REGULAR PAPER

Overwintering ecology and movement of anadromous Arctic char (*Salvelinus alpinus*) in a large, ice-covered river in the Canadian Arctic

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Abstract

Arctic char (*Salvelinus alpinus*) is a facultatively anadromous fish species that is critically important to many Inuit communities in the Canadian Arctic. Plasticity in life history has allowed the species to persist in a diversity of challenging Holarctic environments. Despite their ecological and cultural importance and their presence in aquatic ecosystems that are ice-covered for much of the year, few under-ice studies of Arctic char have been conducted. Most winter studies of adult Arctic char have focused on lakes, where they typically overwinter. Several populations of Arctic char, however, overwinter in large river systems, and subsistence fishers have reported that Arctic char overwinter in the lower reaches of the Coppermine River. The Coppermine River is a large Arctic river that flows into Coronation Gulf near Kugluktuk, Nunavut, Canada. The authors used acoustic telemetry to investigate the overwintering ecology of Arctic char in the region. Consistent with local knowledge, they detected Arctic char overwintering within the fluvial environment of the Coppermine River from 2018 to 2020. Unlike other fluvial environments known to be used by overwintering Arctic char, the lower reaches of the Coppermine River are completely ice-covered throughout the winter, are of moderate depths (3.8–14.1 m) and have no known groundwater inputs. Acoustic telemetry observations indicated long-distance movement (7–8 km) within the river in early winter (October) in response to dynamic ice formation. Under-ice movement generally declined 2 weeks after river freeze-up but continued throughout winter in the lower 5 km of the river, where there were fewer under-ice disturbances. Migration into the marine environment before river ice break-up (June), as well as winter (November–May) movements into and within the marine environment, was unexpectedly observed for some fish. Under-ice use of the marine environment is unusual for Arctic char at the distances observed (up to 18 km) and has not previously been documented at the temperatures (fish body temperatures from −0.76 to 1.90°C) observed. Results allow further understanding of the diverse life-history tactics employed by Arctic char and lay a foundation for

future research into fluvial and other diverse overwintering tactics employed by the species.

1 | INTRODUCTION

Arctic char *Salvelinus alpinus* (L.) is a critically important subsistence food fish for Inuit communities across the Canadian Arctic (Priest & Usher, 2004; Van Oostdam *et al.*, 2005) and is the terminal predator in the majority of Arctic freshwater ecosystems where it is found (Johnson, 1980). The species is cold-adapted, has a Holarctic distribution and is the most northerly distributed freshwater fish in the world (Johnson, 1980; Scott & Crossman, 1973). Plasticity in life history is common and has likely allowed Arctic char to persist across a range of climatic conditions and to exploit a diversity of variable environments, including both lotic and lentic freshwater ecosystems, as well as marine ecosystems (*e.g.*, Beddow *et al.*, 1998; Gilbert *et al.*, 2016; Harwood & Babaluk, 2014; Johnson, 1989). Arctic char may be freshwater resident or anadromous (*i.e.*, they are facultatively anadromous), and populations of Arctic char that have access to marine environments are often partially anadromous; some individuals migrate to marine environments, whereas others remain in fresh water (Jonsson & Jonsson, 1993). Within- and among-population variability in life-history tactics, including age at first migration, frequency of spawning and time required to complete migrations to spawning locations (up to 2 years; Johnson, 1989), make it difficult to develop effective management and monitoring plans without site-specific data, and these data are challenging to obtain in remote Arctic environments (Roux *et al.*, 2011).

Anadromous Arctic char begin migrations to marine environments after an initial period of 2–11 years rearing in fresh water (Johnson, 1980; Power & Reist, 2018). There are numerous costs and benefits of adopting an anadromous life history. In temperate and Arctic regions, ocean waters are typically more productive and provide greater foraging opportunities than freshwater systems (Gross *et al.*, 1988). An anadromous life history can thus result in higher growth rates (Gulseth & Nilssen, 2001; Rikardsen *et al.*, 2000; Tallman *et al.*, 1996), probability of overwinter survival (Jensen *et al.*, 2018) and reproductive output (Tallman *et al.*, 1996) relative to a freshwater-resident life history. Energetic costs associated with anadromy include expenditures during long-distance movement, as well as those associated with changes in physiology that allow transitions between freshwater and salt water (Gross *et al.*, 1988). There may be a higher risk of mortality associated with marine migrations (Gross *et al.*, 1988; Jensen *et al.*, 2019; Quinn *et al.*, 2016), and anadromous Arctic char are typically shorter-lived than freshwater residents (Power & Reist, 2018). In areas where there are harvesting pressures from subsistence and commercial fisheries, it is the anadromous life-history type that is frequently targeted (Gyselman, 1994; Roux *et al.*, 2011; Tallman *et al.*, 2019).

Arctic char is an iteroparous species. Fish spawn in fresh water in the fall and typically reproduce multiple times during their life span (*e.g.*, Johnson, 1980). Due to the high energetic investment associated with spawning and their occupancy of relatively low-productivity environments, Arctic char do not usually spawn annually in northern regions; rather, spawning intervals of 2–4 years are common (Power & Reist, 2018). Both spawning and non-spawning anadromous Arctic char return to freshwater environments in the fall, and it is thought that the species must overwinter in fresh water because salinity tolerance is lower at colder temperatures (Finstad *et al.*, 1989; Wandsvik & Jobling, 1982). Arctic char have only been documented using the marine environment in winter at one location in Norway, where ocean temperatures were typically >2°C and warmer than the nearby river environment (Jensen & Rikardsen, 2012). Use of the marine environment by Arctic char during the ice-covered season remains understudied and is generally understood to be minimal.

Overwintering ecology is important for informing fisheries management and conservation plans (Cunjak, 1996) and has long been identified as a critical knowledge gap (Hubbs & Trautman, 1935). Despite their distribution across latitudes with long winter seasons, the majority of studies on migration patterns and use of marine and freshwater environments by Arctic char have focused on the brief ice-free season, likely for logistical reasons. Arctic char typically overwinter in lakes (Johnson, 1980; Power & Reist, 2018), and thus the studies of Arctic char that have occurred overwinter have focused on lakes (Klemetsen *et al.*, 2003; Mulder *et al.*, 2018b, 2018a, 2019; Svenning *et al.*, 2007). Evidence to date indicates that Arctic char occupy thermal niches that minimize net energy loss; the thermal range occupied by Arctic char overwintering in lakes has been reported to vary between 0.2 and 2.0°C (Klemetsen *et al.*, 2003; Mulder *et al.*, 2018a). These temperatures are at or above the 0.2°C lower thermal limit for feeding (Elliott & Elliott, 2010) but sufficiently cold to reduce metabolic costs. Evidence from lacustrine studies also suggests that Arctic char minimize energy expenditure in winter by reducing movement and remaining relatively stationary (Mulder *et al.*, 2018b), except for diel movements that are likely associated with foraging during daylight hours (Mulder *et al.*, 2019).

Although relatively rare, overwintering by adult Arctic char in fluvial environments has been observed across much of the species' range, including in the western Canadian Arctic in the Northwest Territories (Harwood & Babaluk, 2014), in the eastern Canadian Arctic in Labrador (Beddow *et al.*, 1998) and in Norway (Jensen & Rikardsen, 2012). The two tactics employed by Arctic char to minimize overwinter energy expenditure in lakes (thermal habitat selection and movement reduction) may be more challenging to achieve in
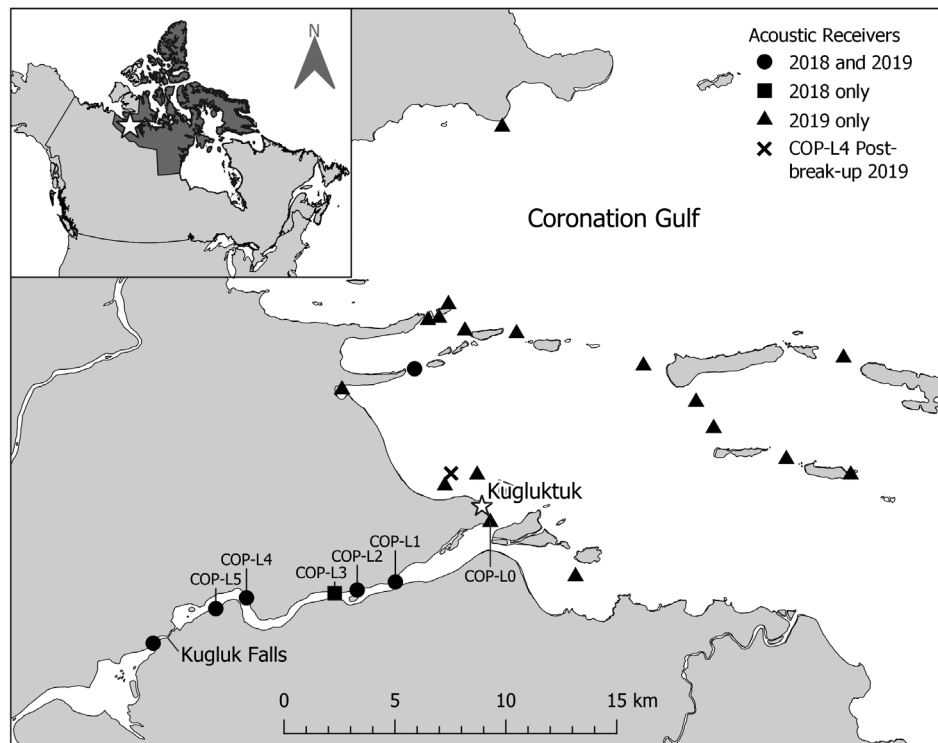
FIGURE 1 Map of the study area and locations of acoustic receivers. Symbols represent the time period each receiver was deployed (and for which data are available). The receiver upstream of Kugluk Falls was retrieved before freeze-up each year to avoid potential winter damage and loss. Note that river receiver COP-L4 was transported into the Coronation Gulf during river break-up in spring 2019, where it remained through the summer. Map was created using QGIS version 3.10.2 (QGIS Development Team, 2020). Shapefiles of Canada and Nunavut boundaries were obtained from Statistics Canada (2016), the US boundary from the United States Census Bureau (2017), Nunavut community place names from the Canadian Geographical Names Data Base (Natural Resources Canada, 2011) and waterbodies from the CanVec hydrographic series (Natural Resources Canada, 2015). ● 2018 and 2019. ■ 2018 only. ▲ 2019 only. ✕ COP-L4 Post-break-up 2019

fluvial systems, where fish must maintain position in flowing water and where mixing of the water column prevents the formation of distinct thermal niches – except in areas with groundwater inputs (Brown et al., 2011; Huusko et al., 2007). Few winter studies have been conducted in large, ice-covered rivers for salmonids in general (Huusko et al., 2007), and to the authors' knowledge only two over-wintering studies of adult Arctic char have been conducted in river systems or estuaries. Either these studies did not have locational data, and investigators inferred habitat use from temperature and salinity measurements (Jensen & Rikardsen, 2012), or locational data were limited to intermittent observations obtained by active tracking (Harwood & Babaluk, 2014). There is thus a clear knowledge gap in the overwintering movements and ecology of Arctic char in large fluvial systems.

