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Seasonal movement and habitat use of Bull Trout (*Salvelinus confluentus*) near the northern geographic range extent

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Abstract

The movement ecology of Bull Trout (*Salvelinus confluentus*) in watersheds at the northern geographic range extent is not well understood. We implanted 54 Bull Trout with acoustic transmitters in the Prairie Creek watershed, Northwest Territories, Canada and tracked fish from July 2011 to October 2012 using 19 stationary hydrophones. Bull Trout movement patterns generally corresponded to two groups, as a result of individual variation within and across seasons. The first group exhibited seasonal variations in movement and habitat use, moving most (range 11.7–115.9 km) and occupying the largest home ranges in summer and autumn, while exhibiting little movement during winter and spring. The second group made negligible movements within seasons and resided in localized areas. Restricted movement in winter resulted in a severe range contraction. The average distance moved within a season was 11.5 km (range 0.3–64.9 km per fish). The unusually high prevalence of stationarity in this watershed suggest fish can complete all life processes (spawning, feeding, and rearing) in short reaches (<10 km) of Prairie Creek and tributaries. We encourage researchers to replicate our work in other northern watersheds to determine if the life history we describe represents a regional divergence from more southerly populations.

Key words: movement ecology, acoustic telemetry, life history, restricted movement paradigm

Introduction

Fundamental knowledge of movement ecology of freshwater fishes has become increasingly important for the management, conservation, and recovery of at-risk fishes, especially in areas where anthropogenic stressors are prevalent (Lucas and Baras 2008; Favaro et al. 2014; Castañeda et al. 2021). Fish move in response to external state dynamics (e.g., maintain homeostasis) and internal abiotic and biotic factors (e.g., environmental gradients, competition) of their environment, whereby individuals balance expending resources to move with acquiring sufficient resources to grow and reproduce (Brownscombe et al. 2017, 2022). The extent and timing of these movements shape population dynamics, structure fish communities, and influence energy pathways (Nathan et al. 2008; Brownscombe et al. 2017). Despite acknowledging the importance of fish movement in structuring aquatic communities and facilitating energy flow (Torgersen et al. 2021), many questions remain regarding the variability in dispersal patterns within and across freshwater fish taxa (Lennox et al. 2019). Fundamental knowledge of movement ecology of freshwater fishes has become increasingly important for management and recovery of at-risk fishes found in areas where anthropogenic stressors are prevalent (Favaro et al. 2014; Castañeda et al. 2021).

Changes in the structure and function of habitat related to climatic and anthropogenic stressors (e.g., linear development, mining, dams) can alter movement patterns of stream fishes or have direct consequences on abundance and recruitment (Tamario et al. 2019). For migratory stream fishes, alteration or fragmentation of habitat can lead to changes in life history (i.e., migratory to lacustrine or resident; Nelson et al. 2002), reduction in habitat quality and extent, and declines in abundance and range contraction (Fuller et al. 2015; Tamario et al. 2019; van Puijenbroek et al. 2019). Understanding the prevailing movement patterns of stream fish populations is essential for predicting population responses to environmental change. More specifically, an important question directing management of mobile stream fish is whether populations align with the restricted movement paradigm (RMP), which describes populations as heterogeneous mixes of mostly stationary and few mobile fish, or alternatively if populations are comprised of primarily mobile individuals (Gerking 1959; Gowan et al. 1994; Radinger and Wolter 2014).

The magnitude and extent of effects of stressors on stream ecosystems can fluctuate seasonally, based on the interplay of variations in habitat availability and fish movement dynamics. For example, during the open water season migratory fish found in large, free flowing river networks move long distances between discrete habitats to feed, rear, and reproduce (Homel and Budy 2008; Brennan et al. 2019; Hodgson et al. 2020). Conversely during winter, movements are often shorter and less frequent because this season is more energetically costly for freshwater fishes (Cunjak et al. 1998; Shuter et al. 2012; McMeans et al. 2023). Moreover, during the winter fish often become sedentary because they are forced to occupy a narrow range of habitats, due to severe limitations in the extent and quality of habitat relative to the open water season (Cunjak 1995; Brown et al. 2011). Constraints on the distribution of suitable habitat can be amplified across spatio-temporal dimensions (e.g., Dolly Varden (*Salvelinus malma*) spawning habitat, Mochnacz et al. 2020; Pacific Salmon (genus *Oncorhynchus*), Brennan et al. 2019) and emphasizes the importance of understanding the diversity of habitat use and movement patterns throughout the year to mitigate impacts of disturbance on migratory stream fishes (Tamario et al. 2019).

Bull Trout (*Salvelinus confluentus*) are a cold-water char found in North America that exhibit resident, fluvial, adfluvial, and anadromous life history strategies (Dunham et al. 2008). While populations can occur in lakes, the species is most common in stream networks across its geographic range. Research on the movement of this species suggests that life history diversity exists below the population level (Bahr and Shrimpton 2004; Homel and Budy 2008). For example, adult, sub-adult, and juvenile life stages display a broad spectrum of movement patterns (i.e., stationary, mobile) across both temporal and spatial scales (Muhlfeld and Marotz 2005; Homel and Budy 2008; Monnot et al. 2008). Such life history plasticity shapes the distribution of populations at both regional and local scales and facilitates persistence in highly stochastic systems (Dunham and Rieman 1999). In addition, populations found in large, connected watersheds with minimal perturbations are likely to persist over long time periods (Dunham and Rieman 1999; Rieman and Dunham 2000). However, in fragmented systems some populations have either shifted from a fluvial to an adfluvial life history (Nelson et al. 2002; Gutowsky et al. 2015, Al-Chokhachy et al. 2019), or are in decline (Schmetterling 2003). Currently, the species is listed as threatened and special concern in Canada and endangered in the United States (United States Fish and Wildlife Service 1999, 2015; COSEWIC 2012, Government of Canada 2021). While our understanding of Bull Trout movement ecology has advanced in the southern and central portions of the geographic range, parallel research is lacking in the north where wild populations exist in minimally perturbed systems (Mochnacz et al. 2013, 2021).

