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Annual survival probabilities of anadromous Arctic Char remain high and stable despite interannual differences in sea ice melt date[1]

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Abstract: Throughout their range, anadromous Arctic Char (*Salvelinus alpinus* (Linnaeus, 1758)) support commercial, recreational, and subsistence fisheries that are important economically, socially, and culturally. However, drivers of interannual variation in survival in this species remain poorly understood. Here, we aimed to quantify the impact of environmental and biological parameters on the survival probability of anadromous Arctic Char near the community of Cambridge Bay, Nunavut, Canada. To do so, we tracked 183 Arctic Char tagged with acoustic transmitters and used capture–mark–recapture methods to estimate survival probabilities over six years. Annual survival probabilities for individuals was high, varying between 0.79 and 0.88, whereas recapture probabilities varied between 0.64 and 0.90. Interannual variation in survival probability was low and neither the environmental (air temperature and sea ice cover) nor biological (sex) variables influenced survival probability. These estimates suggest that annual survival probability is high for anadromous adult Arctic Char in the Cambridge Bay area, despite clear differences in the ice cover melt date among years. These results further our understanding of the demographic parameters of Arctic Char in the region, which will be important for future assessments of the sustainability of commercial fisheries as well as for predicting population responses to a rapidly changing Arctic.

Key words: acoustic telemetry, Arctic Char, *Salvelinus alpinus*, capture–mark–recapture, fisheries management.

Résumé : Dans la région arctique, l'omble chevalier (*Salvelinus alpinus* (Linnaeus, 1758)) anadrome supporte les pêches commerciales, sportives et de subsistance qui sont d'une grande importance économique, sociale et culturelle. Cependant, les facteurs influant sur la variation interannuelle de la survie des individus de cette espèce sont peu connus. L'objectif de cette étude était de quantifier l'impact de paramètres environnementaux

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et des caractéristiques individuelles des poissons sur la probabilité de survie de l'omble chevalier anadrome près de la communauté de Cambridge Bay, Nunavut, Canada. Pour ce faire, 183 ombles chevaliers ont été équipés d'émetteurs acoustiques et suivis pendant plus de 6 ans avec des méthodes de capture–marquage–recapture pour estimer la probabilité de survie. La probabilité de survie annuelle était haute variant entre 0.79 et 0.88 et la probabilité de recapture variait entre 0.64 et 0.90. La variation interannuelle au niveau de la survie était faible et ni les caractéristiques environnementales (couverture de glace de mer, température de l'air) ni les caractéristiques individuelles des poissons (sexe) n'ont influé sur la probabilité de survie des ombles chevaliers. Ces estimations suggèrent que la probabilité de survie est élevée pour les individus anadromes adultes dans la région de Cambridge Bay malgré des variations claires de la date de fonte de la couverture de glace entre les années. Nos résultats permettront d'augmenter notre compréhension des paramètres démographiques des ombles chevaliers de la région, nécessaires pour évaluer la durabilité de la pêche commerciale ainsi que pour prédire la réponse des populations dans l'Arctique qui change rapidement.

Mots-clés : télémétrie acoustique, omble chevalier, *Salvelinus alpinus*, capture-marquage-recapture, gestion des pêches.

Introduction

Estimating demographic parameters such as population abundance, birth rate, or survival probability is important as it provides information about the viability of a population (Lettink and Armstrong 2003). Tools such as capture–mark–recapture (CMR) methods have been developed to enable the estimation of these demographic parameters (Burnham et al. 1987; Williams et al. 2002) and have been used extensively in fisheries management (Schwarz and Dempson 1994; Gresswell et al. 1997; Cox and Walters 2002; Michielsens et al. 2006). However, CMR methods require considerable effort because the precision of the parameter estimates are directly related to the number of recaptures (Lettink and Armstrong 2003). With traditional tagging methods such as T-bar anchor tagging, loss of tags and low number of returns can limit the performance of CMR methods in aquatic populations (see Muoneke 1992). Acoustic telemetry offers a solution to this challenge because it relies on an array of receivers instead of tag returns from harvesters or scientists. Furthermore, as tags are surgically implanted in the body cavity, loss of tags is usually not a problem (Thorstad et al. 2013). This allows for the monitoring of aquatic animals over long, consecutive periods of time, and increases the likelihood of recapture via detection (Hussey et al. 2015). Thus, acoustic telemetry can improve our knowledge of population dynamics, habitat use, and movements, thereby contributing valuable insights into the management of aquatic resources (Crossin et al. 2017). The combined use of acoustic telemetry and CMR methods offers a promising approach for deriving individual encounter histories to precisely estimate demographic parameters (Pine et al. 2003; Dudgeon et al. 2015).

