



Movement behaviour of endangered white sturgeon *Acipenser transmontanus* responds to changing environmental conditions below a dam

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ABSTRACT: Acoustic telemetry allows for fine-scale, or positional, tracking of fish in localised environments, and advancement in analytical techniques allows for quantifiable patterns in fish movement and behaviour. White sturgeon *Acipenser transmontanus* in the regulated Upper Columbia River are listed as endangered in Canada due to their considerable decline over the last century. An improved understanding of where, when, and why white sturgeon move in relation to river regulation is important for species recovery. A VEMCO Positioning System was used to collect the positions of white sturgeon in critical habitats immediately downstream of a dam on the Upper Columbia River over a 1 yr period. We applied hidden Markov models and generalised linear mixed models to (1) identify ecologically meaningful movement behaviours within the positions dataset; and (2) investigate the relationships between movement behaviour and biological (sex) and environmental (e.g. discharge, temperature, habitat) factors. Two behaviour states were identified: 'residential', characterised by short movements with less frequent turns, and 'exploratory', characterised by longer movements with more frequent turns. Water temperature largely influenced the mean weekly probability of a behaviour state, while discharge influenced the spatial distribution of movement behaviours. Changes in movement patterns were also apparent across seasons, with a higher occurrence of residential behaviour in the winter and spring and exploratory behaviour in the summer and fall. Results will help inform species recovery measures, such as overall flow management and optimization of operations to reduce impacts of river regulation.

KEY WORDS: White sturgeon · Hidden Markov models · Movement ecology · Behaviour · Acoustic telemetry · River regulation

1. INTRODUCTION

Riverine fishes are some of the most threatened species globally (Ricciardi & Rasmussen 1999, Cooke et al. 2012, Darwall & Freyhof 2016). This is in part a result of anthropogenic impacts that include habitat fragmentation from the construction of dams for hydroelectric generation and river regulation (Nilsson et al. 2005, Dudgeon et al. 2006, Grill et al. 2015,

2019). Dams have modified natural flow regimes, impacted water quality (e.g. temperature), and altered or prevented access to critical habitats required to complete life stages (e.g. spawning; Cooke et al. 2016). Alterations to water temperature and flow regimes particularly affect fish movement. Water temperature, as a main driver of fish metabolism and physiology, can influence movement by altering metabolic demands for resource (e.g. prey) consump-

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tion and the need to thermoregulate (Volkoff & Rønnestad 2020). Flow can influence movement by altering the energetic demands of fish to maintain position and move (Shepard et al. 2013), as well as by changing the abundance and distribution of resources within and across habitats (Brittain & Eike-land 1988, Taylor & Cooke 2012, Turschwell et al. 2019). Over the past few decades, the study of animal movement in relation to environmental conditions has become a critical component of fisheries management and recovery (Allen & Singh 2016, Crossin et al. 2017).

Advancements in animal tracking technology (Hussey et al. 2015, Lennox et al. 2017), analytical tools (Whoriskey et al. 2019, Joo et al. 2020), and movement theory (Mueller & Fagan 2008, Nathan et al. 2008) have enabled the assessment of intrinsic (biological) and extrinsic (environmental) factors that influence how animals move across time and space (Patterson et al. 2017). Methods increasingly applied are those popularised by Morales et al. (2004) and Jonsen et al. (2005), which deconstruct animal movement track data into underlying behaviours. Assessing movement in terms of behaviour (e.g. resting, foraging, migrating) and the factors that influence switches in behaviour, can assist in understanding what drives growth, survival, and the reproductive success of an animal (Shaw 2020). For example, multiple fish species appear to adopt low-energy sit-and-wait movement behaviours when prey is abundant, and high-energy search behaviours when prey is scarce (Grant & Noakes 1987, O'Brien et al. 1989, Fausch et al. 1997, Killen et al. 2007, Higgingson & Ruxton 2015). As fish must manage finite energy budgets, there will be trade-offs between expending energy on movement or other physiological functions such as growth and reproduction (Rennie et al. 2005). For threatened species inhabiting regulated rivers, understanding how fish adjust their movements in response to changing conditions is needed to support management and recovery efforts (Tuomainen & Candolin 2011, Cooke et al. 2022).

White sturgeon *Acipenser transmontanus* are a species at risk almost everywhere they occur (Hildebrand et al. 2016, Crossman & Hildebrand 2022), with a majority of their historical range being altered by river regulation and fragmented by dams (Dynesius & Nilsson 1994, Haxton & Cano 2016). In the regulated Upper Columbia River, 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 Canada 2014). The population has criti-

cal 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 in regulated rivers (Haxton & Cano 2016), and use of habitat for spawning, feeding, and overwintering has been observed in other populations (Cooke et al. 2012, Hildebrand et al. 2016, Gillespie et al. 2020). Understanding how these endangered species interact with operations and associated environmental conditions is imperative for management and recovery.

The objective of this study was to describe and quantify endangered white sturgeon movement behaviour in relation to hydroelectric operations and river regulation. Acoustic telemetry was used to obtain positional data and track the fine-scale movements of white sturgeon occupying critical habitat immediately downstream of a dam on the Upper Columbia River. Specifically, we applied hidden Markov models (HMMs) and generalised 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 positions dataset; and (2) assessing the influence of biological (i.e. sex) and environmental (water temperature, discharge, season, photoperiod) factors on movement behaviour.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in the Transboundary Reach of the Upper Columbia River, an impounded section of river between the Hugh L. Keenleyside Dam (HLK) in British Columbia (Canada) and the Grand Coulee Dam in Washington (USA) (296 river kilometres; rkm). Wild adult white sturgeon movements were tracked in the 2 rkm section immediately downstream of the HLK and Arrow Lakes Hydro (ALH) (Fig. 1). HLK is a storage-only facility (i.e. no hydroelectric power generation) and was constructed in 1968 under the Columbia River Treaty. ALH, located adjacent to HLK, is a hydroelectric 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 USA under Columbia River Treaty agreements (BC Hydro 2021). While discharge volume is held consistent through