Given the importance of Arctic char to subsistence fisheries, their vulnerability to climate-induced changes in hydrology and water temperature (e.g., Reist et al., 2006) and a severe paucity of data, the objective of this study was to use acoustic telemetry to identify and characterize overwintering movements and locations used by anadromous Arctic char that are known by local Inuit fishers to overwinter in a large Arctic river. The authors also aimed to investigate out-migration to marine environments in spring, including timing of marine entry and extent of marine travel under ice.

2 | MATERIALS AND METHODS

2.1 | Study location

This study was conducted in the lower reaches of the Coppermine River and surrounding marine environment. The Coppermine River provides a unique opportunity to study Arctic char in a large fluvial system with atypical (i.e., non-lacustrine) overwintering habitat. The mouth of the Coppermine River is adjacent to the Hamlet of Kugluktuk (formerly known as Coppermine), which is located on the Coronation Gulf in the western Kitikmeot region of continental Nunavut (67° 49′ N, 115° 06′ W; Figure 1). The average date of sea ice break-up in the Coronation Gulf near Kugluktuk (determined over a 30 year period from 1981 to 2010) is 2 July (Canadian Ice Service, 2018). The average date of freeze-up is 22 October, yielding an ice-free season of 16 weeks. The hydrological regime of the Coppermine River is subarctic nival, and the watershed comprises a 50,800 km^2 area that spans a river length of 520 km (Wedel et al., 1988). The lower reaches have a mean peak discharge during spring freshet of 1330 m^3 s^{-1}, whereas mean summer discharge is 473 m^3 s^{-1} (Coulombe-Pontbriand et al., 1998). Minimal flows (mean winter discharge of 118 m^3 s^{-1}) are sustained during the winter months and are primarily derived from lake storage located in the

upper *c*. 200 km of the Coppermine River (Coulombe-Pontbriand *et al*., 1998).

For anadromous Arctic char that use the Coppermine River system, the nearest lakes that are suitable for overwintering and are known to have consistent connectivity to the Coppermine River are the Dismal Lakes, which are located more than 160 river kilometres upstream from Coronation Gulf. This is considerably farther than overwintering lakes used by other populations of Arctic char in the western Kitikmeot region of Nunavut (0.2–50.4 km; Gilbert *et al*., 2016; Gyselman, 1994; Moore *et al*., 2017). Approximately 17 km upstream of the river mouth lies Kugluk (or Bloody) Falls (Figure 1; photos in Supporting Information Figure S1). Kugluk Falls is a cascade that poses a substantial obstacle to migrating fish, but it is passable during the ice-free season. This cascade is impassable to fish after freeze-up, and there is no lacustrine habitat available to fish below Kugluk Falls. In addition to ascending the falls, upstream migration to the Dismal Lakes requires traversing several other sets of rapids before a final 30 km migration up the Kendall River, which connects the Dismal Lakes to the main stem of the Coppermine River. The Kendall River is relatively shallow. The deepest areas measure 2.0–3.2 m during spring freshet in June, and water levels decrease rapidly through July and August (Environment and Climate Change Canada, 2008; Wedel *et al*., 1988). Avoidance of this long and challenging migratory pathway by using the lower reaches of the Coppermine River for overwintering may thus result in a net fitness benefit for anadromous Arctic char, and local fishers report catching Arctic char by setting nets through the ice in the Coppermine River (below Kugluk Falls) throughout the winter (E. Hitkolok and A. Dumond, pers. obs.).

2.2 | Ethical statement

All fish captures and tagging were conducted under Animal Utilization Project Protocols 18-07 and 30071, which were approved by the University of Waterloo Animal Care Committee.

2.3 | Fish capture and tagging

A total of 165 healthy, adult Arctic char were live-captured in the Coppermine River and Coronation Gulf from 8 to 23 August 2018 ($n = 48$) and from 19 July to 8 September 2019 ($n = 117$). Fish were captured using continuously monitored sets of 127 mm (5 in.) mesh monofilament gillnets ($n = 151$ fish), 51 mm (2 in.) mesh gillnets ($n = 1$ fish), angling ($n = 11$ fish), and dip-netting ($n = 2$ fish). Fork length was measured for each individual. Individuals with fork lengths <600 mm were weighed to verify that tags were <2% of body mass (body mass >1700 g) (Winter, 1996). To minimize stress on the tagged animals, sex was not recorded unless an individual displayed a prominent kype or spawning colours, and the only tissue sample collected from individuals was a small piece of adipose fin for genetic analysis (related project). Captured fish were monitored

in 75 L fish crates before and after handling and surgery. Aerated water in crates was kept at ambient temperature, and water was changed frequently.

During surgery, fish were electro-immobilized using a TENS 3000 unit (Roscoe Medical, Middleburg Heights, OH, USA). Electro-immobilization was employed because this method allows rapid recovery and induces a similar physiological response relative to chemical anaesthetics (*e.g*., tricaine methanesulfonate; see Reid *et al*., 2019). In addition, the use of electro-immobilization did not require transportation of hazardous materials to remote field locations and ensured that fish were safe for human consumption after release; Arctic char are actively harvested by subsistence fishers throughout the study area. One electrode was held on the dorsal surface of the fish, posterior to the opercula. A second electrode was held on the dorsal surface of the caudal peduncle. Pulse width was 30 μS, pulse rate was 150 Hz and the unit was run in modulation mode with a constant timer and an initial current setting of 5 mA. Water was pumped continuously over the gills for the duration of the tagging procedure (typically less than 4 min).

Acoustic tags (V16T, diameter 16 mm, length 98 mm, weight 34 g, InnovaSea) were surgically implanted into the coelomic cavity of each fish. The interval between tag transmissions randomly varied between 60 and 180 s. Tags transmitted both tag ID and fish body temperature. Surgeries were performed by a single surgeon. Tags were inserted through a 3–3.5 cm incision that was made on the ventral surface of the fish, *c*. 1 cm right of the midline and ending 4–5 cm anterior to the pelvic girdle. Incisions were closed with two to three simple interrupted sutures with square knots in a 3-2 pattern, using 3-0 PDS II violet absorbable monofilament sutures with 26 mm, ½ circle, taper-point needles. Fish were held and observed for *c*. 15 min after surgery to ensure adequate recovery before release and were observed to recover immediately upon removal of the electrodes.

2.4 | Acoustic receivers

As part of a larger telemetry study, 8 VR2Tx and 4 VR2AR omnidirectional acoustic receivers (InnovaSea) were deployed in the Coppermine River and Coronation Gulf in July and August 2018, and 1 VR2W and 23 VR2AR receivers were deployed in July 2019 (Figure 1). Receivers were deployed with hydrophone (sensor) tips located *c*. 1–1.5 m above river or ocean bottom. Detection ranges of river receivers were tested at the time of deployment to verify that receivers could detect tag transmissions across the full width of the river during the ice-free season.

A sub-set of receivers was left in place to record movement and habitat use during the ice-covered seasons (October–June) of 2018 ($n = 7$ receivers) and 2019 ($n = 23$ receivers; Figure 1). One river receiver was lost during each winter. The total number of retrieved receivers after winter 2018 and winter 2019 was thus 6 and 22, respectively. In 2018, the mooring of receiver COP-L4 (Figure 1) was damaged during winter, and the receiver was carried into Coronation Gulf during break-up of river ice (river break-up) on 19 June

TABLE 1 Summary statistics for body temperatures of Arctic char *Salvelinus alpinus* recorded in the marine environment during the ice-covered season

| Period | Number of fish | n | Body temperature (°C) | | | |
			Minimum	Maximum	Overall mean (S.D.)	Range of individual means
Winter (November 2019 to May 2020)	4	46,974	−0.76	0.34	−0.17 (0.16)	−0.17 to 0.02
Pre-break-up (June) 2019	5	735	−0.14	1.28	0.29 (0.26)	0.02 to 0.49
Pre-break-up (June) 2020	7	2431	−0.29	6.77	0.91 (1.62)	0.02 to 2.73
Pre-break-up (June) 2020, excluding location with inputs from small stream	7	2159	−0.29	1.90	0.34 (0.27)	0.02 to 0.50

Notes: Minimum, maximum, mean and S.D. were calculated using all observations from all fish. Ranges of mean body temperatures for each individual fish are also presented. Measurements from the "Winter" period are from fish that were detected using the marine environment and subsequently returned to fresh water before commencing summer marine migration ($n = 3$) or were detected using the marine environment throughout the winter with no return to fresh water ($n = 1$). Measurements from "Pre-break-up" are from fish that commenced summer marine migration in June, before sea ice and river break-up.

2019. The receiver buoys became detached in the gulf, which caused the receiver to sink and remain stationary *c*. 3 km from the river mouth, where this receiver was then opportunistically able to detect marine entry of Arctic char in late June (Figure 1). In 2019, receiver COP-L3 was transported during river freeze-up *c*. 1.6 km downstream to station COP-L2, where it remained for the duration of the ice-covered season. A sub-set of receivers were deployed during winter 2020–2021; however, coverage was reduced due to logistic difficulties. Movement and location data for winter 2020–2021 are thus not presented here.

2.5 | Detection data

All receiver log and detection data were imported into VUE software version 2.6.2 (InnovaSea). The VUE VRL File Editor was used to account for receiver clock drift and to correct recorded times. The VUE False Detection Analysis Tool was used to identify potential cases of interference between transmitter signals and incomplete transmissions. All flagged detections were manually reviewed, and invalid observations were removed. All subsequent data manipulation and analyses were conducted using R version 3.6.1 (R Core Team, 2019), including data visualization using the packages ggplot2 (Wickham, 2016) and ggalluvial (Brunson & Read, 2020). Locations were assigned to each observation. Detection data were simplified into residence periods (start, end and length of time a tag was detected continuously at a given location). Mortalities or cases of tag shedding/expulsion were estimated and removed from the data set (Supporting Information S2).

