

Modelling migratory behaviour and habitat use of fish in a large, uninterrupted river network: A case study of a migratory salmonid

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Abstract

Bull trout (*Salvelinus confluentus*) research has historically focused on highly impacted systems or occurred in a reactionary manner following overharvest. Here, we used telemetry and multi-state capture–recapture modelling to inform management decision-making for this highly migratory, conservation-listed species in British Columbia's upper Fraser River watershed (UFW). Our work reduced critical information gaps surrounding the seasonal migration patterns, distribution, and survival rates of fluvial bull trout within the region. By using results of an existing microsatellite DNA analysis, we were able to assign each tagged individual to one of five spawning populations. This assignment allowed us to investigate potential differences in migratory behaviour and seasonal habitat use among the different spawning populations. We identified that the majority of tagged UFW fluvial bull trout made repeated, long-distance migrations (>300km one direction) to appropriate spawning, overwintering and foraging habitats. The five populations did not vary in their seasonal transition probabilities at the spatial scale investigated, suggesting key habitats are important to multiple populations. We also detected post-spawning migration and distribution patterns that suggest UFW bull trout exploit seasonal resource pulses during salmon smolt outmigration. Our results highlight the importance of protecting, restoring and maintaining a diverse assemblage of complex habitats and the natural connections between them (e.g. between tributary spawning habitats and larger rivers) at a spatial scale that supports migratory bull trout life histories. This work provides valuable information for prioritizing conservation actions and identifying restoration opportunities both in the UFW and across the species' range.

KEYWORDS

bull trout, Cormack-Jolly-Seber, meta-population, seasonal movement, spatial transitions, telemetry

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1 | INTRODUCTION

Bull trout's (*Salvelinus confluentus*) life history diversity has facilitated the species' persistence through North America's last glaciation and is fundamental to their long-term stability and persistence (Power, 2002). The species exhibits adfluvial, anadromous, fluvial and resident ecotypes; all except resident populations are migratory (McPhail & Baxter, 1996). Like many highly migratory species, bull trout undertaking large-scale seasonal movements use multiple, spatially segregated, distinct habitats (McIntyre et al., 2016). These habitats vary in their associated mortality threats and population risks, with impacts dependent on the duration of habitat use and the severity of threat(s) (Carvalho & Hauser, 1994; Hilborn & Walters, 1992; Ihssen et al., 1981). Though meta-population structure present in many systems can function to spread risk and support bull trout's persistence, understanding where and when stock mixing occurs is also critical to management and conservation efforts aimed to protect less productive stocks and/or genetic diversity (Paulik et al., 1967; Secor, 2014; Taylor et al., 2014).

Bull trout have designated conservation status across the species' range within the United States ('Threatened') under the United States *Endangered Species Act* (USFWS, 2015). In Canada, bull trout have been assessed under the *Species at Risk Act* (SARA) as five separate conservation units, which range in designated status from 'Not at Risk' to 'Threatened' (COSEWIC, 2012; Government of Canada, 2021). In both nations, bull trout are a conservation concern in many regions due to population declines and increased prevalence of local extirpations (COSEWIC, 2012; USFWS, 2015).

Most research focused on bull trout migratory behaviour comes from artificially fragmented systems, where damming or the presence of other movement barriers significantly impact habitat connectivity and thus migratory behaviours (e.g. Pend Oreille River drainage, DuPont et al. (2007); Mill Creek, Howell et al. (2016) and Starcevich et al. (2012); upper Flathead River, Muhlfeld and Marotz (2005); Blackfoot River drainage, Swanberg (1997)). We have less understanding of bull trout behaviour and dynamics where the full life history expression of the species is possible (e.g. connected systems). Understanding where and when bull trout move and how populations and population complexes distribute both temporally and spatially is important for the species' riverscape-level management. Without this knowledge, it is not possible to ensure that population structure is maintained and that the full mosaic of important habitats are incorporated within management and recovery initiatives (Hilborn & Walters, 1992; Rudd et al., 2014; Taylor et al., 2021).

Telemetry studies are increasingly prevalent for estimation of seasonal movement patterns (e.g. dispersal) and vital population rates (e.g. mortality) in marine systems, lakes and linear stretches of river corridors (Cagnacci et al., 2010; Hussey et al., 2015; Sippel et al., 2015). However, work in large, interconnected freshwater systems is rare. In addition, bull trout telemetry work has often occurred over a relatively short duration (i.e. <3 years; Bahr & Shrimpton, 2004; DuPont et al., 2007; Hogen & Scarnecchia, 2006; Howell et al., 2016; Muhlfeld & Marotz, 2005; Schoby & Keeley, 2011). Bull trout's

late maturity and the complex nature of non-resident populations' migratory behaviours (e.g. non-consecutive or skip spawning, when individuals forgo spawning in a particular year; Rideout & Tomkiewicz, 2011) make it difficult for these investigations to capture the full extent of behaviours that are important for the species' long-term management (Rieman & McIntyre, 1993).

Watershed-level management of the species requires a clear understanding of bull trout dispersal patterns, the timings and locations of aggregations and the presence of shared habitat use. Here, we apply a multi-state, capture-recapture model to a multi-year radio-telemetry study to inform management decision-making for bull trout in the upper Fraser River watershed (UFW) of British Columbia. The goal of our investigation is to reduce critical information gaps surrounding the seasonal movement patterns, distribution and survival rates of bull trout within the region by estimating population-specific apparent survival and population-, seasonally- and spatially-specific movement (transition) probabilities. We test the hypothesis that each bull trout spawning population in the region exhibits different migratory behaviours among shared critical overwintering and foraging habitats. Results of our investigation are valuable in the development of spatial-temporal management strategies for bull trout populations in the UFW specifically, while also having broader applications to bull trout populations across the species' range as well as for other migratory species.

2 | METHODS

2.1 | Study area and species background

Our study region comprises approximately 98,000 km² of the UFW of British Columbia (Figure 1). The region contains an extensive network of freshwater habitats encompassing Stuart, Fraser and François lakes, the Nechako and Stuart rivers, portions of the upper Fraser River and multiple low-order, cold-water tributaries of the Fraser River. Bull trout habitats across the UFW are highly interconnected with one another. Two major exceptions, however, are the upstream barriers formed by the Kenny Dam on the Nechako River approximately 160 km upstream of the confluence between the Fraser and Nechako rivers and Cheslatta Falls, a naturally occurring barrier to fish passage upstream into the Cheslatta watershed, located on the Nechako River approximately 9 km downstream from the dam. The presence of Kenney Dam does not fragment historic bull trout habitat. Prior to dam construction, upstream passage of bull trout from the Nechako River and into Natalkuz Lake (inundated at reservoir infilling) was not possible due to the presence of gradient barriers and significant falls and cascades within the Nechako River Canyon, which served as naturally occurring barriers to fish passage (EDI, 2003).