The Arctic Char (*Salvelinus alpinus* (Linnaeus, 1758)) has a circumpolar distribution and is the northern-most distributed freshwater fish species (Johnson 1980; Klemetsen et al. 2003; Reist et al. 2013). In the Arctic, many individuals are anadromous and migrate to the sea in the summer to feed. In contrast with many other salmonid species, Arctic Char must return to freshwater every fall to overwinter (Johnson 1980; Klemetsen et al. 2003). The species is thought to feed almost primarily during summer to accumulate enough energy to reproduce and survive through winter (Dutil 1986; Jensen et al. 2017). In Nunavut, Arctic Char is a crucial resource for Inuit across the territory where it supports commercial, recreational, and subsistence fisheries (Roux et al. 2011) that are important economically, socially, and culturally (Myers et al. 2005). Thus, the sustainable management of anadromous Arctic Char in Nunavut is a key priority (Government of Nunavut 2016) and requires knowledge of the demographic parameters regulating populations.

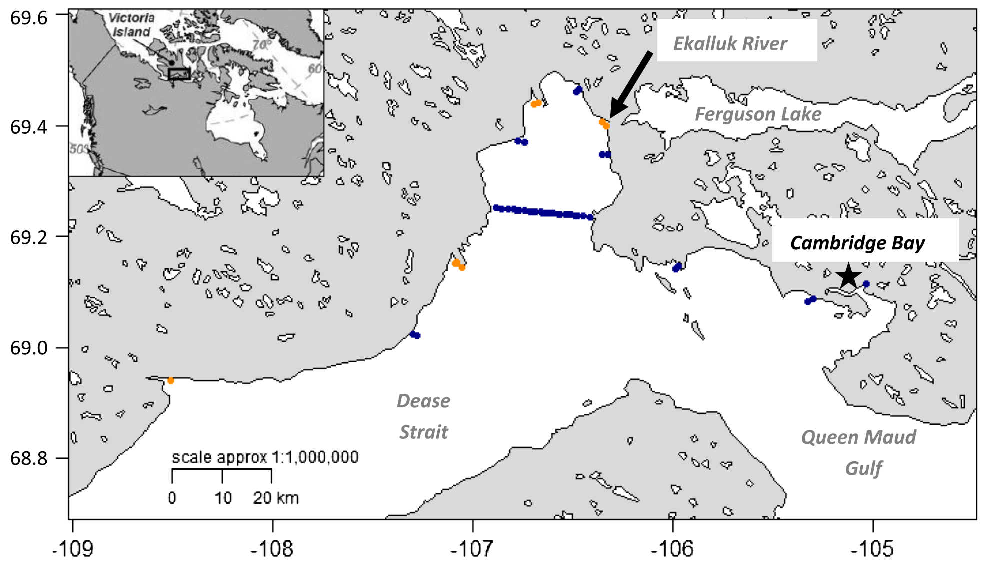
The goal of this study was to quantify the influence of environmental and biological parameters on adult Arctic Char survival in the central Canadian Arctic. To do so, we estimated the survival probability of anadromous Arctic Char in the Cambridge Bay region of Nunavut by combining acoustic telemetry and CMR methods. We tested the influence of environmental and biological parameters on the survival probability of Arctic Char in the marine environment. We first tested the hypothesis that survival probability is lower during years with high sea surface temperature and later melt of the sea ice cover. Survival probability could be reduced with a later date of sea ice melt because the feeding period is shortened, thus limiting energy acquisition (Berg and Berg 1993). Also, Arctic Char are less tolerant of higher temperatures than other salmonids (Larsson 2005); thus, increased temperatures could lead to a lower survival probability. Second, we tested the hypothesis that survival probability is higher in females than in males. Females likely invest more energy in reproduction than males, as observed with Atlantic Salmon (*Salmo salar* Linnaeus, 1758) (Fleming 1996), which could lead to higher mortality in females, especially if the feeding period is shortened. Also, because females benefit more from increased growth, they have been found in some species of salmonids to engage in more risky or costly behaviour to increase their energy intake, which could increase their mortality (Holtby and Healey 1990; Tamate and Maekawa 2004).