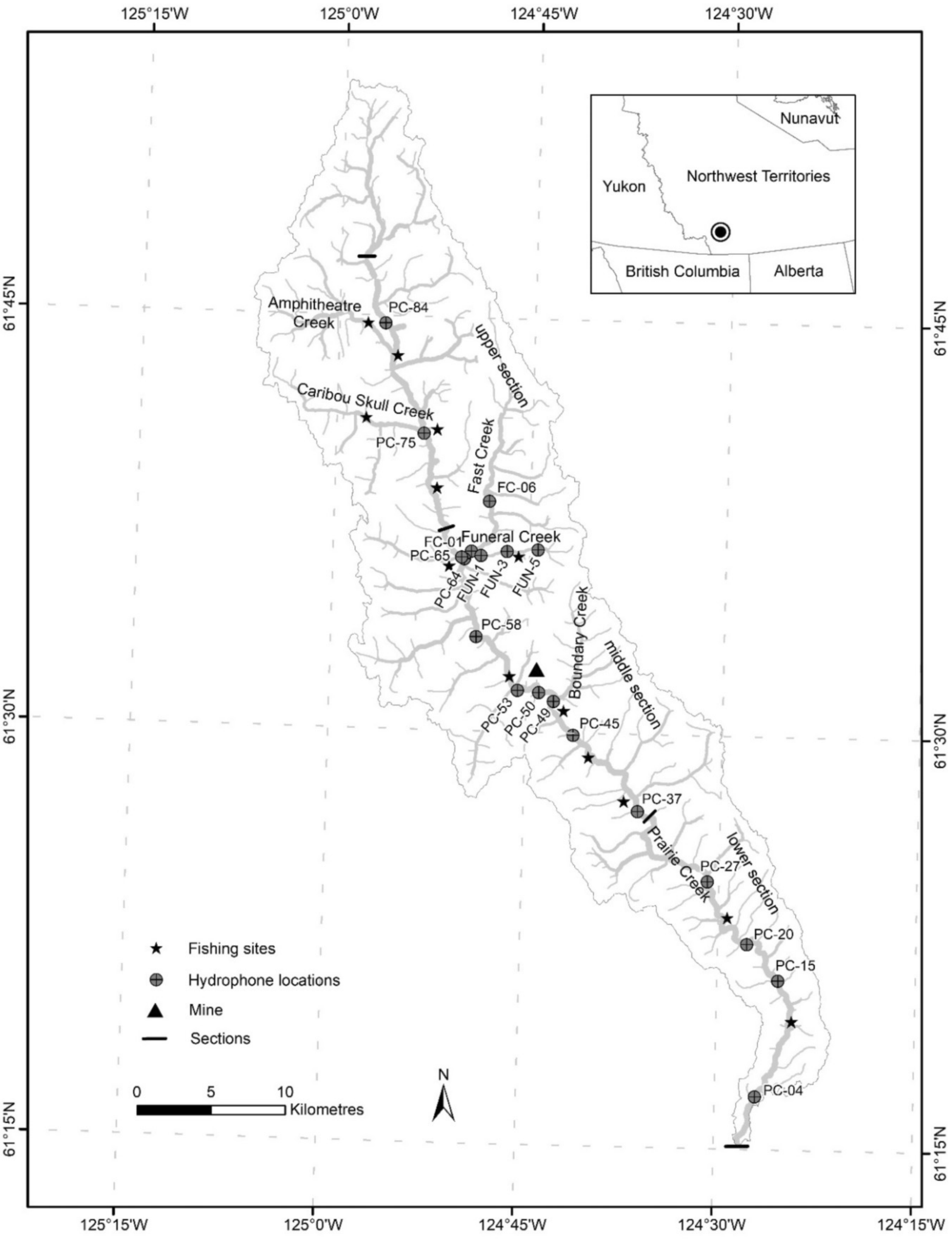
Given northern stream fishes experience short growing seasons and long, cold winters, during which suitable habitat can be spatially limiting (Reist et al. 2006), we sought to document the year-round movement ecology of Bull Trout in a minimally perturbed and highly connected, northern stream network. We expected that some individuals would make minimal movements, within and across seasons, as a life history strategy to conserve energy in this harsh northern environment. To do this, we used telemetry data from Bull Trout tagged in the Prairie Creek watershed, Northwest Territories (NT), Canada, to describe movements and habitat use patterns of this population and discuss implications for conservation of northern populations.

Materials and methods

Study site

Prairie Creek (61°N, 124°W) is a montane sub-basin of the South Nahanni River watershed comprising 498 km of first to fourth order streams with suitable fish habitat (<10% gradient) and encompasses an area of approximately 870 km^2 (Fig. 1). Peak precipitation in Prairie Creek occurs from June to August with approximately 508 mm/year, of which 300 mm/year falls as rain and is approximately half of the annual precipitation experienced by Bull Trout populations in southern watersheds (Monnot et al. 2008). Given its latitude, the climate of the study area is characterized by cool summers (mean air temperature = 9 °C) and cold winters (mean air temperature = −19.5 °C; Halliwell and Catto 2003). Flow rates peak in May–June during the spring freshet and in July–August during high precipitation events (Environment Canada 1991). Flow rates range from 0.5 m^3/s in the winter up to 30 m^3/s during summer (Environment Canada 1991). The lower section of the creek is turbulent and fast flowing, characterized by deep plunge pools, pools created by stabilized rock fall, and swift run and riffle sequences (Fig. 1). Flood cycles in this reach have removed much of the finer clasts, leaving cobble and mid- to large-size boulders. The few tributaries feeding the lower half of Prairie Creek are short and almost entirely ephemeral. The middle section contains well-defined pool, run, riffle sequences and some of the deepest pools available to fish in this stream network (Fig. 1). Above this, the upper section of Prairie Creek changes dramatically to rolling hills dominated by shale, calcareous shale, and minor sandstone (Halliwell and Catto 2003). Most first order tributaries to the upper half section remain steep (>15%), ephemeral for portions with surface flow largely dependent on summer rain events, with occasional cascades preventing fish passage (Fig. 1). Several areas in the middle and upper sections of the watershed are lower gradient and fish bearing, and experience perennial groundwater contributions to baseflow that prevent shallower streams from completely freezing in the winter (Halliwell and Catto 2003; Mochnacz et al. 2021, 2023). Bull Trout, Slimy Sculpin (*Cottus cognatus*), Mountain Whitefish (*Prosopium williamsoni*), and in the lower reaches, Arctic Grayling (*Thymallus arcticus*) are present in Prairie Creek, but the latter two species are not very abundant and have patchy distributions (Babaluk et al. 2015). A recent study indicated that Bull Trout spawn in eight tributaries to Prairie Creek and previous work, based on size-at-age

Fig. 1. Study area and locations of fish tagging events and acoustic receivers deployed in the Prairie Creek (PC) watershed, Northwest Territories, Canada between 19 July 2011 and 15 October 2012. Prefixes in receiver IDs indicate if they were located in the main stem of PC or in a tributary (FC = Fast Creek or FUN = Funeral Creek). Numbers in receiver names following prefixes indicate river km from the southern extent of PC or from the confluence with the main stem for tributaries. Map projection is NAD83. Sources: 1:50 000 Canadian Digital Elevation Data, Natural Resources Canada; province polygons: Statistics Canada Catalogue No. 92-160-X; state polygons: US Department of Commerce, US Census Bureau, Geography Division, Cartographic Products and Services Branch. This map was created using ArcGIS software by Esri (2019).



data, hypothesized that resident forms evolved in several of these locations (Mochnacz et al. 2013, 2021).

An advanced exploration mine, which is not yet operational, occurs in the middle section of the creek. It was established to extract exposures of zinc-lead-copper-silver deposits and zinc-lead-silver veins that bisect the valley. The mine is the only human development footprint in the watershed, and includes the main mill, one water storage pond and two catchment ponds, housing and office infrastructure for 180 people, and a 3000 ft gravel airstrip. There is one road that runs adjacent to the mine and a third of the way up Funeral Creek (~10 km), but this represents the only linear development in the watershed (Mackenzie Valley Land and Water Board, https://mvlwb.com/registry/mv2020l2-0003).