2.6 | Identification of freshwater migration destination and spring marine entry

Freshwater migration destinations of individual fish were classified as being either above or below Kugluk Falls. A designation of "above falls" was applied if an individual fish was detected by the receiver located

above Kugluk Falls after the summer marine migration. Fish that migrated above Kugluk Falls may have overwintered in the Dismal Lakes, but this is currently unknown because there are few suitable locations for receiver placement above Kugluk Falls. Thus, overwintering habitat for fish that migrated above the falls cannot be characterized as either fluvial or lacustrine. A designation of "below falls" was applied if an individual fish was detected by at least one receiver in the fluvial environment below Kugluk Falls during the ice-on period (freeze-up on 1 October 2018 to river break-up on 19 June 2019, 14 October 2019 to 21 June 2020 or 15 October 2020 to 18 June 2021). Individuals were also identified as overwintering below Kugluk Falls if they were captured through the ice by local harvesters during this period.

Spring dates of last detection in fresh water are not available, as the receiver located at the river mouth was lost during winter 2018–2019 and detection ranges were not tested during the ice-covered periods or during dynamic spring break-up. Instead, the date of ocean entry was defined as the earliest date that an individual was detected by overwintering receivers in the marine environment (Figure 1) and not subsequently detected in the river until fall freshwater entry.

Freshwater migration destination and date of spring marine entry were related to fork length. Fork lengths were measured only when fish were tagged, and thus fork lengths for each individual were estimated in subsequent study years by applying a von Bertalanffy growth model. The model parameters were estimated using age and fork length data from 225 fish that were harvested by subsistence fishers. The nls function in the stats package (R Core Team, 2019) was used, and the starting values were determined using the vbStart function in the FSA package (Ogle *et al.*, 2021). Generalized linear mixed models were implemented using the glmer function in the lme4 package in R (Bates *et al.*, 2015) to relate the explanatory variable of fork length to the binary response variable of freshwater migration destination (1, above falls; 0, below falls). Both individual and year were included as random factors. Similarly, linear mixed models were implemented using the lmer function in the lme4 package (Bates *et al.*, 2015) to relate fork length to the continuous response variable of time difference (days) between entry and river break-up. Models with both random factors of individual and year or one random factor of year produced singular fits, so only

individual was included as a random factor. Models were compared to null models (only random factors) using AIC.

2.7 | Environmental data

In addition to recording transmissions from fish tags, VR2AR receivers recorded hourly temperature (°C), depth (m), tilt (°) and noise (mV). Fish body temperatures (transmitted by acoustic tags) had a finer temporal scale than receiver temperature records and often varied from the temperatures that were recorded by receivers. Differences between receiver temperatures and fish temperatures may have occurred because fish were located in different thermal habitats (e.g., higher in the water column) than receivers but were still within detection range. Receiver records of environmental data also varied by receiver; the water column of the river was well mixed and had no groundwater inputs (i.e., temperatures were uniform throughout the lower reaches), yet one receiver consistently recorded temperatures of 0.5°C, whereas another recorded temperatures of −0.8°C during the same period (temperature panel in Supporting Information Figure S2). Therefore, the range and mean of tag temperatures were used to describe thermal environments occupied by individual fish. Receiver logs were visually assessed to identify disturbances (e.g., changes in tilt) and aided in characterizing the under-ice environment (e.g., noise, depth of water/ice) of receivers that remained in place overwinter.

3 | RESULTS

3.1 | Fish tagging

Fork lengths of the 165 tagged individuals ranged from 539 to 889 mm (mean = 709 mm, s.d. = 66 mm). Tags ranged from 0.4 to 1.8% of fish body weight; all were below the 2% rule of thumb (Winter, 1996), and the ratios of tag to body weight were far below the values observed to affect growth, behaviour and survival in salmonid species (e.g., Ammann et al., 2013; Chittenden et al., 2009; Collins et al., 2013; Darcy et al., 2019; Newton et al., 2016; Smirich & Kelly, 2014).

Of the 165 Arctic char tagged in this study, only 1 did not recover after surgery. Five fish were never detected, nine were suspected to have shed their tags or were mortalities after release and one was a confirmed mortality. After removal of false detections and known or suspected mortalities, there were 928,232 transmissions representing 149 individual Arctic char detected by the receivers over the study period (8 August 2018 to 30 September 2020). Sixty-three of these 149 individuals were detected at least once below Kugluk Falls during one or both ice-covered seasons.

3.2 | Freshwater migration destination

There was interindividual and interannual variation in freshwater migration destination. Fork length was not an important predictor of
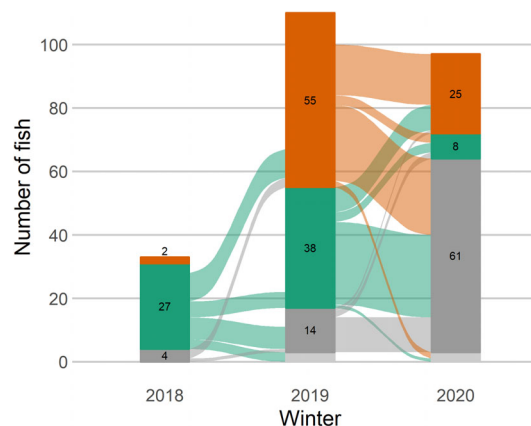

FIGURE 2 Overwintering locations of tagged fish in each study year. Colour of connections between years indicates the overwinter destination of an individual fish in the previous year (e.g., an orange connection to a green bar indicates an individual that overwintered above the falls in the previous year and below the falls in the subsequent year). In 2018, fish were tagged late in the season, likely after most fish would have migrated above the falls, if that was their destination (Smith, 2020). Fish that were detected during the ice-free season but were not detected above the falls or by river receivers (i.e., Below Falls) during the ice-covered season were categorized as "Unknown." It is likely that some individuals with "Unknown" destinations in 2020 were overwintering below the falls but were not detected due to reduced receiver coverage below the falls. ■ Above Falls. ■ Below Falls. ■ Unknown. □ Mortality

overwintering destination; the AIC score of a generalized linear mixed model that included fork length as the explanatory variable for overwintering destination (195.1) was higher than that of the null model (193.7; only random factors were included in the model). Some individuals overwintered in the same general location (i.e., above falls or below falls) for two consecutive years (Figure 2). Others were detected for at least one winter in each location. Migration above Kugluk Falls was detected for 2 fish in fall 2018, 55 fish in fall 2019 and 25 fish in fall 2020 (Figure 2). Twenty-seven fish were detected overwintering in fluvial environments below the falls in 2018. Thirty-eight individuals were detected overwintering below the falls in 2019, including five that had also overwintered below the falls in 2018 (Figure 2). Eight individuals were detected overwintering below the falls in 2020. Freshwater migration destination was unknown for 4 individuals in 2018, 14 individuals in 2019 and 61 individuals in 2020 (Figure 2). The high number of fish with unknown overwintering location in 2020 is likely due to reduced receiver coverage in the river during the ice-covered season.

3.3 | Fluvial overwintering environment

3.3.1 | Under-ice conditions

Data recorded by receivers on depth, tilt and noise, as well as the general condition of receivers upon retrieval, provide insight into the
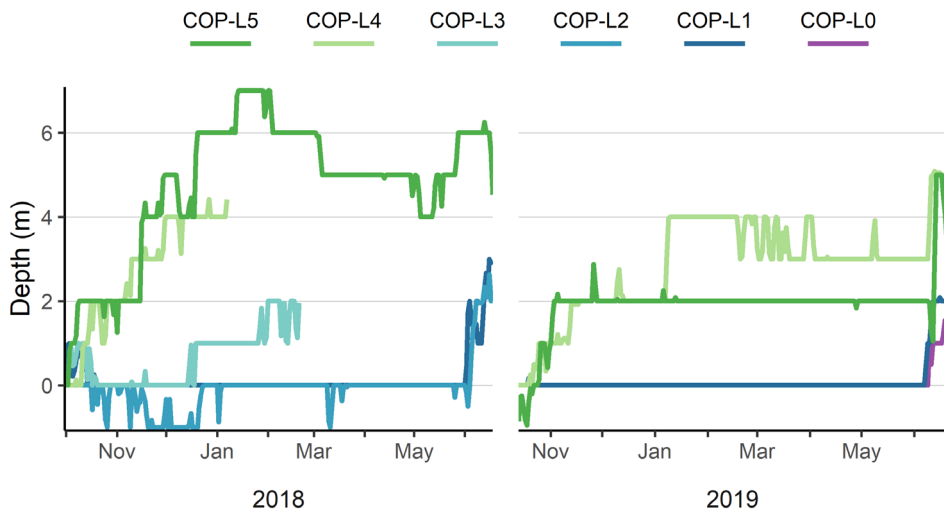
FIGURE 3 Water depth recorded by river receivers during the ice-covered periods of 2018 and 2019. Depths of 0 m represent the surface of the water in late September, before freeze-up. The legend for receiver locations ranges from most upstream (near Kugluk Falls – COP-L5) to most downstream (the river mouth – COP-L0). Depth measurements for receivers COP-L3 and COP-L4 in winter 2018 are shown only until the dates the moorings broke. Note that receiver COP-L3 was displaced shortly after freeze-up in 2019, and data are not shown here

under-ice conditions of the Coppermine River. All data recorded by receivers are available in Supporting Information Figure S2. In general, ice cover was more consistent, and under-ice conditions were more stable as distance increased from Kugluk Falls. Depth data indicated that surface height (distance between the receiver sensor and the water or ice surface) was relatively consistent throughout winter at receivers located either at (COP-L0) or close to (COP-L1 and COP-L2) the river mouth (Figures 1 and 3). At the two receivers located closest to Kugluk Falls (COP-L4 and COP-L5), however, there were 2–7 m increases in surface height throughout the winter, and measurements were more variable over time (Figure 3). Local community members have observed over-ice flow and large build-ups of ice at certain locations within the Coppermine River, in particular the stretch of river below Kugluk Falls, where receivers COP-L4 and COP-L5 were placed. Increases in surface heights at these locations were likely due to ice accumulation caused by periods of over-ice flow from Kugluk Falls that subsequently froze, as well as potential compression and buckling of surface ice.

