 27 fish resided for at least 1 day in a spawning area during the spawning seasons (June 1 – July 31) of 2019 and 2020, spending an average of 18 days (range: 1.50 - 60.25 days) in a spawning area. Around 44% of those fish were female and 56% were male, with an average age of 15 years (range: 9 - 19 years). Of these fish, five (18.5%) visited spawning areas across years and all selected the same spawning area from the prior year. On average, fish spent 52% of their time in a given year (range: 1 - 100%) residing within the same spawning area, with an average maximum displacement of 13.8 rkm (range: 0 - 89 rkm) from the spawning area. Only one fish (a 10-year old male) exhibited a cross-border movement and resided in a spawning area outside their country of initial tagging.

#### Movement behaviour analysis

Hatchery-origin sturgeon spent 95% of their time expressing residential behaviour and 5% expressing transitory behaviour. Mean speed (m/h) for transitory behaviour was 343.4 (± 270.0) with a zero mass parameter of 0.18 (i.e. 18% of speed values were 0 m/h). Transitory behaviour consisted of 44% directed movement and 56% undirected movement. Residential behaviour had a zero mass parameter of 1, representing speed values of 0 m/h or continuous residence at a single receiver station. Consequently, the proportion of directed movement for residential behaviour was zero, representing no directed movement across receivers in the array. Residential behaviour was therefore characterized as localized and undirected movement at a single receiver, and transitory behaviour as larger movements between receivers that were both directed and undirected.

The top model ranked by  $AIC_c$  predicting the probability of residential behaviour given the behaviour state of a fish at time *t-1* (i.e. 6-hours before) included water temperature, relative condition, sex, and a discharge and river zone interaction as covariates (Table 3.1). Five other candidate models also closely explained the dataset and met criteria for inclusion in a 95% confidence set for the best model. Consequently, these candidate models in addition to the top model were included in model averaged predictions. All covariates except season appeared in at least one of the averaged models. Water temperature and the discharge and river zone interaction were included in all averaged models. My results demonstrated that the behaviour state of hatchery-origin sturgeon varied considerably depending on the prior state. When having expressed residential behaviour at time t-1, fish were very likely to express residential behaviour at time t depended more strongly on the values of other covariates.

Averaged model predictions saw the discharge and river zone interaction as having the greatest influence on residential behaviour given transitory behaviour at time *t*-1 (Figure 3.10). Notably, increases in discharge led to large increases in the probability of residential behaviour in Zones 3 – 6. Zones 2 and 10 also demonstrated increases in residential probability in relation to increased discharge. Remaining river zones related to discharge having a negative effect on the probability of residential behaviour, however these results were not statistically significant (i.e. coefficient standard errors overlapping 0) (Table 3.1). Water temperature had the next largest influence. Warming water temperatures related to decreased probabilities of residential behaviour at time *t*-1 (Figure 3.11). The biological covariates of sex and relative condition had less influence, with the probability of residential behaviour decreasing slightly if fish were female or in better relative condition. Age was the least influential covariate. There was minimal influence on the probability of residential behaviour as fish got older.

#### Maximum displacement analysis

Maximum displacement of hatchery-origin white sturgeon varied across time and space. On average, fish traveled farther during the summer and fall compared to the winter and spring (Figure 3.12), and fish in the United States traveled three times farther than fish in Canada (39 rkm, 13 rkm). The top model ranked by AIC<sub>c</sub> predicting maximum displacement included water temperature, age, and a country and discharge interaction as covariates (Table 3.2). Twelve other candidate models including also closely explained the dataset and met criteria for inclusion in a 95% confidence set for the best model. Consequently, these 12 candidate models in addition to the top model were included in model averaged predictions. All possible covariates appeared in at least one of the averaged models. Country and time-varying environmental covariates (i.e. season or water temperature and discharge) were included in all top-ranked models.

The country and discharge interaction was a strong predictor for the probability of white sturgeon moving (i.e. binomial) and the extent of movement (i.e. gamma) when they did decide to move (Figure 3.13). While fish were less likely to move in the United States compared to Canada, averaged model predictions demonstrated higher maximum displacement in the United States when fish did move (Figure 3.14). Increases in discharge led to a decreased likelihood of movement and extent of movement, with maximum displacement in Canada decreasing more rapidly than that in the United States. Warming water temperatures related to decreased probabilities of movement but increased maximum displacement when fish did decide to move (Figure 3.15). The covariates of season, sex, age, and relative condition were less influential and not statistically significant (i.e. binomial and gamma coefficient standard errors overlapping 0) (Figure 3.13 and 3.16). Averaged model predictions resulted in summer and fall having slightly higher maximum displacement compared to winter and spring. Male hatchery-origin sturgeon

were predicted to displace slightly less than females. Fish that were older or in better relative condition were also predicted to travel greater distances.

