Title

Characterization of anadromous Arctic char winter habitat and egg incubation areas in collaboration with Inuit fishers

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Abstract

In Nunavik, anadromous Arctic char spend more than six months under ice-covered habitats, mainly in lakes. Their winter habitats in this region have been scarcely studied due to the challenging logistics in the Arctic. In this study, we worked with Inuit fishers to characterize the winter habitat and incubation areas used by Arctic chars in five overwintering lakes and one lentic river reach. The collaborating fishers determined char occupancy of certain areas related to fishing sites (presence, absence, spawning) and conducted measurements to characterize the sites while performing their fishing activities. The data showed that incubation areas were associated with significantly shallower depths and warmer (albeit not statistically significant) lake bottom temperatures than sites where no spawning occurs, which is beneficial for egg maturation. The productivity of these areas is also beneficial for fry that hatch during winter. Adults and post-smolt habitats tended to be associated with cold littoral zone but their habitat did not show any other distinct characteristics. This exploratory study adds insights into the cryptic characteristics of the Arctic char winter habitat use, thanks to the Inuit fishers' knowledge of fish habitats and movements, and the experience and expertise they have acquired working in the local environment.

Keywords

Overwintering, fish winter habitat, Inuit knowledge, spawning, Arctic fish.

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1 Introduction

Anadromous Arctic char (*Salvelinus alpinus, Iqaluppik* in Inuktitut) is one of the northernmost distributed freshwater fish and has a circumpolar distribution (Klemetsen et al., 2003). Adults and non-mature post-smolts anadromous Arctic char exclusively feed in marine environment during one to two summer months. They return to freshwater systems in fall, for reproduction and/or overwintering. Anadromous Arctic char typically use lakes to overwinter but can also use large river reaches that are not prone to freeze to the bottom (Boivin et al., 1989; Power and Barton, 1987; Smith et al., 2022). Although the overwintering period covers more than half of the year, this is the least studied part of the Arctic char life cycle, probably because conducting Arctic remote fieldwork in winter remains challenging and costly.

Recently, studies of winter habitat use have provided insight into winter behavior, activity level, and movements of lake-resident Arctic char on a broad scale (Hawley et al., 2017), as well as anadromous char in their overwintering lakes (Mulder et al., 2019; Monsen, 2019) and rivers (Smith et al., 2022). The use of acoustic telemetry in these studies allowed us to get a range of temperatures used by Arctic char in winter. In lakes, the char tended to use the upper water column, where water is colder (Mulder et al., 2018a). In rivers, since the water column was well mixed, the char could not select a specific thermal habitat. Depth and temperature were the only variables analyzed for habitat use. Experimental gillnet sampling and simultaneous oxy-thermal measurements of lake water were conducted to assess habitat use of resident and anadromous Arctic char in Cumberland Sound, Nunavut. Although the abundance of anadromous Arctic char was negatively correlated to pelagic area in the fall, no significant correlation was found between abundance and habitat variables in winter. The authors pointed out the necessity to assess the variability of its habitat use across its distribution range given the plasticity of the species (Klemetsen, 2010). To our knowledge, anadromous char winter habitat has not been characterized in Nunavik.

In Ungava Bay and particularly in Kangiqsualujjuaq, anadromous Arctic char is one of the few species caught year-round by the Inuit for subsistence fisheries. Winter is a good fishing season since Arctic char are in specific areas known to harvesters, and access by snowmobile allows easier transportation than in other seasons (Boivin et al., 1989). Char are usually harvested by gillnets installed under the ice for a few hours or overnight, or by gigging with a hook (ice fishing). Both mature adults and non-mature (post-smolts) are caught. Knowledge of the sites used by char is passed on from generation to generation of harvesters. Hence, traditional Inuit knowledge is a relevant source of information on Arctic char life cycle and habitat, especially in winter.

Given the paucity of scientific data on the physical characteristics of anadromous Arctic char winter habitat in Nunavik, we collaborated with Inuit fishers to characterize Arctic char habitat during their traditional subsistence fishing activities. The idea was to use their knowledge of fishing sites in selected overwintering lakes to infer and characterize fish habitat use. The objectives of the study were to assess (1) whether overwintering habitat used by adults and post-smolts Arctic char at traditional fishing sites have different characteristics than non-fishing sites and (2) whether egg incubation areas identified at certain overwintering sites showed specific physical characteristics. Improved knowledge of the characteristics of habitats used by the adults and post-smolt will help to predict the impact of climate change and could be incorporated into fish habitat models. Moreover, some Nunavik communities consider increasing productivity with *in situ* hatchery in depleted rivers, where artificially fertilized eggs would be deposited. Hence, knowledge of the specific characteristics favorable for incubation areas will be useful to choose potential sites.

2 Methods

2.1 Study area

The study was conducted in popular fishing lakes and river reaches used by Arctic char to overwinter around Kangiqsualujjuaq, Ungava Bay, Nunavik, Québec, Canada. The ice cover in overwintering lakes is usually present from mid-November to the end of May. The mean annual temperature of the region is between -5°C and -6°C, and the total annual snow water equivalent varies from 300 to 400 mm, with a snow cover duration on the land between 241 to 260 days (Charron, 2015). The fishing sites were located in four different hydrographic systems. Three of them were located north-east of the village, Ujarasutjulik (Barnoin River),

Koroc River, and Tasikallak (Short Lake), while Tunnullik was located in the south-west portion of the territory (Figure 1). Ujarasutjulik (~2.5 km²) and Ujarasutjuliup Qullinga (~10.7 km²) are two consecutive fluvial lakes formed by a widening of the Barnoin River. Kuururjuaq (~8.4 km²) is also a fluvial lake, formed by the Koroc River in its lower reach, while Koroc Allipaak is a lentic river reach, about 25 km upstream. Tasikallak is a relatively small lake (~1.2 km²) that flows directly into a fjord of Ungava Bay through a short rapid stretch of 350 meters, and Tunnullik is also a small lake (~1.2 km²) that flows into Ungava Bay through a lentic river of 4 km. In Tunnullik, the measured sites were located at the entrance of the main tributary in the lake. Even if some studied sites were located in 'rivers' according to classic hydro-geomorphological characteristics (Koroc Allipaak), the relatively low velocity and the stable ice conditions make them very similar to lakes. All the sites are also qualified as lakes by Inuit. Hence, for simplicity, the six sites are called overwintering 'lakes'.
Anadromous Arctic char is the main fish species encountered in the studied lakes, but other salmonids are also present. Lake-resident Arctic char (*Nutillik* in Inuktitut), brook trout (*Salvelinus fontinalis; Aanaak*) and a few lake trout (*Salvelinus namaycush; Isiuralitaak*) are present in Ujarasutjulik and Ujarasutjuliup Qullinga. Brook trout, lake trout and Atlantic salmon (*Salmo salar; Saamaak*) are present in the Koroc River and thus, can be