Receiver tilt records in both study winters showed abrupt and substantial changes in tilt that indicated events or periods of under-ice disturbance (Supporting Information Figure S2). Changes in tilt were generally greater and more frequent at upstream locations. More physical damage to receivers was also observed at upstream locations (see additional details in Supporting Information Figure S4). Damaged buoy attachment hardware, abrasion on receiver casings and wear between mooring cables and receiver attachments suggested that the receivers and mooring cables were subject to considerable friction and force, which corroborates inferences of substantial under-ice disturbances from receiver logs.

On 22 March 2019, an attempt was made to communicate with receiver COP-L3 after drilling through the ice; communication was not possible as the water column was comprised of unconsolidated frazil ice. Local community members have observed that unconsolidated frazil ice is more prevalent near Kugluk Falls and decreases in concentration and frequency of occurrence at more downstream locations (A. Dumond and E. Hitkolok, pers. obs.). Consistent with this, a historic hydrological station near Kugluk Falls had to be relocated due to slush ice conditions over multiple years (Coulombe-Pontbriand et al., 1998). Frazil ice crystals consolidate to form anchor ice and hanging dams (Brown et al., 2011; Huusko et al., 2007). The authors thus infer stable, low noise levels that coincided with constant tilt angles and temperatures of 0°C as periods when receivers were frozen into ice structures (Supporting Information S2). Fish were not detected by receivers during these periods of time. Ice surrounding receivers appeared to melt in early June each year, which was inferred from an increase in noise levels and temperature (Supporting Information Figure S2), and from greater variability in depth (Figure 3) and tilt (Supporting Information Figure S2) measurements before break-up.

3.3.2 | Location and temperature

Detection patterns in the Coppermine River mirrored patterns in under-ice conditions (and inferred ability of receivers to detect tag transmissions); as winter progressed, detections of fish decreased or ceased at each receiver in an upstream to downstream pattern (Figure 4). During freeze-up in each study year, fish were detected by all available river receivers (Figure 4). Detections largely ceased at the two upstream receivers, COP-L4 and COP-L5, 10 days after freeze-up in fall 2018 and 15 days after freeze-up in fall 2019. The exception was three individuals detected at COP-L5 in winter 2018–2019: one was detected for 1.8 h at this same receiver in early February, another was detected for 74.3 h in mid-March and then immediately before river break-up on 18 June and one was consistently detected from mid-March to mid-May (Figure 4). In winter 2019–2020, fish were detected later in the winter by the downstream receivers; detections continued throughout the ice-covered season at COP-L1 and the river mouth (COP-L0); 455,616 detections were recorded over the two ice-covered study seasons. During these seasons, individual detections of fish body temperature in fresh water ranged from −0.14 to 1.28°C, and 98.6% of detected temperatures were ≤0.02°C (Supporting Information Figure S3).
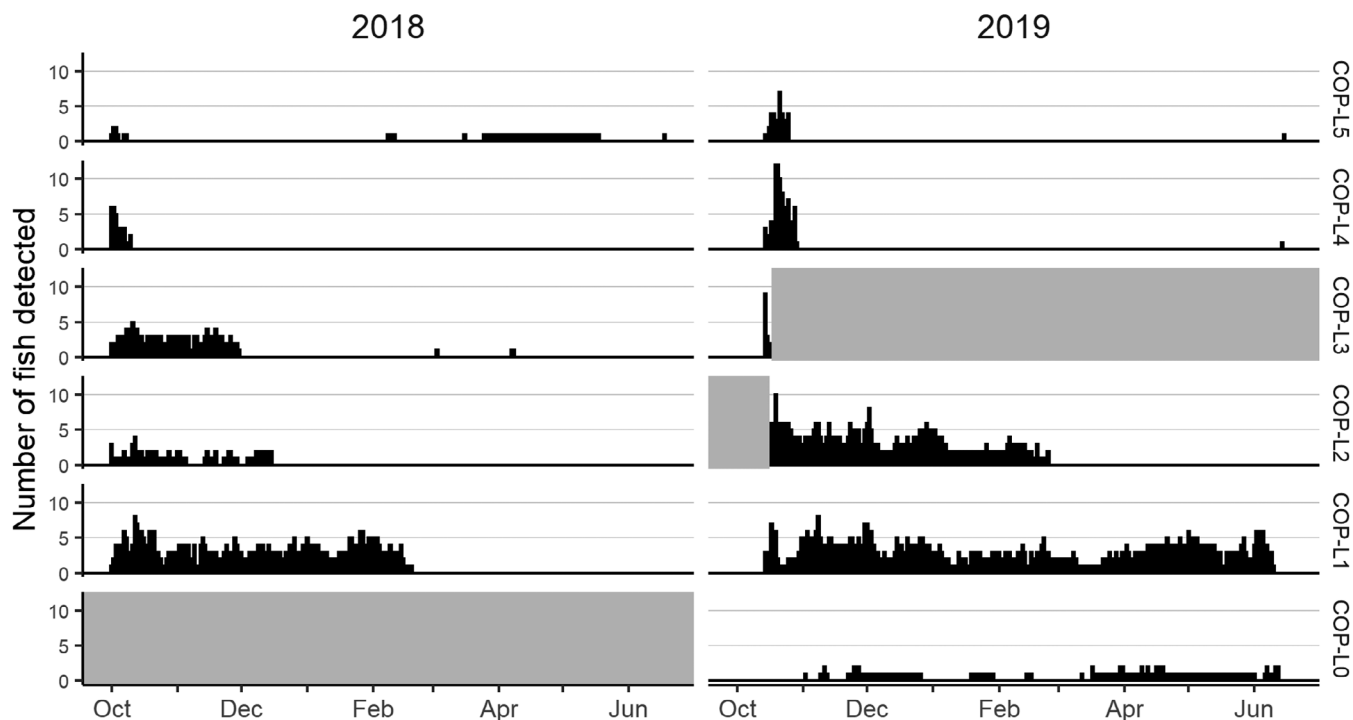
FIGURE 4 Number of unique fish detected each day by river receivers during the ice-covered season (1 October 2018 to 19 June 2019 and 14 October 2019 to 21 June 2020). Receivers are presented from most upstream (COP-L5; located closest to Kugluk Falls) at the top of the figure to most downstream (COP-L0; located at the river mouth) at the bottom of the figure. Periods when receivers were missing are indicated by grey shading. Note that receiver COP-L2 was not recovered after winter 2019; however, receiver COP-L3 was pushed c. 1.6 km downstream to the approximate location of station COP-L2 on 17 October 2019

3.4 | Overwinter movement

Fish movement was observed under ice in the Coppermine River in the 2 weeks after freeze-up in both fall 2018 and fall 2019 and appeared to decrease as winter progressed. During the 2 weeks after freeze-up in 2018, 4 of the 12 individuals (33%) located at the upstream receivers (COP-L4 and COP-L5; Figure 1) moved c. 7 km to the downstream receivers (COP-L1, COP-L2 and COP-L3), where they were again detected later in the winter (Figure 5). Four of 19 individuals (21%) displayed similar downstream movement overwinter in 2019 (Figure 5). During freeze-up on 17 October 2019, three individuals moved 5–6.5 km from receiver COP-L3 to the upstream receivers. This movement coincided with the movement of four other individuals from COP-L3 to receivers further downstream, as well as the displacement of receiver COP-L3 to station COP-L2 (Supporting Information Figure S2).

Movement was reduced and limited to the downstream receivers in mid- to late winter (November–May; Figure 5). The receiver at the river mouth (COP-L0) and COP-L1 detected fish throughout the ice-covered season of 2019–2020, and 11 individuals were detected travelling c. 5 km between these two receivers at least once. Although testing of receiver detection ranges was not conducted in winter, ice conditions likely reduced the detections by the other receivers in winter 2019–2020 and all receivers in winter 2018–2019. Data from the limited detections recorded suggested that many individuals exhibited

minimal winter movement (Figure 5). In 2018, three of eight individuals that remained within the range of the upstream receivers after freeze-up were detected again by upstream receivers either in mid-winter or before river break-up in June. These individuals likely remained upstream as they were not detected at any other location during the winter. All 12 individuals that were recorded by the downstream receivers during freeze-up in 2018 (and were not subsequently harvested) remained downstream, where they were detected later in the winter (Figure 5). Similarly, fish remained relatively stationary in mid- to late winter 2019–2020; 6 of 18 individuals (33%) that were occupying or moved to the upstream receivers during freeze-up remained upstream, where they were again detected in late winter or after river break-up, and 13 of 19 individuals (68%) that were occupying or moved to the downstream receivers during freeze-up remained downstream (Figure 5).