#### Discussion

Understanding the movement of threatened fish whose habitat range crosses international boundaries is useful for the cooperative management and recovery of a species. In this study, I used coarse-scale acoustic telemetry to track the movements of hatchery-origin white sturgeon located within the Transboundary Reach of the Upper Columbia River. I identified distinct residential and transitory patterns in movement behaviour, with the former representing localized movement at a single receiver station and the latter representing directed and undirected movements between receiver stations. Overall, hatchery-origin white sturgeon moved very little and demonstrated strong site fidelity. Fish spent most of their time expressing residential behaviour and residing in a single river zone. In my analyses, location (i.e. country, river zone), discharge, and water temperature had the greatest influence on maximum displacement and behaviour probability when fish were already in a transitory state. Sturgeon moving within the United States, whose river zones can be characterized as more reservoir-like than riverine, exhibited maximum displacements far greater than fish moving within Canada. Discharge also interacted with fish location. Increases in discharge related to faster declines in maximum displacement in Canada compared to the United States, as well as fish in more channelized river zones having increased probabilities of expressing residential behaviour when previously in a transitory state. These channelized river zones often resided near the international border and all observed border-crossing fish were initially tagged from border adjacent zones. Warming water temperatures were related to increases in maximum displacement and decreases in the

probability of residential behaviour when previously in a transitory state. Trends could be observed seasonally, with warmer waters in the summer and fall being associated with increased movement.

While movement ecology analyses can help us understand animal movement in terms of biological and ecological processes, interpreting movement from coarse-scale acoustic telemetry can be challenging. Acoustic telemetry arrays are imperfect and their performance in tracking animal movement will depend on array design and environmental conditions. Array design, including the number of receiver stations and how they are distributed throughout the study area, influences animal detection and data resolution (Heupel et al. 2006). Larger distances between receiver stations (e.g. receiver every 1 rkm versus 10 rkm) offer more space for animals and their movements to go undetected. When animals are undetected, uncertainty arises on where an animal is and what it is doing (Crossin et al. 2017). Environmental conditions, such as noise caused from discharge or human activities, can also lead to error in positional accuracy (Kessel et al. 2014). Increases in noise will have a negative effect on the detection range (i.e. distance from receiver that tag can be detected) and detection efficiency (i.e. number of successful detections of a tag out of possible detections) of an acoustic telemetry array. In this study, both array design and environmental conditions appeared to influence fish detection. Periods of sturgeon going undetected between receiver stations peaked during winter months (Figure 3.6). Detection efficiency also declined during the summer as flows increased, especially in more channelized river zones (Figures 3.3 and 3.4).

Even when fish are detected, intent of movement can be difficult to determine with complete certainty. This is especially true for river systems, such as the UCR, where biological and ecological processes (e.g. feeding, spawning, overwintering) overlap temporally and spatially (Hildebrand et al. 2013). While incorporating empirical data (e.g. feeding or spawning documentation) into movement analyses can benefit ecological interpretations, such data is often difficult to acquire in swift and deep aquatic environments (Cooke et al. 2012). In this study, these river system characteristics did limit the certainty of movement intent. Additionally, due to acoustic telemetry array design and performance, the full extent of hatchery-origin sturgeon movement could not be determined (e.g. missed detections of fish residing outside of receiver range or moving during high flows). Recognizing the uncertainty in the data and modelling process is essential for the honest and transparent communication of findings to recovery and management agencies (Crossin et al. 2017). Such recognition does not immediately discount the results of movement ecology analyses, but rather implores researchers to use their own intuition and knowledge when interpreting the ecological meaningfulness of movement.

White sturgeon movement can be driven by multiple biological and ecological processes, such as feeding, overwintering, and spawning (Hildebrand et al. 2016). Feeding is necessary for the growth, survival, and reproduction of an animal. Fish will move within and between habitats to take advantage of feeding opportunities (Cooke et al. 2016). White sturgeon are primarily benthic feeders, meaning they search out food on the river bottom. Depending on resource availability and fish size, sturgeon will feed on a variety of invertebrates and other fish (McCabe et al. 1993; Crossman et al. 2016; Parsley et al. 2010). While the intent of movement cannot be determined with complete certainty, the timing of observed movements by hatchery-origin sturgeon in this study do coincide with known sturgeon feeding ecology. In the Transboundary Reach, movement activity related to feeding is thought to increase during warmer water temperatures (i.e. summer and fall; Figure 3.4) and occur in low-velocity habitats where fish can hold and feed on prey delivered by the river (Hildebrand & Parsley 2013). I observed that

increases in water temperature related to increased maximum displacement and reduced probabilities of residential behaviour when previously in a transitory state (Figures 3.11 and 3.15). As water temperature is a driver of fish metabolism (Volkoff et al. 2020), these results likely reflect how hatchery-origin sturgeon are increasing movement in response to metabolic demands and feeding opportunities.