Bull trout spawning activity within the UFW is believed to be confined to tributaries of the upper Fraser River (Pillipow & Williamson, 2004; Taylor et al., 2021) with past reconnaissance surveys not identifying bull trout spawning habitat in other portions of

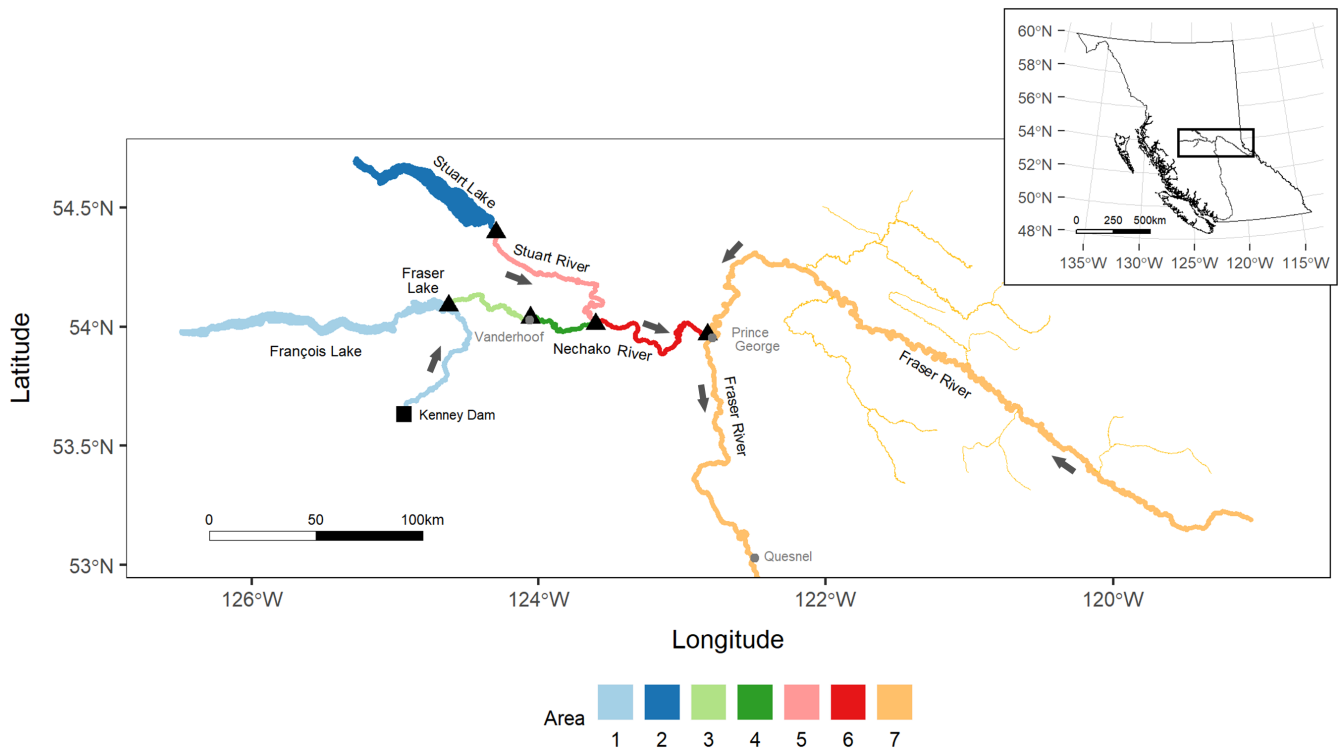


FIGURE 1 Overview map of the study area within the UFW. The seven spatial areas modelled are represented in colour, human population centres are identified by grey circles, distribution of fixed receiver array is identified by black triangles, flow direction is indicated with grey arrows and the location of Kenney Dam is designated with a black square.

the watershed (e.g. Nechako River or associated tributaries; ARC Environmental Ltd, 1998; Taylor et al., 2021). Analyses of UFW bull trout population structure using microsatellite DNA and otolith microchemistry have reported significant genetic differentiation between a number of samples collected from individuals within different spawning tributaries (Taylor et al., 2014, 2021; Taylor & Clarke, 2007). Past work by Pillipow and Williamson (2004) suggests bull trout spawning migrations in the region occur over an approximately 4-week period from late July to late August, with arrival on spawning grounds/spawning staging by the first week of September. Spawning then occurs over an approximately 3-week period concluding in late September, followed by rapid post-spawning dispersal from tributaries into the Fraser River (Pillipow & Williamson, 2004).

Currently, we do not have a clear understanding of bull trout populations' post-spawning dispersal fate within the UFW, but at least portions of the mainstem Nechako and Fraser rivers are thought to be important overwintering and foraging habitats for some fluvial bull trout populations (i.e. those spawning within the Goat, McKale and Holmes rivers and Walker Creek; Pillipow 2021, pers. commun.; Pillipow & Williamson, 2004; Taylor et al., 2021). Habitats within the Nechako and Stuart rivers may provide important foraging opportunities for bull trout following Chinook salmon (*Oncorhynchus tshawytscha*) spawning (i.e. eggs in fall/winter and out-migrant fry in spring) and during sockeye salmon (*O. nerka*) smolt outmigration in spring (Pillipow 2021, pers. commun.). Work elsewhere (e.g. Chilcotin watershed; Furey et al., 2015, 2016, 2021 and Furey & Hinch, 2017; and Skagit River; Lowery & Beauchamp, 2015)

has documented bull trout demonstrating foraging-related aggregating behaviour in response to *Oncorhynchus* spp.

2.2 | Tagging and telemetry tracking

2.2.1 | Fish capture

We observed bull trout movements using radio telemetry. Our primary goal was to tag as many mature fluvial fish as possible with the purpose of generating apparent survival and movement estimates. From May 2011 to October 2015, we captured a total of 525 bull trout within both spawning and foraging/overwintering habitats of the UFW and tagged 169 individuals with a fork length >400mm to ensure that transmitter weight was <2% of the individual's body weight (Table 1; Winter, 1996). Our use of minimum fish size criteria also decreased potential size-selective impacts on an individual's migratory behaviour by reducing the potential capture of juveniles and stream-resident fish, the latter of which are generally <330mm (Craig & Bruce, 1982; Pollard & Down, 2001; Robinson & McCart, 1974).

We conducted annual tagging surveys in the Nechako River from ice off (i.e. approximately mid-April through May) until the date when temperatures exceeded bull trout's thermal preference (i.e. in the summer when temperatures preclude bull trout residency in the Nechako River; Fraley & Shepard, 1989; Gutowsky et al., 2017; Hass, 2001; Islam et al., 2019). To provide spatial separation of

TABLE 1 Tag deployment (number of bull trout, grouped by genetic assignment and tagging location) within the UFW.

Assigned population	Tagging location	Year					Total
		2011	2012	2013	2014	2015	
Chalco Creek	UFRT	1	8	15	10	0	34
	NSR	0	0	2	0	2	4
	Population total	1	8	17	10	2	38
Goat River	UFRT	25	5	0	0	0	30
	NSR	0	0	5	1	5	11
	Population total	25	5	5	1	5	41
Milk River	UFRT	0	3	9	11	0	23
	NSR	0	0	0	0	0	0
	Population total	0	3	9	11	0	23
Walker Creek	UFRT	24	9	0	0	0	33
	NSR	0	0	1	0	2	3
	Population total	24	9	1	0	2	36
Outgroup	UFRT	0	2	5	3	2	12
	NSR	0	0	8	2	9	19
	Population total	0	2	13	5	11	31
Grand Total		50	27	45	27	20	169

Note: Genetic assignments were performed by Taylor et al. (2021).

Abbreviations: NSR, Nechako or Stuart River mainstem; UFRT, Upper Fraser River tributaries.

sites and to avoid only sampling hyper-concentrated areas, we angled multiple sites along the Nechako River. Our site selection was primarily based on local knowledge and professional judgement of which areas were most likely to yield bull trout (i.e. locations with known or suspected bull trout aggregations) and locations that permitted routine, feasible accessibility for crews and vessels. We repeatedly sampled selected sites over several years.

Our tagging efforts in the Nechako River were primarily exerted via vessel-based angling using an 18' jetboat. In 2015, angling efforts were supported by additional effort via boat-electrofishing using a 23' research vessel equipped with a Smith-Root GPP 2.5 gas-powered electrofisher (settings=60hz Low Range DC - 120v). Over the study period, these efforts resulted in our capturing 333 bull trout (37 radio tags deployed as a result of sized-based criteria, see Table 1). Annual electrofishing effort was not recorded but would not be expected to impact mean model outcomes. However, this effort could impact variance associated with estimated movement probabilities and apparent survival. Our mean annual angling CPUE was 2.61 fish/angler day (range 0.67–4.25 fish/angler day). We caught a total of five individuals who died as a result of hooking mortality (we did not tag these fish).