3.5 | Winter use of marine environment and spring marine entry

Timing of entry into the marine environment was highly variable among individuals (Figure 6). Dates that fish entered the marine environment in spring were identified for 81% (n = 21) of individuals that had known overwintering locations (above or below Kugluk Falls) in 2018 (and were not harvested; n = 26) and for 79% (n = 73) of
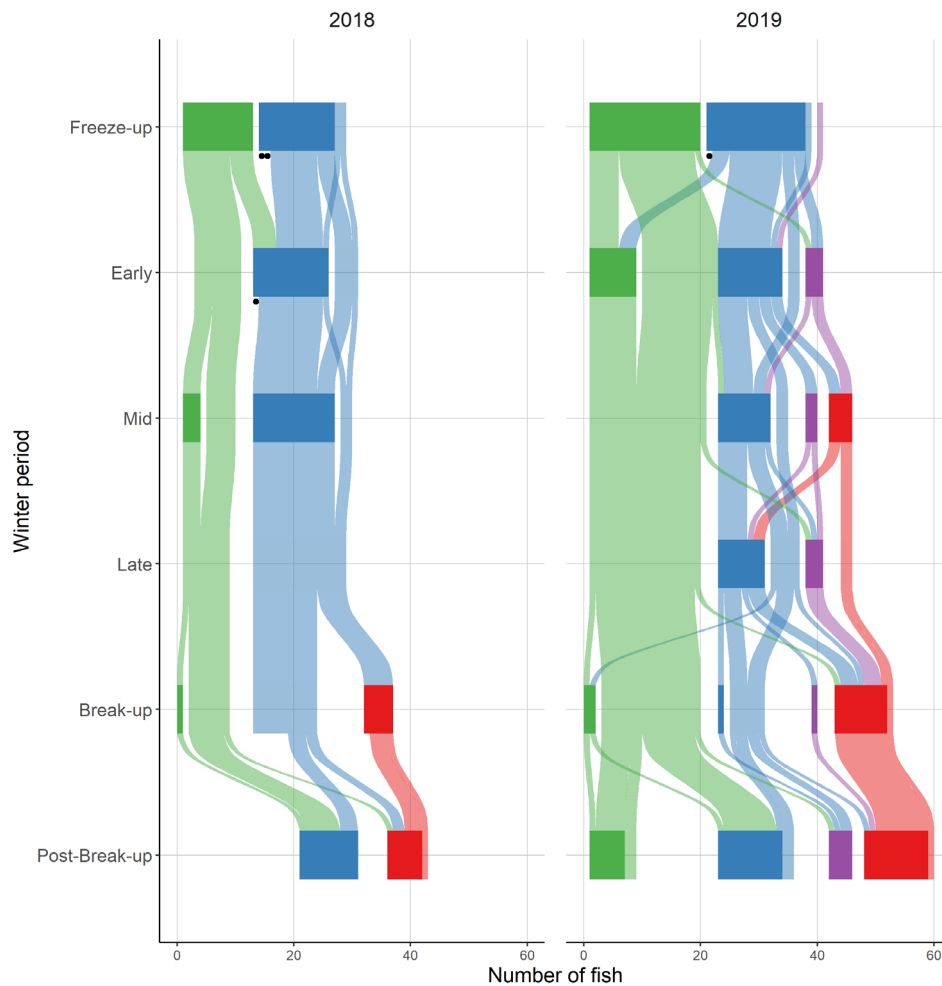
FIGURE 5 Detections and movement of tagged Arctic char *Salvelinus alpinus* below Kugluk Falls in the Coppermine River and the marine environment during the winter season. Upstream represents detections by receiver COP-L4 or COP-L5, and downstream represents detections by receivers COP-L1, COP-L2 and COP-L3. The width of the bars along the *x*-axis represents the number of unique individuals detected in a given location and period. The winter periods on the *y*-axis represent periods of 2 weeks ("Freeze-up," on or within 2 weeks of river freeze-up; "Early," 2–4 weeks after freeze-up; "Late," 2–4 weeks before river break-up; "Break-up," in or within 2 weeks before break-up), with the exception of "Mid," which is condensed to include all detections from 1 month after freeze-up to 1 month before break-up, as detections were limited during this period and few movements were recorded. Semi-transparent bars within a given time period represent locations where an individual was not detected within that time period but was assumed to be present based on detections from prior time periods. Black dots indicate fish that were harvested by subsistence fishers. ■ Upstream. ■ Downstream. ■ River mouth. ■ Ocean

individuals with known overwintering locations in 2019 (*n* = 92). Marine entry dates ranged from 5 June to 2 July 2019 and from 7 June to 1 July 2020 (Figure 6). Date of marine entry was not influenced by fork length; the AIC score of a linear mixed model with fork length as an explanatory variable (590.4) was substantially higher than that of the null model (581.1).

Of individuals with identified marine entry dates, the majority began their marine migration after river break-up (76% in spring 2019 and 89% in spring 2020; Figure 6). This includes most individuals that overwintered below the falls (76% in winter 2018–2019 and 73% in winter 2019–2020) and all individuals that overwintered above the falls. Five individuals began marine migration before river break-up (19 June) in spring 2019. Only one marine receiver was present before break-up in 2019 (Figure 1). This receiver was located *c.* 7 km

northwest of the river mouth, thus requiring substantial under-ice travel. Seven individuals began marine migration before river break-up (21 June) in spring 2020 (Figure 6), including one individual that was detected 18 km north of the river mouth from 15 to 17 June (Supporting Information Figure S5). All individuals that began marine migration before river break-up had overwintered below the falls. After river break-up in spring 2020, individuals that overwintered below the falls entered the marine environment at a similar time as those that had overwintered above the falls (Figure 6).

Because use of the marine environment during winter is unusual for Arctic char, the authors examined the body temperatures of fish that were detected in the marine environment while the Coppermine River and Coronation Gulf remained ice covered. Recorded body temperatures of the five individuals that began their marine migration

FIGURE 6 Date of spring marine entry for each tagged individual with known overwintering location (either above or below Kugluk Falls). Each point represents the date that an individual tagged fish entered the marine environment and did not return to fresh water until the fall migration. Some individuals were detected earlier in the marine environment but subsequently returned to the river; those marine detection dates are not included in this figure. ●Above Falls. ○Below Falls. ┊River Break-up
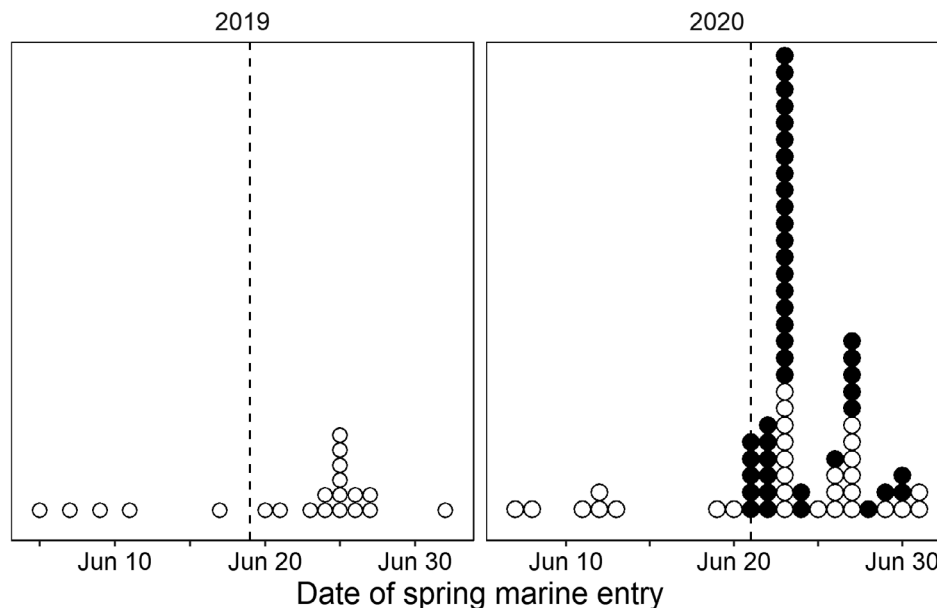
before river break-up (19 June) in spring 2019 ranged from −0.14 to 1.28°C, with an overall mean of 0.29°C (s.d. = 0.26, n = 735; Table 1; Supporting Information Figure S3). Recorded body temperatures of the seven individuals that began their marine migration before river break-up (21 June) in spring 2020 ranged from −0.29 to 6.77°C, with an overall mean of 0.91°C (s.d. = 1.62, n = 2431; Table 1; Supporting Information Figure S3). Recorded body temperatures >2°C before river break-up represented three individuals that were detected by a receiver located in a shallow bay near the outflow of a small stream. When detections from this receiver were excluded (11.2% of ocean detections in June 2020 before river break-up), body temperatures before river break-up in spring 2020 were colder; the overall range was −0.29 to 1.90°C, with an overall mean of 0.34°C (s.d. = 0.27, n = 2159; Table 1).

Three individuals were detected in the marine environment during the ice-covered season of 2019–2020 and subsequently returned to fresh water before river break-up (Supporting Information Figure S5). One individual was detected periodically from 22 November to 3 December 2019, another was detected on 29 March 2020 and the third was detected by two receivers over a period of 5 h on 15 April 2020. A fourth individual was detected in the marine environment on 3 December 2019. This individual did not re-enter fresh water and was detected by that same marine receiver throughout the winter, until it was detected moving through the marine environment by five other receivers, beginning on 11 June 2020. Recorded body temperatures of tagged individuals during these marine excursions ranged from −0.76 to 0.34°C, with an overall mean of −0.17°C (s.d. = 0.16, n = 46,974; Table 1; Supporting Information Figure S3). Winter environmental data are not available in the marine environment for locations where fish were detected; nonetheless, vertical profile data obtained by Fisheries and Oceans Canada and Canadian Rangers Ocean Watch at several times and locations near the study area indicate the presence of a layer of water with low salinity and

temperatures c. 0°C at the water surface (unpubl. data; Supporting Information Figure S6).

4 | DISCUSSION

4.1 | Freshwater migration destination

Although overwintering in fluvial environments has been documented for other populations of Arctic char (e.g., Beddow et al., 1998; Harwood & Babaluk, 2014; Jensen & Rikardsen, 2012), it is rarer than overwintering in lacustrine environments. Consistent with local Inuit knowledge, the authors detected Arctic char overwintering within the lower reaches of the Coppermine River, where fluvial overwintering conditions are unique. The fluvial overwintering habitats used by other populations include systems with minimal ice cover due to disturbance from a hydroelectric plant (Jensen & Rikardsen, 2012) or with large, deep (>30 m) pools (Beddow et al., 1998). In contrast, the Coppermine River below Kugluk Falls is fully ice-covered and of moderate depth (3.8–14.1 m). Adult Arctic char have also been observed to overwinter in fluvial habitats where there are groundwater inputs (Harwood & Babaluk, 2014). Groundwater buffers fluctuations in water temperature and creates microhabitats with cooler water in summer and warmer water in winter (Power et al., 1999). The Coppermine River has spatially uniform water temperatures in summer (Kugluktuk Ikaarvik youth group, unpubl. data), and individual fish body temperatures were consistently cold throughout the ice-covered season (99.98%, ≤0.02°C), which suggests that there are no substantial groundwater inputs. Several lines of evidence, including noise, tilt and surface height data collected by receivers, historical water station observations (Coulombe-Pontbriand et al., 1998) and movement/loss of receivers during the ice-on season, indicate that there are large-scale under-ice disturbances in the lower reaches of the Coppermine

River in winter. These disturbances likely include scouring, anchor ice, hanging dams and substantial formation of frazil ice. Adult Arctic char have not been previously documented to overwinter in fluvial systems under such ice conditions.