Material and Methods

This study took place in the Kitikmeot Sea on southern Victoria Island focussing specifically on Arctic Char from the Ekalluk River system in Nunavut, Canada (69°07′N, 105°03′W, Fig. 1). The most significant commercial fishery for Arctic Char in Canada occurs at the Ekalluk River with an annual available quota of 20 000 kg (Day and Harris 2013). This system is also home to a long-term acoustic telemetry study that was initiated in the region in 2013 (Moore et al. 2016, 2017; Harris et al. 2020*a*). Between 2013 and 2017, 183 adult Arctic Char (fork length >400 mm) were captured and surgically implanted with acoustic transmitters (V16, Vemco, Halifax, Nova Scotia, Canada). The transmitters have a detection probability of more than 50% within ~500 m of a marine receiver (see Moore et al. 2016 for details). A piece of pectoral fin of approximately 1 cm^2 was preserved in 95% EtOH to determine genetically the sex of individuals based on the method of Yano et al. (2013). After release of the individuals, their movements were continuously monitored with an array of 21–36 Vemco VR2W receivers deployed in the area (Fig. 1). Some receivers with limited detections were removed from the array or relocated, which explains the variation of the number of receivers among years (see Harris et al. 2020*a* for details). The observation period in the marine environment was approximately 10 weeks, which corresponds to the feeding period at sea for anadromous Arctic Char during the ice-free season before their return to freshwater to overwinter (Klemetsen et al. 2003). Additional details for all tagging and tracking methodologies can be found in Moore et al. (2016) and Harris et al. (2020*a*).

Air temperature and ice cover data were obtained from the "Cambridge Bay A" and "Cambridge Bay GSN" stations from Environment Canada (https://weather.gc.ca/; consulted on 18 October 2019). These stations are located less than 9 km from Cambridge Bay. Water temperatures were not available and likely vary between stations (see, for example, Harris et al. 2020*a*). As a result, we used air temperature as an indicator of overall environmental conditions. The temperature value used for each year was the average of the average daily air temperature during the feeding period for Arctic Char at sea, which we defined based on the first and last day of detections recorded during each year of the study. The week of

Fig. 1. Map of the study area showing the location of the receivers used from 2013 to 2019. Fish were tagged at the Ekalluk river. Orange dots represent estuarine receivers, and blue dots represent marine receivers (see Harris et al. 2020*a* for station descriptions). The map was made in R 3.6.3. (R Core Team 2020). Base maps were made using the "maps" and "mapdata" package (Becker and Allan 2018*a*, 2018*b*). River and lake layers are from the National Topographic Data Base (Government of Canada 1994–2005).



sea ice melt was defined as the week when the ice cover on the marine water in the Cambridge Bay area fell to less than 10% ice cover (Supplementary Table S2[1]).

Because each transmitter had a unique identification code associated with an individual, we determined whether it was detected during each 10-week summer period between 2013 and 2019. We removed detections that did not match individuals from our study, as these were most likely the result of detection interference when many individuals are detected simultaneously at a receiver. Every individual with fewer than 20 detections for a given year was manually verified for potential false detections caused by interference and a minimum of three detections per year was set to consider an individual as observed that given year. This threshold resulted in removing six observations from the analysis. We included data from 2019 in the analyses even though receivers were retrieved four weeks before the presumed end of the marine feeding phase. During all previous years, only three fish that had not been detected before those four final weeks were detected later, so we assumed that this shortened sampling season would not have a significant impact on estimates of annual survival. Some transmitters used in 2013 had shorter battery life than those used in other years (three year estimated battery life compared with >five years for all other sampling years). Thus, we removed 20 individuals with these shorter-lived transmitters after their last detection to prevent underestimating survival probability.