Within tributaries, angling effort was deployed in such a way as to ensure the selection of fluvial fish. Our effort only occurred in tributaries without access barriers. Effort timing (i.e. between July 1 to August 31 annually) also coincided with known run timing/population spawning staging (Phillipow, 2021, pers. commun.) to ensure staging fish would be broadly distributed throughout the natal system. We selected specific angling sites that were accessible via helicopter or road. We angled a total of 192 bull trout (132 radio tags deployed due to minimum size criteria) between August 3, 2011

and August 20, 2015, in eight tributaries of the upper Fraser River upstream of Prince George (see Table 1).

Our tributary angling efforts were primarily focused on three study watersheds, containing (1) Goat and Milk River, (2) Chalco Creek and Holmes River and (3) Walker Creek (Figure 2). Annually, our angling effort (as angler days) in each watershed averaged between five to 11 angler days, equating to average annual CPUEs ranging from 1.34 fish/angler day (Chalco Creek and Holmes River combined), 1.64 fish/angler day (Goat and Milk rivers combined), and 5.25 fish/angler day (Walker Creek). In comparison, our efforts in other tributary habitats (i.e. Fontaniko Creek, Haggen Tributary and McKale River) were substantially lower (two angler days per stream), and we visited these streams only in one study year. We angled bull trout in both the mainstem Nechako River and upper Fraser River tributaries using a variety of lures and baits and did not observe evidence of selectivity (i.e. strong behavioural evidence of non-selective aggression; fish were aggressive to hooks, bait, floats, weights and each other).

2.2.2 | Tag specifications and tagging procedure

We used uniquely coded transmitters (a combination of Lotek model MCFT2-3L and Sigma Eight model TX-PSC-I-1200-M radio tags) to identify individual fish. These tags emitted signals with a 5-s burst rate (frequencies in mHz: 150.300, 150.520, 150.580, 150.780 and 150.800) and had operating lives from six (Sigma Eight) to eight (Lotek) years. Prior to tag application, we individually anesthetized all captured fish using a 10% clove oil-ethanol stock solution diluted with river water to a concentration of approximately 50mg/L. Each

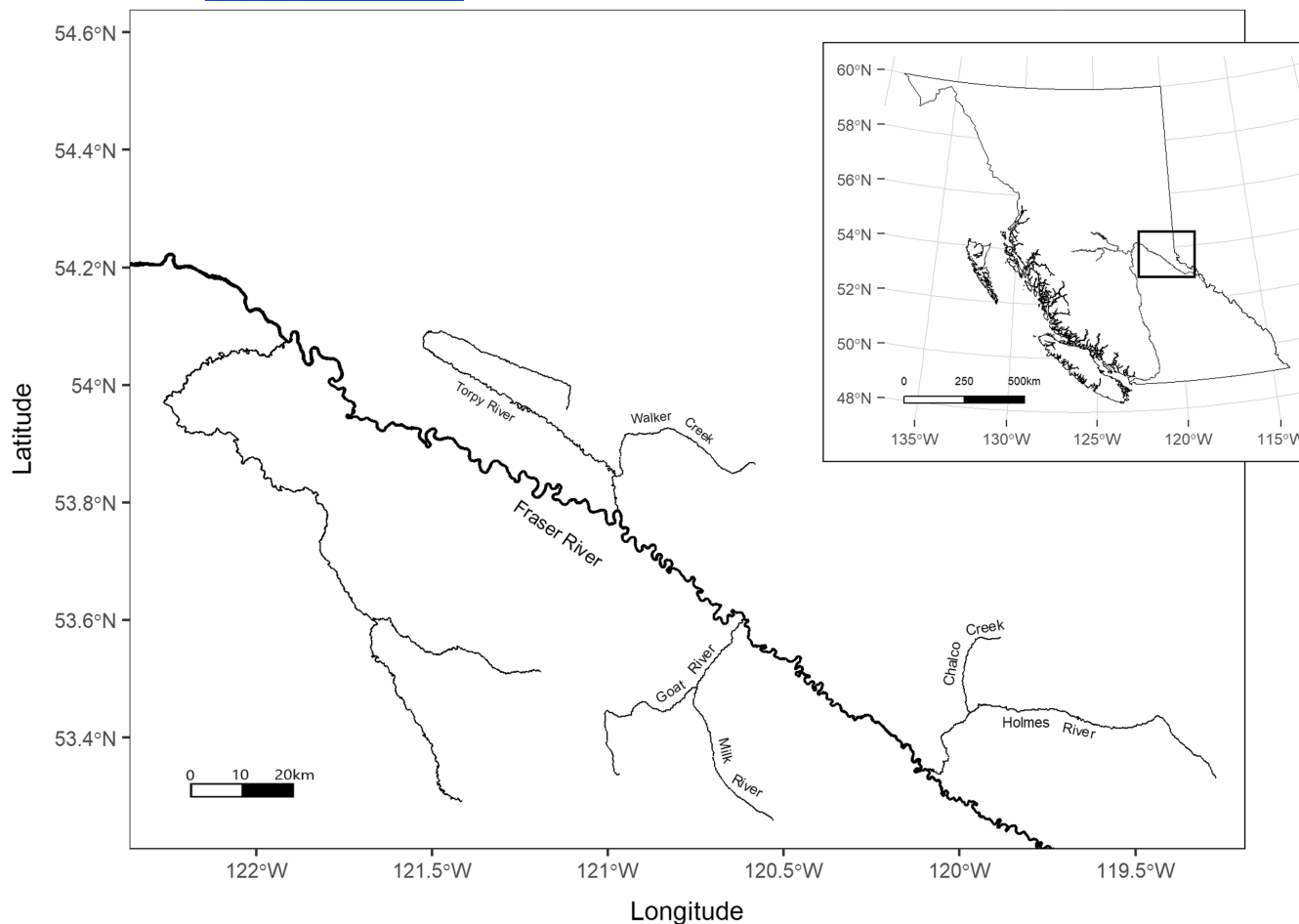


FIGURE 2 Locations of bull trout spawning tributaries for modelled populations.

fish remained in the anaesthetic until it reached a total loss of reflex reactivity (Schreck & Moyle, 1990). Using a pistol grip-style gun applicator, we tagged each captured fish with an individually coded T-Bar anchor tag on the dorsal surface along the dorsal fin base. Each tagged fish also received a passive integrated transponder tag which we inserted in the left cheek. We removed the leading edge of one pectoral fin with a scalpel, clipping the ray as close as possible to its insertion into the body. Fin rays were then dried and used to determine individual age. We also collected genetic samples from each individual via an adipose fin punch (see details in Taylor et al., 2021). Briefly, we assessed each individual's most likely population (tributary) of origin using microsatellite DNA variation across 10 loci. We then used these assignments within the multi-stock model to allocate fish of unknown origin to known bull trout populations within the UFW (see Table 1).

When using radio telemetry tags, we implanted these abdominally (intraperitoneally) in fish over ~400 mm. We oriented anaesthetized bull trout ventral side up on a moist surgical trough and made a 2.5 cm incision into the abdominal cavity on the mid-ventral line immediately anterior to the pelvic girdle. Looking into the incision site, we visually assessed gonadal maturity while attempting to minimize tissue disturbance. We then passed the transmitter antenna through the body wall using a 16-gauge shielded cannula pierced through

the body wall posterior to the pelvic girdle near the incision. We closed the incision using three or four interrupted sutures. Surgeries lasted less than five minutes. After the procedure, we transferred tagged bull trout from the surgical trough to a temporary live well and monitored them until recovery. Finally, we released fish with a dip net back to the water as close to the capture location as possible.