Despite physical conditions that would pose challenges for overwintering fish, there are several potential reasons for Arctic char to overwinter within the river below Kugluk Falls. It is possible that individuals enter the river each year with the intent of migrating above Kugluk Falls, but some individuals are unable to ascend the cascade. Environmental conditions such as discharge (*e.g.*, Lennox *et al.*, 2018) and temperature (*e.g.*, Gowans *et al.*, 1999; Kennedy *et al.*, 2013) have been shown to influence the ascent of Atlantic salmon *Salmo salar* L. over migration obstacles, but similar studies have not been conducted for Arctic char. Although the mean environmental conditions were similar between study years (Supporting Information Table S1), fine-scale temporal variation in conditions may influence the ability of individuals to ascend the falls. The observed interannual variation in the proportion of individuals that migrated above the falls may reflect an interaction between environmental conditions, body condition, and fishing pressure. A longer-term study is required to investigate the relative influences of these potential factors.

Although failure to ascend Kugluk Falls is one possible reason why fish may overwinter in the lower reaches of the Coppermine River, it is also possible that fish intentionally overwinter in this location. The nearest suitable lakes for overwintering that are known to be reliably connected to the river are >160 km upstream from the Coronation Gulf. In other populations of Arctic char in the region, where migration routes are substantially shorter (0.2–50.4 km; Gilbert *et al.*, 2016; Gyselman, 1994; Moore *et al.*, 2017), fluvial overwintering has not been observed. Overwintering within the river would allow fish to avoid the likely strenuous passage above Kugluk Falls and a long migration under potentially unfavourable hydrological conditions.

If fluvial overwintering in the Coppermine River is employed as a tactic, rather than by chance, the observed interindividual and interannual variation in migration destination may be related to the spawning status of tagged individuals. Although generalized linear mixed models indicated fork length did not influence overwintering location, all tagged fish had fork lengths >539 mm. Smaller Arctic char (*c.* 300 mm in length) are known to overwinter below Kugluk Falls (E. Hitkolok, pers. obs.). Tagged fish thus did not represent the full size range of anadromous Arctic char and were all likely at or near maturity. Arctic char are intermittent spawners (Power & Reist, 2018), and overwintering in non-natal habitats in non-spawning years has been noted in other populations of Arctic char (Gilbert *et al.*, 2016; Gyselman, 1994; Moore *et al.*, 2013; Spares *et al.*, 2015). Use of non-natal freshwater habitats in non-spawning years has been suggested to be more likely if the migratory pathway to spawning grounds is long or has a higher gradient (Moore *et al.*, 2017), as is the case in this study system. There is no known spawning habitat downstream of Kugluk Falls; fish overwintering below the falls may thus be non-spawners, and those overwintering above the falls may be spawners, but this requires further study.

Overwintering in fluvial habitat below the falls in non-spawning or prespawning years may confer a fitness benefit to Arctic char in this system. Marine feeding is associated with benefits for nutrition and fecundity (Gross *et al.*, 1988; Gulseth & Nilssen, 2001; Rikardsen *et al.*, 2000; Tallman *et al.*, 1996), and fish that overwinter nearer to the ocean would save an expensive migration to upstream lakes. Fish that overwinter nearer the ocean may also have earlier access to marine food resources and thus greater potential gains in condition and energy storage. Authors' data indicated that some individuals (27%) that overwintered below Kugluk Falls entered the marine environment before river break-up. Movement patterns during fall migration (*e.g.*, timing, speed, directedness of travel) may allow the identification of intended migration destination, which, along with further investigation of spawning status, under-ice foraging opportunities, body condition and environmental conditions, would provide additional insight into factors that influence the frequency, prevalence and intra-individual variation in use of overwintering environments below Kugluk Falls.

4.2 | Fluvial overwintering conditions and movement

Although overwintering within the lower reaches of the Coppermine River may be energetically advantageous due to a relatively shorter migration, there are also likely energetic costs associated with overwintering in this environment. Arctic char that overwinter in lakes minimize metabolic costs by occupying selected thermal niches that represent only a sub-set of available temperatures (Mulder *et al.*, 2018a). As the water column is mixed and there are no known groundwater inputs in the lower reaches of the Coppermine River, Arctic char overwintering within the river are likely unable to select preferred thermal environments. The body temperatures of Arctic char overwintering within the Coppermine River (98.6% ≤0.02°C) were lower than those observed in lakes (0.2–2.0°C; Klemetsen *et al.*, 2003; Mulder *et al.*, 2018a) and below the 0.2°C lower thermal limit for feeding (Elliott & Elliott, 2010). Arctic char that overwinter in the Coppermine River would likely thus have low metabolic costs due to the cold temperature but would also be unable to take advantage of any feeding opportunities.

Another energy conservation tactic observed for Arctic char overwintering in lakes is a reduction in movement (Mulder *et al.*, 2018b). Reduced winter movement has been observed in other Salmonidae species that overwinter within rivers, including Atlantic salmon kelts (Komadina-Douthwright *et al.*, 1997), cutthroat trout *Oncorhynchus clarkia* (Richardson 1836) (Jakober *et al.*, 1998) and rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) (Muhlfeld *et al.*, 2001). During freeze-up in October of each study year, the authors observed movements of fish over distances of *c.* 5–7 km that coincided with the timing of ice accumulation and under-ice disturbances. Movements to avoid dynamic ice formation in early winter have been observed for other Salmonidae species overwintering in rivers, such as brook trout *Salvelinus fontinalis* (Mitchell 1814)

(Lindstrom & Hubert, 2004), bull trout *Salvelinus confluentus* (Suckley 1859) (Jakober *et al.*, 1998) and cutthroat trout (Brown, 1999; Lindstrom & Hubert, 2004). Movement of Arctic char between upstream and downstream receivers in the Coppermine River decreased as winter progressed, and 33–100% of fish (depending on year and receiver location) were detected at the same location in mid- to late winter (November–June). Nonetheless, some individuals continued moving in the lower 5 km of the river and even into the marine environment throughout the winter months, and a greater number of fish displayed movement within the 2 weeks before river break-up in June. Whether to avoid under-ice conditions or to forage, movement overwinter would increase the energy expenditures associated with fluvial overwintering.

Atlantic salmon kelts (Komadina-Douthwright *et al.*, 1997), brook trout (Chisholm *et al.*, 1987), brown trout *Salmo trutta* L. (Heggenes *et al.*, 1993; Lindstrom & Hubert, 2004) and cutthroat trout (Lindstrom & Hubert, 2004) in fluvial environments have been observed to preferentially overwinter in lower-velocity areas, where less movement is required to maintain position. Although the authors expected fish to overwinter in a large, deep (14 m) pool with low water velocity that was identified during summer field research, receiver records suggested that this area experienced substantial ice accumulation, frequent under-ice disturbances and likely scouring; few fish detections were observed at this receiver. The accumulation of ice and restriction of river channels may be greater in areas with lower water velocity (Brown *et al.*, 2011; Huusko *et al.*, 2007), and the accumulation of frazil ice in deep pools can actually result in less under-ice fish habitat than predicted, or compared to shallower areas (Cunjak, 1996; Komadina-Douthwright *et al.*, 1997). Water velocity may also increase in deep pools during the winter months (Brown *et al.*, 2000). Overwintering in rivers affected by frazil ice, such as the Coppermine River, may thus result in substantial energy expenditures. Future research that includes the estimation of field metabolic rates and comparisons of overwinter metabolic rates and energetic costs between fish that overwinter above *vs.* below migration obstacles would be useful in assessing how plasticity in migration destination and utility of a dynamic fluvial environment for overwintering affect fitness of individual fish, especially in the context of a species known to be partially migratory through a conditional life-history strategy (Jonsson & Jonsson, 1993).

4.3 | Winter use of marine environment and spring marine entry

Although it was previously suggested that Arctic char enter the marine environment while rivers remain frozen (Grainger, 1953), it has otherwise been observed by western scientists that Arctic char do not enter the marine environment until after river break-up (Dempson & Green, 1985; Gilbert *et al.*, 2016; Mathisen & Berg, 1968; Spares *et al.*, 2015). In contrast to the majority of recent data, the authors found that movement into the marine environment occurred while both the river and Coronation Gulf remained ice covered, which is

consistent with local observations that Arctic char can be caught under the sea ice from April through mid-June (Prno, 2019; Eric Hitkolok, pers. obs.).

Winter use of the marine environment is unusual for Arctic char, as they have lower salinity tolerance at colder temperatures (Finstad *et al.*, 1989; Wandsvik & Jobling, 1982). Although hypoosmoregulatory capacity is correlated with body size for Arctic char (Arnesen *et al.*, 1992), linear mixed models suggested that fork length did not influence the timing of marine entry. Previous authors have reported, however, that in June, when Arctic char were acclimated to spring photoperiod conditions, fish were more tolerant of high salinities (Arnesen *et al.*, 1992), or of both high salinities and low temperatures (Finstad *et al.*, 1989), than in other seasons. Similarly, Aas-Hansen *et al.* (2005) found that Arctic char captured through the ice in fresh water in late winter (May and June) had greater osmoregulatory capacity (*i.e.*, salinity tolerance) and greater liver metabolic capacity (in preparation for feeding season) relative to earlier in the winter (April). These results suggest that physiological adaptations in response to seasonal cues may allow Arctic char to not only travel under the ice in cold, marine waters in June, as observed, but also forage in marine habitats; body temperatures recorded for some individuals were above the lower thermal feeding limit (0.2°C; Elliott & Elliott, 2010).

There are two other documented locations where Arctic char used the marine environment under sea ice (Bégout Anras *et al.*, 1999; Hammer *et al.*, 2021). In both locations, under-ice travel was observed after (Bégout Anras *et al.*, 1999) or likely after (Hammer *et al.*, 2021) river break-up in late spring. In contrast, the authors observed Arctic char using the marine environment in winter, while both the Coppermine River and Coronation Gulf remained ice covered. The only other documented occurrence of Arctic char using the marine environment in winter is in Norway (Jensen & Rikardsen, 2008), where the marine habitat used by Arctic char was not ice-covered and was typically warmer than the nearby river environment (>2°C; Jensen & Rikardsen, 2012). Jensen and Rikardsen (2008) suggested that accumulation of frazil ice within the freshwater environment promoted winter use of the marine environment. This, in addition to perhaps exploiting foraging opportunities, may be the case in the Coppermine River.

The authors detected fish at marine receivers before river break-up at colder temperatures (−0.76 to 1.90°C) than has been previously observed (Jensen & Rikardsen, 2012). Fish travelled up to 18 km under ice from the mouth of the Coppermine River during late winter. To authors' knowledge, under-ice travel of this distance has been observed only once (Hammer *et al.*, 2021), and use of the marine environment by Arctic char at these cold temperatures has not been previously documented. In addition, four individuals were detected using the ice-covered marine environment earlier in the winter (November–March) than has been previously documented, and well in advance of when seasonally cued physiological adaptations would facilitate marine habitat use (Aas-Hansen *et al.*, 2005; Arnesen *et al.*, 1992; Finstad *et al.*, 1989). The potential for under-ice movement to marine environments by other populations of Arctic char that overwinter in fluvial environments is understudied and warrants further investigation.