Fish sampling and tagging

A total of 54 Bull Trout were collected from Prairie Creek during 18–23 July 2011 by angling in Prairie Creek at the confluences of suspected spawning tributaries and electrofishing in streams where fish were known to occur (Fig. 1). Mean fork lengths and wet weights of tagged fish were 351 mm (range 288–628 mm) and 458 g (range 240–2500 g), respectively. In northern watersheds, Bull Trout reach maturity at fork lengths between 225 and 400 mm (Mochnacz et al. 2013). Once captured, fish were placed in a 100 L cooler of fresh river water that was refreshed regularly. Bull Trout were then transferred to another cooler where they were anesthetized in 30 L of river water containing 3 g (i.e., 100 mg/L) of tricaine methanesulfonate (MS-222) buffered with sodium bicarbonate. Fish were considered to be fully anesthetized, once equilibrium was lost and ventilation had nearly stopped. Anesthetized fish were placed ventral side up on a V-shaped cradle lined with styrofoam that was kept moist. Gills were continually bathed in freshwater with the exception of flushing the gills with diluted anesthetic solution (20 mg/L) 3–4 times per minute. An incision, 80–120 mm long, was made anterior to the pelvic fins and 10–15 mm adjacent to the ventral midline to expose the abdominal cavity. Before insertion, transmitters were disinfected in 95% ethanol. Incisions were closed by three simple interrupted stiches of polydioxanone (PDS) suture material 3–0 (CP-2 reverse edge cutting needle, Ethicon, Markham, Ontario). Fish were then held in a recovery tub until they were able to re-establish equilibrium and subsequently released.

Two models of transmitters were used, so a broad size range of fish could be tagged and to not exceed the recommended threshold of 2.0% body weight (Brown et al. 1999). Model V9-1 L and V13-1 L acoustic coded tags were implanted in fish and had random pulse rates ranging between 35 and 300 s intervals and battery lives of 239 days (V9) and 531 days (V13) (Innnovasea-Vemco, Bedford, Nova Scotia, Canada). This research was reviewed, approved, and conducted in accordance with Parks Canada Agency Research and Collection permit #NAH-2011-8999 and Fisheries and Oceans Canada, Animal Care Committee, Animal Use Protocol #FWI-ACC-2011-039. All animals were cared for in accordance with the Guide to the Care and Use of Experimental Animals (Vol. 1, 2nd ed., 1993, and Vol. 2, 1984, available from the Canadian Council on Animal Care, 190 O'Connor St., Suite 800, Ottawa, ON K2P 2R3, Canada).

Acoustic receiver deployment

To track fish, an array of 19 omni-directional receivers (model VR2W, Innovasea-Vemco, Bedford, Nova Scotia, Canada) was deployed in the Prairie Creek watershed (Fig. 1). Receivers were attached to 23 kg concrete blocks with the hydrophone oriented toward the surface at depths ranging between 1.0 and 5.0 m. Receivers were systematically placed in locations along the mainstem, and at the mouth, or in suspected spawning tributaries. A cluster of receivers was systematically deployed in the Funeral-Fast Creek stream network because historic occurrence records suggested this could be an important spawning area for this population. Deeper pools, where water velocity was slower, were the preferred receiver locations relative to plunge pool, glide, or riffle habitat, as these locations had the least noise and therefore the highest acoustic tag detectability (Shroyer and Logsdon 2009). Range testing was done and showed that the average detection diameter of each receiver was between 50 and 150 m, which aligns with results of other studies (Shroyer and Logsdon 2009). Because several short sections of Prairie Creek were unsuitable for receiver deployment in the downstream section, we designed the array to try and have an equidistant arrangement of continuous receivers positioned approximately every 8–10 river kilometers (km). In some cases, receivers were placed closer together due to river structure (i.e., confluences of tributaries). Receivers were retrieved, downloaded, and subsequently redeployed in fall 2011, and spring (before freshet), summer, and autumn of 2012.

Data analyses

Data management and statistical model covariates and diagnostics

Raw detection data for individual fish were exported into Microsoft Access for databasing and later exported in raw format for analysis in the R Statistical Computing Platform v. 4.3.2 (R Core Team 2023). Prior to analyses, detection data for each transmitter were filtered based on the minimum tag pulse rates to remove possible erroneous detections and echoes. See results for details.

We used linear mixed effects models (LMMs) to model home ranges and generalized additive mixed effects models (GAMMs) to model probability of movement. Information on model specification and estimation of each of these movement metrics are provided in their respective sections below. In addition to a fixed effect of seasonality (coded as season (factor) in LMMs and week of year (continuous) in GAMMs), models included fish fork length and year as fixed effects. Fish fork length (z-scored) was treated as a continuous fixed effect because body size has been shown to influence movement and habitat use in Bull Trout (Gutowsky et al. 2015) and year was treated as a fixed factor to account for potential differences in movement between years. LMM and GAMM were fit using the R packages *lme4* (Bates et al. 2015) and *mgcv* (Wood 2017), respectively.

Model diagnostics for the LMM and GAMM were performed by examining q–q plot, boxplot, and scatterplots of the normalized residuals, as well as residual lag and auto-correlation function plots (Zuur et al. 2009; Fox and Weisberg 2011). Model diagnostics indicated that no autocorrelation was present in either LMM or GAMM models, but that home range areas needed to be $\log_{10}$-transformed for LMM analysis.

Spatial distribution

Seasonal spatial distribution at the population level was quantified by calculating the proportion of tagged fish detected at each receiver during each season. Proportions were used to account for unequal numbers of individual fish encountered among seasons. Estimates were imported into ArcGIS version 10.5.1 (ESRI, Redlands, CA) and interpolated using ordinary kriging to generate raster layers summarizing the proportion of unique fish detected across the watershed relative to the position of hydrophones across the stream network. The similarity of tagged fish distributions among seasons was assessed using the Fuzzy Kappa statistic, which measures the degree of similarity of each map cell on a scale of 0–1 (Hagen 2003). Fuzzy Kappa statistics were calculated using the Map Comparison Kit software version 3.2.3 Research Institute for Knowledge Systems, BV, Maastricht, the Netherlands (Hagen-Zanker et al. 2006; available from http://www.riks.nl/mck/index.php). Only kriging results that were located within our receiver array were retained and included in resulting figures.

Home ranges

We estimated the home range of each fish separately by season because Bull Trout habitat use changes seasonally based on the need to carry out key life processes (e.g., spawning migrations). Due to generally low movement (i.e., not enough unique relocations per fish/season) and the linear nature of the study system, typical methods to estimate home ranges were not applicable (e.g., minimum convex polygon, kernel density; Kraft et al. 2023). Instead, we calculated the distance between receivers that each fish was detected on during each season and multiplied this by the corresponding average stream widths between these receivers to get a total area of river occupied in km^2. Average stream widths were the mean bankfull channel width throughout the year. Note, that if a river segment between receivers was traversed multiple times, this distance was only added once to the linear distance before multiplying by segment width. Thus, our method provides a method of river area used each season. Although this method is simple, it avoids having to interpolate or position average to meet minimum number of relocations needed for the methods mentioned above and also provides what we feel is the most accurate estimate of the area fish occupied during that season (i.e., a home range) based on our detection histories. For fish that were only detected at a single receiver within a season, the home range occupied was calculated as half the distance between the two neighboring receivers multiplied by the average stream width at the receiver location. This was a conservative estimate where we assumed fish could move part way between neighboring receivers without being detected.

The seasonal estimates of Bull Trout home range sizes ($\log_{10}$-transformed) were then modeled with a LMM with normal distribution and p values were estimated using the *lmerTest* R package (Kuznetsova et al. 2017). Seasonality was incorporated into the LMM as a grouping variable (i.e., factor), with seasons defined based on the timing of key life history events and abiotic conditions. Winter was defined as 1 December–28 February, a period where streams are ice covered and temperatures remain stable; spring as 1 March–31 May, where temperatures begin to increase and streams become ice free; summer as 1 June–31 August, which coincides with open water conditions and the warmest temperatures; and autumn as 1 September–30 November, when temperatures decline and staging and spawning occur. Fish fork length and year were also included as fixed effects in the model. While it would be most appropriate to include a random slope and intercept for each individual fish, the number of random effects needed to be estimated ($n = 168$) would have exceeded our sample size ($n = 138$). Therefore, to test for mean differences in home range area between seasons, while accounting for year and fish size and repeated measures, we ran a LMM with a random intercept for fish ID. Estimated marginal means and post hoc pairwise comparisons of seasons were calculated with the "*emmeans*" package (Lenth et al. 2018). Prior to emmeans, any nonsignificant fixed effects were removed from the model. To illustrate the contribution of individual variation in home range areas between seasons (i.e., that would have been estimated with a random slope and intercept model), we plotted all individual home range estimates superimposed over a boxplot and presented this below marginal means estimates from the random intercept model.