Spatially, maximum displacement and behaviour probabilities differed depending on fish location and discharge. Hatchery-origin sturgeon moving within Canada displaced far less than fish moving within the United States, with increases in discharge relating to faster declines in maximum displacement in Canada compared to the United States (Figures 3.12 and 3.14). Increases in discharge also related to sturgeon in more channelized river zones (e.g. Zones 3 and 4) having increased probabilities of expressing residential behaviour when previously in a transitory state (Figure 3.10). These results may reflect differences in feeding habitat between countries and river zones. While Canada consists of a more riverine environment with lowvelocity habitat interspersed between rapids, the United States is more reservoir-like with lowvelocity habitat covering entire river zones. Fish must make trade-offs when deciding between allocating energy to movement or maintenance of other physiological functions such as growth and reproduction (Rennie et al. 2005). Discharge has also been shown to alter the energetic demands of fish movement, with greater energy required to move in higher flows (Shepard et al. 2013). Consequently, less energy expended moving in low-velocity water may be promoting the greater displacement of hatchery-origin sturgeon in the United States to capitalize on feeding habitat.

While water temperature, discharge, and fish location (i.e. country, river zone) were influential in predicting movement, in general hatchery-origin sturgeon expressed strong site fidelity. Sturgeon spent most of their time expressing residential behaviour and movement typically did not extend beyond two river zones. These results support site fidelity predictions from direct capture assessments of hatchery-origin sturgeon in the Transboundary Reach (BC Hydro 2018a,b). It also supports the observed distribution and seasonal movements of wild adult sturgeon in the Transboundary Reach who have been well documented since the 1990s through the use of mark-recapture and acoustic telemetry (BC Hydro 2018a; Irvine et al. 2007; Hildebrand et al. 1999). These assessments have shown that wild adults demonstrate high site fidelity to deep and low water velocity areas, with individuals spending more than 60% of the year at a single location and 90% of the year within a 10 rkm river section. Similar trends in site fidelity have been observed in other sturgeon populations as well (Robichaud et al. 2017; Kynard et al. 2016). I observed the least amount of movement in the winter and spring (Figure 3.11). This reduction in movement is likely a reflection of overwintering, a biological process in which fish activity levels and metabolic rates decline in response to cooling water temperatures (Crawshaw 1984). Overwintering may also explain why larger numbers hatchery-origin sturgeon went undetected during winter months (Figure 3.6), as overwintering in habitats between receiver stations (i.e. outside of receiver range) would lead to long periods of no detection.

Spawning can also be a driver of movement in sturgeon. In this study, residence and movement of hatchery-origin sturgeon to spawning areas was observed in 2019 and 2020. Around 40% of the study population resided in a spawning area for at least one day during a spawning period, and 7% were repeat visitors of a spawning area across years. While males were of interest due to their earlier sexual maturity and greater likelihood of spawning activity, the sex ratio of fish present in spawning areas was similar to the ratio of the entire study population. The average age of both female and male hatchery-origin sturgeon occupying spawning areas was

around 15 years. This age is below average for expected female spawning in the UCR (~25 years) and on par for expected male spawning (~15 years), with the youngest age of a sexually mature hatchery-origin surgeon in the UCR being a 9-year old male (Maskill et al. 2022, unpublished). Although residence of hatchery-origin sturgeon in spawning areas suggests possible spawning activity, especially by males, spawning areas in the Transboundary Reach can also overlap with productive feeding habitat (Hildebrand et al. 2013). The presence of likely sexually immature female hatchery-origin sturgeon in spawning areas might be representative of feeding opportunity in spawning areas. Incorporating supporting independent data in future studies, such as timestamped embryo collection and reproductive staging, could help better determine spawning activity in relation to sturgeon movement (Buderman et al. 2021).