(Coregonus sp.) was observed at this site, although they do not seem to be a common species in the area.

present in Kuururjuaq and Koroc Allipaak. Tunnullik Lake also supports brook trout and a white fish

2.2 Identification of site occupancy

According to the knowledge of experienced local fishers, Arctic char are generally harvested only in certain areas of the overwintering lakes, which can vary during the season. Hence, each lake has sites of presumed fish 'presence' and 'absence', based on this local knowledge. Sites used for winter fishing during the sampling period were hypothesized as sites of 'presence', whereas places where fishing was not practiced at any time of the year, were hypothesized as sites of 'absence'. In addition, some sites located in known spawning areas were characterized and qualified as 'incubation' sites. Most of the spawning areas identified here were also identified on maps by elders who had spent a lot of time along the studied lakes (Dubos et al., 2023). The sites were not characterized during the spawning season, but their winter characterization provided a better understanding of the egg incubation conditions. The sites not identified as spawning areas were analyzed as 'non-spawning' sites, although some might just be unknown spawning sites. Fishing/Non-fishing (associated with Presence/Absence by fishers) and Incubation/Non-spawning sites were analyzed independently as an incubation site could be either a winter habitat for adults or a site of absence, and vice-versa. The type of occupancy was described qualitatively for each site characterized by the local fishers participating in the data collection and was confirmed by other knowledge holders from the community of Kangiqsualujjuaq during informal meetings. The characterized sites of absence were chosen randomly in areas never used for fishing. In addition to this Inuit knowledge, when fishing was carried out during the measurements, the occupancy of the sites was confirmed by catch or absence of catch. At most sites, confirmation of absence was also tested with the installation of nets or by fishing with hook. Underwater videos were also recorded occasionally at sites of presence and sites of absence, using GoPro Hero 3 and Hero 5 cameras attached to a stick. Absence of char on the video was not used to infer site unoccupancy but only to confirm that previously identified sites of absence were indeed not used by the char. No fish were observed or caught at sites of absence, Nevertheless, the fishing effort was lower than at sites of presence, since fishers knew that those sites were not suitable for fishing.

2.3 Fieldwork planning and sites characterization

The project was proposed to the municipal authorities in the fall 2019, during an in-person meeting, as part of complementary work for Arctic char habitat characterization already underway. Two experienced fishers, who have extensive knowledge of Arctic char local habitats and movements, were hired successively to identify the sites and measure their characteristics. Fishermen, including a long-term collaborator, were suggested by the municipal authorities. They were met in person the fall prior to the study and briefed on the study objectives. The sampling method was co-developed to minimize the impact of measurements on the fishing activities of our collaborators. The equipment, adapted to fishing holes, was easy to handle in cold conditions and took up

minimal space in a snowmobile sled. Initially, sampling techniques with sketched instructions were sent by email, but a short in-person training was conducted for the use of a multiparameter water quality probe. The on-site training was done at first with one researcher (author, VD) and one of the fishers. The fisher then carried out the characterization of sites himself, during his fishing activities. However, as he was not available until the end of the winter, the other collaborator was trained in person by a biologist from the Makivik Research Center, based in Kuujjuaq. After each day of fieldwork, the fisher sent pictures of the data collected on the notebook, site occupancy, and GPS locations to the researcher. A subsequent phone call or message ensured that all the information had been noted down and clearly understood. A follow-up of the results and interpretation was made online during the analyses to receive the feedback of the collaborating fishers and the final results were presented in person in summer 2022 to each of the fishers and to the municipal authorities. Data collected, including site locations, were also transmitted to the new LNUK manager (Local Nunavimmi Umajulirijiit Katujiqatigininga, local association of Hunters and fishers) and to Nunavik Parks since the sampling in the Koroc River was carried out in a Regional Park.

At each of the studied overwintering lakes, some sites of char 'presence' and 'absence', or identified 'incubation' areas were physically characterized by drilling holes through the ice. 43 measurements were conducted between January and May 2020, while snow and ice conditions allowed for safe access to the fishing areas. Five sites were sampled between March and April 2021, and two in May 2022. The equipment included a chain of thermographs, and/or a thermometer and/or a YSI multiparameter probe; insulation materials and hand warmers to prevent the probe from freezing between two measurements; a weighted measuring tape (30 m) and an underwater GoPro camera mounted on a telescopic pole. Prepared notebooks were provided and were useful for the hunters to follow a standardized sampling. At each site, char occupancy, GPS location, snow depth, water depth, and oxy-thermal properties of the water column were collected. Of the 50 vertical profiles conducted, 34 were obtained using a YSI multiparameter probe (either YSI 650 or YSI ProSolo) collecting temperature (accuracy $\pm 0.15^{\circ}$ C) and dissolved oxygen (DO; accuracy $\pm 0.1\%$). The YSI instrument's cable had a maximum length of 30 m, which was therefore the maximum length of the profiles for two sites with greater depths. For the other profiles, only temperature was measured, either with a Hanna thermometer

(9 profiles, accuracy $\pm 0.1^{\circ}$ C) or with a vertical chain equipped with Hobo Pro V2 ($\pm 0.2^{\circ}$ C) and Pendant ($\pm 0.5^{\circ}$ C) thermographs, positioned at different elevations (7 profiles). In most cases, the data produced were validated shortly after each day of measurements to ensure their quality. In addition to the *in situ* measured variables, the distance from the shore and the bed slope were estimated. The distance from the shoreline was derived from topographic maps. The mean bed slope was calculated as the ratio of the measured depth and the distance from the shoreline.