2.2.3 | Radio tracking

We used an array of five stationary telemetry receivers and additional, limited opportunistic mobile telemetry effort to track tagged individuals. The stationary receiver array included three permanent stations (Lotek Wireless SRX400, located in Prince George, Vanderhoof and the upper Stuart River near Stuart Lake) and two seasonal stations (Lotek Wireless SRX600, located at the confluence of the Stuart and Nechako rivers and Lotek Wireless SRX400, located at the confluence of the Nechako and Nautley rivers) which were operated from early May through late October of each year (Figure 1; Table 2). All stationary receivers had a minimum of two directional antennas.

We extended the spatial resolution of movement data by leveraging opportunistic mobile telemetry effort (Lotek model SRX600

TABLE 2 Location and operating details of stationary telemetry receiver array.

Station name	Antenna (count)	Antenna Direction	River monitored	River Kilometer (rKM)	Operational dates
Prince George	2	Antenna 1: Upstream Antenna 2: Downstream	Nechako Nechako	2.5 (Nechako)	Year-round
Lower Stuart	3	Antenna 1: Upstream Antenna 2: Downstream Antenna 3: Upstream	Nechako Nechako Stuart	91.7 (Nechako)	May-October
Upper Stuart	2	Antenna 1: Upstream Antenna 2: Downstream	Stuart Stuart	104.9 (Stuart)	Year-round
Vanderhoof	2	Antenna 1: Upstream Antenna 2: Downstream	Nechako Nechako	136.1 (Nechako)	Year-round
Nautley	3	Antenna 1: Upstream Antenna 2: Downstream Antenna 3: Upstream	Nechako Nechako Stuart	191.7 (Nechako)	May-October

receiver), conducted primarily by helicopter but also by truck where road access permitted. Once per month in each February and March, we conducted telemetry overflights over the mainstem Stuart, Nechako and Fraser rivers. Our flight paths included the full extent of both the Nechako and Stuart rivers and the Fraser River from Prince George upstream to the uppermost spawning tributary included in the study (i.e. Holmes River). Within tributary habitats, our mobile effort occurred primarily via telemetry overflights or truck-based telemetry during capture and tag deployment activities (i.e. one flight or drive per tributary per year in mid-August). We also opportunistically conducted a single overflight per tributary during annual redd surveys each September (2013–2016 Chalco Creek surveys, 2014–2016 Goat River and Walker system surveys). Flights included the full extent of habitat from the tributary mouth to its headwaters, while our truck-based effort was limited to the extent of road infrastructure (~28 rkm of ~30 rkm driven). We recorded each individual's unique identification and the time and date of each detection.

To validate detections within the receiver detection zones, we evaluated detection ranges annually at each of the five stationary receiver stations by passing test tags of the same model and frequency as deployed in the study animals through the detection zone at varying distances from shore. We minimized telemetry error (e.g. false positive detections) by validating the time step and power of each tag's acquisition in the receiver data logs prior to classification as a true detection. Through this process, we removed false positives by assigning the designation of 'true detections' based on multiple, repeat detections of a specific code on a specific day, with detection strength and signal noise serving as additional accuracy indicators of true detections.

2.3 | Analysis

2.3.1 | Data preparation

Telemetry data was analysed using two methods. First, all field observations (i.e. detections) were used to quantify specific movement patterns related to suspected UFW bull trout spawning and

post-spawning dispersal, overwintering and foraging behaviours (i.e. as counts of fish or proportion of the total tagged population). Second, we used radio telemetry data as "virtual recaptures" (Hightower et al., 2001) to estimate inter-seasonal transition (movement) probabilities and apparent survival rates using a multi-state Cormack Jolly Seber (CJS) model in a Bayesian state-space modelling framework (Table 3; Lebreton et al., 2009; Kéry & Schaub, 2012).

For both analyses, we divided the study area into seven discrete spatial areas based on the location of fixed telemetry receivers (see Figure 1 and Table 2). We assigned each individual to one of the seven spatial areas for each detection as follows. First, we assigned individuals detected by mobile telemetry effort to the area where they were detected (e.g. individuals detected in Chalco Creek were assigned to area 7, individuals detected in Stuart River were assigned to area 5). Second, we assigned individuals detected by stationary telemetry receiver stations to a spatial area based on their last detected location each day. For example, we assigned fish detected on downstream receivers to the area immediately downstream of the station (e.g. downstream detection at Prince George station assigned to area 7) while we assigned fish detected on an upstream receiver to the area immediately upstream of the station. Within the model, we defined eight possible process model states: 1–7: 'individual being alive and in one of the seven spatial areas' or 8: 'dead'. There were also eight possible detection model states, where an individual could be 'detected in one area (1–7) or be 'not detected' (8).

To explore differences in inter-seasonal transition (movement) probabilities within the CJS model, we divided each study year into two unequal time-blocks to account for seasonal variations in movement. Time-block one (TB1, 'moving') spanned April 15 through October 31 while time-block two (TB2, 'stationary') spanned November 1 through April 14. We set the dates included in each time-block based on previous research on bull trout movement within the UFW and known bull trout movement patterns across other portions of the species' range. We initiated TB1 on April 15 to account for potential bull trout movements in spring in response to Stuart and Nechako River Chinook fry emergence and dispersal (Bradford, 1994; Healey, 1987; NFCP, 2005) and Stuart

Symbol	Value(s)	Prior	Description
Indices			
i	(i, \dots, I)		Individual
st	(1:5)		Stock number
se	(1, 2)		Season (1 = TB1 "moving", 2 = TB2 "stationary")
a_O	(1:8)		Detected state of departure
k_O	(1:8)		Detected state of arrival
a	(1:8)		Estimate state of departure
k	(1:8)		Estimate state of arrival
Parameters			
\emptyset	++	$B(2, 2)$	Survival probability
p	++	$B(2, 2)$	Redetection probability
G			Logit space transition probability
g	++	$N(0, 2)$	Gravity
v	++	$N(0, 2)$	Viscosity
ψ	++		Transition probability
f_{s_i}	++		Detected state at first capture (i.e., tagging event)
Z_{i,f_i}	++		True state of individual
Likelihood estimation		<i>Likelihood function</i>	
$Z_{i,t+1} Z_{i,t}$	++	$C(\Omega_{z_{i,t}, 1 \dots S, i, t})$	State membership development
$Y_{i,t} Z_{i,t}$	++	$C(\theta_{z_{i,t}, 1 \dots O, i, t})$	Estimation linking detected and true states

Note: The symbol ++ indicates estimated parameters, TB1 refers to time-block 1, and TB2 refers to time-block 2. We assigned priors and likelihood functions abbreviated distribution names as follows: B = Beta (shape parameters), N = Normal (mean, precision) and C = Categorical, respectively.

River sockeye salmon smolt outmigration (Taylor & Bradford, 1993) based on field observations of bull trout foraging in the Nechako River and research by Furey et al. (2015, 2016, 2021, Chilcotin watershed) and Lowery & Beauchamp (2015; Skagit River) which have shown bull trout move in response to these seasonal resource pulses. We ended TB1 on October 31 to ensure it extended through known bull trout spawning run timing and post-spawning dispersal in the UFW based on work by Pillipow and Williamson (2004). The expectation of bull trout stationarity throughout TB2 was based on past research on bull trout overwintering behaviour (e.g. see Bahr & Shrimpton, 2004; Jakober et al., 1998; Muhlfeld & Marotz, 2005; Starcevic et al., 2012). Our choice of the two time-blocks over the 6-year study resulted in 11 detection occasions within the state-space model.