Probability of movement

To compliment spatial distributions and home ranges occupied by each fish, we also estimated the probability of movement across seasons. To do this, we summarized the number of unique receivers each fish visited by week of the year. Given receivers were spaced <1–10 km apart and Bull Trout are capable of covering such a distance over several days or less, one calendar week (1–52) was selected as an adequate time period in which to detect movement—i.e., detections on $\geq$2 receivers. Movement was coded as 0 (detected at only a single receiver) and 1 (detected on $\geq$2 unique receivers) for Bull Trout during each calendar week of the study. Given the data were assessed for 52 weeks a year, seasonal trends in probability of movement were estimated with a binomial GAMM. The preferred method would be to fit a GAMM with a common smoother for week of year plus group-level smoothers for each fish that either differ or are similar in wiggleness (see GI and GS models in Pederson et al. (2019)), but these models did not converge due to our sample size. Therefore, we modeled our data in two ways to obtain both global and fish-specific weekly probability of movement curves. In the first model (GAMM-1), probability of movement was modeled as a function of two smoothers: a thin-plate regression spline for week of year and a random effect for Fish ID to model fish-specific intercepts (see G model in Pederson et al. (2019)). This provided a means to obtain a global seasonal trend while accounting for repeated measures. The second model (GAMM-2) fit probability of movement as a shared smoother model (model S in Pederson et al. (2019)), where an individual smoother is fit for each fish with the same smoothness but the individual shapes of the smooth terms are not related (i.e., factor-smoother interaction). This model allows the seasonal response in movement probability to be modeled individually for each fish to depict individual variation in weekly probability of movement. Both models also contained fish fork length and year as fixed effects (see above). GAMMs fit using *mgcv* use cross-validation which automatically determines the optimal amount of smoothing (Zuur et al. 2009; Wood 2017). Prior to plotting GAMM fits, any nonsignificant fixed effects were removed from the model. In addition to our GAMM modeling, we also calculated the number of movements that occurred across sections of Prairie Creek. Due to the very low sample size, we were forced to summarize the findings by season. These results are qualitatively described rather than modeled.

Results

Of the 54 Bull Trout tagged, 9 (or 17%) were never detected following their release. An additional three fish were detected 2–4 times only within the tagging period (July 18–23 July 2011) and never detected again, so we excluded these fish from our analyses. From the 42 remaining fish, 92 129 detections from a total of 1 179 483 (or <8%) were removed as the time between detections were less than the minimum 35 s tag pulse rate (i.e., the second detection was removed in these cases). The 42 remaining Bull Trout were detected 1 087 312 times with an average of 25 888 times per fish (range 1–201 058 per fish) and ranged in fork length between 288 and 628 mm, while those that went undetected ranged between 293 and 565 mm. The mean fork lengths did not differ between those fish that were detected (345 mm) and those never detected (369 mm) by the array (*t*-test: $t = 0.99$, df $= 14.5$, $p = 0.34$). For those fish detected, the number of detections per fish was not correlated to fish fork length (Pearson correlation: $n = 42$, $r = 0.19$, $p = 0.23$). Fish were detected at 16 of the 19 receivers deployed during the study, but the number of detections varied widely by receiver (range 8–360 599; Fig. 2).

The 42 fish that were detected displayed high individual variation in movement patterns (Fig. 2). Some fish ($n = 16$ or 38%) were detected traveling total linear distances exceeding 10 km during the study (mean 26.9 km, range 11.7–115.9 km). Another group of fish ($n = 9$ or 21%) was detected traveling total distances < 10 km (mean 4.6, range 1.4–9.5 km). The rest of the 42 fish ($n = 17$ or 41%) were not detected making any within season movements during the study (i.e., detected at a single receiver within a season). For the fish that were detected moving, they moved an average of 11.5 km (range 0.3–64.9 km per fish) in distance per season.

Spatial distribution

Bull Trout distribution varied seasonally throughout the study (Figs. 2 and 3). Of the 1 087 312 post-filtered detections, 93.6% occurred in the middle section of Prairie Creek, while only 5.9% and <1% were in the lower and upper sections, respectively (Fig. 2). Overall, fewer fish were detected in winter ($n = 16$) and spring ($n = 14$) compared to summer ($n = 39$) and autumn ($n = 31$) (Fig. 2). During summer, fish were detected in all sections of Prairie Creek, with six individuals detected in each of the upper and lower sections, respectively, and 37 detected in the middle. During spring and winter, no fish were detected in the upper section and only one and two fish were detected in the lower section during these seasons, respectively (Figs. 2*a* and 3). Most tagged Bull Trout stayed within a single section of Prairie Creek (particularly the middle) for the entirety of the study (Fig. 2*a*). In fact, only one fish (tag 8) was detected in all three sections of Prairie Creek during the study, and 12 fish were recorded in two sections (Fig. 2*a*). Fuzzy Kappa statistics indicated that the greatest spatial similarity in Bull Trout distribution occurred between winter–spring (0.80) and summer–autumn (0.74), whereas the greatest difference between seasons occurred between summer–winter (0.34) and summer–spring (0.33) (Fig. 3). A larger proportion of fish were detected in tributaries during summer and autumn than in the winter and spring (Figs. 2 and 3).

Analysis of variance (ANOVA) tests of fixed factors in the LMM found that season was a weakly significant factor describing differences in the sizes of the home ranges of tagged Bull Trout during the study period ($F_{3,99.0} = 2.969$, $p = 0.04$), while fish fork length and study year were not significant (Table 1). On average, home ranges were largest in summer (marginal mean (95% confidence interval; CI): 0.17 (0.11–0.26) km^2) and autumn (0.13 (0.08–0.20) km^2) and smallest in winter (0.08 (0.04–0.14) km^2) and spring (0.07 (0.03–0.15) km^2) (Fig. 4*a*). Pairwise multiple comparison post hoc tests between seasons found that on average summer home ranges were larger than those in winter ($t = 2.57$, $p = 0.01$) and in spring ($t = -2.15$, $p = 0.03$). No other significant between-season differences in home range size were found (all $p \geq 0.1$; Fig. 4). Fixed effects in the LMM only accounted for 5% of total 36% variation in home ranges explained, while the random effects accounted for 31% (Table 1). Individual seasonal home ranges spanned < 0.01 km^2 to nearly 10 km^2 (Fig. 4*b*). The variation between individuals was accounted for mainly by 11 individuals who displayed seasonal home ranges >2 km^2, all of which occurred only in summer or autumn (Fig. 4*b*). Notably, two of these individuals (Fish IDs 8 and 43) were found to have home ranges >2 km^2 in both summer and autumn. Larger home ranges in summer and autumn were mainly due to movement only being detected during these seasons (Fig. 4*b*).