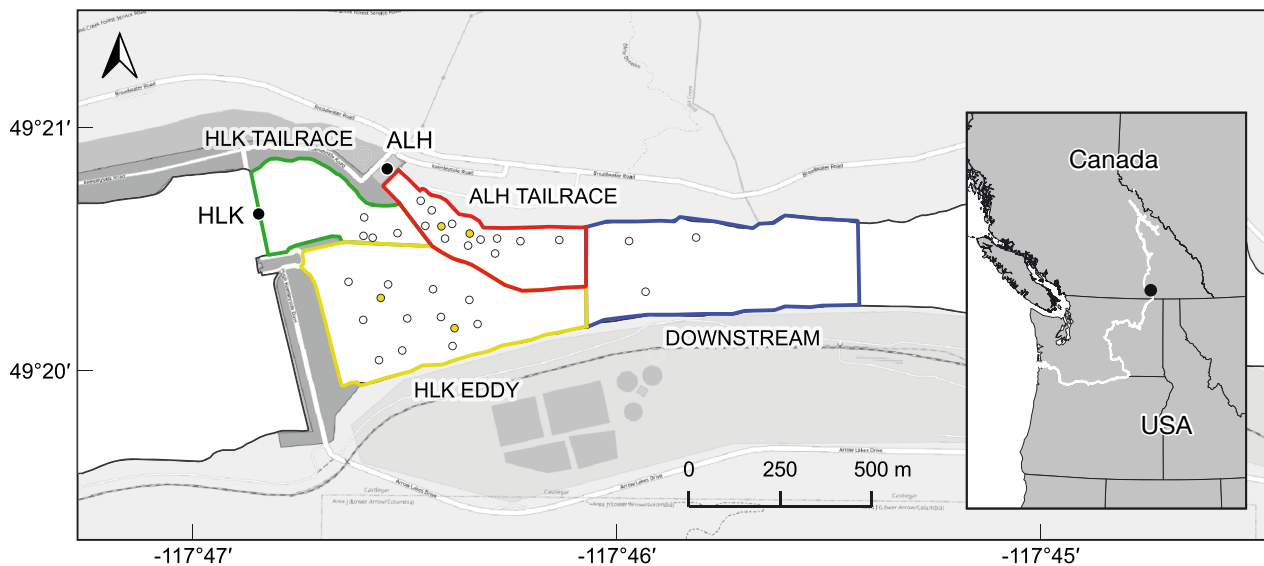


Fig. 1. Study area below the Hugh L. Keenleyside Dam (HLK) and Arrow Lakes Hydro (ALH) (black dots), British Columbia, Canada. Habitat zones are highlighted by colour, acoustic receivers are represented by white circles, and anchored sentinel tags are represented by yellow circles. Black dot in the inset shows the study site

the week, hourly or daily adjustments are sometimes required for maintenance activities or other demands around power generation. Fluctuations in discharge alter water surface elevations several metres but do not affect the availability of habitats for white sturgeon anywhere in the study area.

The study area includes federally protected critical habitat and was divided into 4 habitat zones based on river structure and environmental parameters: HLK Eddy, HLK Tailrace, ALH Tailrace, and Downstream (Fig. 1). HLK Eddy is a large, deep (>15 m) circulating eddy caused by discharge from both tailraces. High use of the HLK Eddy for feeding (e.g. benthic prey; Crossman et al. 2016) and overwintering has been identified for white sturgeon (Fisheries and Oceans Canada 2014, BC Hydro 2016). The HLK Tailrace consists of discharge from HLK and is a deep pool (10 m) that shallows (<5 m) where it joins the ALH Tailrace. Increased turbulence and total dissolved gas (TDG) occur in the HLK Tailrace during periods of high discharge from HLK (Li et al. 2022). TDG was not monitored continuously in the study area, but we know sturgeon are able to depth compensate in habitats where TDG is elevated (>120%; Pleizier et al. 2020). Use of the HLK Tailrace is primarily for feeding on seasonally abundant fish, such as spawning Kokanee *Oncorhynchus nerka* and mountain whitefish *Prosopium williamsoni* in the fall (Hildebrand et al. 2016). The ALH Tailrace consists of discharge from ALH and is a shallow section of the

study area. Prior research has identified spawning in the ALH Tailrace (Terraquatic Resource Management 2011). Lastly, Downstream consists of more riverine (i.e. channelized) habitat from combined HLK and ALH discharge. It is a transitional area in which fish move in and out of the study area.

2.2. Fish sampling and tagging

Our study population consisted of wild adult white sturgeon in the Transboundary Reach with already existing acoustic tags ($n = 132$). These fish were captured and tagged in the Canadian portion of the Transboundary Reach (rkm 1261–1204) between the years 2007 and 2013 for prior research to inform recovery programmes. Fish capture abided by capture protocols and set line configurations commonly used for white sturgeon throughout the Columbia River (Nigro et al. 1988, BC Hydro 2015). Sturgeon captured over this period were tagged with uniquely coded VEMCO V16-4x acoustic transmitters (69 kHz, 120–180 s ping rate). Surgical procedures were used to implant the transmitter 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 mid-line. Using an otoscope, the gonad tissue was visually assessed for sex (Webb et al. 2019). Afterwards, fish were implanted with an acoustic transmitter 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). Fork length and weight (i.e. size) was recorded at the time of capture; however, these measurements were not included in our study due to the variation in size that could occur between time of capture and time of study. Age was also not included in our study, as it was not available for all tagged fish, and confidence in the age estimates that exist for adult sturgeon is low (Rien & Beamesderfer 1994, Paragamian & Beamesderfer 2003, Bruch et al. 2009). After processing, sturgeon were returned to the water near their location of capture (BC Hydro 2015).

2.3. Acoustic array

The movement of tagged white sturgeon was monitored with a VEMCO Positioning System (VPS) deployed between 1 December 2013 and 15 November 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 from at least 3 separate receivers are then processed using a hyperbolic positioning technique to estimate positions 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 used in this study consisted of an array of 29 acoustic receivers (VEMCO VR2W) deployed in the 2 rkm study area (Fig. 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. To account for receiver clock drift and horizontal position error (HPE), each receiver was equipped with a synchronisation tag, and 4 separately anchored sentinel tags were placed within the array (Golder Associates Ltd 2015).