2.4 Data analysis

To assess if the measured variables (Table 1) differed significantly between lakes, regardless of site occupancy, the non-parametric Kruskal-Wallis statistical test was used due to the not-normal distribution of the data (Shapiro-Wilk test). If a difference between lakes was significant, a post hoc pair-wise Dunn test with Bonferroni correction was conducted to detect which location showed different characteristics. The absence of Dunn test difference allowed us to pool the data together. The post hoc power of the Kruskall-Wallis test was calculated using the software G*Power (Faul et al., 2009).

The Kruskal-Wallis test was also applied to assess if there were significant differences between sites of presence and absence. The Fligner-Killeen test was used to compare the variance between sites of presence and absence. Given that very few studies have investigated habitat variables for overwintering and spawning habitat, a correlation analysis was performed to identify potential variables that co-vary. Pearson linear correlation and Spearman rank correlation factor were calculated for each pair of studied variables, for all locations pooled together. Testing rank correlation allowed us to verify potential non-linear relationships between variables that could be missed by linear correlation. Assessing potential correlations helped to ensure that results on the habitat use were related to variable under study and not the result of a correlation between variables.

3 Results

3.1 Characteristics of overwintering lakes

A total of 50 sites were characterized in the six overwintering lakes, distributed as follows: Ujarasutjulik (n=4), Ujarasutjuliup Qullinga (n=7), Kuururjuaq (n=19), Koroc Allipaak (n=5), Tasikallak (n=13) and Tunnullik Lake (n=2) (see Table S3 in Supplementary material). During the studied period, the water temperature of all sites varied between -0.04°C \leq T \leq 1.90°C, with a mean of 0.24°C and a median of 0.19°C. Regardless of site occupancy by Arctic char, the measured variables were significantly different by location for mean and bottom temperature (Kruskall-Wallis test, $\chi^2=13.80$; p=0.017 and $\chi^2=12.61$; p=0.027 respectively), water depth $(\chi^2=13.21; p=0.007)$ and shore distance $(\chi^2=12.84; p=0.025)$. However, a pair-wise comparison of lakes with the Dunn test for these variables did not show any significant differences between the characteristics of the compared lakes. This might be due to the low statistical power of Kruskall-Wallis test, given the small number of sites in some lakes (1- β err. prob=0.20 for temperature, 1- β = 0.21 for water depth and shore distance). The bottom temperature between Ujarasutjulik and Tasikallak was almost significantly different (p=0.053), with Tasikallak Lake showing a warmer median bottom temperature than Ujarasutjulik (0.62°C vs 0.12°C). All the characterized sites from the six overwintering lakes (Ujarasutjulik, Ujarasutjuliup Qullinga, Kuururjuaq, Koroc Allipaak, Tasikallak, and Tunnullik) were pooled for the analyses since the number of sampled sites was too limited for some lakes to be analyzed on their own. The sampled sites were located at depths varying between 0.68 m and > 30 m. Water depth was correlated with mean temperature (Figure 2, values are given in Supplementary material). Recorded bottom temperatures varied between -0.03°C and 1.90°C, and vertically averaged temperature varied between -0.04°C and 1.1°C. Water temperature was negatively correlated with mean DO saturation [79,8% - 106.6%] and bottom DO values [67.4% - 107.1%]. Snow depth was negatively correlated with both mean and bottom DO with rank correlation, but the linear correlation was not significant for any variable, including shore distance.

3.2 Characteristics of incubation areas in winter

The sites characterized as incubation areas showed significantly shallower depths than non-spawning sites, with respectively a mean depth of 3.0 m and 6.2 m (χ^2 =5.38; p=0.02) (Figure 3 and Table 1). The median depth value of incubation areas was 2.4 m, whereas the median depth of non-spawning sites was 4.5 m. The depth of incubation areas [0.7 m - 8.4 m] showed a significantly smaller variance than non-spawning areas [0.9 m - > 30 m] (χ^2 =7.15; p=0.007). Even if they were located at shallower depths, incubation areas showed a median bottom temperature of 0.60°C, which is higher than the median bottom temperature of non-spawning areas (0.30°C), but the difference is not significant (χ^2 =3.38; p=0.066). Bed slope variance was also significantly different at incubation areas than at non-spawning sites (χ^2 =2.70; p=0.010), with the former mainly located on slopes varying between 0.031 m.m⁻¹ and 0.045 m.m⁻¹ (first and third quartile). Other variables, including DO, did not show any statistically significant difference between incubation and non-spawning sites. However, incubation areas also tended to have lower snow depths (median of 0.30 m) compared with non-spawning areas (median of 0.37 m), and, as expected from the depth, they tended to be at a closer shore distance than non-spawning sites (mean distance of 83 m compared to 123 m).

3.3 Characteristics of winter habitat use by adults and post-smolts

None of the variables used to characterize sites of presence of anadromous Arctic char was significantly different from sites of absence (Figure 3 and Table 2). Char used a mean and median vertical temperature of respectively 0.25°C and 0.20°C [0°C - 0.66°C] and a mean dissolved oxygen saturation of 91.9% [80.3% - 106.6%]. Although statistically not different, the mean and median depth of sites used by Arctic char were respectively 4.1 m and 3.6 m, whereas the mean and median depth measured at sites of absence were 7.7 m and 2.9 m. The water depth variance was significantly lower (χ^2 =3.83; p=0.050) at sites of presence, with depth used by char varying between 1.3 m and 9.7 m, whereas the depth of sites of absence was comprised between 0.7 m and > 30 m. The bed slope of sites used by Arctic char also tended to have a smaller variance than the slope of sites of absence, with char using mainly sites with a slope comprised between 0.034 m.m⁻¹ and 0.066 m.m⁻¹ (respectively for first and third quartile; χ^2 =3.12; p=0.077). Sites of presence tended to have a lower

snow accumulation than sites of absence (mean and median of 0.30 m compared to 0.38 m; $\chi^2=1.71$; p=0.191), with a higher variance towards lower values of snow accumulation.