Probability of movement

Bull Trout did not move often during the study, with only 44 instances where an individual fish was detected on more than a single receiver per week (only 6% of unique

Fig. 2. Abacus plot depicting the weekly distribution of detections of acoustic-tagged Bull Trout within the receiver array of Prairie Creek (PC), Northwest Territories between 19 July 2011 and 15 October 2012. (A) shows the number of unique receivers that each fish was detected on during each week. (B) depicts the number of unique fish detected at each receiver during each week. (C) displays number of days during each week that fish were detected at each receiver. The dates on the *x*-axis correspond to the mid-point of each week of the study. FC, Fast Creek; FUN, Funeral Creek.

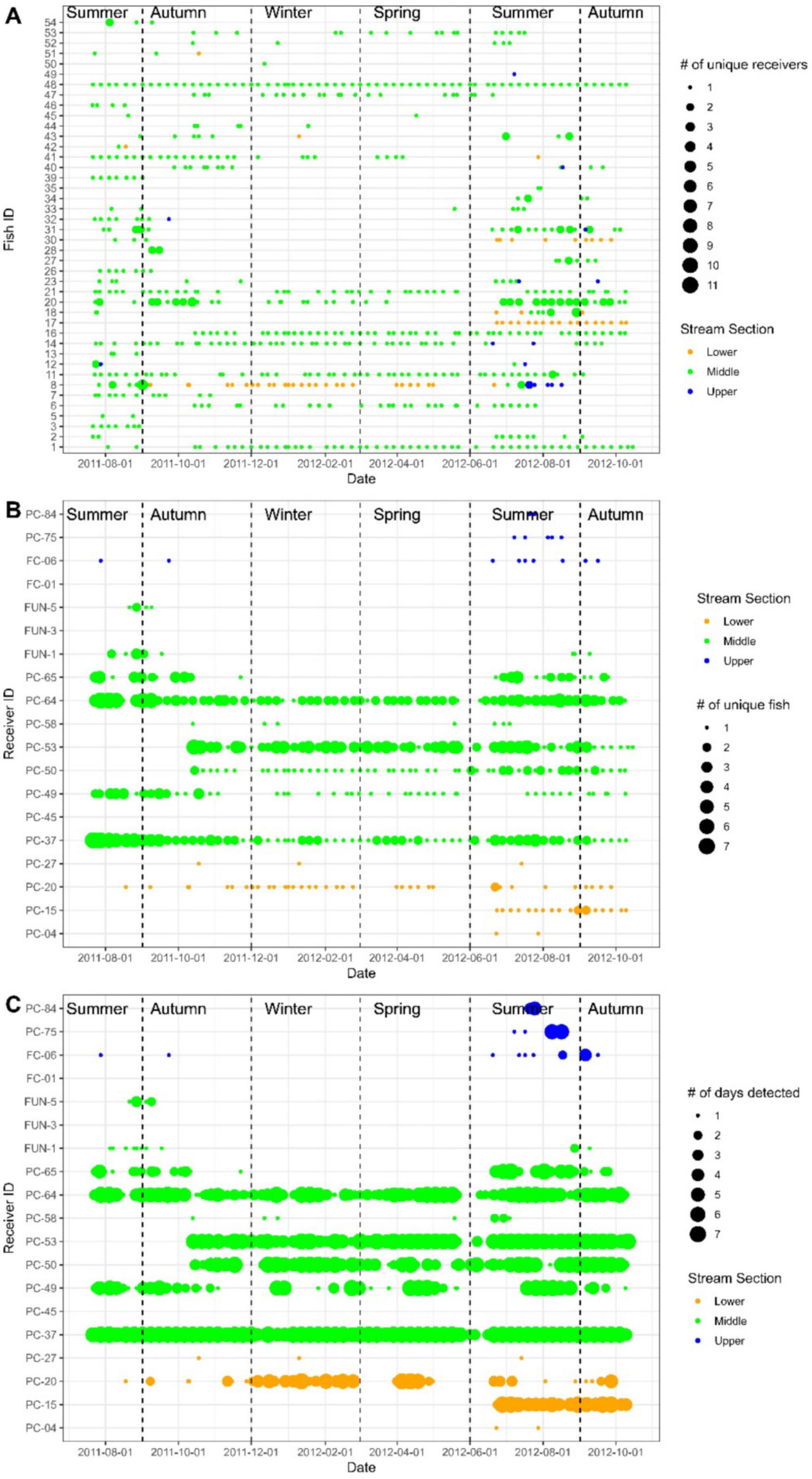


Fig. 3. Seasonal distribution maps of tagged Bull Trout in Prairie Creek, Northwest Territories estimated by kriging (see methods). The number of fish detected in each season is shown in parenthesis. Streams not suitable for occupancy ($\geq$10% gradient) or outside the telemetry array are shown in gray. Map projection is NAD83. Sources: 1:50 000 Canadian Digital Elevation Data, Natural Resources Canada; province polygons: Statistics Canada Catalogue No. 92-160-X; state polygons: US Department of Commerce, US Census Bureau, Geography Division, Cartographic Products and Services Branch. This map was created using ArcGIS software by Esri (2019).

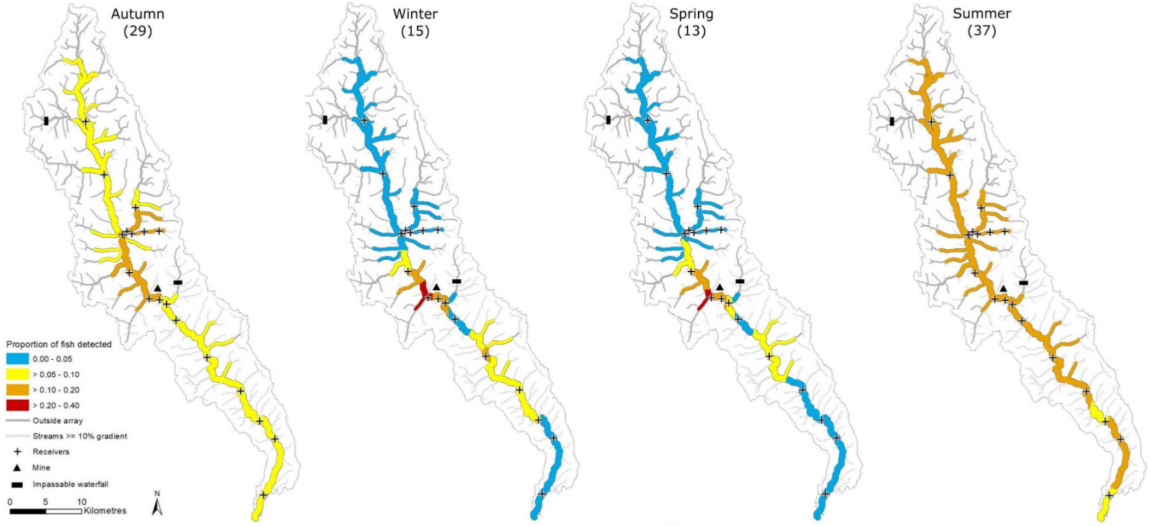


Table 1. Estimates from the linear mixed effects models (LMMs) with normal distribution and binomial generalized additive mixed effects models (GAMMs) of seasonal Bull Trout home range area and movement probability. DF = degrees of freedom; SE = standard error; FL = fork length.