2.4. Data filtering

Factors such as the spatial configuration of acoustic receivers (e.g. density) and surrounding environment (e.g. water velocity) can affect both detection efficiency (resulting in tracks with irregular time interval) and positional error in an array (Bergé et al.

2012, Roy et al. 2014). Assessments of positional error were performed using HPE, which is a relative and unitless estimate of error potential for a calculated position. This estimate is derived by analysing the error of calculated positions for synchronisation and sentinel tags, calibrated to local environmental conditions (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 Ltd 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.

2.5. Movement behaviour state estimation with hidden Markov models

Hidden Markov models (HMMs; R package 'momentuHMM'; McClintock & Michelot 2018) were used to analyse the white sturgeon track data obtained with the VPS. HMMs are statistical models used to analyse sequences of observable quantities that depend on unobservable or 'hidden' discrete states of the study system (McClintock et al. 2020). In the analysis of animal tracks, HMMs use the probability distribution of movement metrics computed from sequential animal locations to decompose movement tracks into distinct hidden states, which are assumed to represent different behaviour states of an animal (Jonsen et al. 2005). For this study, step length (metres; gamma distribution with zero-inflation) and turning angle (radians; Von Mises distribution) were used as the movement metrics for a 2-state HMM. Formally selecting the appropriate number of states for an HMM can be challenging, and the decision often has to rely on expert knowledge (Pohle et al. 2017, McClintock et al. 2020). Prior research on the general movement tendencies of white sturgeon as a species and in the Transboundary Reach has shown that individuals often express high fidelity to a single location (e.g. study area) where they feed year-round (Hildebrand et al. 2016, BC Hydro 2018). Based on this knowledge, as well as the inherent difficulties of estimating more than 2 biologically meaningful movement states with only 2 data streams (step length and turning angle; McClintock et al. 2017), we determined a 2-state model to be appropriate for assessing the effects of biological and environmental conditions on white sturgeon movement behaviour.

HMMs are well suited to analyse movement datasets that are recorded at regular time intervals and with negligible positional error (Patterson et al. 2017). Fish detections in this study often occurred on an irregular time interval due to fluctuations in detection efficiency and because tags were programmed to transmit at random intervals between 120 and 180 s (to minimise code collisions). To regularise the data, fish movement tracks were first split into unique bouts if time between consecutive positions was greater than 2 h. Using bouts in this way is required when there are large gaps in detection due to periods in which fish location cannot be determined or when fish temporarily leave 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 min time interval using the 'crawlWrap' function in the R package 'momentuHMM' (McClintock & Michelot 2018), which implements a continuous-time correlated random walk model to predict locations at the selected time interval (Johnson et al. 2008). Positional error associated with intervals of 1 HPE between 0 and 16 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 & London 2018) from positional error data acquired by the study's sentinel tags (i.e. difference between true and calculated sentinel tag positions).

After movement interpolation, a 2-state HMM was fit to the data in 'momentuHMM' using multiple imputation, an approach which repeatedly fits the HMM to multiple realisations of the track reflecting positional error and generates pooled parameter estimates to reflect uncertainty in positioning (McClintock 2017, McClintock & Michelot 2018). Instead of a definite behaviour state estimated for each interpolated location, 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. Starting parameters (i.e. movement metric distributions of each behaviour state) used to fit the 2-state HMM 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. The 2 states identified by the HMM fit to the white sturgeon dataset were characterised by (1) short step length with less frequent changes in direction (hereafter, residential behaviour) and (2) longer

step lengths with more frequent changes in direction (hereafter, exploratory behaviour).

2.6. Movement behaviour state modelling with GLMMs

Once the probability of a behaviour state was estimated for each position using our 2-state HMM, the influence of biological and environmental covariates on movement behaviour was assessed. As some environmental covariates changed on a coarser timescale than the 15 min interval (e.g. HLK and ALH discharge adjusted on a weekly basis), movement behaviour was assessed using 2 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 at time $t - 1$ (i.e. 1 wk before; means calculated from 15 min intervals). Both methods applied 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 fit all GLMMs to the data. Analyses of movement behaviour in this study focused on reporting the probability of residential behaviour; however, it is important to note that the probability of exploratory behaviour would be the complement of these results.

For GLMMs assessing the probability of residential behaviour at 15 min intervals, candidate models included combinations of biological (sex) and environmental (water temperature, discharge, photoperiod, habitat zone, season) covariates. Discharge was assessed in 2 formats: models with a single parameter representing combined ALH and HLK discharge, or models with 2 separate parameters each representing ALH or HLK discharge. As temperature and discharge varied seasonally, the covariates were not included in models with a season factor. Interactions between discharge covariates and habitat zone, as well as season and habitat zone, were also included in candidate models. A random intercept by bout nested within individual was included in all models, and all combinations of covariates (i.e. candidate models) were fitted to the data. For GLMMs assessing mean weekly probability of residential behaviour, 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 by individual was included in all models, and all combinations of covariates (i.e. candidate models) were fitted to the data.

Temperature data were acquired from BC Hydro's Birchbank gauging station (rkm 1290), and discharge data were obtained from the ALH and HLK facilities. Temperature and discharge data were measured at 1 h increments, and values were interpolated across 15 min time intervals to match the locations estimated at a 15 min interval. Discharge was only changed on a weekly basis, and a 6 h lag effect was applied to the discharge data to ensure that all discharge changes had stabilised in the downstream environment. Photoperiod was categorised 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 (<https://nrc.canada.ca/en/research-development/products-services/software-applications/sun-calculator/>). Season was categorised as winter (December–February), spring (March–May), summer (June–August), and fall (September–November) and was included to represent general biological patterns (e.g. overwintering) and allow for comparison to other species.

We used the bias-corrected Akaike's information criterion (AIC_c) to rank and select candidate models. AIC_c is a relative measure of how close a model approximates the data generating process and of the predictive ability of a model (McElreath 2020), with the lowest AIC_c representing the best or top model. Due to model selection uncertainty (Burnham & Anderson 2004), models included in a set defined by a cumulative weight AIC_c residing just at or above 0.95 were used for model-averaged predictions. Model averaging was performed using the R package 'MuMIn' (Bartoń 2020), and all analyses in this study were performed in R (R Core Team 2021).

