

Estimating survival probabilities of Cambridge Bay Arctic char using acoustic telemetry data and Bayesian multistate capture–recapture models

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Abstract

Arctic fishes are threatened by climatic change and other anthropogenic stressors, yet information on how such changes impact survival remains scarce. Acoustic telemetry has become valuable for studying aspects of fish ecology, including survival, which is invaluable in understanding potential responses to changing conditions. In Cambridge Bay, NU, we have been using acoustic telemetry to study movements and habitat use of the culturally and commercially important Arctic char (*Salvelinus alpinus*). Here, we combine acoustic telemetry data and Bayesian multistate mark–recapture models to study the survival of Arctic char from 2014 to 2018 in the region in freshwater and marine/estuarine habitats. We found that survival probabilities were high (>0.87) and models considering two environments (freshwater and marine) perform better than those considering three (including estuarine habitats). Furthermore, the survival in fresh water was higher than survival in marine/estuary environments. Overall, the results of this study further our understanding of important demographic parameters (i.e., survival) for Arctic char in the region, which will be useful in refining fishery management plans for the largest commercial fishery for this species in Canada.

Key words: acoustic telemetry, Arctic char, Bayesian statistics, mark–recapture models, survival ecology

Résumé

Si les poissons de l'Arctique sont menacés par les changements climatiques et autres facteurs de stress d'origine humaine, l'information sur l'incidence de ces changements sur leur survie demeure rare. La télémétrie acoustique est devenue prisée pour étudier divers aspects de l'écologie des poissons, notamment la survie, un paramètre essentiel pour comprendre les possibles réactions à des conditions changeantes. Nous utilisons la télémétrie acoustique pour étudier les déplacements et l'utilisation d'habitats par les ombles chevaliers (*Salvelinus alpinus*), une espèce d'importance culturelle et commerciale, dans la baie Cambridge (Nunavut). Nous combinons des données de télémétrie acoustique et des modèles bayésiens multi-états de marquage–recapture afin d'étudier la survie des ombles chevaliers de 2014 à 2018 dans des habitats d'eau douce et marins/estuariens de cette région. Nous relevons que les probabilités de survie sont élevées ($>0,87$) et que les modèles qui intègrent deux types de milieux (d'eau douce et marin) donnent de meilleurs résultats que ceux qui en intègrent trois (incluant les habitats estuariens). La survie en eau douce s'avère en outre plus grande que la survie dans les milieux marins/estuariens. Globalement, les résultats de l'étude améliorent la compréhension de paramètres démographiques importants (c.-à-d., la survie) pour l'omble chevalier dans la région, ce qui sera utile pour peaufiner les plans de gestion des ressources pour la plus importante pêche commerciale de cette espèce au Canada. [Traduit par la Rédaction]

Mots-clés : télémétrie acoustique, omble chevalier, statistiques bayésiennes, modèles de marquage–recapture, écologie de la survie

Introduction

Climate change in the Canadian Arctic is occurring at some of the fastest rates on Earth (Prowse et al. 2006; Barber et al. 2008; Pithan and Mauritsen 2014). This rapid climate change,

coupled with other human-related factors such as increased harvesting and negative impacts from increased shipping activities, poses clear and significant threats to the survival and population persistence of many freshwater and anadro-

mous Arctic fish species (Caza-Allard et al. 2021). Due to a paucity of data and a subsequent poor understanding of the biology and ecology of many Arctic fish species, predicting how those species will respond and adapt to changing climatic conditions and anthropogenic pressures has been challenging (Reist et al. 2006; Crossin et al. 2017). Some climate change effects noted for Arctic anadromous fishes include, among other things, changes in trophic positioning and diet (Ulrich and Tallman 2021), declines in fish condition (Lehnherr et al. 2018), impacts to early year growth, and life history variation (Grenier and Tallman 2021), shifting geographic ranges and potentially local extinctions (Reist et al. 2006). Few studies to date, however, have assessed changes in survivorship and mortality in anadromous fishes relating to climate change in the Canadian North. All told, the impacts of Arctic climate change on anadromous fishes remain enigmatic and future studies at high latitudes will be important for understanding the potential and realized impacts on this important group of fishes.