Model	Term	DF	Estimate	SE	Test statistic	*p*-value	R^2
LMM: random intercept log$_{10}$ home range	Intercept	94.8	−0.93	0.10	$t = -8.66$	<0.001	R$^2{}_{m =}$ 0.05 R$^2{}_{c =}$ 0.36
	FL (standardized) ($F_{1,27.9} = 0.43$, $p = 0.52$)	27.9	−0.05	0.07	$t = -0.66$	0.52	
	Year 2012 ($F_{1,108.5} = 0.73$, $p = 0.39$)	108.5	0.08	0.10	$t = 0.85$	0.39	
	Season ($F_{3,99} = 2.96$, $p = 0.03$)	100.1	Spring −0.25	0.18	$t = -1.43$	0.16	
		97.0	Summer 0.11	0.11	$t = 1.02$	0.31	
		101.4	Winter −0.23	0.14	$t = -1.68$	0.09	
GAMM-1: random intercept probability of movement (0, 1)	s(weeks)	3.28	–	–	$\chi^2 = 11.79$	0.02	R$^2{}_{\text{adj}} = 0.45$
	s(fish ID)	21.9	–	–	$\chi^2 = 73.94$	<0.001	
	Intercept	42	−6.07	1.75	$z = -3.48$	<0.001	
	FL (standardized)	1	0.07	0.42	$z = 0.16$	0.87	
	Year 2012	1	0.21	0.48	$z = 0.44$	0.66	
GAMM-2: factor-smoother probability of movement (0, 1)	s(week, fish ID)	34.8	–	–	$\chi^2 = 95.7$	<0.001	R$^2{}_{\text{adj}} = 0.47$
	Intercept	1	−3.70	0.71	$z = 5.22$	<0.001	
	FL (standardized)	1	0.19	0.52	$z = 0.36$	0.72	
	Year 2012	1	−0.10	0.46	$z = -0.21$	0.84	

Note: For LMM, type 3 ANOVA *F*-values and corresponding *p*-values for test of fixed factor significance are provided before each model term and a marginal (fixed effects only) and conditional (fixed + random effects) R^2 value are provided for the model. For GAMM, test statistics are given from the χ^2 for the GAMM component and *z* value for the linear effects components of the model. GAMM-1 model treats individual fish as a random intercept with a global smoother for week of year and GAMM-2 uses a factor smoother interaction between week of year and fish ID. See methods for model details.

fish/week combinations; Fig. 2*a*). However, there was a significant weekly global trend in the probability of movement that followed a uni-modal pattern beginning in late-spring (GAMM-1 in Table 1 and Fig. 5*a*). On average, detections at multiple receivers were low, with average probability peaking in mid-summer (week 33; 0.08 ± 0.02–0.15, 95% CI) and becoming unlikely by early autumn (week 44; Fig. 5*a*). There was no significant effect of body size or year (Table 1), but there was a significant global weekly effect on movement probability, with the intercepts of the weekly pattern varying greatly between individual fish (Figs. 2 and 5*a*). Most fish had negligible movement probabilities throughout the year, 10 fish having low-moderate (20%–50%) peak probabilities, and 2 fish having high peak movement probabilities (>75%). The

Fig. 4. Seasonal home range area (km^2) of 42 tagged Bull Trout in Prairie Creek, Northwest Territories tracked using acoustic telemetry. Panel A presents the global mean ± 95% CI marginal home range estimates for each season from the linear mixed effects model and panel B presents raw seasonal home range estimates for individual fish and corresponding boxplots. Moved relates to whether a fish was detected at more than one receiver during each season. Note that the *y*-axis in panel B is on the scaled to the log$_{10}$, but the values are untransformed.

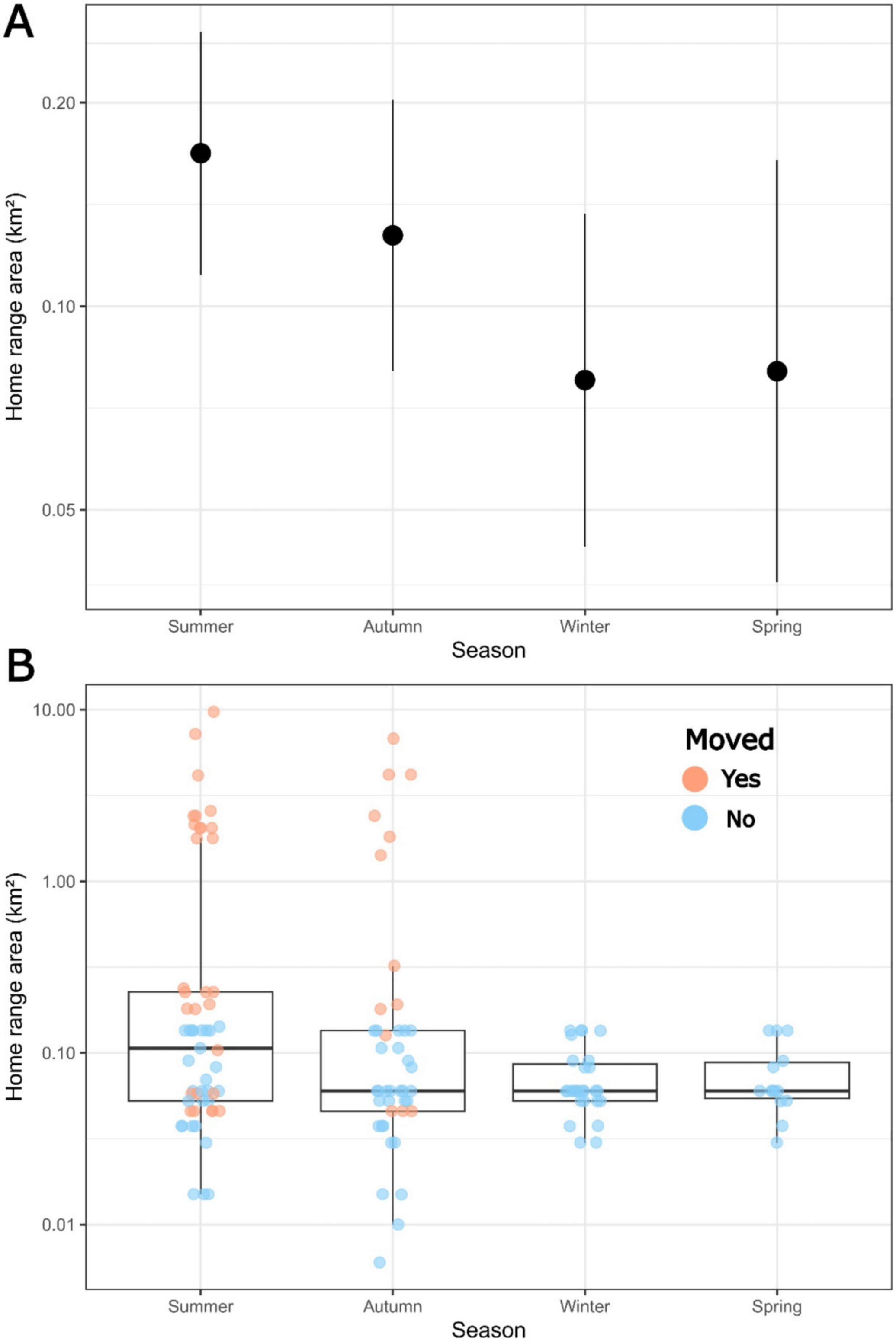
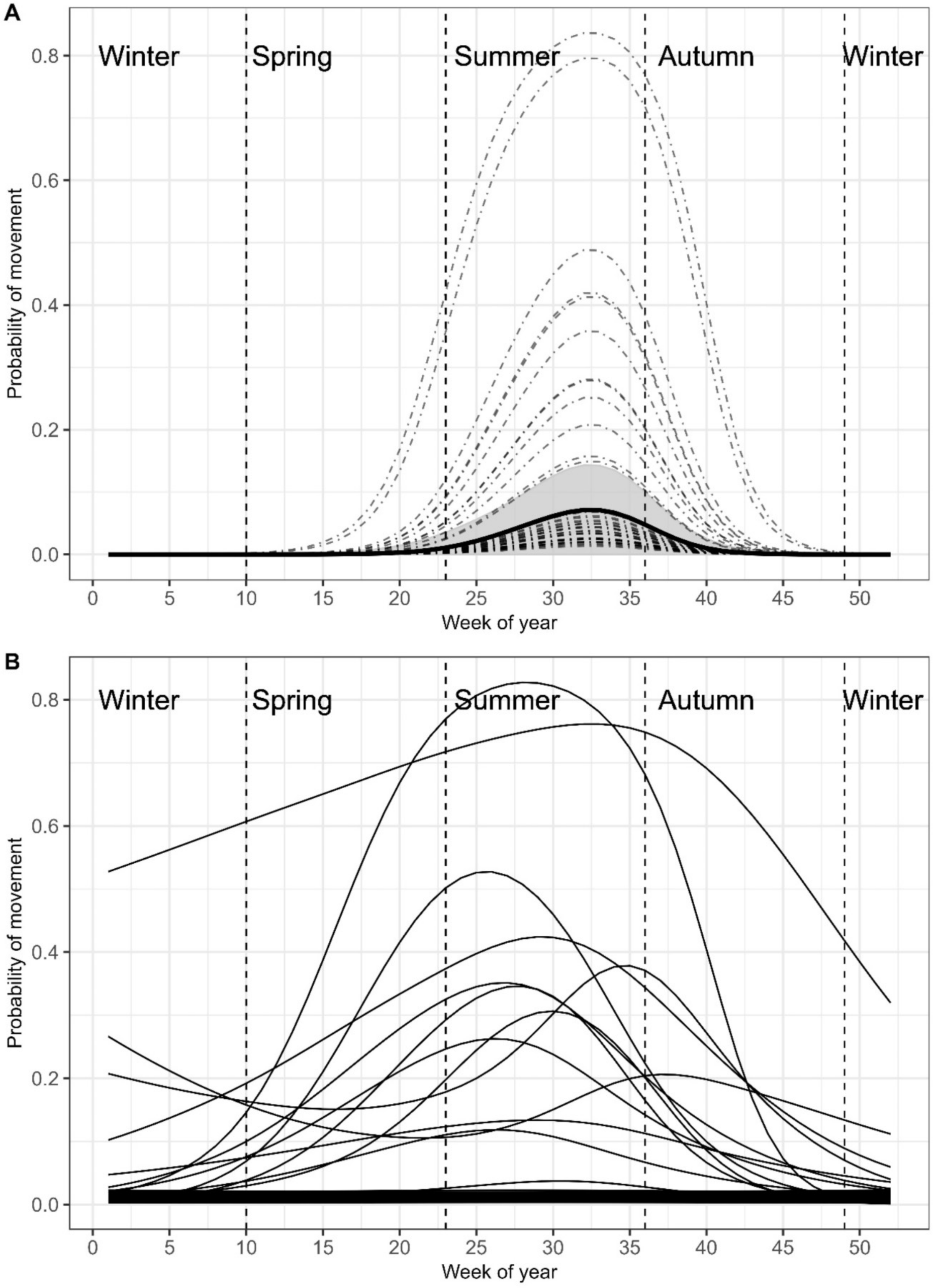