4 Discussion

In this study, we compared the physical characteristics of sites used by Arctic char with sites of absence and spawning areas with non-spawning sites in six overwintering lakes of Nunavik. We worked in collaboration with Inuit fishers as they carried out their traditional fishing activities, to measure and determine the char habitat occupancy using evidence-based cumulative knowledge. The spawning areas identified in the overwintering lakes were located at significantly shallower depths with higher bottom temperatures than sites not identified as spawning areas. On the other hand, the winter habitats used by adults and post-smolts anadromous Arctic char did not present significantly different characteristics than the sites of absence. However, winter habitats were typically found in the littoral zone, at depths less than 10 meters.

4.1 Incubation zones

The location of the spawning areas at shallower depths and at a limited distance from the shore makes them favorable environments for egg development. Indeed, they might benefit from recirculating downslope density currents which brings more oxygenated water from under the ice, while the benthic zone suffers oxygen depletion at the center of the lake during winter (Jansen et al., 2020; Welch and Bergmann, 1985; Magnuson and Karlen, 1970). In addition, spawning sites are likely selected for their warmer bottom temperatures in winter, possibly to prevent the eggs from freezing and improve the incubation conditions. Indeed, whereas below 4°C bottom temperature usually increases with water depth due to water density, incubation areas were warmer despite being shallower. Among the non-spawning areas characterized, some temperature profiles even showed a vertical profile of 0°C throughout the depth that could be detrimental to egg incubation (Elliott and Elliott, 2010). Hyporheic or groundwater upwelling flow might explain the locally warmer temperature (Baxter and Hauer, 2000) and could be detected by the char during the spawning season. More detailed studies

are needed to investigate the role of hyporheic flow for egg incubation of the Arctic char through the monitoring of local piezometric pressure and temperature as it was done for brook trout (Franssen et al., 2013).

Shallower depths used as incubation areas might likewise be selected as a favorable post-hatching environment for fry. Eggs are hatching in winter, between January and April depending on incubation conditions (Dubos et al., 2023; Granier, 2013; Johnson, 1980a). In our study, in addition to being at shallower depths, the incubation areas tended to have less snow accumulation (although not statistically significant). Snow depth has a critical impact on light penetration under the ice (Welch et al., 1987) and is thus related to productivity. Notably, the littoral zones are favorable for the development of macrophytes and periphyton, which are themselves associated with the growth of chironomid larvae (Jansen et al., 2020). During the winter, the littoral zones of high Arctic lakes were indeed associated with a high occurrence of zoobenthos, especially chironomid larvae, which are an important part of the diet of juvenile Arctic char (Svenning et al., 2007; Klemetsen et al., 2003). Although metabolic demand decreases at low temperatures, young-of-the-year need to feed in winter (Byström et al., 2006). Therefore, it is likely that shallower depths are selected as spawning areas for their increased productivity.

Due to the transitory nature of the reproduction period, identification of the incubation areas is more difficult than the winter habitat of adults. The spawning areas were first identified on maps by elders who had spent a lot of time along the studied lakes and had observed the spawning (Dubos et al., 2023). Since spawning areas were in part associated with visual observation of spawning behavior, the identified sites might be at depths that allowed such observations. The identified spawning areas were also confirmed by the collaborating fishers who had already caught many individuals in spawning colours in these areas during the fall. Hence, the restricted range of depths associated with spawning areas may not be due to the identification method, but to a true specificity of the habitat. A similar observation was done in the shallow littoral zone of a Baffin Island lake by Young and Tallman (2021) who caught in the fall aggregated large Arctic char returning from migration. The char were suspected to be in pre-spawning behavior, although their reproductive status or their colour was not specified.

4.2 Adult and post-smolt habitat use

None of the lakes in the present study showed the presence of an inverse stratification with bottom temperatures at 4°C as typically observed in more southern latitudes. The measured temperature in our overwintering lakes always remained below 1.90°C, and Arctic char occupied a narrow range of temperature [0°C - 0.66°C]. This range of temperature is comparable with the body temperature of Arctic char from the Coppermine River, NWT, implanted with acoustic transmitters ([-0.14°C - 1.28°C], with over 98% of temperatures below 0.02°C; Smith et al., 2022), the river being slightly cooler than the lakes studied here. In two subarctic lakes in Norway presenting a similar range of temperature than our study site, the large lake-resident Arctic char also used the cold water layer $[0.2^{\circ}C - 0.7^{\circ}C]$ located in the littoral zone (Klemetsen et al., 2003). Arctic char are highly tolerant to low temperatures and can even bear supercooling temperatures (Spares et al., 2012; Johnson, 1980a; Scholander et al., 1957), limited to -0.1 °C in freshwater. The lake-resident char were thought to use the littoral for the presence of light and prey availability. However, according to Inuit observations and studies on stomach contents, anadromous Arctic char stop feeding or eat very little during the winter season (Dubos et al., 2023; Young et al., 2021; Moore and Moore, 1974). In Tasikallak Lake, winter fasting has been confirmed by a sampling of 237 Arctic char which all had empty stomachs for, at least, several days (Boivin and Power, 1990). As anadromous Arctic char are fasting for several months in winter (Jørgensen and Johnsen, 2014), the use of a cold-water habitat, and thus the littoral zone, is favorable to survival as it slows down their metabolic rate. Thus, anadromous Arctic char are not only adapted to the lower temperatures of Arctic lakes, but they generally seem to avoid higher temperature areas of these cold systems.

The DO saturation levels were well above the Arctic char minimum requirements in all studied lakes (60%; Sæther et al., 2016). A minimum value of 67.4% was observed at a depth of 30 m at Ujarasutjuliup Qullinga, at the end of March, but other lake areas were accessible. Therefore, DO cannot be considered a significant variable for winter habitat selection by char, at least for the years covered by our study. Nonetheless, DO can vary from one site to another on the same lake but also from year to year because it depends on the concentration at the time of ice cover formation (Clilverd et al., 2009; Chambers et al., 2008). For example,

during the winter 2021-2022 in Tasikallak, DO decreased constantly from 92 to 73% below the ice cover at a depth of 15 m (unpublished data). This same lake experienced a major winter fish kill in 2002, possibly due to oxygen depletion (Côté, 2002). DO depletion in the deepest areas of the lakes could explain the lack of fish (or fishing sites) in the pelagic zone as an interannual adaptative behavior. Telemetry studies showed that Arctic char do occasional incursions in deeper water but only for a limited time (Monsen, 2019; Hawley et al., 2017).