The model was informed by individual detection histories for each tagged fish. Since the focus of the model was to explore broad scale, inter-seasonal movement patterns, detection histories did not include in-season movements. Instead, individual detection histories were built based on only the first detection event for each fish in each time block over the 11 sampling periods (e.g. if a fish was detected in TB1 of 2013 in area 3 and subsequently detected in area 4 in the same time-block in the same year, the detection was assigned as area 3). Further, since detection histories used within the model

were based only on the first detection in each time-block, transitions that occurred within seasons but across multiple spatial areas were inferred by the model (Kéry & Schaub, 2012; Lebrenton et al., 2009).

We generated two modelling frameworks based on two alternative assumptions of bull trout population structure in the UFW: (1) A parametrically concise model where movement probabilities of all tagged individuals were assumed independent of stock (termed the single-stock model) and (2) a more complex, multi-stock model that used genetic assignment information obtained from Taylor et al. (2021) to allocate individuals to one of five possible stocks (i.e. Goat River, Milk River, Chalco Creek, Walker Creek or a single outgroup), each with its own movement matrix. Our choice of tributaries included within the multi-stock model was based on sample size (i.e. we included populations where >20 individuals were tagged).

We assigned individuals to one of the five populations based on their probability of genetic assignment to the population based on Taylor et al. (2021). We ran the multi-stock model three times under 75%, 85% and 95% assignment confidence to explore the impact of the inclusion cut-off on model results. The composition of the outgroup varied by model run and was comprised of two data types: (1) any tagged individual(s) with probability of genetic assignment below the model run assignment confidence cut-off (i.e. 75%, 85%

TABLE 3 Notation of indices and parameters for bull trout state-space capture–recapture model including prior probability distributions and likelihood functions.

or 95% confidence) and (2) any individual(s) (with assignment confidence above the percentage cut-off) belonging to a tributary with a sampled population size <20 individuals.

2.3.2 | Model structure

We built our multi-state capture–recapture model with two components: (1) state equations describing the true development of state membership through time and (2) detection equations that map detected states, recorded as individual detection histories, to true states. We used a four-dimensional state transition matrix (Ω) (where dimensions represent stock, season, state of departure and state of arrival) to describe the true state. We applied this matrix form in both the single stock (i.e. stock fixed at one) and multi-stock (i.e. five stock) models. In Table 3, we define all indices and parameters presented within the model. We define each element $\omega_{i,t,a,k}$ of Ω , the probability of an individual's true state (S) at time t given its state in the previous time-step using two parameters: the probability of apparent survival (\emptyset) and the transition probability between states (ψ).

While apparent survival can represent either tag loss or individual mortality, for the purpose of the model discussion here, we label both fates as 'dead'. We defined the transition probability from a living to a dead state as $1 - \emptyset$, and once dead, we could no longer encounter a fish (i.e. they remained in the dead state with a probability of one, and the probability of transitioning between dead and alive states was zero). We also assumed no additional mortality occurred during transition events and ordered events such that survival occurred prior to movement. We define the probability of moving between alive states (i.e. spatial areas) by

$$\Omega_{st,se,a,k} = \emptyset * \psi_{st,se,a,k}, \quad (1)$$

where a represents the state at time t , and k represents the state at $t + 1$. To estimate the probability of apparent survival (\emptyset), we assumed that this parameter was uniform across stocks, areas and sampling occasions. We calculated area-dependent transition probabilities (ψ) using a gravity model and then calculated the transition probability of an individual moving from area a to area k ($\psi_{st,se,a,k}$) using a logit function to constrain all rows of the state transition matrix to sum of 1:

$$\psi_{st,se,a,k} = \frac{e^{G_{st,se,a,k}}}{\sum_k e^{G_{st,se,a,k}}} \quad (2)$$

We did not estimate the first term in each row of the transition matrix ($G_{st,se,a,1} = 0$; i.e. fixed at zero) and jointly estimated G terms in all subsequent sampling occasions as:

$$G_{st,se,a,k} = \begin{cases} g_k & a \neq k \\ g_k + v & a = k \end{cases} \quad (3)$$

such that state transitions (i.e. from state a to state k) were proportional to the gravity weight of each area k , and the probability of remaining in the same area was proportional to that gravity, with slope v .

To define detection probabilities, we used a four-dimensional detection matrix (Θ) with dimensions 'true state', 'detected state', 'stock' and 'season'. We used site-specific redetection probabilities (ρ_{i,t,a_0,k_0}) to estimate individual detection probability in one of the seven location states and estimated the probability of an individual not being detected as $1 - \rho_{i,t,a_0,k_0}$.

2.3.3 | State-space estimation

The state-space model was conditional on first capture, and therefore, we did not estimate initial capture probabilities for each individual. Instead, we used the vector of first capture f_{s_i} for each individual as the individual's detected state at first capture (i.e. tagging event) such that

$$z_{i,f_i} = f_{s_i}, \quad (4)$$

where matrix z with elements $z_{i,t}$ denoted the true state of each individual i at time t . We estimated the development of state membership of each individual for each subsequent occasion as

$$z_{i,t+1} | z_{i,t} \sim \text{categorical}(\Omega_{z_{i,t},1 \dots S,i,t}), \quad (5)$$

with the likelihood estimation linking detected and true states given by

$$y_{i,t} | z_{i,t} \sim \text{categorical}(\theta_{z_{i,t},1 \dots O,i,t}), \quad (6)$$

We approximated posterior density functions for parameters of interest using the Markov chain Monte Carlo algorithm implemented using JAGS (Just Another Gibbs Sampler; available from <http://mcmc-jags.sourceforge.net/>; Plummer, 2016) implemented through R (R Core Team, 2022) using the R2Jags package (Yu-Sung & Yajima, 2015). We ran three chains for 40,000 iterations after a burn-in of 20,000 iterations and thinned final posterior estimates by 20. We evaluated convergence using the Gelman-Rubin diagnostic tool (Brooks & Gelman, 1998) and visual inspection of Markov chain trace plots for each parameter.

2.3.4 | Model assumptions

To use the above model, we had to make several assumptions: (1) no loss of implanted radio telemetry tags during the study, (2) both fixed and mobile telemetry receivers recorded states without assignment error, (3) all states and all individuals were independent, (4) all states and individuals shared a single probability of survival and (5) transition and detection probabilities were shared across all individuals within the single stock model, or in the case of the multi-stock model, within stocks.

2.3.5 | Sensitivity analysis

We conducted a sensitivity analysis to determine if alternative genetic assignment cut-offs of 75%, 85% and 95% assignment probability visually impacted predicted probabilities of transition as estimated in transition matrices. To assist with model selection, we also compared goodness of fit between the single- and multi-stock model using the deviance information criterion (DIC; Spiegelhalter et al., 2002) with the 'best' performing model providing the most statistically robust characterization of bull trout in the UFW.

3 | RESULTS

3.1 | Demographics of the tagged population

We radio-tagged 169 unique individuals over the 6-year study period. We tagged the majority of fish (132 fish, 78%) within the months of July and August in low-order tributaries of the Fraser River (i.e. known spawning habitats; Figure 2) and tagged the remaining 37 fish (22%) within the months of April, May and October within the mainstem Nechako River (see Table 1). Individual fork lengths ranged from 395 to 865 mm with an average length of 596 mm (± 94 mm). Individual weights ranged between 430 and 5500 g with an average weight of 2217 g (± 1041 g). We were able to identify the sex of 128 of 169 individuals during tagging surgical procedures (sex ratio of 70 males to 58 females) and all 128 individuals were classified as reproductively mature. Our telemetry tracking network of stationary receiver stations and mobile effort resulted in a total of 943 detections over the 6-year period. We detected a total of 148 individuals (~88%) at least twice while we did not detect the remaining 21 individuals (~12%) again. Further, we detected 94 individuals (~56%) over a multi-year period (i.e. greater than 1-year duration).