Long-distance migrations of hatchery-origin sturgeon to spawning areas were uncommon. Most fish spent a majority of their time in a given year within a spawning area or moved less than one river zone to reach a spawning area. In studies of other sturgeon populations, spawning migrations have been observed in response to water temperature and discharge. For lake sturgeon (Bruch & Binkowski 2002) and Kootenay River white sturgeon (Paragamian & Kruse 2001), increases in water temperature during a spawning season was a good predictor of female migration. Increases in discharge have been thought to cue spawning migration (Forsythe et al. 2012; Dammerman et al. 2018), with increased movements by white sturgeon following peak flows in the Kootenay River (Paragaminan et al. 1999). While spawning activity could not be confirmed in this study, increases in water temperature, which occurred during the summer spawning period (Figure 3.4), did relate with increased maximum displacement and decreased probabilities of residential behaviour (when in a transitory state at time *t-1*) (Figures 3.11 and 3.15). Discharge however, which also peaked during the summer (Figure 3.4), related to decreased maximum displacement and increased probabilities of residential behaviour (when in a transitory state at time t-1) in more channelized river zones (Figures 3.10 and 3.14). While this might suggest that discharge is limiting the displacement of hatchery-origin white sturgeon during spawning periods, my results are likely biased by significant drops in detection efficiency during the summer in response to increased discharge (Figure 3.3). I recommend that future research attempt to incorporate detection efficiency into movement analyses, as it is possible that hatchery-origin sturgeon could be expressing greater spawning movements, and movement in general, than observed in this study.

Although hatchery-origin sturgeon demonstrated high site fidelity overall, heterogeneity in movement was present in the study population, with individual displacement ranging between 0-89 rkm over the study period. Similar examples of heterogeneity in movement have been observed in other sturgeon populations (Robichaud et al. 2017) and fish species (Moser et al. 2013; Rodríguez 2002). Variability in movement among individuals may be related to biological factors such as age, relative condition, and sex. While biological covariates were not statistically significant in predicting maximum displacement, my study observed decreases in the probability of residential behaviour (when in a transitory state at time t-1) related to fish that were female or in better relative condition (Figure 3.11). Age was the least influential predictor and there was minimal influence on the probability of residential behaviour as fish got older. Other researchers have observed that older lake sturgeon demonstrate greater maximum displacement (Trested et al. 2011) and that relative condition was a good indicator of individual energetic state (Neff & Cargnelli 2004). Outside of spawning migrations, sex has not been observed as a factor influencing the movement of sturgeon. It is important to note that the duration of this study only lasted 1.5 years. As individual sturgeon movement can differ across years, more time is likely

needed to better understand how biological as well as environmental variables influence movement patterns and behaviour states.

Table 3.1. Models predicting the probability of residential behaviour given the behaviour state at time *t*-1 ranked by increasing order of the bias-corrected Akaike Information Criterion (AIC<sub>c</sub>). Differences in AIC<sub>c</sub> relative to the top model ( $\Delta$ AIC<sub>c</sub>), weighted AIC<sub>c</sub> (wAIC<sub>c</sub>), cumulative weighted AIC<sub>c</sub> (cwAIC<sub>c</sub>), log-likelihood (log(*L*)), and the number of parameters in a model (K) are shown. The top six models were selected for averaged predictions.

| Model   | K | AICc    | ΔAIC <sub>c</sub> | wAICc | cwAICc | log(L)   |
|---|---|---------|-------------------|-------|--------|----------|
| $ztemp + zdisc \times zone + zcond + sex + tm1$ | 6 | 6208.97 | 0.00              | 0.40  | 0.40   | -3076.46 |
| $ztemp + zdisc \times zone + sex + tm1$         | 5 | 6210.33 | 1.37              | 0.20  | 0.60   | -3078.15 |
| ztemp + zdisc×zone + zcond + zage + sex + tm1   | 7 | 6210.70 | 1.73              | 0.17  | 0.76   | -3076.33 |
| ztemp + zdisc×zone + tm1                        | 4 | 6211.93 | 2.97              | 0.09  | 0.85   | -3079.95 |
| ztemp + zdisc×zone + zage + sex + tm1           | 6 | 6212.30 | 3.34              | 0.07  | 0.93   | -3078.13 |
| ztemp + zdisc×zone + zcond + tm1                | 5 | 6212.34 | 3.37              | 0.07  | 1.00   | -3079.15 |
| ztemp + tm1                                     | 2 | 6238.15 | 29.18             | 0.00  | 1.00   | -3114.07 |
| seas + tm1                                      | 2 | 6307.49 | 98.52             | 0.00  | 1.00   | -3146.74 |
| zone + tm1                                      | 2 | 6368.90 | 159.94            | 0.00  | 1.00   | -3170.45 |
| zdisc + tm1                                     | 2 | 6380.24 | 171.28            | 0.00  | 1.00   | -3185.12 |
| sex + tm1                                       | 2 | 6384.64 | 175.68            | 0.00  | 1.00   | -3187.32 |
| tml   | 1 | 6385.34 | 176.37            | 0.00  | 1.00   | -3188.67 |
| zcond + tm1                                     | 2 | 6386.26 | 177.30            | 0.00  | 1.00   | -3188.13 |
| zage + tm1                                      | 2 | 6387.18 | 178.22            | 0.00  | 1.00   | -3188.59 |

zage, Age of fish; zdisc, Discharge; tm1, Probability of residential behaviour at time *t-1*; zcond, Relative condition of fish; zone, River zone; seas, Season; sex, Sex of fish; ztemp, Water temperature. All models include bout nested within individual as a random effect.