3. RESULTS

Of the 132 acoustically tagged white sturgeon in the Transboundary Reach, 51 resided in the study area during the study period. The VPS calculated a total of 818 577 positions from the 51 white sturgeon ($16\,050 \pm 14\,777$ positions per fish; range: 14–67 176). Fish were positioned in the study area most frequently in the winter (35%), followed by the spring (31%), summer (18%), and fall (15%). When broken down by habitat zone, fish positions were highest in the HLK Eddy (62%), followed by the ALH Tailrace

(27%), Downstream (7%), and HLK Tailrace (4%). HPE filtering resulted in 459 569 positions for the 51 sturgeon (9011 ± 8223 positions per fish; range: 11–28 432), with excluded positions varying proportionally across season and habitat zone to total positions ($\pm 8\%$). Six fish did not meet the minimum requirements identified for fitting the HMM (bouts of at least 100 positions), resulting in a sample of 45 white sturgeon (Table S1 in the Supplement at www.int-res.com/articles/suppl/n050p295_supp.pdf). The final dataset resulted in a total of 596 bouts, with an average of 13 bouts per fish (range: 1–53) and 5 d per bout (range: 0.4–89.6 d). Mean water temperature for the study period was 9.3°C (range: $2.0\text{--}18.4^\circ\text{C}$; Fig. S1). Mean discharge for the ALH and HLK facilities was $635\text{ m}^3\text{ s}^{-1}$ (range: $0\text{--}1109\text{ m}^3\text{ s}^{-1}$) and $462\text{ m}^3\text{ s}^{-1}$ (range: $0\text{--}1182\text{ m}^3\text{ s}^{-1}$), respectively (Fig. 2).

3.1. Movement behaviour states

The 2-state HMM identified behaviour states characterised by movements with short step lengths and less frequent turns (residential), and movements with

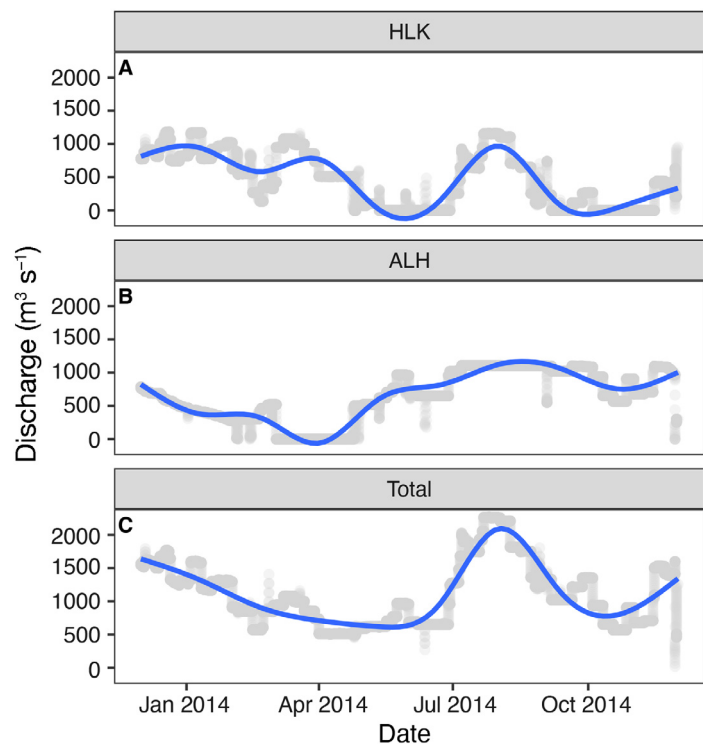


Fig. 2. Discharge from (A) Hugh L. Keenleyside Dam (HLK), (B) Arrow Lakes Hydro (ALH), and (C) total discharge from December 2013 to November 2014. Total discharge is the combination of HLK and ALH. Blue lines represent LOESS-smoothed data and grey points represent raw data

longer step lengths and more frequent turns (exploratory) (Fig. 3). The movement metric of step length had the greatest difference between behaviour states, with mean step length of residential and exploratory behaviour being 1.9 ± 2.0 and 27.4 ± 28.5 m, respectively (Fig. S2). Both behaviour states had step length zero-mass parameters ($\in (0, 1)$) close to 0, representing few instances of no movement between consecutive positions. For turning angle, residential and exploratory behaviour states had angle concentrations (i.e. concentration at 0 radians) of 0.8

and 0.3, respectively. While both behaviours involved changes in direction, these concentrations describe residential behaviour as having more instances of directed movement than exploratory behaviour, with residential and exploratory behaviour having 62 and 56% of turning angles concentrated between -0.5 and 0.5 radians, respectively (Fig. S2).

White sturgeon were detected in the acoustic array for an average of 65 d (range: 1–193 d), or 19% (range: 0.3–55.8%) of the study period. During that period, white sturgeon spent 50% of the time with residential probabilities >0.75 (likely residential) and 36% of the time with residential probabilities <0.25 (likely exploratory). A total of 14% of time was spent with residential probabilities between 0.25 and 0.75, representing instances with less certainty of behaviour state. Using these intervals of residential probability (<0.25 , $0.25-0.75$, >0.75), patterns in what behaviour state fish exhibited changed across habitat zones and seasons (Fig. 4). When broken down by