Fig. 5. Generalized additive mixed effects models (GAMMs) derived predicted probability of weekly movement for Bull Trout in Prairie Creek, Northwest Territories based on acoustic telemetry data from the 42 detected individuals. Panel A provides the global mean ± 95% CI (black solid line ± grey shading) and mean individual fish probability curves (dashed lines) obtained from a GAMM with random intercept for fish ID (GAMM-1). Panel B provides the mean probability curves for each fish (black lines) obtained from a GAMM with group-level smoothers for fish ID (i.e., factor-smoother interaction between week and fish ID; GAMM-2).



44 weekly between receiver movements were made by 13 different individuals, with 18 being made by tag 20, 7 by tag 31, and 5 by tag 8. The rest of the fish that moved only did so two times each (Fig. 2). In addition to large variation in probability of movement among fish, the timing of the peak probability also varied between fish (GAMM-2 in Table 1 and Fig. 5*b*). Of the 13 fish whose individual movement probability curves were not flat lined at zero, all but one peaked during summer, with one fish peaking in early autumn (Fig. 5*b*). Together, results of the random intercept (GAMM-1) and group level smoother (GAMM-2) GAMMs both indicate that probability of movement was on average greatest in summer with a large degree of individual variation in peak probability existing between tagged fish.

Bull Trout made even fewer large scale movements between the lower, middle, and upper sections of the Prairie Creek watershed. At a weekly scale, only five between section movements occurred, three in summer and two in autumn. At the seasonal scale, fish traversed between sections 12 times, with eight trips occurring in summer and the remaining four in autumn. No between-section movements were detected in spring or winter (Fig. 2).

Discussion

Using acoustic telemetry, we observed large individual variation in movements and spatial distributions of Bull Trout in Prairie Creek, NT corresponding to two groups. The first group exhibited the greatest seasonal variations in habitat use, moving most (range 11.7–115.9 km) and occupying the largest home ranges in summer and autumn, while exhibiting little movement during winter and spring. The second group made negligible movements within and across seasons and resided in localized areas. The average distance that fish traveled within a season was 11.5 km (range 0.3–64.9 km per fish). Movements outside late summer and early fall migrations were limited in spatial extent, suggesting individuals were able to fulfill their seasonal habitat requirements (e.g., foraging, overwintering) in relatively short river reaches of Prairie Creek or tributaries. High site fidelity, small home ranges, and stationarity for long periods by many individuals aligns with the RMP; however, evidence of this life history strategy should be viewed cautiously, given the capability of our hydrophone array to detect small-scale movements (<10 km). We encourage others to formally test the RMP hypothesis in other northern Bull Trout populations to determine if the life history we describe for the Prairie Creek Bull population represents a regional divergence from more southerly populations.

We observed a large degree of individual variation in movement, where most tagged Bull Trout (62%) exhibited negligible or low movement, while the remaining fish (38%) moved greater distances. All of the within-season movements took place in summer and autumn. The strong seasonal effect on movements in the Prairie Creek watershed is consistent with patterns reported in other Bull Trout populations (Bahr and Shrimpton 2004; Starcevich et al. 2012; Chudnow 2021). Despite similar timing of movements, the fish tagged in our study traveled considerably shorter distances and had much smaller home ranges than reported elsewhere (Salmon River, Schoby and Keely 2011; Columbia-Snake rivers, Starcevich et al. 2012; Fraser River, Chudnow 2021). Although body size is acknowledged as a strong predictor of home range size (Burbank et al. 2023), it was not a strong predictor in our study, which aligns with other telemetry studies on adfluvial and fluvial Bull Trout (Schoby and Keeley 2011; Gutowsky et al. 2015). Interestingly, water body size has emerged as a strong predictor of home range size in lotic fishes (Burbank et al. 2023) and could partly explain the disparity in home range size between our study and those done in much larger watersheds (e.g., Fraser River, Chudnow 2021; Kinbasket Reservoir, Gutowsky et al. 2015).