Table 3.2. Models predicting maximum displacement ranked by increasing order of the biascorrected Akaike Information Criterion (AIC<sub>c</sub>). Differences in AIC<sub>c</sub> relative to the top model ( $\Delta$ AIC<sub>c</sub>), weighted AIC<sub>c</sub> (wAIC<sub>c</sub>), cumulative weighted AIC<sub>c</sub> (cwAIC<sub>c</sub>), log-likelihood (log(L)), and the number of parameters in a model (K) are shown. The top 13 models were selected for averaged predictions.

| Model                                   | K | AICc    | ΔAIC <sub>c</sub> | wAICc | cwAICc | log(L)  |
|---|---|---------|-------------------|-------|--------|---------|
| ztemp + zdisc×ctry + zage               | 4 | 1278.59 | 0.00              | 0.19  | 0.19   | -623.25 |
| ztemp + zdisc×ctry + zage + zcond + sex | 6 | 1279.99 | 1.40              | 0.10  | 0.29   | -621.65 |
| ztemp + zdisc×ctry + zage + sex         | 5 | 1279.99 | 1.40              | 0.10  | 0.38   | -621.65 |
| ztemp + zdisc×ctry + zage + zcond       | 5 | 1280.02 | 1.43              | 0.09  | 0.48   | -623.96 |
| ztemp + zdisc×ctry + zcond + sex        | 5 | 1280.10 | 1.51              | 0.09  | 0.57   | -619.36 |
| seas + ctry + zage                      | 3 | 1280.21 | 1.62              | 0.09  | 0.66   | -621.75 |
| seas + ctry + zage + sex                | 4 | 1280.62 | 2.03              | 0.07  | 0.72   | -626.52 |
| seas + ctry + zage + zcond + sex        | 5 | 1280.75 | 2.16              | 0.07  | 0.79   | -624.33 |
| ztemp + zdisc×ctry + zcond              | 4 | 1280.77 | 2.18              | 0.06  | 0.85   | -622.04 |
| ztemp + zdisc×ctry                      | 3 | 1281.49 | 2.90              | 0.05  | 0.90   | -620.06 |
| ztemp + zdisc×ctry + sex                | 4 | 1281.53 | 2.94              | 0.04  | 0.94   | -624.72 |
| seas + ctry + zage + zcond              | 4 | 1282.38 | 3.79              | 0.03  | 0.97   | -622.84 |
| seas + ctry + zcond + sex               | 4 | 1282.53 | 3.94              | 0.03  | 1.00   | -622.92 |
| seas                                    | 1 | 1305.27 | 26.68             | 0.00  | 1.00   | -641.07 |
| ctry                                    | 1 | 1310.01 | 31.42             | 0.00  | 1.00   | -647.77 |
| ztemp                                   | 1 | 1312.04 | 33.45             | 0.00  | 1.00   | -648.78 |
| zdisc                                   | 1 | 1326.31 | 47.72             | 0.00  | 1.00   | -655.92 |
| zage                                    | 1 | 1330.53 | 51.94             | 0.00  | 1.00   | -658.03 |
| null                                    | 0 | 1335.89 | 57.30             | 0.00  | 1.00   | -662.82 |
| sex                                     | 1 | 1336.60 | 58.01             | 0.00  | 1.00   | -661.06 |
| zcond                                   | 1 | 1339.41 | 60.82             | 0.00  | 1.00   | -662.47 |

zage, Age of fish; zdisc, Discharge; ctry, Country; zcond, Relative condition of fish; seas, Season; sex, Sex of fish; ztemp, Water temperature. All models include individual as a random effect.



Figure 3.1. Transboundary Reach of the Upper Columbia River from HLK in British Columbia, Canada, through Gifford in Washington, USA. River kilometers of interest are labeled as white dots.



Figure 3.2. Canadian section of the Transboundary Reach in British Columbia, Canada, (left) and United States section of the Transboundary Reach in Washington, USA (right). River zones are distinguished by grey and white sections of river. Dashed lines represent the extent of the six environmental monitoring zones. White dots represent aggregated acoustic receiver locations (some locations may contain more than one receiver). Yellow dots represent capture locations of tagged fish. Shaded blue circles represent known white sturgeon spawning areas.



Figure 3.3. Detection efficiency (DE) from May 2019 – August 2020. A) Mean daily detection efficiency by season and year. B) Mean daily detection efficiency by river zone. Solid blue lines represent river zone mean and dashed blue lines represent river zone median for the study period.