Recent advances in animal tracking technologies such as acoustic telemetry have enabled researchers to collect enormous amounts of data on animal movement and habitat use over large geographic scales (Klimley et al. 1998; Donaldson et al. 2014; Hussey et al. 2015), significantly increasing the overall understanding of the ecology and biology of high-latitude fish species (Peklova et al. 2012; Hussey et al. 2015, 2017). For example, data from acoustic telemetry have primarily been used for studying spatiotemporal aspects of animal movements in both marine and freshwater environments (Heupel and Simpfendorfer 2002; McMichael et al. 2010; Lees et al. 2021). More recently, acoustic telemetry data have been used to estimate demographic parameters such as survival probability and population size, with comparable or better precision than conventional capture–mark–recapture studies (Pollock et al. 2004; Dudgeon et al. 2015; Lees et al. 2021). Estimating survival using acoustic data has become particularly important for understanding how fishing and natural mortality impact population persistence (Crossin et al. 2017; Lees et al. 2021).

Incorporating acoustic telemetry data, the most popular approach for estimating survival probabilities has been the use of the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965). However, when there are few detection records from certain sites, the estimated survival probabilities with CJS models suffer from low precision due to low recapture rates (Pollock et al. 1990; O'Brien et al. 2005; Morris et al. 2006). As such, using CJS models, it is often not possible to obtain stable estimates for individual survival probabilities for all sites and (or) environments. In this context, multistate mark–recapture models can be used to deal with sparseness in data by borrowing information across regions (Calvert et al. 2009). Early applications of multistate mark–recapture models can be found in Arnason (1972), Hestbeck et al. (1991), and Brownie et al. (1993). Parameter estimation of the multistate mark–recapture models can be done using either the frequentist or Bayesian framework. The Bayesian framework has been gaining popularity for a variety of reasons, including its extreme flexibility, greater precision, and ability to incorporate prior knowledge about param-

eters (Harwood and Stokes 2003; Calvert et al. 2009; Kéry and Schaub 2011). Through simulation studies and real-world applications, Calvert et al. (2009) showed that using a hierarchical Bayesian approach to multistate mark–recapture, one can obtain more precise and accurate parameter estimates than nonhierarchical approach. Thus, hierarchical Bayesian approaches using acoustic telemetry data and mark–recapture methods hold promise for estimating demographic parameters using nonconventional methods.