The Cormack–Jolly–Seber (CJS) model was used for the analysis of the individual encounter histories (Williams et al. 2002). These encounter histories are the product of two probabilities, (1) the apparent survival probability (ϕ) (hereafter, survival), and (2) the recapture (or re-encounter) (p) probability. With the encounter history of each of the tagged individuals, it is then possible to obtain the estimates of these probabilities independently

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Table 1. Candidate models of the Cormack–Jolly–Seber analysis on Arctic Char from the Cambridge Bay region using acoustic telemetry data collected from 2013 to 2019.

Model	K	$QAIC_c$	$\Delta QAIC_c$	Akaike weight
ϕ(melt) p(year)	9	588.09	0.00	0.59
ϕ(1) p(year)	8	591.72	3.63	0.10
ϕ(sex) p(year)	9	592.92	4.83	0.05
ϕ(temperature) p(1)	4	593.49	5.40	0.04
ϕ(year) p(year)	12	593.70	5.62	0.04
ϕ(temperature) p(year)	9	593.78	5.69	0.03
ϕ(1) p(1)	3	594.17	6.08	0.03
ϕ(melt) p(1)	4	594.36	6.27	0.03
ϕ(temperature) p(effort)	5	595.31	7.22	0.02
ϕ(sex) p(1)	4	595.37	7.28	0.02
ϕ(year) p(1)	8	595.63	7.55	0.01
ϕ(temperature × sex) p(1)	6	596.02	7.93	0.01
ϕ(1) p(effort)	4	596.03	7.95	0.01
ϕ(melt) p(effort)	5	596.39	8.30	0.01
ϕ(temperature × sex) p(year)	11	596.43	8.34	0.01
ϕ(sex) p(effort)	5	597.25	9.16	0.01
ϕ(year) p(effort)	9	597.65	9.57	0.00
ϕ(temperature × sex) p(effort)	7	597.87	9.78	0.00
ϕ(year × sex) p(year)	18	602.69	14.60	0.00
ϕ(year × sex) p(1)	14	604.45	16.37	0.00
ϕ(year × sex) p(effort)	15	606.55	18.47	0.00

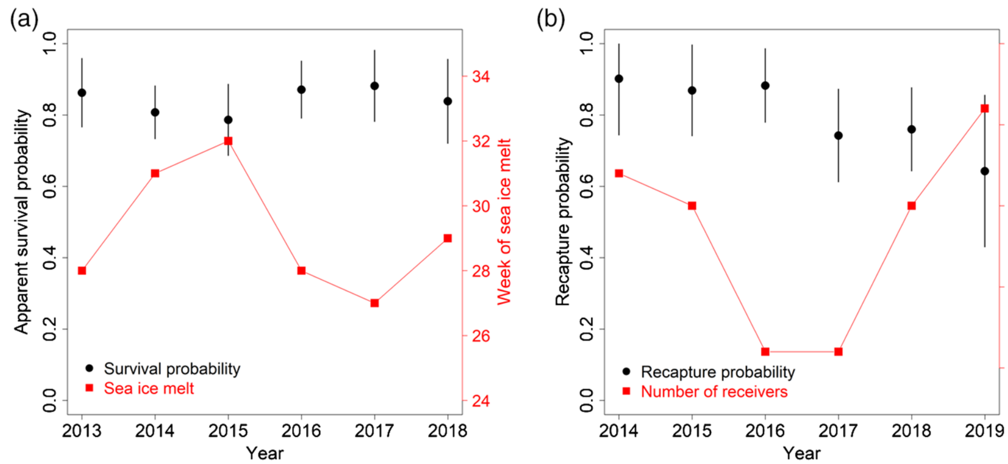
Note: Models estimate probabilities of apparent survival (ϕ) and of recapture (p). K represents the number of parameters used for each model. $QAIC_c$ is the Akaike information criterion for small samples and adjusted for overdispersion ($\hat{c} = 1.06$).

by maximum likelihood with the program MARK (White and Burnham 1999; Cooch and White 2019). We used the package RMark (Laake 2013) in R 3.6.3 (R Core Team 2020) to conduct these analyses. We formulated 21 candidate models to test our biological hypotheses (Table 1). We considered the date of sea ice melt of the current year, the temperature, the sex, and the time (year) as the parameters influencing ϕ. Because the duration of the accessibility of marine feeding habitats in the previous year may influence an individual's capacity to acquire resource and survive another year, we also performed the analysis with the date of sea ice melt from the preceding year (Supplementary Table S3[1]). We also considered the interaction between sex and temperature and the interaction between sex and time. For the recapture probability, we considered the number of receivers (effort) and the year. The global model fit was assessed with the fletcher-$\hat{c}$, and it showed some low overdispersion ($\hat{c} = 1.06$). Therefore, we used model selection and multimodel inference based on Akaike's information criterion corrected for small samples and overdispersion (Burnham and Anderson 2002).