Figure 3.4. Mean daily water temperature (A) and discharge (B) from May 2019 – August 2020. Line type represents gauges at Hugh L. Keenleyside Dam (rkm 1261.2) and Border (rkm 1204.2).



Figure 3.5. Tagged hatchery-origin white sturgeon used in study. A) Fork length and weight of tagged fish, with shades of gray describing sex, shape describing country of capture, and line type representing expected values based on country of capture (relative condition of 0). B) Number of fish tagged by age and sex. C) Number of fish tagged by habitat zone of capture and sex. D) Boxplot of fish tagged by age and habitat zone of capture. Dashed line represents the border between countries.



Figure 3.6. Distribution of tagged hatchery-origin white sturgeon by month and river zone between May 2019 – August 2020. Fish were counted for the river zone in which they spent the longest duration of time in a month. Last box represents the number of fish not detected during a month.



Figure 3.7. Daily number of tagged hatchery-origin white sturgeon in each river zone between May 2019 – August 2020. Dashed line represents the border between countries.



Figure 3.8. Presence of tagged hatchery-origin white sturgeon between May 2019 – August 2020. Presence indicated by black lines with instances of movement across zones highlighted by points. Point colour represents river zone fish are crossing into and shape represents country where the river zone is located. Crosses represent date and river zone of fish release after tagging.


Figure 3.9. Model averaged coefficients and standard errors (SE) of the binomial generalized linear mixed model parameters predicting the probability of residential behaviour given the behaviour state at time *t*-1. Model averaged intercept estimate of -0.50 ( $\pm$  0.34 SE).



3.10. Model averaged predictions of the probability of being in the residential behaviour state by river zone, discharge, and the behaviour state at time t-l. Shaded areas denote 95% confidence interval. To isolate the effect, other numeric model covariates were fixed at their mean and the categorical covariate sex was set to Female.



Figure 3.11. Model averaged predictions of the effect of water temperature (A), sex (B), age (C), and relative condition (D) on the probability of being in the residential behaviour state. Behaviour state at time *t*-1 represented by colour with 95% confidence interval (shaded area and whiskers). To isolate the effect, other numeric model covariates were fixed at their mean and the categorical covariates sex and river zone were set to Female and Zone 1 respectively.



Figure 3.12. Maximum displacement (rkm) of tagged hatchery-origin white sturgeon by season and country where movement took place between May 2019 – August 2020.



Figure 3.13. Model averaged coefficients and standard errors (SE) of the gamma hurdle generalized linear mixed model parameters predicting maximum displacement. Results are separated by binomial and gamma components of the gamma hurdle model. Model averaged intercept estimates are -0.75 ( $\pm$  0.52 SE) and 1.58 ( $\pm$  0.42 SE) respectively.



Figure 3.14. Model averaged predictions of the effect of country (A) and discharge and country (B) on maximum displacement (rkm) with 95% confidence interval (shaded area and whiskers). To isolate effects, other model covariates were fixed at their mean. Categorical covariates of sex and season were set to Female and Summer respectively.



Figure 3.15. Model averaged predictions of the effect of water temperature on maximum displacement (rkm) with 95% confidence interval (shaded area). To isolate effects, other model covariates were fixed at their mean. Categorical covariates of sex, season, and country were set to Female, Summer, and USA respectively.



Figure. 3.16. Model averaged predictions of the effect of season (A), sex (B), age (C), and relative condition (D) on maximum displacement (rkm) with 95% confidence interval (shaded area and whiskers). To isolate effects, other model covariates were fixed at their mean. Categorical covariates of sex, season, and country were set to Female, Summer, and USA respectively.

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## **CHAPTER 4**

## CONCLUSION

The goal of this study was to investigate the movement patterns and behaviour states of white sturgeon who occupy a regulated and transboundary section of the Upper Columbia River. Acoustic telemetry was utilized to capture movement and behaviour at two different spatial scales. In Chapter 2, an overlapping acoustic telemetry array covering 2 rkm was implemented to track the fine-scale movements of wild adult white sturgeon immediately downstream of a hydroelectric operation on the UCR. In Chapter 3, an acoustic telemetry array covering 296 rkm was implemented to track the coarse-scale movements of hatchery-origin white sturgeon residing throughout the Transboundary Reach of the UCR. Hidden Markov models (HMMs) and generalized linear mixed models (GLMMs) were then applied in both chapters to identify ecologically meaningful movement behaviours and determine how movement and behaviour is influenced by biological factors and environmental conditions (e.g. water temperature and discharge) that are frequently altered by river regulation. Results from this study described in detail white sturgeon interactions with dams and river regulation and will help inform recovery measures and management decisions for this threatened species.