Adults Arctic char preferentially used the littoral zone in the present study (at depths < 10 m with a mean of 4.1 m), a behavior corroborated by other studies (Klemetsen et al., 2003; Svenning et al., 2007). Sites of presence showed slightly less snow accumulation, although differences were not significant. The study area in Nunavik is located at a latitude with a daylight period of several hours in winter. The studied lakes are all clear and oligotrophic, with limited snow over the ice allowing the penetration of a certain amount of light in the water column, likely enough for fish with good vision such as chars (Ali and Wagner, 1980). However, since anadromous Arctic char do not feed in winter, other potential factors explaining habitat selection must be considered. During the measurements, char were observed or filmed in shallow areas, slowly swimming in groups for most of them, but also staying close to the lake bottom and hiding behind rocks for some of them (video accessible in Dubos and Snowball, 2020; captures in Supplementary material). One Inuit elder mentioned that *«at the beginning of the winter, all the char get together, the adults and the small. They are* together but not always aggregate» (Local fisher, Kangigsualujjuag 2019, pers. communication). Hence, the use of nearshore areas could allow them to use the substrate at the bottom of lakes to rest during periods of slow metabolism while benefiting from the available light for social behavior like shoaling. Although they show low activity in winter (Mulder et al., 2018b; Hawley et al., 2017), the anadromous Arctic char have some daily movements as they are caught in fixed gill nets installed by Inuit harvesters for a few hours or for the night. Further studies are needed to determine whether other variables may impact the selectivity of winter habitat for these fish, such as the proximity to a tributary or the presence of a bay or irregular shorelines, the local topography, but also the light penetration and its link to the shoaling social behavior.

The habitats used by the char were determined from the knowledge of fishers who seldom use the deepest lake areas to harvest fish. Thus, according to our results, depths greater than 10 m were not considered as used habitats as they are not fishing areas. It remains however possible that harvesters avoid the deepest areas for practical reasons regarding the length of ropes needed for setting nets at a suitable depth, which could result in a bias in the assignment of habitat based on fishing sites only. Nonetheless, during fieldwork, attempts for fishing were unsuccessful, albeit of shorter duration than at fishing sites. Furthermore, fish catchability can be linked not only to the fish presence/absence but also to the level of activity linked to environmental conditions as was shown for sand flathead (*Platycephalus bassensis*) (Stehfest et al., 2015). Some barely active Arctic char using deeper habitats could be indeed hard to catch. However, underwater videos taken at sites of absence did not show any char and previous telemetry study has shown that anadromous Arctic char tagged with depth sensor tag spent between 81.2% and 99.8% of their time within the top 5 m of the water column (Mulder et al., 2018b). We nonetheless recognize that Inuit knowledge of fishing integrates hundreds of years of transmitted observations and practices, equivalent to extensive sampling (Berkes and Berkes, 2009) and thus we considered, as mentioned by our collaborators, that Arctic char habitat use is correlated with known fishing sites.

The usual fishing sites were located in specific areas of the lakes. For example, in Tasikallak, the sites of presence were delineated in four specific areas. Hence, it is likely that several fishing sites can exhibit similar characteristics and smaller variance, as observed. In addition, there were differences between lakes in sampling efforts; for example, only two sites were sampled in Tunnullik while 19 sites were sampled in Kuururjuaq, reflecting the fishers' practices. Future work would benefit from a more systematic sampling of sites in each lake, at least for sites of absence, and the participation of more fishers, to increase characterization in undersampled lakes.

4.3 Specificities of the collaboration with Inuit fishers

This community-based monitoring approach and partnership was valuable because Inuit fishers have great depth of knowledge of the area and frequently access Arctic Char at these sites. This collaborative method allowed the efficient sampling of several lakes on a large territory, difficult to access for southern researchers in the winter season. A much larger number of sites were sampled than could be done by a team of southern scientists on one-time visits (Moller et al., 2004). A short training of participating fishers enabled them to carry out the work and transmit collected data effectively. Logistical or material considerations related to working in cold and sometimes harsh weather conditions were not always within the control of participating fishers, and the planning of the work was subject to different considerations between scientists and Inuit (Bates, 2007). In addition, since we worked with fishers practicing subsistence fishery, their interest and timing were related to their need to provide food for their family or community. For these reasons, the lakes and measurement dates were chosen by fishers since the methodological approach relied on their availability. Fishers were interested in characterizing sites used by the char, especially since they were using an underwater camera. Hence, they tended to characterize more sites of presence than sites of absence even if, from a Western scientific point of view, both sites of presence and absence had to be characterized equally for an unbiased comparison. Overall, the methodology and results intrinsically benefited from Inuit knowledge. For example, their knowledge of where and when fish are present has enabled them to synchronize with the char in specific sites. The study was exploratory and proved to be relatively efficient. It is an example of the complementarity of traditional qualitative knowledge, used to locate Arctic char habitats and science, used to characterize those habitats. Reciprocally, the involvement of fishers in data collection during their traditional fishing activities motivated them to learn more about fish habitat characteristics and sparked their interest in the research process.

In addition to knowing of winter anadromous Arctic char movements, Inuit fishers provided additional details on the study sites. For example, a site of absence in Kuururjuaq (not characterized) was a site of presence in the 1980s-1990s. According to the fishers, the reason for this habitat change was a drop in the water level of the Koroc River. In addition, one site along this river, located in a bay, has ceased to be used as a spawning area, apparently because macrophyte growth is blocking fish passage to this area. This information therefore allows us to relate fish occupancy to local environmental changes. Hence, traditional monitoring methods, used intuitively by Inuit harvesters, similar to catch-per-unit-effort (CPUE), should be considered more formally for assessing fish populations (Moller et al., 2004).