Results

The annual survival probability of the Arctic Char from the Ekalluk River was high and did not show marked interannual variation (range: 0.79 ± 0.10 (2015) to 0.88 ± 0.10 (2017); Fig. 2*a*). The recapture probability was also high with values ranging from 0.64 ± 0.21 (2019) to 0.90 ± 0.10 (2014), suggesting that our acoustic array was effective at detecting Arctic Char with acoustic transmitters in the marine area (Fig. 2*b*). The most parsimonious model included the effect of sea ice melt date on survival probability, but with a constant recapture probability (Table 1). This model had most of the support (Akaike weight = 0.59) and was 5.9 times better than the second-ranked model consisting of constant survival probability and recapture probability varying across years (Table 1). However, a second model

Fig. 2. Apparent survival probabilities (*a*) and recapture probabilities (*b*) of Arctic Char (*Salvelinus alpinus*) acoustically tracked between 2013 and 2019 in Cambridge Bay ($n = 183$ individuals). Estimates obtained with multimodel inference on the entire set of candidate models. The vertical lines denote 95% confidence intervals. The red squares represent the week of sea ice melt (*a*) and the number of receivers (*b*) for each year of the study. Estimates of survival and recapture probabilities and measures of precision are presented in Supplementary Table S1[1].



allowing the survival probability to vary with the date of sea ice melt only had an Akaike weight of 0.03. As a result, the effect size of sea ice melt on survival probability did not differ from 0 (model-averaged estimate: −0.24, 95% confidence interval: (−0.72 to 0.23)). Several of the top models included the effect of year on the recapture probability, but recapture probability did not differ among years (Fig. 2*b*). Models with the sex of the individuals or temperature had little support, suggesting no effect of these variables on survival (Akaike weight ≤0.05).

Discussion

In this study, 183 anadromous Arctic Char were tagged with acoustic transmitters and tracked by an array of 21–36 receivers between 2013 and 2019 in the Cambridge Bay region of Nunavut. In contrast with our expectations, survival probability did not vary with any of the environmental (temperature and sea ice cover) and biological (sex) variables assessed. Indeed, results show that both survival (range: 0.79–0.88) and recapture probabilities (range: 0.64–0.90) are high and that there is minimal interannual variation in these parameters. The high and non-variable recapture probability was expected because the receivers were placed at strategic locations such as the river mouths or along the coast that are frequented by Arctic Char during their annual migrations to freshwater after summer marine foraging (Moore et al. 2016).

The low interannual variability in survival was not expected, especially given that the years included in this study showed clear variability in environmental conditions. Despite important interannual variability in the date of sea ice melt during the study period, it did not clearly influence survival probability, which showed very little variability among years. Indeed, although the best-supported model included sea ice melt date, other models including this variable were not very well supported. In short, although our results do not currently support an effect of this variable, at least in part because of very low interannual variability in survival, additional years of data might allow us to unambiguously determine its influence on survival probability. In the years of our current study, there was a difference of four weeks between the earliest (2017) and the latest (2015) date of ice cover melt among years (Supplementary Table S1[1]), which is considerable as the marine feeding period for Arctic Char lasts approximately six to seven weeks on average in the region (Moore et al. 2016). Berg and Berg (1993) reported that Arctic Char migrated to the sea earlier when ice cover from rivers melted earlier. Consequently, winter sea ice persisting later in the year could reduce the duration of the feeding period for Arctic Char. Indeed, the date of first detection in our study occurred later during years with a later sea ice melt date (Supplementary Fig. S1[1]). Delayed sea ice melt could also have a negative impact on primary productivity and the onset of major phytoplankton blooms (Janout et al. 2016). A later bloom due to a later melt of sea ice cover might increase zooplankton mortality due to a timing mismatch, and therefore negatively impact the trophic chain by reducing marine food availability (Søreide et al. 2010; Janout et al. 2016). During these few weeks of ice-free waters, Arctic Char acquire most of their energy reserves required for reproduction and winter survival (Dutil 1986; Jensen et al. 2017). It is surprising that shorter feeding periods with presumably less food availability did not reduce survival. However, a reduction in the feeding period could potentially impact body condition, which could have some repercussions on other demographic parameters such as reproductive investment and success or recruitment, which were not studied here.