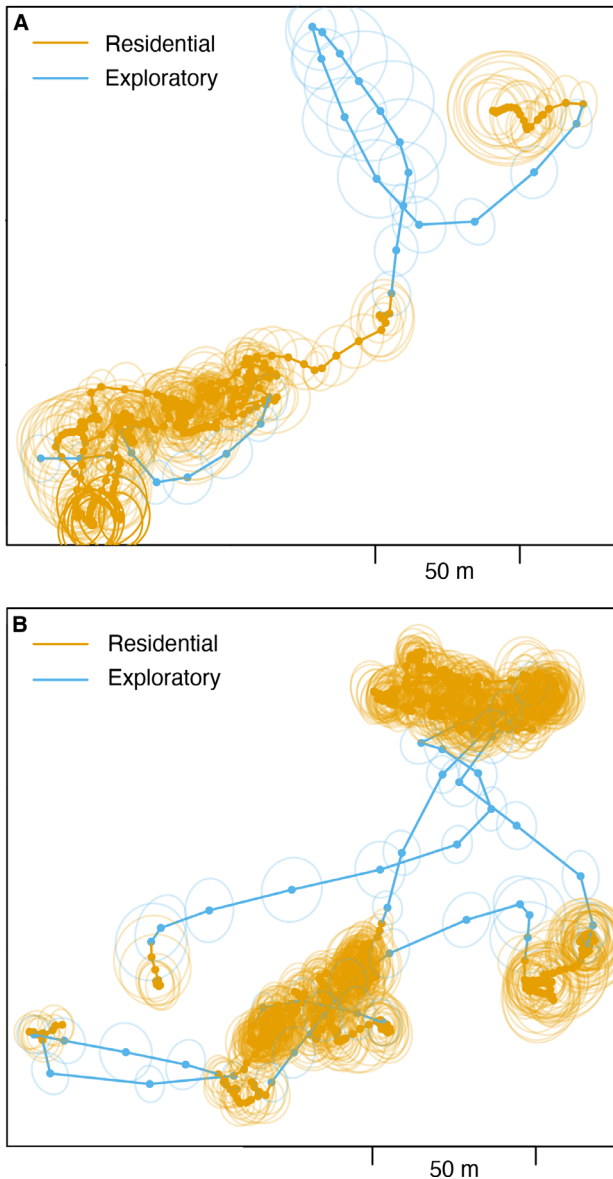


Fig. 3. Individual bouts from 2 white sturgeon in the study area with behaviour state of a position (dot) estimated by the hidden Markov model represented by colour. Ovals represent the error ellipse associated with a position

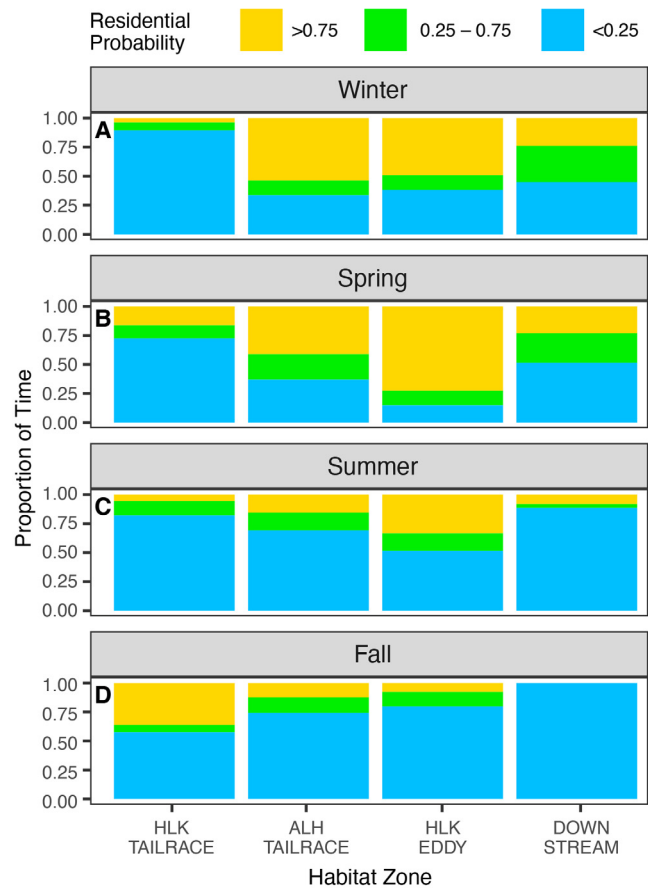


Fig. 4. Proportion of time white sturgeon spent having an upper (>0.75), middle ($0.25-0.75$), or lower (<0.25) probability of being in a residential behaviour state. Results are separated by season and habitat zone (see Fig. 1)

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%). 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%). These seasonal trends were observed in all habitat zones except the HLK Tailrace, where white sturgeon spent a larger proportion of time as residential during the fall (36%) compared to other seasons. Among individual fish, about 18% had bouts in all 4 seasons, and they exhibited substantial variability in time spent in a behaviour state within seasons (Fig. S3).

When examined spatially, residential behaviour during the winter and spring was concentrated in large areas (>100 m²) of the ALH Tailrace and HLK Eddy (Fig. 5). In the summer and fall, however, movement was more dispersed, with exploratory behaviour more often exhibited across all habitat zones and residential behaviour concentrated in smaller areas (<100 m²) of the ALH Tailrace, HLK Tailrace, and HLK Eddy. The Downstream zone had the lowest fish presence and exhibited similar seasonal shifts from residential behaviour in the winter and spring to exploratory behaviour in the summer and fall.

3.2. Model selection and predictions

The top model ranked by AIC_c 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 1). One other candidate model including sex as a covariate also had support from the dataset and was included in the 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 strong persistence in expressing a behaviour state. When a fish had a high probability of a given state at time $t - 1$ (e.g. residential probability of >0.75), it was very likely to remain in that state at time t . When fluctuations occurred, it was when there was less certainty about residential behaviour in the previous timestep (e.g. residential probability of 0.5). The season and habitat zone interaction was the most influential predictor in these instances (Figs. S4 & S5). Fish in the HLK Eddy demonstrated increased probabilities of residential behaviour in the winter and spring when probabilities at time $t - 1$ were 0.5. In the Down-

stream 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. Photoperiod and sex had the smallest effect sizes of model-averaged covariates, with minimal differences between photoperiods and sexes (Fig. S4).