Chapter 2 identified two distinct behaviour states from the fine-scale movement dataset of wild adult white sturgeon occupying critical habitat immediately below a hydroelectric operation. These states consisted of a residential and transitory behaviour, with the former representing short movements with more persistent direction and the latter representing longer movements with more frequent turns. The influence of biological factors and environmental

conditions on behaviour was assessed using two response variables: 1) the probability of fish expressing residential behaviour given the probability of residential behaviour at time t-1 (i.e. 15-min before), and 2) the mean weekly probability of residential behaviour given the mean weekly probability of residential behaviour at time t-1 (i.e. 1 week before). In both analyses, white sturgeon were very likely to remain in the same behaviour state. Environmental covariates influenced behaviour only when there was less certainty of a behaviour state in the previous timestep (i.e. probability of 50%). At a fine timescale, the interaction of season and zone was the strongest predictor of residential behaviour given probabilities at time t-1 were 50%. HLK Eddy, for example, was sensitive to seasonal changes and demonstrated lower probabilities of residential behaviour in the summer and fall. At a coarser timescale, mean weekly probabilities of residential behaviour were influenced by water temperature, discharge, and habitat zone. Warming water temperatures related to decreased probabilities of residential behaviour and higher flows from ALH related to increased probabilities of residential behaviour. Fish located in the HLK Tailrace and Downstream habitat zones also demonstrated decreased mean weekly probabilities of residential behaviour when probabilities at time t-1 were 50%.

While the exact biological and ecological processes that dictate behaviour cannot be known for certain (Patterson et al. 2017), the movement behaviours in Chapter 2 were likely correlated to feeding ecology and foraging strategies as observed for other sturgeon (McLean et al. 2014) and fish species (Killen et al. 2007; Grant et al. 1987; Fausch et al. 1997; O'Brien et al. 1989). Residential behaviour and transitory behaviour fluctuated temporally and spatially. Residential behaviour, possibly representing a low-energy sit-and-wait foraging strategy, was expressed most frequently in the winter and spring as energy levels and metabolism likely declined due to cooler water temperatures (Volkoff et al. 2020). On the other hand, transitory behaviour, possibly representing a high-energy foraging strategy that can cover larger areas, was expressed more frequently as metabolic demands for energy increased with warming water temperatures. Additionally, I observed that the spatial distribution of behaviours shifted seasonally, likely in response to facility discharge changing the downstream energetic landscape (e.g. energy demands for movement) and resource (e.g. prey availability) environment (Taylor et al. 2012; Turschwell et al. 2019; Shepard et al. 2013). Patches of residential behaviour, for example, were observed to shift seasonally so as to possibly capitalize on low-velocity feeding habitat adjacent to fast waters. Overall, my results demonstrated that hydroelectric operations in the study area did appear to have some influence on white sturgeon movement behaviour.

Results from Chapter 2 can help inform recovery measures and management decisions. Discharge, for example, could be adjusted in future mitigative measures so as to optimize flows during periods of increased sturgeon feeding (e.g. summer and fall). These measures would be especially important for habitat such as the HLK Eddy which has been identified as critical for white sturgeon feeding (Fisheries and Oceans 2014). Patches of residential behaviour in the HLK Eddy (likely representing feeding activity) were most prominent during the summer when discharge was highest at both HLK and ALH facilities. In the fall, however, patches of residential behaviour largely disappeared from the HLK Eddy as flows deceased and came mainly from the ALH facility. I hypothesize that elevated summer flows provides upstream food resources and extending the period of HLK discharge into the fall, or for a longer period of time, may therefore improve white sturgeon feeding in the HLK Eddy during periods of increased metabolic demand. I recommend future research utilize more detailed spatial analyses (e.g. coordinates versus habitat zones) to further investigate the relationship between white sturgeon behaviour and environmental variables related to hydroelectric operations.

In Chapter 3, two behaviour states were identified from my coarse-scale movement dataset of hatchery-origin white sturgeon residing in the Transboundary Reach of the UCR. These states also consisted of a residential and transitory behaviour, with the former representing localized movement at a single receiver station and the latter representing longer movements between receiver stations. The influence of biological factors and environmental conditions on behaviour was assessed using the probability of fish expressing a behaviour state given the state at time t-1 (i.e. 6-hours before). In my analysis, sturgeon spent most of their time expressing residential behaviour and were unlikely to change behaviour when already in a residential state (i.e. state at time t-1). However, when transitory behaviour was expressed at time t-1, the probability of residential behaviour at time t depended more strongly on environmental covariates. With increases in discharge, I observed sturgeon in more channelized river zones (e.g. Zones 3 and 4) having increased probabilities of residential behaviour (when in a transitory state at time t-1). Additionally, warming water temperatures were related to decreased probabilities of residential behaviour when previously in a transitory state. Similar results were observed in my assessment of maximum displacement. Warming water temperatures were related to increased maximum displacement. Hatchery-origin sturgeon moving within Canada, whose river zones are characterized as more channelized, also displaced far less than fish moving within the United States, with increased flows related to faster declines in maximum displacement in Canada compared to the United States.