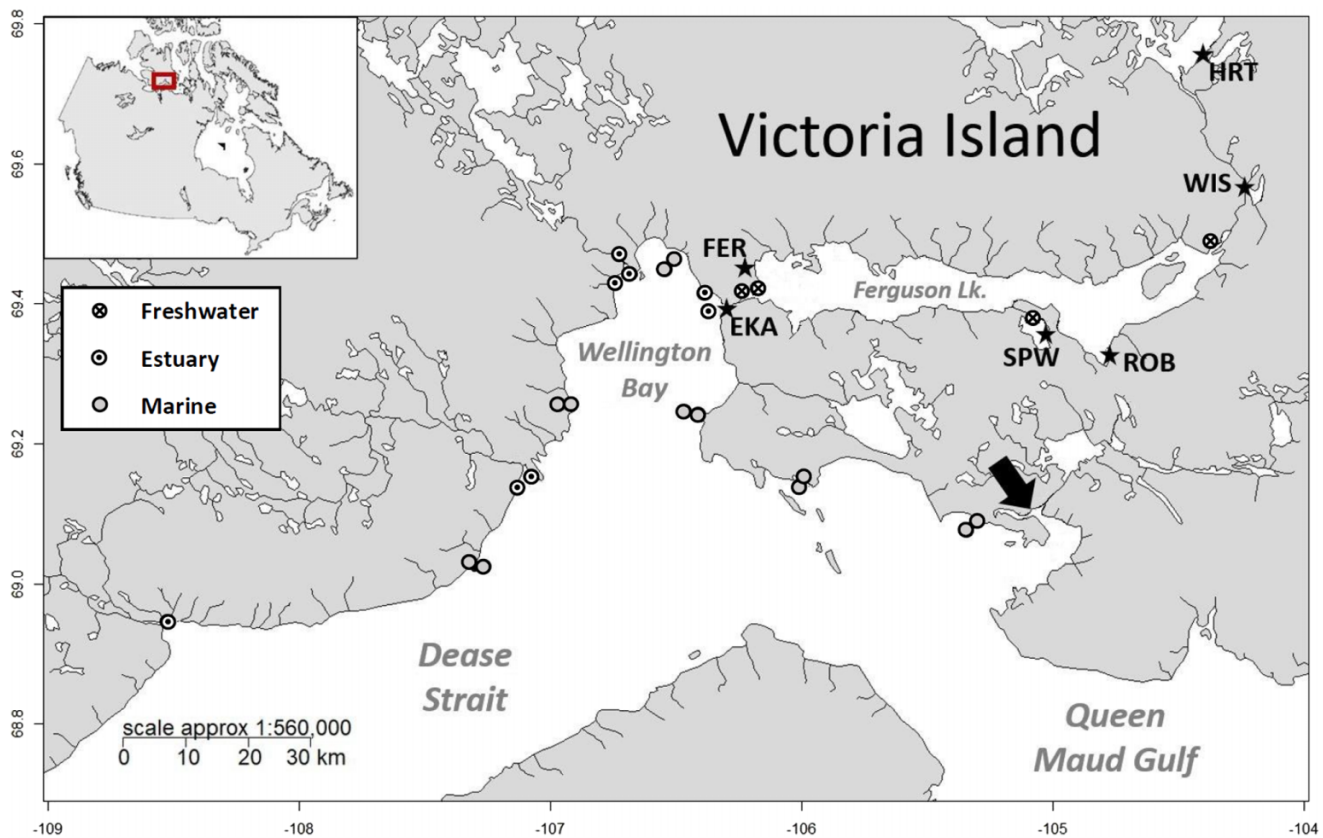
The objective of this study was to use the multiyear acoustic telemetry data set that has been generated for Arctic char (*Salvelinus alpinus*) in the Cambridge Bay region of Nunavut to estimate survival probabilities of this culturally and commercially important species. Here, we have been using acoustic telemetry since 2013 to further our understanding of movements and freshwater and marine habitat use of Arctic char in the region (Moore et al. 2016; Harris et al. 2020a). The region is home to the largest commercial fishery for this species in Canada; yet, there is still a paucity of information on many demographic parameters highlighting the need to employ nonconventional methods for parameter estimation. Previously, Caza-Allard et al. (2021) employed conventional CJS methodology to estimate survival and encounter probabilities for Arctic char in the region. However, due to low recapture rates in freshwater and estuary environments, CJS models are not ideal to estimate survival probabilities of Arctic char in those environments. Furthermore, Caza-Allard et al. (2021) estimated survival solely in the marine environment despite the fact the Arctic char in the region spend more than 10 months of the year in fresh water. Hence, in this study, we used more flexible hierarchical Bayesian multistate mark–recapture models to estimate survival probabilities over multiple years (2014–2018) in marine/estuarine and freshwater environments for Arctic char tagged specifically in the Ekalluk River/Ferguson Lake system, where much of our acoustic telemetry efforts have been focused.

Materials and methods

Study area and fishery information

The study takes place on southern Victoria Island in the Cambridge Bay region of Nunavut (Fig. 1). Our acoustic telemetry array in the area consists of stations that cover marine (Wellington Bay and adjacent coastal areas), estuary (Lauchlan, Halokvik, Surrey and Ekalluk river estuaries), and freshwater (Ferguson Lake) environments. Detailed descriptions of the acoustic array and station information can be found in Moore et al. (2016) and Harris et al. (2020a). Commercial fishing for Arctic char in the Cambridge Bay region started in 1960, and as mentioned above, the region now accounts for the largest commercial fishery for Arctic char in Canada (Harris et al. 2020a). Presently, five waterbodies are actively fished with a combined available annual quota of 56 100 kg (Harris et al. 2020b). The Ekalluk River commercial fishery, which now takes place in Ferguson Lake targeting Arctic char after they have returned to fresh water from summer foraging, is the largest in the region with a 20 000 kg quota (DFO 2014).

Fig. 1. Study area on southern Victoria Island within the Kitikmeot Sea region of Nunavut showing receivers that we considered in this study (circles), and acoustic tagging locations (stars). The location of the community of Cambridge Bay is shown with a black arrow. Tagging information is described in Table 1. Map was modified from Harris et al. (in press). The original map was created with R package "maps" (Becker et al. 2018) using NAD83 projection, and layers for rivers and lakes were downloaded from the National Topographic Database of Canada.