3.2 | Field detections of individual movements

We detected a large proportion of tagged individuals tracked over a multi-year period making repeated, seasonally specific movements between spatially segregated habitats within the upper Fraser watershed. Specifically, 74 of 94 individuals (i.e. 78.7%) were detected using the upper Fraser River as a migration corridor between overwintering and foraging habitats within areas 3–6 (i.e. mainstem Nechako and Stuart rivers) and spawning habitats within area 7 (i.e. upper Fraser River mainstem and tributaries) during the annual spawning and post-spawning dispersal periods. Generally, we did not detect fish in the monitored lakes at any time of year (i.e. only 17 of 169 tagged individuals were detected entering or leaving via lake outlets, for a total of 23 detections). Individuals were detected migrating significant distances to reach seasonally appropriate habitats, as evidenced by numerous detections of fish initially tagged in spawning habitats within area 7 and later detected in areas 1 to 6,

representing a minimum travel distance of ~250 km (i.e. 77 of 108 tributary tagged fish for which more than one detection event occurred). The furthest migration distance we detected was greater than 600 km for an individual tagged within the spawning habitat in Chalco Creek and later detected in area 1.

Following the spawning period (i.e. August–early September), most tagged fish initially demonstrated the same post-spawning dispersal pattern from area 7. Across stocks, 74 of 94 individuals (i.e. 78.7%) detected over a multi-year period initially made post-spawning movements downstream from tributaries into the mainstem Fraser River in September and October then proceeded downstream to the confluence of the Fraser and Nechako rivers. All of these individuals then dispersed broadly across areas 3 to 6, migrating upstream within the Nechako and Stuart rivers for distances greater than 190 km. Individuals were also detected returning to the same river to overwinter from year to year (i.e. only five of 94 individuals were detected overwintering in both the Stuart and Nechako rivers).

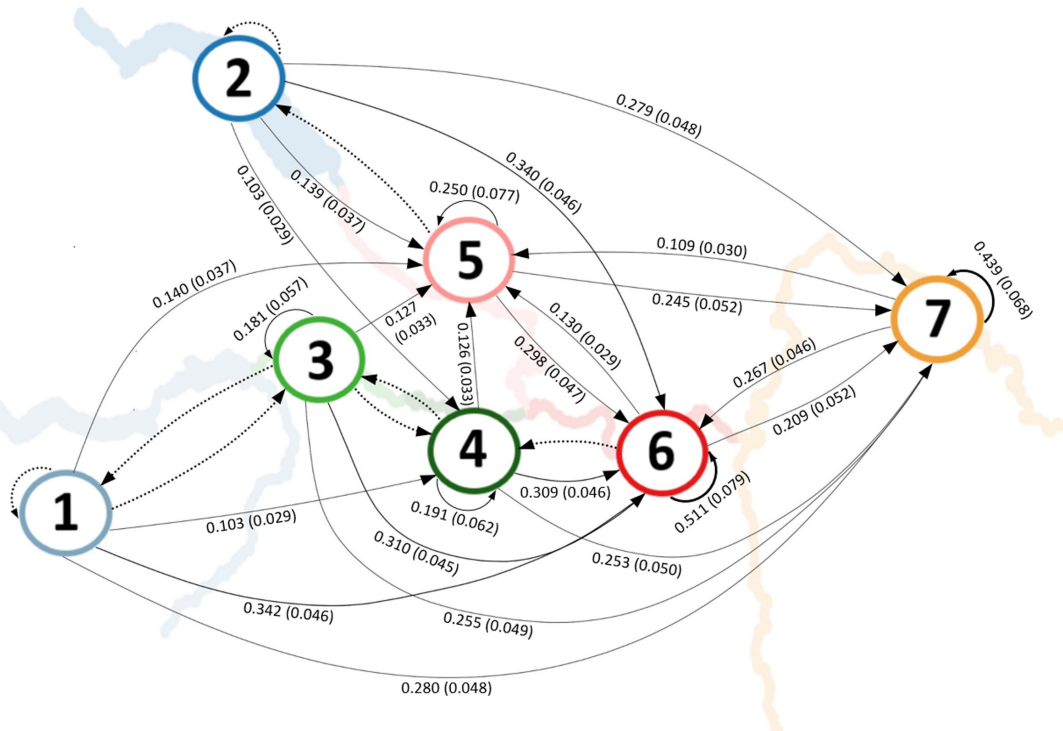
3.3 | Model choice and apparent survival rates

Our sensitivity analysis did not demonstrate an effect of varying assignment accuracy cut-offs on transition probabilities in the multi-stock model. The parametrically concise single-stock model was the DIC-preferred model with a DIC of 1631 relative to 1676 for the stock-specific model (i.e. multi-stock model). Our results suggest that the data support the single-stock model, implying no broad differences in movement probabilities between the four stocks or the outgroup at the spatial scale investigated. All results presented here are based on the selected best model (i.e. the single-stock model). We estimated the apparent survival rate across populations and seasons as $\phi = 0.832$ (median, MD) with a 95% credible interval (CI) of 0.793–0.868.

3.4 | Model predicted inter-season transitions

For the transition from TB2 ('stationary') to TB1 ('moving') (TB2 \rightarrow TB1), the multi-state model predicted the highest transition probabilities as stationarity in area 7 or area 6 (MD = 0.809, CI = ± 0.061 and MD = 0.504, CI = ± 0.071 , respectively; Figure 3; Supplement). The model also predicted higher probabilities of state transitions in a downstream direction from areas 1 to 6 (representing Stuart, Fraser and François lakes and the Nechako and Stuart rivers) into area 7 (Fraser River and associated tributaries) than any other directional movement pattern. Fish were also predicted to remain in habitats within areas 3–6 with median transition probabilities > 0.300 , potentially reflecting station-keeping behaviour. In contrast, fish were not predicted to make transitions away from area 7 or between areas 1 and 6 in an upstream direction (median transition probabilities < 0.100). Fish were also not predicted to transition to or remain within areas 1 or 2, which represented François Lake, the upper Nechako River (i.e. upstream of Nautley River) and Stuart Lake (median transition probabilities < 0.100).

(a)



(b)

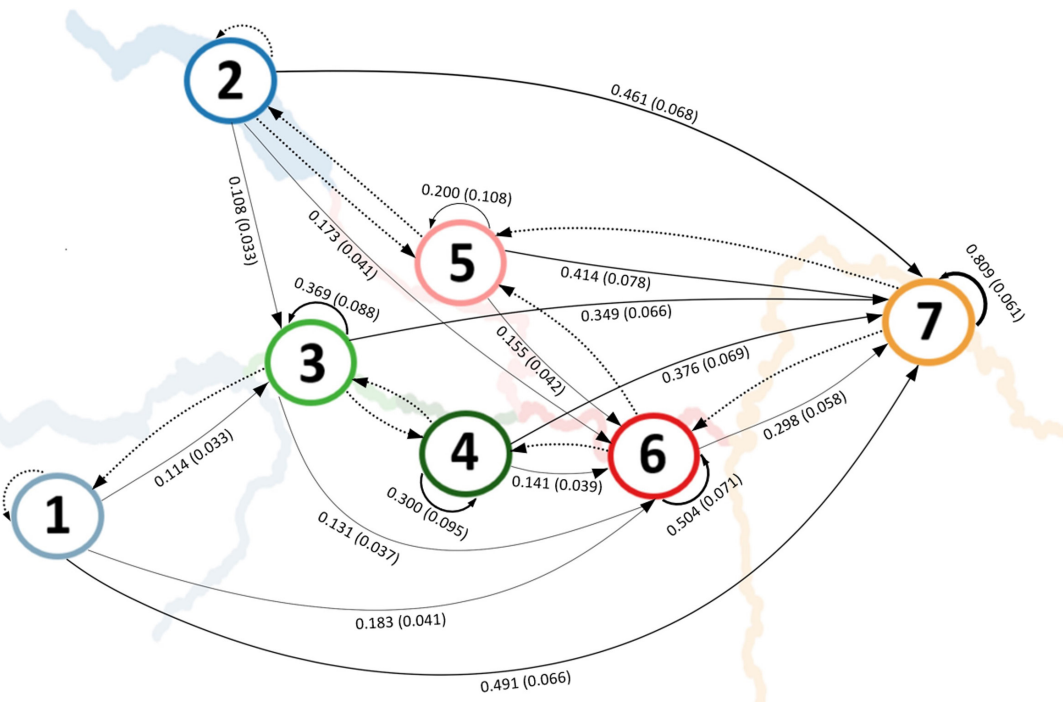


FIGURE 3 Inter-seasonal, area-to-area estimated state transitions (movement probabilities) for bull trout within the UFW. Transitions from time-block 1 to time-block 2 are presented in panel (a), and transitions from time-block 2 to time-block 1 are presented in panel (b).