The large proportion of small movers relative to large movers (~2:1 ratio) we observed in Prairie Creek differs from what others report (7%, Starcevich et al. 2012; 22%, Chudnow 2021) and may reflect a life history adjustment to maximize growth opportunities in a barren northern watershed. Prairie Creek differs from more southerly stream systems (<60°N) in the following ways: it has a less abundant and patchy fish community; a smaller proportion of spawning, rearing, and winter habitat in tributaries (Mochnacz et al. 2021); and has longer (8 months), colder winters (mean air temperature = −19.5 °C) and shorter growing seasons. Given these differences, it is possible that fish move less often and shorter distances because higher energetic costs of longer movements do not yield higher foraging opportunities (Brownscombe et al. 2022). Occupying areas with higher flow in mid to lower reaches of Prairie Creek could be more energetically profitable than upstream reaches and tributaries, where riparian vegetation is particularly sparse and prey species are rare (N.J. Mochnacz, unpublished data) (Kawaguchi and Nakano 2001; Allan et al. 2003; Tank et al. 2010). Additionally, completing all life processes (spawning, feeding, and rearing) in small areas (e.g., <10 km reach) requires fish to expend less energy migrating longer distances to reproduce. Other chars commonly exhibit similar life history plasticity to optimize growth and persistence in unique environments (Klemetsen 2010; Chavarie et al. 2016).

Few and short movements of tagged Bull Trout in Prairie Creek implies high habitat specificity throughout the year, despite having access to a broad suite of streams across this watershed. Such restricted movement has several plausible explanations. First, the most energetically profitable habitats (prey bearing, thermally optimal) are not wide-spread throughout the year in stream networks (Armstrong et al. 2021) and these habitats are even more sparsely distributed across sub-Arctic watersheds (Prowse et al. 2006*b*; Reist et al. 2006). In the Prairie Creek watershed, the availability of suitable spawning and rearing is much lower than similar stream systems further south where this species occurs (Rich et al. 2003; Rodtka et al. 2015; Mochnacz et al. 2021). Consequently, our results suggest that Bull Trout are able to fulfill all life cycle requirements in short reaches of the middle and lower sections of Prairie Creek and some tributaries. Second, individuals may seek to inhabit areas that lack predators. However, predation pressure seems unlikely to restrict movement in Prairie Creek because Bull Trout are the apex aquatic predator in this system (Mochnacz et al. 2021). Lastly, it is possible that many of the fish we tagged did not move to spawning locations because they were not mature or did not spawn during our study. The latter (alternate year spawning) is commonly seen in Bull Trout populations, including this one (Johnston et al. 2007; Mochnacz et al. 2013; Chudnow 2021). Similar full year residence in local areas has been observed in other populations, but far less frequently than what we report (Starcevich et al. 2012; Chudnow 2021).

Habitat specificity was most pronounced during the winter where fish were seldomly observed moving even small distances (>1 km), and most fish resided in the middle section of Prairie Creek. Others report similar lack of movement during winter (Bahr and Shrimpton 2004; Starcevich et al. 2012; Chudnow 2021), but to our knowledge this is the least amount of movement reported during the winter for any fluvial population across the geographic range. Such limited movement in Prairie Creek could be driven by limited availability of suitable winter habitat, also seen in stream networks south of 60°N, but exacerbated by extreme winter conditions in sub-Arctic river systems (Prowse et al. 2006*a*). Recent research in this watershed demonstrates that the availability of thermally viable winter habitat is severely limited by ice conditions in tributaries (Mochnacz et al. 2023) and emphasizes that Prairie Creek serves as an essential winter habitat for this population. As latitude increases the availability of viable spawning and overwintering habitat becomes even more limited for ecologically similar species (Dunmall et al. 2016; Mochnacz et al. 2020). Another important contextual consideration is that winter movement ecology is not well-reported for this species (Al-Chokhachy et al. 2010), due to the challenge of collecting data during winter—a common problem that limits the depth of knowledge on movement patterns for many fishes in North America (Brown et al. 2011; Shuter et al. 2012). Therefore, the limited movement we report for the Prairie Creek population could be common for this species in the winter but not well-documented across the geographic range.

Of the 54 fish tagged in this study, 42 were relocated, while 12 (22%) were either not detected by the array or detected a few times immediately following tagging and never again. There were also a number of fish detected a few receivers (2–4) throughout the study but had large gaps (weeks to several months) in their detection history. There are several possible explanations for nondetection of some tags. First, failing to detect some proportion of fish after tagging is common due to mortality, tag loss, or tag malfunction. In other telemetry studies on Bull Trout, nondetection after tagging ranged between 13% and 45% (Schoby and Keeley 2011; Gutowsky et al. 2015; Chudnow 2021) and our results fall well within this range. Second, the ability of our array to detect movements was limited by the spatial arrangement (on average ~10 km between receivers), rate of movement, and detecting environment. For example, there were three fish that were detected by our array immediately following tagging and then never detected again. These fish either moved to local areas not capable of detection by our receiver array (e.g., moved into tributaries or between receiver detection ranges), or they migrated downstream at a rapid rate without being detected and moved into the South Nahanni River. Even in larger river systems, where hydrophones are presumably detecting tags more effectively because they are in better receiving environments (i.e., less noise), nondetection rates are similar to what we observed (16% nondetection, Gutowsky et al. 2015), providing confidence in our findings.

Conclusion

Bull Trout in Prairie Creek, NT exhibit a large degree of stationarity and individual variation in movement, with most fish having small home ranges but with a few having large home ranges. Our findings suggest that even small losses of habitat could have implications for the Prairie Creek Bull Trout population, especially during the winter, where movement was negligible and habitat specificity was highest (Cunjak 1995). The value of understanding movement patterns and habitat use of stream fish in minimally perturbed stream networks should not be understated, given so few stream networks have not experienced flow modifications in North America (Dudgeon et al. 2006; Olden and Naiman 2009). More broadly, our results add to existing evidence (e.g., Pacific Salmon, Brennan et al. 2019), which demonstrates that migratory stream fish require spatially discrete and disparate habitats to complete their annual life cycle and maintain the full life history expression of populations. This highlights the importance of maintaining habitat complexity and connectivity across contiguous stream networks to preserve biodiversity at the intraspecific level.

Acknowledgements

We thank the following individuals for their tireless effort doing field work in extreme conditions: L. Brekke, P. Marcellais, C. McDougall, M. Carroll, A. Chapelsky, M. Gillespie, B. Lewis, A. Okrainec, B. Robinson, and J. Sabourin. Parks Canada Agency (Nahanni National Park) provided in-kind and technical support. We thank D. Teleki for developing the maps. Comments from two anonymous reviewers substantially improved the manuscript. Financial support was provided by Fisheries and Oceans Canada; Government of the Northwest Territories, Cumulative Impacts Monitoring Program; National Research Council of Canada, Program for Energy Research and Development; and Parks Canada Agency.

Article information

Editor

Trevor Pitcher

History dates

Received: 30 November 2023
Accepted: 12 June 2024
Version of record online: 4 October 2024

Notes

This paper is part of a collection entitled Progress and Priorities for the Recovery of Aquatic Species at Risk in Canada.

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Data availability

This research was reviewed, approved, and conducted in accordance with Parks Canada Agency Research and Collection permit #NAH-2011-8999 and Fisheries and Oceans Canada Animal Use Protocol #FWI-ACC-2011-039. Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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