The top model ranked by AIC_c predicting the mean weekly probability of residential behaviour given the probability at time $t - 1$ (i.e. 1 wk before) included the covariates of water temperature, ALH discharge, and habitat zone (Table 1). Three other candidate models including HLK discharge and sex as covariates were also supported by the dataset and were included in the 95% confidence set for the best model. Averaged model predictions again demonstrated that white sturgeon were very likely to remain in the same state at time t that they expressed at time $t - 1$, although fluctuations in mean weekly residential probability occurred when probabilities at time $t - 1$ were less certain (e.g. residential probability of 0.5). Habitat zone and water temperature were the most influential predictors in these instances (Fig. 6; Fig. S6). Fish in the HLK Tailrace and Downstream habitat zones demonstrated decreased mean weekly probabilities of residential behaviour, 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. Discharge from the ALH facility was the next strongest predictor. Increased discharge from ALH resulted in increased mean weekly residential probabilities. Sex and HLK discharge had the smallest effect sizes of model-averaged covariates, with minimal differences between sexes and across HLK discharge (Fig. S6).

4. DISCUSSION

We used positioning of endangered white sturgeon located below a hydroelectric facility to identify distinct residential and exploratory patterns in movement behaviour, with the former characterised by short movements with less frequent turns and the latter by longer movements with more frequent turns. Our results indicate that environmental covariates influenced behaviour when there was less certainty of a behaviour state in the previous timestep (i.e. residential probability of 0.5). At a fine timescale (i.e. 15 min timestep), the interaction of season and zone was the strongest predictor of residential behaviour.

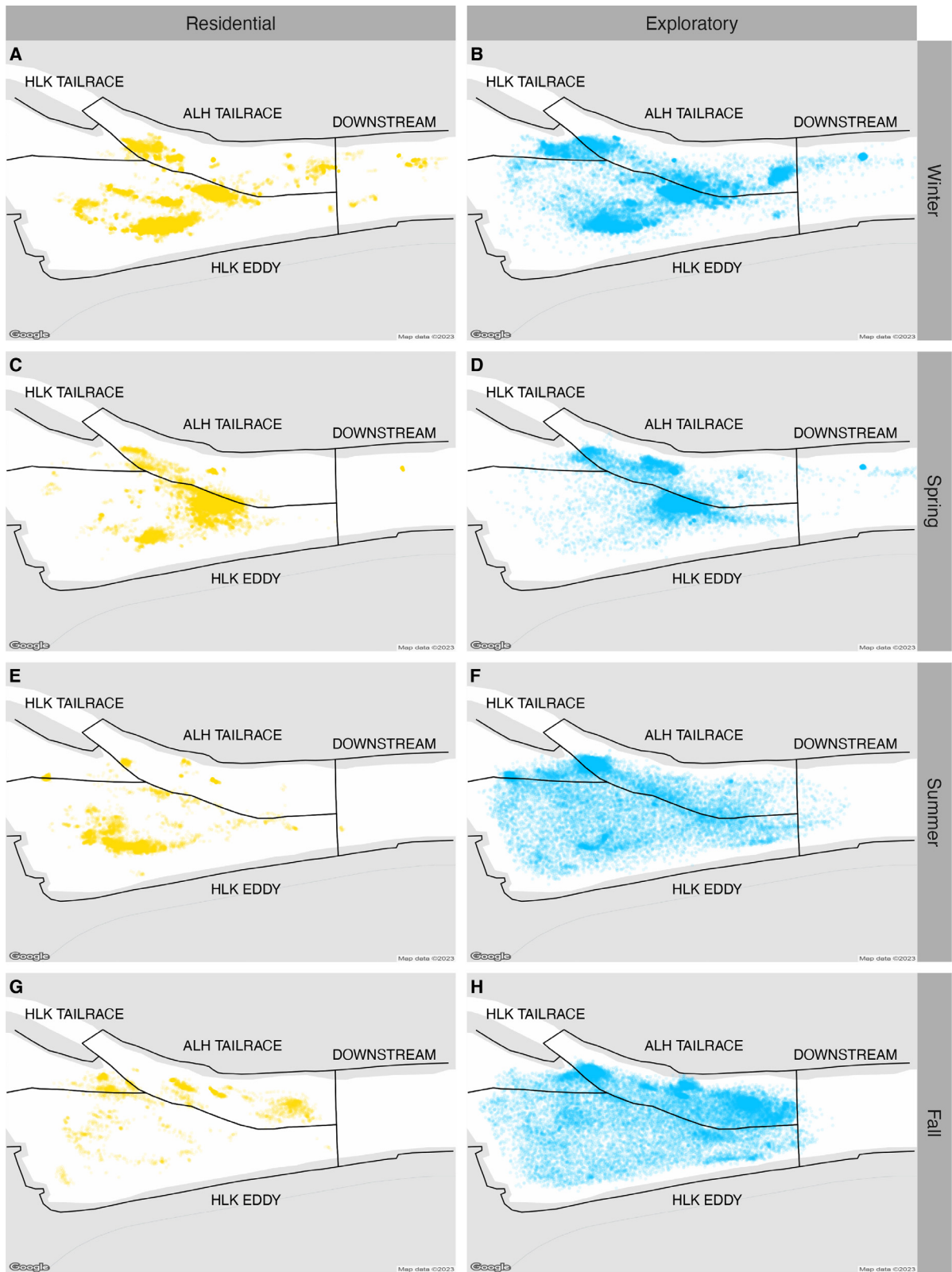


Fig. 5. White sturgeon positions having greater than 0.75 probability of being in a (A,C,E,G) residential or (B,D,F,H) exploratory behaviour state. Positions are shown by season (winter: A,B; spring: C,D; summer: E,F; fall: G,H), with black lines distinguishing habitat zones (see Fig. 1)

Table 1. Top models predicting the probability of residential behaviour at 15 min and mean weekly intervals ranked by increasing order of the bias-corrected Akaike's information criterion (AIC_c). Differences in AIC_c relative to the top model (ΔAIC_c), weight AIC_c ($wAIC_c$), cumulative weight AIC_c ($cwAIC_c$), log-likelihood ($\log(L)$), and the number of parameters in a model (K) are shown. Top models comprised the 95% confidence set for the best model and were used to generate model-averaged predictions. All models included track bout nested within individual as random effects (15 min) or individual as random effect (mean weekly), as well as a probability of residential behaviour at time $t - 1$ variable. alh: discharge from Arrow Lakes Hydro; hlk: discharge from the Hugh L. Keenleyside Dam facility; light: photoperiod; sex: sex of fish; temp: water temperature; zone: habitat zone (see Fig. 1)