5 Conclusion

The study filled a gap in the knowledge of winter habitat use of anadromous Arctic char in Nunavik by showing that incubation areas have significantly different characteristics than non-spawning areas. Winter habitat of adult Arctic char, associated with traditional fishing areas, was also linked with the littoral zone. However, the habitat used did not exhibit characteristics significantly different from those of non-fishing areas, associated with an absence of fish by Inuit fishers. By using the littoral zone, the char can use the lake bottom during this period of slow metabolism while benefiting from the presence of light. Collaborating with local knowledgeable fishers has led to a recurrence of sampling and observations that surpasses the one-time observations that scientists can make alone in the field. This collaboration made it possible to investigate the close relationship between char habitat use and traditional fishing sites. The study remains exploratory as the sites characterized depended on the availability, needs, and practices of the fishers and are limited to specific fishing lakes, although they are the most popular. The active participation of Inuit collaborators in the measurements simultaneously with their fishing activities raised their interest in the study results. Combining traditional fishing activities and fishers' knowledge of site occupancy with simple measurements is a promising approach to characterizing Arctic char habitat and learning more about the winter ecology of this important species.

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Competing interests: The authors declare there are no competing interests.

Data Availability Statement: Data generated or analyzed during this study are provided in full within

the published article and its supplementary materials. Geographical coordinates of sites are kept confidential

at the request of the partner community.

References

- Ali, M.A., Wagner, H.-J., 1980. Vision in charrs: a review and perspectives., in: Charrs: Salmonid Fishes of the Genus Salvelinus. Dr. W. Junk Publishers. The Hague, The Netherlands., pp. 391–422.
- Angela L. Young, Tallman, R.F., Ogle, D.H., 2021. Life history variation in Arctic charr (*Salvelinus alpinus*) and the effects of diet and migration on the growth, condition, and body morphology of two Arctic charr populations in Cumberland Sound, Nunavut, Canada. Arct. Sci. 1–18. https://doi.org/10.1139/as-2019-0036
- Bates, P., 2007. Inuit and Scientific Philosophies about Planning, Prediction, and Uncertainty. Arct. Anthropol. 44, 87–100. https://doi.org/10.1353/arc.2011.0065
- Baxter, C.V., Hauer, F.R., 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout. Can J Fish Aquat Sci 57, 12.
- Bégin, P.N., Rautio, M., Tanabe, Y., Uchida, M., Culley, A.I., Vincent, W.F., 2020. The littoral zone of polar lakes: inshore–offshore contrasts in an ice-covered High Arctic lake1. Arct. Sci. https://doi.org/10.1139/as-2020-0026
- Berkes, F., Berkes, M.K., 2009. Ecological complexity, fuzzy logic, and holism in indigenous knowledge. Futures 41, 6–12. https://doi.org/10.1016/j.futures.2008.07.003
- Boivin, T., Olpinski, S., May, P., 1989. The Arctic charr (*Salvelinus alpinus*) experimental-commercial winter fishery in Kangiqsualujjuaq, Québec, November, 1988-April, 1989.
- Boivin, T.G., Power, G., 1990. Winter condition and proximate composition of anadromous arctic charr (*Salvelinus alpinus*) in eastern Ungava Bay, Quebec. Can. J. Zool. 68, 2284–2289. https://doi.org/10.1139/z90-319
- Byström, P., Andersson, J., Kiessling, A., Eriksson, L.-O., 2006. Size and Temperature Dependent Foraging Capacities and Metabolism: Consequences for Winter Starvation Mortality in Fish. Oikos 115, 43–52.

- Chambers, M.K., White, D.M., Lilly, M.R., Hinzman, L.D., Hilton, K.M., Busey, R.C., 2008. Exploratory Analysis of the Winter Chemistry of Five Lakes on the North Slope of Alaska1. JAWRA J. Am. Water Resour. Assoc. 44, 316–327. https://doi.org/10.1111/j.1752-1688.2007.00164.x
- Charron, I., 2015. Élaboration du portrait climatique régional du Nunavik. Ouranos.
- Clilverd, H., White, D., Lilly, M., 2009. Chemical and Physical Controls on the Oxygen Regime of Ice-Covered Arctic Lakes and Reservoirs. JAWRA J. Am. Water Resour. Assoc. 45, 500–511. https://doi.org/10.1111/j.1752-1688.2009.00305.x
- Côté, I., 2002. Massive fish-fill at lake Tasikallak, Nunavik. Final report.
- Dubos, V., Peter, M., Gillis, C.-A., St-Hilaire, A., Bergeron, N.E., 2023. Nunavik anadromous Arctic char life histories, behaviour and habitat use informed by both Inuit knowledge and western science: A year in Ungava Bay. Arct. Sci. Just In. https://doi.org/10.1139/AS-2022-0019.
- Dubos, V., Snowball, E., 2020. Arctic char under ice at night in Tasikallak (Short Lake).
- 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. J. Fish Biol. 77, 1793–1817. https://doi.org/10.1111/j.1095-8649.2010.02762.x
- Faul, F., Erdfelder, F., Buchner, A., Lang, A.-G., 2009. Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. Behav. Res. Methods 41, 1149–1160.
- Franssen, J., Pépino, M., Lapointe, M., Magnan, P., 2013. Alternative tactics in spawning site selection by brook trout (*Salvelinus fontinalis*) related to incubation microhabitats in a harsh winter environment. Freshw. Biol. 58, 142–158.
- Granier, S., 2013. Alimentation, réserves énergétiques et qualité des oeufs chez l'omble chevalier (*Salvelinus alpinus*) et le doré jaune (*Sander vitreus*) (phd). Université du Québec à Rimouski, Rimouski, Québec.
- Hawley, K.L., Rosten, C.M., Haugen, T.O., Christensen, G., Lucas, M.C., 2017. Freezer on, lights off! Environmental effects on activity rhythms of fish in the Arctic. Biol. Lett. 13, 20170575. https://doi.org/10.1098/rsbl.2017.0575
- Jansen, J., MacIntyre, S., Barrett, D., Chin, Y.P., Cortes, A., Forrest, A., Hrycik, A.R., Martin, R., McMeans, B.C., Rautio, M., Schwefel, R., 2021. Winter limnology: how do hydrodynamics and carbon biogeochemistry shape unique ecosystems under ice? 126, B018-0015.
- Johnson, L., 1980. Analysis of the dolly varden charr, Salvelinus malma, of northwestern North America and northeastern Siberia., in: Charrs: Salmonid Fishes of the Genus Salvelinus. Dr. W. Junk Publishers. The Hague, The Netherlands.
- Jørgensen, E.H., Johnsen, H.K., 2014. Rhythmic life of the Arctic charr: Adaptations to life at the edge. Mar. Genomics, Marine Rhythms 14, 71–81. https://doi.org/10.1016/j.margen.2013.10.005
- Klemetsen, A., 2010. The Charr Problem Revisited: Exceptional Phenotypic Plasticity Promotes Ecological Speciation in Postglacial Lakes. Freshw. Rev. 3, 49–74. https://doi.org/10.1608/FRJ-3.1.3

- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., Mortensen, E., 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol. Freshw. Fish 12, 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x@10.1111/(ISSN)1600-0633.Editors-Choice-2011
- Klemetsen, Anders, Knudsen, R., Staldvik, F., Amundsen, P.-A., 2003. Habitat, diet and food assimilation of Arctic charr under the winter ice in two subarctic lakes. J. Fish Biol. 62, 1082–1098. https://doi.org/10.1046/j.1095-8649.2003.00101.x
- Magnuson, J.J., Karlen, D.J., 1970. Visual Observation of Fish Beneath the Ice in a Winterkill Lake. J. Fish. Board Can. 1059–1068. https://doi.org/10.1139/f70-122
- Martin, N.V., Olver, C.H., 1980. The lake charr, Salvelinus namaycush., in: Charrs: Salmonid Fishes of the Genus Salvelinus. Dr. W. Junk Publishers. The Hague, The Netherlands., pp. 205–277.
- Moller, H., Berkes, F., Lyver, P.O., Kislalioglu, M., 2004. Combining Science and Traditional Ecological Knowledge: Monitoring Populations for Co-Management. Ecol. Soc. 9.
- Monsen, G.-J., 2019. Behavioral study of coexisting populations of anadromous brown trout and arctic char that overwinter in a subarctic lake (Master thesis). Nor. Univ. Life Sci. NMBU.
- Moore, J.W., Moore, I.A., 1974. Food and growth of arctic char, *Salvelinus alpinus* (L.), in the Cumberland Sound area of Baffin Island. J. Fish Biol. 6, 79–92. https://doi.org/10.1111/j.1095-8649.1974.tb04525.x
- 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. https://doi.org/10.1007/s10750-019-3926-7
- Mulder, I.M., Morris, C.J., Dempson, J.B., Fleming, I.A., Power, M., 2018a. Winter movement activity patterns of anadromous Arctic charr in two Labrador lakes. Ecol. Freshw. Fish 27, 785–797. https://doi.org/10.1111/eff.12392
- Mulder, I.M., Morris, C.J., Dempson, J.B., Fleming, I.A., Power, M., 2018b. Overwinter thermal habitat use in lakes by anadromous Arctic char. Can. J. Fish. Aquat. Sci. 75, 2343–2353. https://doi.org/10.1139/cjfas-2017-0420
- Power, G., Barton, D.R., 1987. Some Effects of Physiographic and Biotic Factors on the Distribution of Anadromous Arctic Char (*Salvelinus Alpinus*) in Ungava Bay, Canada. Arctic 40, 198–203. http://dx.doi.org/10.14430/arctic1767
- Sæther, B.-S., Siikavuopio, S.I., Jobling, M., 2016. Environmental conditions required for intensive farming of Arctic charr (*Salvelinus alpinus* (L.)). Hydrobiologia 783, 347–359. https://doi.org/10.1007/s10750-015-2572-y
- Scholander, P.F., Dam, L. van, Kanwisher, J.W., Hammel, H.T., Gordon, M.S., 1957. Supercooling and osmoregulation in arctic fish. J. Cell. Comp. Physiol. 49, 5–24. https://doi.org/10.1002/jcp.1030490103
- Smith, R., Hitkolok, E., Loewen, T., Dumond, A., Kristensen, K., Swanson, H., 2022. Overwintering ecology and movement of anadromous Arctic char (*Salvelinus alpinus*) in a large, ice-covered river in the Canadian Arctic. J. Fish Biol. 100, 1432–1446. https://doi.org/10.1111/jfb.15054

- Spares, A.D., Stokesbury, M.J.W., O'Dor, R.K., Dick, T.A., 2012. Temperature, salinity and prey availability shape the marine migration of Arctic char, *Salvelinus alpinus*, in a macrotidal estuary. Mar. Biol. 159, 1633–1646. https://doi.org/10.1007/s00227-012-1949-y
- Stehfest, K.M., Lyle, J.M., Semmens, J.M., 2015. The use of acoustic accelerometer tags to determine seasonal changes in activity and catchability of a recreationally caught marine teleost. ICES J. Mar. Sci. 72, 2512–2520. https://doi.org/10.1093/icesjms/fsv115
- 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. Ecol. Freshw. Fish 16, 70–77. https://doi.org/10.1111/j.1600-0633.2006.00183.x
- Welch, H.E., Bergmann, M.A., 1985. Water Circulation in Small Arctic Lakes in Winter. Can. J. Fish. Aquat. Sci. 42, 506–520. https://doi.org/10.1139/f85-068
- Welch, H.E., Legault, J.A., Bergmann, M.A., 1987. Effects of Snow and Ice on the Annual Cycles of Heat and Light in Saqvaqjuac Lakes. Can. J. Fish. Aquat. Sci. 44, 1451–1461. https://doi.org/10.1139/f87-174
- Young, A.L., Tallman, R.F., 2021. The comparative lake ecology of two allopatric Arctic Charr, Salvelinus alpinus, populations with differing life histories in Cumberland Sound, Nunavut. Arct. Sci. 7. https://doi.org/10.1139/AS-2019-0037

Figure captions

Figure 1. Location of the sampling sites. They are located in winter fishing areas that are popular with Kangiqsualujjuammiut. However, winter fishing is not limited to these areas. Map sources: Esri, "Ocean Basemap", GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other contributors; and Esri, "Light Gray Canvas Map", DeLorme, HERE, MapmyIndia. Source: QGIS, Esri topo World. Coordinate references: EPSG:4326 - WGS 84, Projection: Pseudo-Mercator.