We found no variation in survival linked with average air temperature during the feeding season. Some studies have reported that cardiorespiratory capacities decreased with increasing temperatures (Penney et al. 2014; Gilbert and Tierney 2018; Gilbert et al. 2020). This could increase the difficulty of migration and potentially impact survival. Temperatures during our study remained within the optimal ranges for the Arctic Char and did not vary widely among the years. Thus, the lack of influence of temperature on survival probability is perhaps not surprising. Arctic Char prefer water temperatures between 9 and 12 °C (Larsson 2005) but could tolerate temperatures up to 23.2 °C in an experimental study (Larsson et al. 2005). Recent field-based evidence on wild populations, however, suggested temperatures above 16 °C are physiologically stressful on Arctic Char and temperatures around 21 °C can lead to arrhythmia (Gilbert et al. 2020). Another explanation for the lack of an impact of temperature on survival probability could be our use of air temperature as opposed to water temperature, which would have been more appropriate, but which was not available. We note that water temperature varies widely among regions and with depth, and that linking interannual differences in water temperatures with survival remains challenging.

In contrast to our prediction, survival probability did not vary between males and females. Fleming (1996) found that Atlantic Salmon females invested more energy into gonad production than males (20%–25% vs. 3%–6%) that resulted in higher mortality in females due to the stress of migration. Indeed, Holtby and Healey (1990) and Tamate and Maekawa (2004) reported that mortality of females (Masu salmon (*Oncorhynchus masou* (Brevoort, 1856)) and Coho salmon (*Oncorhynchus Kisutch* (Walbaum, 1792)), respectively) at sea was higher because of their more active feeding behavior. Fishing-related mortality could also entail differences in survival between sexes. Studies on Chinook (*Oncorhynchus tshawytscha* (Walbaum in Artedi, 1792)) and Sockeye (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) salmon have reported that males tend to be caught more often in subsistence and commercial fisheries (Molyneaux et al. 2005; Kendall and Quinn 2013). However, of the 33 transmitters returned by fishers (commercial and subsistence) during the present study, 17 were from males (21% of tagged males) and 16 from females (16% of tagged females), which suggests no differences in fishing mortality between sexes.

Another potential explanation for the lack of interannual variability in survival is that we only considered individuals with a length of >400 mm. These individuals might have reached a size where mortality is low and constant because they have few predators in the Arctic. It is a well-known fact that mortality in anadromous salmonids is much higher in juveniles than in adults (Jensen et al. 2017). Furthermore, Arctic Char is a species with a high longevity that commonly reach an age of 25–30 years in the region (Harris et al. 2020*b*). For the Ekalluk River, the commercial harvest is thought to be low with an exploitation rate of 4.1% of the available biomass (Day and Harris 2013). Also, strong modal age classes in the commercial fishery range between 11 and 14 years (Day and Harris 2013), which could explain the low mortality of adult individuals. Finally, quantitative stock assessment models of Arctic Char in the Cambridge Bay area found that natural mortality was typically low ($M < 0.20$) for age classes greater than 10 years old (Zhu et al. 2021). These estimates are remarkably concordant with our results.

In conclusion, annual survival and recapture probabilities remained high and constant for Arctic Char during the six years of the study. These estimates indicated that survival of adults (fork length >400 mm) does not vary with the environmental (temperature and ice melt date) and biological parameters (sex) assessed here. Exploring other types of CMR analyses could also be very useful for furthering our understanding of Char biology and ecology in the region. For example, multi-state models could possibly predict the probability of an individual migrating to the sea or remaining in freshwater during the summer, which could provide valuable information on habitats used on an annual basis. The commercial fishery for Arctic Char at the Ekalluk River is the largest in Canada. Continuing the long-term monitoring of this population using acoustic telemetry will further advance our understanding the environmental drivers of demographic variation in this species that will undoubtedly be valuable for informing the effective management of this key fishery.

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