In contrast, for the transition between TB1 ('moving') to TB2 ('stationary') (TB1→TB2), the model predicted relatively higher state-transition probabilities for the majority of possible transitions compared to that predicted for TB2→TB1. This suggests rather than the directional movement pattern predicted for TB2→TB1, bull trout dispersed broadly across the UFW. The highest transition probabilities were stationarity in area 6

(MD=0.511, CI=±0.079) and area 7 (MD=0.439, CI=±0.068) followed by movements from areas 1, 2, 3, 4, 5 to area 6 (MD range=0.309–0.342). Similar to predictions for TB2→TB1, the lowest transition probabilities were from areas 3–7 to areas 1 and 2 which represented François Lake, the upper Nechako River (i.e. upstream of Nautley River) and Stuart Lake (median transition probabilities <0.100).

4 | DISCUSSION

Bull trout populations across the species' range are regularly impacted by agriculture, mining, forestry, hydroelectric power and human development. Many observed population declines have been strongly linked to anthropogenic impacts resulting from these human activities (Fraleigh & Shepard, 1989; Hagen & Decker, 2011). Populations exhibiting migratory life histories have the potential to be significantly impacted by habitat fragmentation and degradation through reductions or loss of access to seasonally important habitats (Hagen & Decker, 2011; Neraas & Spruell, 2001; Rieman & McIntyre, 1993). Therefore, it is critical that we improve our understanding of bull trout movement behaviour to appropriately prioritise conservation actions, identify restoration opportunities and define where anthropogenic impacts will have the largest negative effects (Cadran & Secor, 2009; Hilborn & Walters, 1992; McIntyre et al., 2016; USFWS, 2015).

We tracked individual bull trout movements, estimated inter-seasonal movement probabilities between key habitats and explored stock-specific variation in movement behaviours and habitat use for UFW fluvial bull trout. To our knowledge, this is the first bull trout investigation to use a multi-state capture–recapture model to estimate seasonally specific movement probabilities and apparent survival rates for the species or to use a combination of telemetry, capture–recapture modelling and genetic information to explore if (and how) post-spawning dispersal patterns differ across spawning populations in a watershed.

4.1 | Seasonal movement patterns

Bull trout movement patterns occurred with high seasonality. Similar to observations in other studies (e.g. Bahr & Shrimpton, 2004; Muhlfeld & Marotz, 2005), we detected peak movement periods in spring and fall, preceding and subsequent to spawning. Individuals were detected to regularly travel significant distances (i.e. >250 km one way) and used the Fraser River as a migration corridor between distinct habitats for spawning, overwintering and foraging. Previous bull trout research has observed similar long-distance migrations and spatial segregation between habitats used for specific behaviours (e.g. spawning, overwintering, foraging); however many of these studies were shorter in duration or used smaller sample sizes than our investigation (e.g. Morice River watershed, Bahr & Shrimpton, 2004; upper Salmon River basin, Schoby & Keeley, 2011) and/or occurred in artificially fragmented systems (e.g. upper Flathead Basin, Muhlfeld & Marotz, 2005; Mill Creek, Starcevich et al., 2012; Blackfoot River drainage Swanberg, 1997).

Importantly the results of the CJS model suggest that at the spatial scale investigated, bull trout from multiple distinct spawning locations are using spatially segregated, key habitats within the UFW in a similar way. Our work builds on past bull trout movement monitoring across the species' range through the use of a relatively large sample size ($n=169$) of tagged migratory fish, composed of several spawning populations, monitored over an extended time period

(approximately 6 years), in a large and highly connected watershed. Taken together, the current investigation and past work, particularly that of Muhlfeld and Marotz (2005), Starcevich et al. (2012) and Taylor et al. (2021), highlight the importance of protecting, restoring and maintaining a diverse assemblage of complex habitats and the natural connections between them. Critically, such actions must occur over a large enough spatial scale to permit the full expression of bull trout migratory life histories (Muhlfeld & Marotz, 2005).

Our findings have implications for both fisheries management and conservation initiatives aimed at identifying and protecting critical habitats. It is important that we resolve uncertainties surrounding the specifics of how and where fish move through time to allow us to develop fisheries management practices that adequately account for population- and community-level processes. This is of particular relevance for species like bull trout that demonstrate migratory or aggregating behaviours, as individuals or population groups may have increased susceptibility to either exploitation or anthropogenic impacts in specific locations and/or at specific times (Hilborn & Walters, 1992; Lucas & Baras, 2000; Taylor et al., 2014).

Many regions of North America are considering or undergoing dam decommissioning and removal to reconnect watersheds (Bellmore et al., 2017; Magilligan et al., 2016; Sullivan et al., 2019). Our findings may provide additional support for the ecological importance of watershed habitat connectivity. This is relevant considering we detected UFW bull trout travelling several 100 km distances between preferred spawning and overwintering habitats. Dams and other barriers to fish passage may not only prevent connection between marine and freshwater systems but can also prevent connection between spatially distinct habitats important to various life history processes within freshwater species like bull trout (Schilt, 2007). Additional studies on large continuous watersheds may further explore the benefits of restoring river connectivity.

4.2 | Post-spawning dispersal patterns

Generally, iteroparous salmonids, including bull trout, make upstream spawning migrations that are followed by downstream post-spawning dispersal to access overwintering and foraging opportunities, which permit higher growth potential (DuPont et al., 2007; McPhail, 2007; Northcote, 1984; Power, 2002). Bull trout in our study demonstrated post-spawning dispersal movements contrasting this pattern. Most of the bull trout we tracked over a multi-year period (~80%) initially dispersed downstream from tributary spawning habitats through the Fraser River to its confluence with the Nechako River, then migrated upstream, dispersing broadly within areas 3–6. Although multiple bull trout movement studies have observed upstream dispersal towards overwintering and foraging habitats, in most cases, this behaviour has been observed in populations exhibiting an allacustrine (i.e. outlet spawning, lake rearing) life history (but see Starcevich et al., 2012) and with reported upstream movements generally <50 km (DuPont et al., 2007;

Herman, 1997; Hogen & Scarnecchia, 2006; Starceвич et al., 2012; Watry & Scarnecchia, 2008). Fluvial fish in our study moved substantially longer distances upstream (up to >190 km).

Past work has not broadly identified causes of bull trout upstream dispersal behaviour. Generally, migrations are triggered by factors such as unfavourable environmental conditions, limited resources (e.g. prey or preferred microhabitats) or competition (Bell, 1991; Northcote, 1984). Bull trout post-spawning dispersal has been linked to multiple environmental cues including decreased water temperature, habitat exclusion and perhaps flow changes (Bjornn, 1971; Jakober et al., 1998; Muhlfeld & Marotz, 2005).