Model	K	AIC_c	ΔAIC_c	$wAIC_c$	$cwAIC_c$	$\log(L)$
15 min						
season×zone + light	3	-2717204	0.00	0.71	0.71	1358624
season×zone + light + sex	4	-2717202	1.84	0.29	1.00	1358625
Mean weekly						
temp + alh + zone	3	-5860.61	0.00	0.35	0.35	2939.37
temp + alh + zone + sex	4	-5860.29	0.32	0.29	0.64	2941.25
temp + alh + hlk + zone	4	-5859.51	1.10	0.20	0.84	2939.84
temp + alh + hlk + zone + sex	5	-5859.10	1.51	0.16	1.00	2941.67

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 (i.e. 1 wk timestep), mean weekly probabilities of residential behaviour were influenced by water temperature, discharge, and habitat zone. Warming water temperatures were related to decreased probabilities of residential behaviour, and higher discharge from ALH was related to increased probabilities of residential behaviour. Given the importance of water temperature and discharge on movement behaviours of sturgeon in our study, we focus our discussion on results from the mean weekly time period.

Interpreting behaviour states in terms of ecological functions (e.g. resting, foraging, migrating) can be a challenging task that comes with uncertainty (Patterson et al. 2017, McClintock et al. 2020). As the movement of fish is often not observed directly due to the difficulties of studying in an aquatic environment (Ogburn et al. 2017), it is impossible to know for certain why a fish is moving. However, an understanding of a species' life functions can offer relevant insight (McClintock et al. 2020). In the case of sturgeon, distinct foraging behaviours have been observed in previous research. A fine-scale telemetry study of Atlantic sturgeon *Acipenser oxyrinchus* within an intertidal summer feeding area (McLean et al. 2014) identified 3 types of movement behaviours which they 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 move-

ments in and out of the study 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 2 types of foraging strategies have also been identified in lab studies of sturgeon (Kasumyan 1999) and other fish species (Grant & Noakes 1987, O'Brien et al. 1989, Fausch et al. 1997, Killen et al. 2007), and changes in strategy are often explained by changes in prey abundance and distribution (Higginson & Ruxton 2015). With descriptions of movements from other studies aligning with the behaviours identified in this study (e.g. residential as Type 1 and exploratory as Type 2), the mechanisms for these behaviour states likely reflect the feeding ecology of white sturgeon and offer insight into how sturgeon are influenced by hydroelectric operations.

This study found that a decreased mean weekly probability of residential behaviour (given 0.5 residential probability at time $t - 1$) was related to warming water temperatures. These results align with observed seasonal trends, with sturgeon spending the lowest proportion of time expressing residential behaviour (>0.75 residential probability) during warmer seasons (i.e. summer and fall; Fig. 4; Fig. S1). It is not uncommon to observe changes in movement activity in response to water temperature for white sturgeon, and changes are observed between seasons (Hildebrand et al. 2016, Robichaud et al. 2017). For example, white sturgeon have been shown to exhibit more frequent forays between deep, high-use habitat (e.g. eddies) and nearby shallower habitat during warmer seasons, with such movements being attributed to feeding activity and higher seasonal use of shallower habitat by potential prey (Hildebrand et al. 1999). As metabolic demands for energy increase with warming water temperatures, declines in residential behaviour may reflect how white sturgeon adopt a more high-energy movement strategy (i.e. exploratory behaviour) which allows the coverage of larger areas in order to find enough prey to meet metabolic demands. This can be observed not only in the more frequent but also more spatially dispersed expression of exploratory behaviour during the summer and fall (Fig. 5).