While the intent of movement exhibited by hatchery-origin white sturgeon in the UCR cannot be known for certain, similar movement patterns have been observed in other sturgeon and fish species. For example, increased movement activity in response to water temperature has been documented in wild white sturgeon in the UCR (Hildebrand & Parsley 2013) and other

sturgeon populations (Robichaud et al. 2017; Kynard et al. 2016). Movement activity during warmer seasons (e.g. summer) is typically driven by feeding and spawning (Hildebrand et al. 2016). While spawning activity could not be confirmed for hatchery-origin sturgeon in this study, feeding ecology may explain observed movements. Water temperature is a driver of fish metabolism (Volkoff et al. 2020) and it would be reasonable to assume hatchery-origin sturgeon are increasing movement during warmer water temperatures in response to increasing metabolic demands. Additionally, discharge has been shown to alter the energetic landscape and demands of fish movement (Shepard et al. 2013), with fish making trade-offs when deciding between allocating energy to movement or maintenance of other physiological functions such as growth and reproduction (Rennie et al. 2005). Consequently, the increased movement of sturgeon observed in the United States may be related to feeding ecology, as lower energy is required to move across its low-velocity and reservoir-like habitat for feeding opportunities. My results could suggest a possible movement component for the growth differences observed in hatcheryorigin sturgeon between countries and river zones in the Transboundary Reach (Crossman et al. 2021; Van Poorten & McAdam 2010). Future research may benefit from integrating stable isotope analyses to better understand feeding-related movements (Brownscombe et al. 2022), as well as timestamped embryo collection or reproductive staging for possible spawning-related movements (Buderman et al. 2021).

Overall, hatchery-origin white sturgeon in the UCR demonstrated strong site fidelity. Fish spent most of their time expressing residential behaviour and movement typically did not extend beyond two river zones. These results support trends observed in wild adult white sturgeon located in the UCR (BC Hydro 2018a; Irvine et al. 2007; Hildebrand et al. 1999), as well as other sturgeon populations (Robichaud et al. 2017; Kynard et al. 2016). There were only a few instances of hatchery-origin sturgeon crossing the international border (4% of study population), and all instances were from fish initially tagging in border adjacent river zones. These results suggest that fishing mortality risk of sturgeon located in Canada migrating to the United States is not substantial enough to warrant adjustments in the hatchery stocking program. However, due to the short duration of the study period (i.e. 1.5 years), more time is recommended to fully understand the movements of hatchery-origin sturgeon in the Transboundary Reach.

A longer study period would also benefit our understanding of how environmental covariates influence movement. Discharge, specifically, varied significantly between years. Peak flows which occurred in the summer were far greater in 2020 than 2019. While increased discharge has been found to increase the movement of sturgeon related to spawning (Forsythe et al. 2012; Dammerman et al. 2018; Paragaminan et al. 1999), this study observed a negative effect of discharge on maximum displacement. Higher discharge has been shown to negatively affect detection efficiency in an acoustic telemetry array (Gjelland et al. 2013; Kessel et al. 2014). Therefore, it is possible that my observed declines in movement during increased flows are a result of such detection efficiency bias. It is recommended that future studies track and correct for detection efficiency so as to better understand the influence of environmental variables on movement (Brownscombe et al. 2020).

A main takeaway from Chapter 3 is that hatchery-origin white sturgeon are moving and residing throughout the Transboundary Reach. Specifically, in Canadian section of the Transboundary Reach, habitats along the entire 57 rkm stretch are used year-round by white sturgeon, with strong individual based site fidelity. Accordingly, maintaining the functionality and connectivity of all habitats, such as eddies and spawning areas (Irvine et al. 2007), should be critical for future recovery measures and management decisions. Currently, the majority of river zones in the Transboundary Reach are not federally protected in Canada or the United States (no critical habitat in river zones 2 - 4 and 6 - 10; Fisheries and Oceans 2014). Since hatchery-origin white sturgeon are moving across and expressing high fidelity to river zones not cited as critical and federally protected, future recovery planning should consider expanding protections to include more, if not all, river zones of the Canadian section of the Transboundary Reach. In the United States section where the population isn't listed, my coarse-scale approach from Chapter 3 applied over a longer period could be used to help inform guidelines for the ongoing fishery to ensure pertinent information on habitat use is available.

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