It is possible that Arctic char detected in the marine environment during the ice-covered season were exploiting a layer of fresh water under the ice surface. Temperature and salinity measurements taken from a vertical profile in the marine environment on 22 March 2019 showed a layer of 0°C fresh water extending from the water surface until a sharp halocline at a depth of *c.* 3 m (Smith, 2020). A similar layer of fresh water was consistently observed at the surface from point measurements obtained between the months of February and April (2013–2020; Fisheries and Oceans Canada and Canadian Rangers Ocean Watch, unpubl. data; Supporting Information Figure S6). Although salinity measurements are not available for the periods and locations Arctic char were detected, it is possible that fish were using a freshwater lens under the sea ice. Recorded body temperatures below 0°C suggest that at least some were occupying salt water. Little is known of oceanographic processes in the region, particularly during the winter months, and future work characterizing the marine environment will greatly improve the understanding of under-ice movements of Arctic char.

5. CONCLUSION

Although overwintering of Arctic char in fluvial environments has been observed in several locations across the Arctic (Beddow *et al.*, 1998; Harwood & Babaluk, 2014; Jensen *et al.*, 2016), it is not commonly observed, and within-river winter movements remain virtually unstudied. The authors observed Arctic char overwintering in a fluvial environment with distinct characteristics from those previously described. They also observed high interindividual and interannual variability in overwintering location (above or below Kugluk Falls). Arctic char that overwintered below Kugluk Falls displayed net movements of up to 7 km in early winter. These movements likely occurred in response to dynamic ice formation. Continued winter movement in environments inferred to be relatively less impacted by ice was also observed. Arctic char used the ice-covered marine environment at cold temperatures throughout the winter months (November–May) and at long distances (18 km) from fresh water in June, when fluvial and marine environments remained ice-covered. The results from this study help to further the knowledge of the diversity of overwintering environments used by Arctic char. Although a potential benefit of fluvial overwintering is avoiding energy expenditures associated with a long and difficult migratory pathway, the challenging ice conditions and winter movement observed here are undoubtedly energetically expensive for Arctic char that overwinter in the lower Coppermine River. Future research will examine the potential benefits (*e.g.*, foraging potential) and drivers (*e.g.*, spawning status, environmental conditions) of fluvial overwintering both within and among individuals. The results of this research will also assist communities and regulators in the management and conservation of this highly plastic and important subsistence species.

AUTHOR CONTRIBUTIONS

R.S. was involved in conceptualization, methodology, data collection and analysis and manuscript preparation (primary author).
E.H. helped with study design, data collection and review.
T.L. assisted with conceptualization, review and editing and funding.
A.D. was involved in conceptualization, review and in-kind support.
K.K. helped with methodology, data collection and review.
H.S. was involved in conceptualization, methodology, data collection, manuscript preparation and funding.

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REFERENCES

Aas-Hansen, Ø., Vijayan, M. M., Johnsen, H. K., Cameron, C., & Jørgensen, E. H. (2005). Resmoltification in wild, anadromous Arctic char (Salvelinus alpinus): A survey of osmoregulatory, metabolic, and endocrine changes preceding annual seawater migration. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 195–204.

Ammann, A. J., Michel, C. J., & MacFarlane, R. B. (2013). The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook Salmon. *Environmental Biology of Fishes*, *96*, 135–143.

Arnesen, A. M., Halvorsen, M., & Nilssen, K. J. (1992). Development of hypoosmoregulatory capacity in Arctic char (Salvelinus alpinus) reared under either continuous light or natural photoperiod. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 229–237.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Beddow, T. A., Deary, C., & McKinley, R. S. (1998). Migratory and reproductive activity of radio-tagged Arctic char (Salvelinus alpinus L.) in northern Labrador. In J.-P. Lagardère, M.-L. B. Anras, & G. Claireaux (Eds.), *Advances in invertebrates and fish telemetry* (pp. 249–262). Dordrecht: Springer Netherlands.

Bégout Anras, M. L., Gyselman, E. C., Jorgenson, J. K., Kristofferson, A. H., & Anras, L. (1999). Habitat preferences and residence time for the freshwater to ocean transition stage in Arctic Charr. *Journal of the Marine Biological Association of the United Kingdom*, *79*, 153–160.

Brown, R. S. (1999). Fall and early winter movements of cutthroat trout, Oncorhynchus clarki, in relation to water temperature and ice conditions in Dutch Creek, Alberta. *Environmental Biology of Fishes*, 55, 359–368.

Brown, R. S., Power, G., Beltaos, S., & Beddow, T. A. (2000). Effects of hanging ice dams on winter movements and swimming activity of fish. *Journal of Fish Biology*, 57, 1150–1159.

Brown, R. S., Hubert, W. A., & Daly, S. F. (2011). A primer on winter, ice, and fish: What fisheries biologists should know about winter ice processes and stream-dwelling fish. *Fisheries*, 36, 8–26.

Brunson, J., & Read, Q. (2020). ggalluvial: Alluvial Plots in 'ggplot2'.

Canadian Ice Service. (2018). Climatic Ice Atlas 1981–2010. http://iceweb1.cis.ec.gc.ca/30Atlas/ (accessed Oct 16, 2018).

Chisholm, I. M., Hubert, W. A., & Wesche, T. A. (1987). Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. *Transactions of the American Fisheries Society*, 116, 176–184.

Chittenden, C. M., Butterworth, K. G., Cubitt, K. F., Jacobs, M. C., Ladouceur, A., Welch, D. W., & McKinley, R. S. (2009). Maximum tag to body size ratios for an endangered Coho Salmon (O. kisutch) stock based on physiology and performance. *Environmental Biology of Fishes*, 84, 129–140.

Collins, A. L., Hinch, S. G., Welch, D. W., Cooke, S. J., & Clark, T. D. (2013). Intracoelomic acoustic tagging of juvenile sockeye salmon: Swimming performance, survival, and postsurgical wound healing in freshwater and during a transition to seawater. *Transactions of the American Fisheries Society*, 142, 515–523.

Coulombe-Pontbriand, M., Reid, R., & Jackson, F. (1998). *Coppermine River: Overview of the hydrology and water quality* (p. 43). Yellowknife, NWT: Water Resources Division, Indian and Northern Affairs Canada.

Cunjak, R. A. (1996). Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 267–282.

Darcy, A. P., Raby, G. D., Johnson, T. B., Pitcher, T. E., & Fisk, A. T. (2019). Effects of intracoelomic transmitter implantation on metabolic rate, swimming performance, growth and survival in juveniles of two salmonids. *Journal of Fish Biology*, 95, 1094–1106.

Dempson, J. B., & Green, J. M. (1985). Life history of anadromous Arctic Charr, Salvelinus alpinus, in the Fraser River, northern Labrador. *Canadian Journal of Zoology*, 63, 315–324.

Elliott, J. M., & Elliott, J. A. (2010). Temperature requirements of Atlantic Salmon Salmo salar, Brown trout Salmo trutta and Arctic Charr Salvelinus alpinus: Predicting the effects of climate change. *Journal of Fish Biology*, 77, 1793–1817.

Environment and Climate Change Canada. (2008). Kendall River near Outlet of Dismal Lakes (10PC001) https://wateroffice.ec.gc.ca/report/historical_e.html?stn=10PC001 (accessed Feb 20, 2020).

Finstad, B., Nilssen, K. J., & Arnesen, A. M. (1989). Seasonal changes in sea-water tolerance of Arctic Charr (Salvelinus alpinus). *Journal of Comparative Physiology B*, 159, 371–378.

Gilbert, M. J. H., Donadt, C. R., Swanson, H. K., & Tierney, K. B. (2016). Low annual fidelity and early upstream migration of anadromous Arctic char in a variable environment. *Transactions of the American Fisheries Society*, 145, 931–942.

Gowans, A. R. D., Armstrong, J. D., & Priede, I. G. (1999). Movements of adult Atlantic Salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology*, 54, 713–726.

Grainger, E. H. (1953). On the age, growth, migration, reproductive potential and feeding habits of the Arctic char (Salvelinus alpinus) of Frobisher Bay, Baffin Island. *Journal of the Fisheries Research Board of Canada*, 10, 326–370.

Gross, M. R., Coleman, R. M., & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science*, 239, 1291–1293.

Gulseth, O. A., & Nilssen, K. J. (2001). Life-history traits of charr, Salvelinus alpinus, from a high Arctic watercourse on Svalbard. *Arctic*, 54, 1–11.

Gyselman, E. C. (1994). Fidelity of anadromous Arctic char (Salvelinus alpinus) to Nauyuk Lake, N.W.T., Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 1927–1934.

Hammer, L. J., Hussey, N. E., Marcoux, M., Pettitt-Wade, H., Hedges, K., Tallman, R., & Furey, N. B. (2021). Arctic char enter the marine environment before annual ice breakup in the high Arctic. *Environmental Biology of Fishes*. https://doi.org/10.1007/s10641-021-01099-3

Harwood, L. A., & Babaluk, J. A. (2014). Spawning, overwintering and summer feeding habitats used by anadromous Arctic char (Salvelinus alpinus) of the Hornaday River, Northwest Territories, Canada. *Arctic*, 67, 449–461.

Heggenes, J., Krog, O. M. W., Lindas, O. R., & Dokk, J. G. (1993). Homeostatic behavioural responses in a changing environment: Brown trout (Salmo trutta) become nocturnal during winter. *The Journal of Animal Ecology*, 62, 295–308.

Hubbs, C. L., & Trautman, M. B. (1935). The need for investigating fish conditions in winter. *Transactions of the American Fisheries Society*, 65, 51–56.

Huusko, A., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., … Alfredsen, K. (2007). Life in the ice lane: The winter ecology of stream salmonids. *River Research and Applications*, 23, 469–491.

Jakober, M. J., McMahon, T. E., Thurow, R. F., & Clancy, C. G. (1998). Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. *Transactions of the American Fisheries Society*, 127, 223–235.

Jensen, A. J., Finstad, B., & Fiske, P. (2018). Evidence for the linkage of survival of anadromous Arctic char and Brown trout during winter to marine growth during the previous summer. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 663–672.