Figure 2. Correlation matrix of the measured variables according to a) Pearson linear correlation and b) Spearman rank correlation.

Figure 3. Boxplot of the analyzed variables associated with the type of occupancy (blue tone: fishing, non-fishing; red tone: incubation, non-spawning). The black inbox line represents the median, with box sides representing the first and third quantiles.

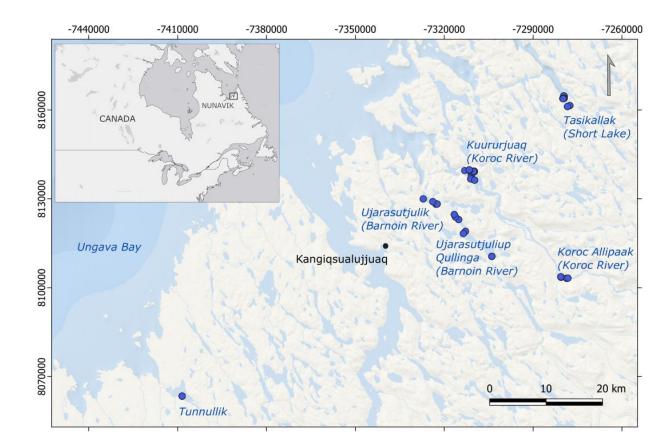


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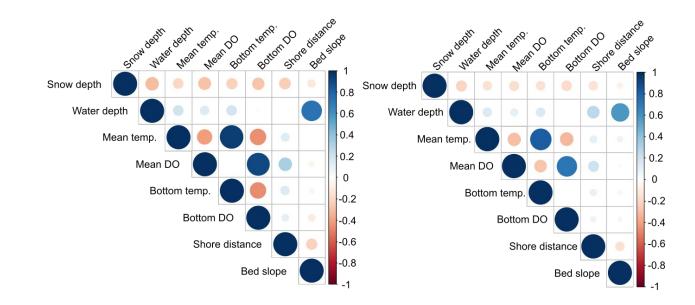


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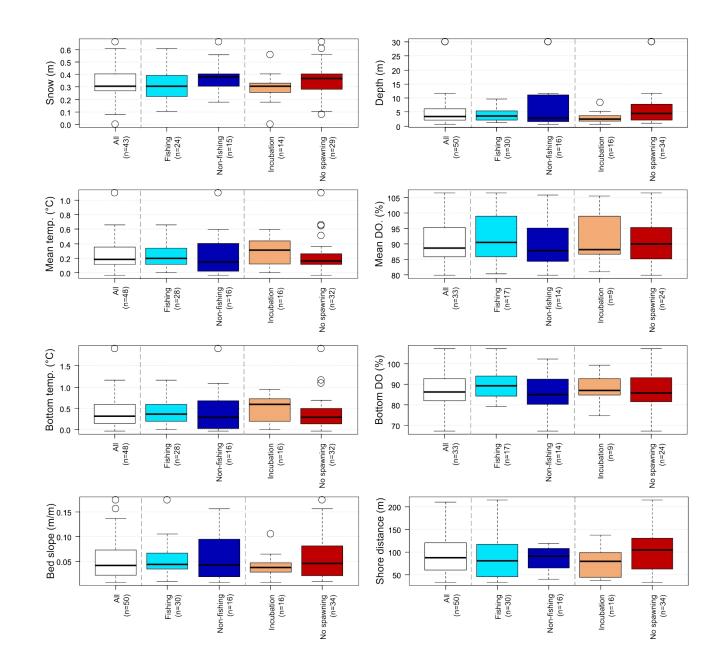


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Table 1. Statistical comparison between characteristics from sites identified or not as an incubation site for the Arctic char. Significant p-values ($\alpha \leq 0.05$) are highlighted with asterisks and the test statistic value is given in parenthesis. The sample size for each variable is given in parenthesis (N spawning / N non-spawning).

	Snow depth	Water depth	Mean temp	Mean DO	Bottom temp	Bottom DO	Shore distance	Bed slope
	(N=14/29)	(N=16/34)	(N=16/32)	(N=9/24)	(N=16/32)	(N=9/24)	(N=16/34)	(N=16/34)
Kruskal-Wallis test	0.121	0.020**	0.108	0.968	0.066	0.716	0.100	0.279
on the median value	(2.406)	(5.379)	(2.584)	(0.002)	(3.381)	(0.132)	(2.700)	(1.170)
Fligner test on	0.235	0.007**	0.253	0.804	0.365	0.725	0.133	0.011**
variance	(1.413)	(7.149)	(1.309)	(0.062)	(0.820)	(0.124)	(2.260)	(6.489)

Table 2. Statistical comparison between characteristics of fishing and non-fishing sites. Significant p-values $(\alpha \le 0.05)$ are highlighted with asterisks and the test statistic value is given in parenthesis The sample size for each variable is given in parenthesis (N presence / N absence).

	Snow depth	Water depth	Mean temp	Mean DO	Bottom temp	Bottom DO	Shore distance	Bed slope
	(N=24/15)	(N=30/16)	(N=28/16)	(N=17/14)	(N=28/16)	(N=17/14)	(N=30/16)	(N=30/16)
Kruskal-Wallis test	0.191	0.926	0.428	0.475	0.435	0.211	0.604	0.854
on the median value	(1.708)	(0.009)	(0.629)	(0.511)	(0.611)	(1.564)	(0.269)	(0.034)
Fligner test on	0.678	0.050**	0.167	0.328	0.106	0.931	0.528	0.077
variance	(0.173)	(3.833)	(1.906)	(0.956)	(2.610)	(0.008)	(0.398)	(3.124)