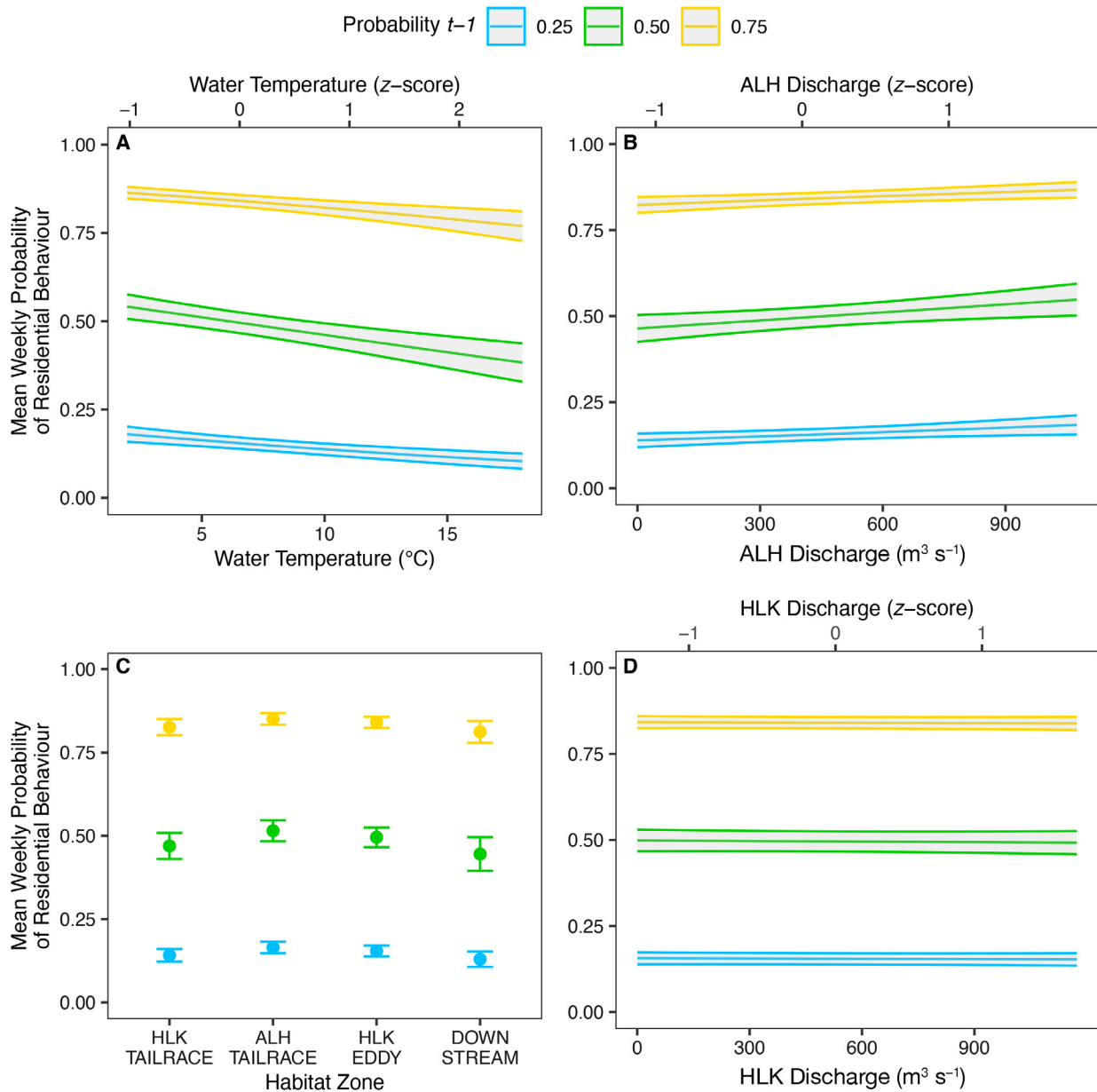


Fig. 6. Model-averaged predictions of the mean weekly probability of being in the residential behaviour state by (A) water temperature, (B) Arrow Lakes Hydro (ALH) discharge, (C) habitat zone (see Fig. 1), (D) Hugh L. Keenleyside Dam (HLK) discharge, and mean weekly probability of residential behaviour at time $t - 1$. Shaded areas and whiskers denote 95% confidence intervals, and top axes (z-scores) denote standardised values of the variable. 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

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 discharge (Shepard et al. 2013). Our study found that increased discharge from the ALH facility was related to increased mean weekly probabilities of residential behaviour (given 0.5 residential probability at time $t - 1$). This result likely reflects the increased likelihood of sturgeon to move

less (i.e. adopt residential behaviour) during high discharge, as well as the importance of ALH discharge on the flow environment (e.g. most consistent source of discharge throughout a given year).

Discharge also influenced the spatial distribution of residential behaviour within habitat zones, with areas of residential behaviour (>0.75 residential probability; Fig. 5) shifting seasonally. For example, in the summer and winter, when ALH and HLK are

both at high discharge (Fig. 2), areas of residential behaviour were observed in the centre of the HLK Eddy, where circulation is strengthened by discharge from both facilities (West et al. 2020). Areas of residential behaviour can also be seen in habitat adjacent to facility outflows 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, areas of residential behaviour either disappear or shift away from the eddy's centre as flow dynamics change and circulation is reduced (West et al. 2020). In terms of feeding ecology, residential behaviour may represent a movement strategy adopted when an area of suitable prey abundance has been found, and discharge has been shown to alter prey abundance and distribution within habitats (Brittain & Eikeland 1988, Taylor & Cooke 2012, Turschwell et al. 2019). For white 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 flows and minimal energy required for movement (Hildebrand & Parsley 2013). Adjustments in facility discharge may therefore be causing the relocation of these productive feeding areas and changing the spatial distribution of residential behaviour through time. Future research might apply spatial analyses, such as hydraulic habitat modelling, to better understand these observed trends in movement behaviour.

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 spawning or overwintering. Residential behaviour was observed in the known spawning area of the ALH Tailrace during the spawning period of June to July. However, mate interactions can be difficult to infer from HMMs (Buderman et al. 2021) and from white sturgeon as a species (e.g. spawning is rarely observed; Hildebrand et al. 2016), and there were no empirical data to support spawning activity during the study period (e.g. embryo or larvae collection; BC Hydro 2016). Overwintering, on the other hand, is a well-known 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, but high-energy movements and foraging in general are greatly reduced (Hildebrand et al. 2016). The increased probability of residential behaviour and a high proportion of time as

residential observed in the cooler winter and spring seasons was likely a reflection of the overwintering biology of these fish. For residential behaviour, feeding and overwintering biology may be overlapping. While metabolic demands and movement are greatly reduced due to overwintering, seasonal shifts in the location of areas of residential behaviour between the winter and spring suggest white sturgeon are still making habitat selections in response to discharge dynamics and possible changing prey availability.

Our study provides a framework for understanding how hydroelectric operational regimes could be used to optimize functionality of critical habitats for sensitive or endangered species. Results suggest that discharge could be stabilised during periods of increased sturgeon feeding (summer and fall). In the fall, residential behaviour largely disappeared from the HLK Eddy as discharge was reduced and flow dynamics changed. A more stabilised flow distribution may promote suitability of the HLK Eddy habitat before the onset of winter, a period where feeding and developing adequate energy reserves are critical for growth and future reproduction (Hildebrand et al. 2016). Prioritising environmental flows comes as a trade-off against other demands for water, and climate change is expected to shift the distribution of water availability, particularly in drier months when sturgeon activity is highest. Understanding how future climate forecasts will influence hydroelectric operational regimes will be important to continued conservation and recovery efforts for endangered sturgeons.

Data availability. Data used in this study are available from the authors upon reasonable request.

Code availability. The code that supports the analyses presented here, developed using R version 3.5.3 (www.r-project.org), are available upon request from the corresponding author.

Acknowledgements. We thank Marco Marrello and Katy Jay from BC Hydro for their contributions to field data collection for this project, as well as Chris Johnson from the University of Northern British Columbia and Kim Whoriskey from Dalhousie University for valuable feedback on previous versions of this paper and analysis. Funding for this project was provided by BC Hydro, Castlegar, through the Columbia River Use Plan. E.G.M. was supported by an NSERC Discovery Grant. The present work was part of C.N.J.'s Master's thesis from the University of Northern British Columbia.

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*Editorial responsibility: Constance M. O'Connor,
Toronto, Ontario, Canada*
Reviewed by: M. Keefer and 2 anonymous referees

Submitted: October 21, 2022
Accepted: February 28, 2023
Proofs received from author(s): April 8, 2023