Jensen, A. J., Finstad, B., & Fiske, P. (2019). The cost of anadromy: Marine and freshwater mortality rates in anadromous Arctic char and Brown trout in the Arctic region of Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 2408–2417.

Jensen, J. L. A., & Rikardsen, A. H. (2008). Do northern riverine anadromous Arctic Charr Salvelinus alpinus and sea trout Salmo trutta overwinter in estuarine and marine waters? *Journal of Fish Biology*, 73, 1810–1818.

Jensen, J. L. A., & Rikardsen, A. H. (2012). Archival tags reveal that Arctic Charr Salvelinus alpinus and Brown trout Salmo trutta can use estuarine and marine waters during winter. *Journal of Fish Biology*, 81, 735–749.

Jensen, J. L. A., Christensen, G. N., Hawley, K. H., Rosten, C. M., & Rikardsen, A. H. (2016). Arctic Charr exploit restricted urbanized coastal areas during marine migration: Could they be in harm's way? *Hydrobiologia*, 783, 335–345.

Johnson, L. (1980). The Arctic Charr, Salvelinus alpinus. In E. K. Balon (Ed.), *Charrs: Salmonid fishes of the genus Salvelinus* (pp. 15–98). The Hague, The Netherlands: Dr. W. Junk bv Publishers.

Johnson, L. (1989). The anadromous Arctic Charr (Salvelinus alpinus) of Nauyuk Lake, N.W.T., Canada. *Physiology and Ecology Japan*, 1, 201–227.

Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, 3, 348–365.

Kennedy, R. J., Moffett, I., Allen, M. M., & Dawson, S. M. (2013). Upstream migratory behaviour of wild and ranched Atlantic Salmon Salmo salar at a natural obstacle in a coastal spate river. *Journal of Fish Biology*, 83, 515–530.

Klemetsen, A., Knudsen, R., Staldvik, F. J., & Amundsen, P.-A. (2003). Habitat, diet and food assimilation of Arctic Charr under the winter ice in two subarctic lakes. *Journal of Fish Biology*, 62, 1082–1098.

Komadina-Douthwright, S. M., Caissie, D., & Cunjak, R. A. (1997). *Winter movement of radio-tagged Atlantic Salmon (Salmo salar) kelts in relation to frazil ice in pools of the Miramichi River. Canadian technical report of fisheries and aquatic sciences. Canadian technical report of fisheries and aquatic sciences 2161 2161*. Moncton, NB: Fisheries and Oceans Canada.

Lennox, R. J., Thorstad, E. B., Diserud, O. H., Økland, F., Cooke, S. J., Aasestad, I., & Forseth, T. (2018). Biotic and abiotic determinants of

the ascent behaviour of adult Atlantic Salmon transiting passable waterfalls. *River Research and Applications*, 34, 907–917.

Lindstrom, J. W., & Hubert, W. A. (2004). Ice processes affect habitat use and movements of adult cutthroat trout and brook trout in a Wyoming foothills stream. *North American Journal of Fisheries Management*, 24, 1341–1352.

Mathisen, O. A., & Berg, M. (1968). Growth rates of the char Salvelinus alpinus (L.) in the Vardnes River, Troms, northern Norway. *Report of the Institute of Freshwater Research Drottningholm*, 48, 177–186.

Moore, J.-S., Harris, L. N., Le Luyer, J., Sutherland, B. J. G., Rougemont, Q., Tallman, R. F., … Bernatchez, L. (2017). Genomics and telemetry suggest a role for migration harshness in determining overwintering habitat choice, but not gene flow, in anadromous Arctic char. *Molecular Ecology*, 26, 6784–6800.

Moore, J.-S., Harris, L. N., Tallman, R. F., & Taylor, E. B. (2013). The interplay between dispersal and gene flow in anadromous Arctic char (Salvelinus alpinus): Implications for potential for local adaptation. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 1327–1338.

Muhlfeld, C. C., Bennett, D. H., & Marotz, B. (2001). Fall and winter habitat use and movement by Columbia River Redband trout in a small stream in Montana. *North American Journal of Fisheries Management*, 21, 170–177.

Mulder, I. M., Morris, C. J., Dempson, J. B., Fleming, I. A., & Power, M. (2018a). Overwinter thermal habitat use in lakes by anadromous Arctic char. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 2343–2353.

Mulder, I. M., Morris, C. J., Dempson, J. B., Fleming, I. A., & Power, M. (2018b). Winter movement activity patterns of anadromous Arctic Charr in two Labrador lakes. *Ecology of Freshwater Fish*, 27, 785–797.

Mulder, I. M., Dempson, J. B., Fleming, I. A., & Power, M. (2019). Diel activity patterns in overwintering Labrador anadromous Arctic Charr. *Hydrobiologia*, 840, 89–102.

Natural Resources Canada. (2011). Canadian Geographical Names of Nunavut (cgn_nu_shp_eng). Canada Centre for Mapping and Earth Observation.

Natural Resources Canada. (2015). *Lakes, Rivers and glaciers in Canada - CanVec series - hydrographic features (canvec_50K_NU_Hydro)*. Ottawa, ON: Natural Resources Canada.

Newton, M., Barry, J., Dodd, J. A., Lucas, M. C., Boylan, P., & Adams, C. E. (2016). Does size matter? A test of size-specific mortality in Atlantic Salmon Salmo salar smolts tagged with acoustic transmitters. *Journal of Fish Biology*, 89, 1641–1650.

Ogle, D., Doll, J., Wheeler, P., & Dinno, A. (2021). *FSA: Simple fisheries stock assessment methods*. Zenodo. https://doi.org/10.5281/zenodo.6098468

Power, G., Brown, R. S., & Imhof, J. G. (1999). Groundwater and fish - insights from northern North America. *Hydrological Processes*, 13, 22–422.

Power, M., & Reist, J. D. (2018). Salvelinus alpinus. In B. W. Coad & J. D. Reist (Eds.), *Marine fishes of Arctic Canada* (pp. 283–289). Toronto, ON: University of Toronto Press.

Priest, H., & Usher, P. J. (2004). *The Nunavut wildlife harvest study*. Nunavut, Canada: Nunavut Wildlife Management Board.

Prno, J. (2019). Traditional Knowledge Study on the Arctic Char Fishery in the Lower Coppermine River, Nunavut. Report prepared for Angoniatit Niovikvia Ltd. (a subsidiary of the Kugluktuk Hunters and Trappers Organization).

QGIS Development Team. (2020). QGIS geographic information system. Open Source Geospatial Foundation Project

Quinn, T. P., McGinnity, P., & Reed, T. E. (2016). The paradox of "premature migration" by adult anadromous salmonid fishes: Patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1015–1030.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reid, C. H., Vandergoot, C. S., Midwood, J. D., Stevens, E. D., Bowker, J., & Cooke, S. J. (2019). On the electroimmobilization of fishes for research and practice: Opportunities, challenges, and research needs. *Fisheries*, 44, 576–585.

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., King, J. R., & Beamish, R. J. (2006). An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. AMBIO: A journal of the human. *Environment*, 35, 381–387.

Rikardsen, A. H., Amundsen, P.-A., Bjorn, P. A., & Johansen, M. (2000). Comparison of growth, diet and food consumption of sea-run and Lake-Dwelling Arctic Charr. *Journal of Fish Biology*, 57, 1172–1188.

Roux, M.-J., Tallman, R. F., & Lewis, C. W. (2011). Small-scale Arctic Charr Salvelinus alpinus fisheries in Canada's Nunavut: Management challenges and options. *Journal of Fish Biology*, 79, 1625–1647.

Scott, W. B., & Crossman, E. J. (1973). *Freshwater fishes of Canada*. Ottawa, ON: Fisheries Research Board of Canada.

Smircich, M. G., & Kelly, J. T. (2014). Extending the 2% rule: The effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. *Animal Biotelemetry*, 2, 16.

Smith, R. L. (2020). Migration timing and overwintering habitat of anadromous Arctic char (Salvelinus alpinus) near Kugluktuk, Nunavut (Master's thesis). University of Waterloo, Waterloo, ON, 84. Available from UWSpace https://uwspace.uwaterloo.ca/handle/10012/16016

Spares, A. D., Stokesbury, M. J. W., Dadswell, M. J., O'Dor, R. K., & Dick, T. A. (2015). Residency and movement patterns of Arctic Charr Salvelinus alpinus relative to major estuaries. *Journal of Fish Biology*, 86, 1754–1780.

Statistics Canada. (2016). *Provinces/territories, cartographic boundary file - 2016 census (lpr_000b16a_e)*. Ottawa, ON: Statistics Canada.

Svenning, M.-A., Klemetsen, A., & Olsen, T. (2007). Habitat and food choice of Arctic Charr in Linnévatn on Spitsbergen, Svalbard: The first year-round investigation in a high Arctic lake. *Ecology of Freshwater Fish*, 16, 70–77.

Tallman, R. F., Ferguson, S. H., Harris, L. N., Hedges, K. J., Howland, K. L., Hussey, N. E., … Moore, J.-S. (2019). Migration, dispersal, and gene flow of harvested aquatic species in the Canadian Arctic. In Y. Bozkurt (Ed.), *Biological research in aquatic science*. London, UK: IntechOpen.

Tallman, R. F., Saurette, F., & Thera, T. (1996). Migration and life history variation in Arctic Charr, Salvelinus alpinus. *Écoscience*, 3, 33–41.

United States Census Bureau. (2017). Cartographic boundary files – Shapefile (cb_2017_us_state_20m). United States Census Bureau

Van Oostdam, J., Donaldson, S. G., Feeley, M., Arnold, D., Ayotte, P., Bondy, G., … Kalhok, S. (2005). Human health implications of environmental contaminants in Arctic Canada: A review. *Science of the Total Environment*, 351–352, 165–246.

Wandsvik, A., & Jobling, M. (1982). Overwintering mortality of migratory Arctic Charr, Salvelinus alpinus, (L.) reared in salt water. *Journal of Fish Biology*, 20, 701–706.

Wedel, J. H., Olding, B. J., & Palmer, M. (1988). *An overview study of the Coppermine River basin*. Yellowknife, NWT: Environment Canada.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag.

Winter, J. (1996). *Advances in underwater Telemetery. Fisheries techniques* (pp. 555–590). Bethesda, Maryland: American Fisheries Society.

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