Field detections and model predictions for TB1 → TB2 transitions demonstrate bull trout disperse broadly across available overwintering and foraging habitats present in the UFW. This dispersal may result in increased individual survival through adverse winter conditions and may also serve to reduce competition (Brown et al., 2011; Howell et al., 2016; Jakober et al., 1998). Portions of the Fraser, Nechako and Stuart rivers all have the capacity to provide suitable bull trout overwintering habitat (i.e. protection from frazil and anchor ice and protection from terrestrial and avian predators; Brown et al., 2011; Jakober et al., 1998). Unfortunately, limitations in the spatial extent of our telemetry receiver network did not permit us to explore the prevalence of bull trout movement south of the Fraser River's confluence with the Nechako River nor were we able to consider potential survival rate variation between these two regions.

It is likely that bull trout dispersing upstream into the Nechako and Stuart rivers encounter improved foraging opportunities that are not available within the mainstem Fraser River upstream of its confluence with the Nechako River. In portions of their range, bull trout have been identified as important Pacific salmon predators (Brown, 1995; Furey et al., 2015, 2016, 2021; Furey & Hinch, 2017; Lowery & Beauchamp, 2015). Bull trout dispersing upstream into overwintering and foraging habitats within the Nechako and Stuart rivers may be exploiting seasonal resource pulses (i.e. emerging and dispersing Pacific salmon fry and smolts). Nechako and Stuart river Chinook salmon peak emergence occurs in spring (Nechako: April through early May; Stuart: mid-May), with Nechako and Stuart Chinook fry and Stuart sockeye smolt dispersal occurring from April to July (Bradford, 1994; Envirocon Ltd., 1984; NFCP, 2005; Taylor & Bradford, 1993). Unfortunately, we were unable to specifically estimate bull trout movement patterns in response to Pacific salmon emergence, fry dispersal and smolt outmigration in the system due to the temporal scale of our two modelled time blocks. However, visual inspection of field detection data showed detections in areas 3, 4 and 6 increased and reached the maximum value observed over the calendar year in April, May and June, corresponding to Chinook and sockeye salmon emergence and dispersal timing. Further, past diet research in the Nechako River (see Brown, 1995) and direct observations during tag deployment identified Bull Trout as Pacific salmon predators.

When deploying radio tags in the Nechako River, we identified the presence of schooling salmon smolts in areas where we captured bull trout. Further, opportunistic diet sampling of five bull trout angling mortalities directly identified bull trout consuming Pacific salmon smolts. We found four of the five mortalities contained stomachs full of smolts (i.e. stomach content smolt counts of 44, 20, two individuals where smolts were not enumerated and one empty stomach). Our findings support the theory that food availability is a strong driver of long-distance seasonal bull trout movements, which could be investigated further with targeted studies. If UFW bull trout are exploiting Pacific salmon smolts during their outmigration, it has strong implications for the management and conservation of these species. For example, management actions impacting the survival and escapement of sockeye or Chinook salmon throughout their adult life stages could drive variations in future juvenile abundance, which in turn could lead to shifts in bull trout behaviour and distribution within the UFW (Taylor et al., 2021).

Generally, we did not detect individuals moving between overwintering/foraging and spawning habitats on an obligatory, annual basis. Further, model outputs of predicted inter-season transitions between both time blocks (i.e. TB1 → TB2 and TB2 → TB1 transitions) showed a relatively high probability of individuals remaining within a specific area (e.g. transition from area 6 to area 6) between time blocks. This behaviour is likely reflective of individuals that skip spawning for a year, a behaviour that has been well observed in bull trout populations across the species' range (Bahr & Shrimpton, 2004; Fraley & Shepard, 1989; Goetz, 1989; Hogen & Scarnecchia, 2006; Johnston & Post, 2009). We detected bull trout stationarity regardless of how recently a fish was tagged, indicating it was not a response to recent tagging (i.e. a tagging effect). In years where individuals left overwintering and/or foraging habitats to spawn, they generally made post-spawning dispersals back to the general location where they had been detected prior to spawning. The spatial extent of each area modelled meant that we could not investigate finer level fidelity to overwintering and foraging habitats within the UFW. However, others have observed bull trout to have high site fidelity to both spawning and overwintering locations (Bahr & Shrimpton, 2004; Starceвич et al., 2012; Swanberg, 1997). The populations we studied here also demonstrated significant levels of genetic differentiation (see Taylor et al., 2021), which also implies some spawning site fidelity.

4.3 | Limitations

Our ability to explore bull trout movements was restricted to the spatial extent of the stationary receiver network. As a result, the inclusion of additional receivers, specifically at the mouths of spawning tributaries could impact our model selection by making population-specific spawning dispersal patterns clearer. However, the research questions we aimed to address within our analysis related to post-spawning dispersal patterns, and if and how these

movements vary between different spawning populations. We therefore strongly believe that our model findings (i.e. single-stock model chosen over the multi-stock model) support that at the spatial scale investigated, populations appear to have similar post-spawning dispersal and overwintering and foraging habitat use.

Our application of the multi-state, capture–recapture model necessitated we make multiple assumptions, all of which have the potential to impact result interpretation. The model required we assume zero tag loss, a common assumption in mark–recapture experiments (Arnason & Mills, 1981). Despite this assumption, we believe it is possible that a small proportion of tags were lost over the 6 year period, which would inflate our estimate of apparent mortality (Arnason & Mills, 1981; Rudd et al., 2014). We attempted to minimize potential tag loss by surgically implanting tags. However, low rates of tag shedding could still occur if sutures dissolved before surgical incisions fully healed (Bridger & Booth, 2003) or as a result of wound infection (Bridger & Booth, 2003; Daniel et al., 2009; Rudd et al., 2014; Thorstad et al., 2014). If high tag shed rates are a concern in future analyses, uncertainty regarding rates of tag shedding could be reduced by applying a different multi-state modelling approach (e.g. see Conn et al., 2004) or by using multiple tag types to explore tag retention rates (e.g. see Rudd et al., 2014).

We also applied a structural assumption of similar apparent survival (θ) across states and individuals. In the study region, the most pertinent parameter for future management decision-making was an overall survival rate, rather than temporally or spatially specific rates. Where information regarding the spatial or temporal variation in survival rate is an important study objective, this assumption could be tested within the capture–recapture model or by using an alternative approach (Lebrenton et al., 2009). We also assumed telemetry error (i.e. assignment of false positives) was zero. Given our data cleaning procedures, error was likely very low given the DIC difference between the single-stock (DIC = 1631) and multi-stock (DIC 1676) models. Any existing telemetry error could have masked population-specific differences in movement.

5 | CONCLUSIONS

Unlike in the UFW, bull trout in many regions exist in artificially fragmented systems where their movements are significantly limited (DuPont et al., 2007; Howell et al., 2016; Muhlfeld & Marotz, 2005; Starcevich et al., 2012; Swanberg, 1997). Our work builds on that of others (e.g. Muhlfeld & Marotz, 2005; Starcevich et al., 2012) to further our understanding of how migratory bull trout populations behave and spatially distribute when able to access diverse habitats spread across the full extent of a watershed. The combination of stock level mixing across available overwintering and foraging habitats, the prevalence of similar movement patterns across populations at the watershed scale and the spatial scale of migrations in the UFW highlight the importance of habitat connectivity between tributary spawning and large riverine

habitats. Also, anthropogenic impacts (e.g. habitat degradation, fishing, etc.) have the potential to affect multiple bull trout spawning populations that share critical seasonal habitats. This could reduce the viability of bull trout population complexes within impacted habitats.

AUTHOR CONTRIBUTIONS

This study was conceived and designed by RC, BvP, RP, IS and NG; performed field and/or laboratory work: RC, RP, IS and NG; analysed the data: RC and BvP; contributed materials, reagents and/or analysis tools: RP, IS, NG and SH; wrote the paper: RC and BvP.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data that support the findings of this study are available from the corresponding author upon reasonable request.

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