Experimental setup and data

This study is based on a sample of 188 Arctic char acoustically tagged (VEMCO V16 transmitters) between 2014 and 2018 focusing on those from, or presumed to be from, the Ekalluk River/Ferguson Lake system (Table 1). Over the years, acoustic data have been collected using 99 receivers (VEMCO VR2W), including estuary and marine stations in the region and freshwater stations in Ferguson Lake (Fig. 1). Some receivers were repositioned during the study. Hence, we incorporated acoustic detections from 30 receivers, which were fixed or moved slightly (less than the detection range of the acoustic tags (Moore et al. 2016)) and continuously in operation between 2014 and 2018. Additional information on the tagging process and the experimental setup can be found in Moore et al. (2016) and Harris et al. (2020a). For each year of study, our acoustic tagging procedure was approved by the Fisheries and Oceans Canada (DFO) Animal Care Committee and the procedure conforms to all animal care laws in Canada (permit number: FWI-ACC-2013-2019). Licenses to Fish for Scientific Purposes were also approved annually by DFO.

Multistate capture–recapture models

The models we present in this paper are based on the multistate capture–recapture with Bayesian framework us-

ing state-space formulation presented in Kéry and Schaub (2011). State-space models are a type of hierarchical models that are increasingly used to model complex ecological data observed with error (King 2012; Auger-Méthé et al. 2021). Using a state-space formulation for capture–recapture data, we can specify the model as two separate submodels (levels) for the demographic process and the observation process (Gimenez et al. 2007; King 2012). This can be generally expressed as

$$(1) \quad x_t = f(x_{t-1})$$

$$(2) \quad y_t = g(x_t, \epsilon_t)$$

where x_t denotes the true state (e.g., alive or dead) and y_t denotes the observed state (e.g., observed or not observed). Here, $f(\cdot)$ and $g(\cdot)$ represent the process model and the observation model, respectively. The process model describes the true state, and the observation model maps the true state to the observed state. The parameter ϵ_t is the observation error.

The process model

Consider a mark–recapture setting where n number of fish were captured and observed in T number of recapture occur-

Table 1. Tagging information for acoustically tagged Arctic char used in this study.

Location/fishery	Lat.	Long.	Year	No. tagged	Dates	Fork length (mm; mean ± SD)	Weight (g; mean ± SD)
Ekalluk River (EKA)	69.406836°	-106.316685°	2013	30	10–12 July	717 ± 57	4013 ± 1065
			2014	30	11–12 July	670 ± 85	3192 ± 1183
			2015	75	9–11 July	729 ± 83	4103 ± 1212
Spawning Lake (SPW)	69.363741°	-105.045023°	2016	23	14–15 August	761 ± 62	4601 ± 1056
Wishbone Lake (WIS)	69.555709°	-104.178389°	2016	19	20–21 August	734 ± 66	4247 ± 8330
Roberts Bay (ROB)	69.366612°	-104.976021°	2016	21	25–26 August	783 ± 68	5319 ± 1467
Ferguson Lake (FER)	69.461544°	-106.107964°	2017	6	13–14 August	784 ± 81	5450 ± 2056
Heart Lake (HRT)	69.76876°	-104.386835°	2017	19	22–23 August	671 ± 52	3345 ± 6980

Note: Shown are the tagging location (and location code), coordinates for the tagging location, dates of tagging, sample sizes, and length and weight information.

rences. Let $x_{i,t}$ denotes the true state of the i^{th} fish at time t , and $y_{i,t}$ denotes the observed state. Let x_{i,e_i} be the true state of the i^{th} fish at the first capture occurs at time e_i that is observed without error. Then, conditioning on the known first capture, the process model (state equation) can be written as

$$(3) \quad x_{i,t+1} | x_{i,t} \sim \text{multinomial}(1, \Omega_{x_{i,t}, 1...K}), \quad i = 1...n, \text{ and } t \geq e_i$$

where K is the total number of true states and $\Omega_{x_{i,t}, 1...K}$ is a vector of length K , where the elements are the transition probabilities of a fish given its true state at time t (i.e., $x_{i,t}$). Given the capture occasion and state, we assume that the survival/transition probabilities ($\Omega_{x_{i,t}, 1...K}$) to be independent of the fish.

First, consider a state-space process with two environments (M: marine/estuary and F: freshwater). Let ϕ_M and ϕ_F be environment-specific survival probabilities for the marine-estuary environment and freshwater environment, respectively. Let ψ_{MF} and ψ_{FM} denote movement probabilities between each environment. Then, the process can be represented by a 3×3 matrix, which is usually referred to as the transition matrix (Table 2). Note that the rows of the transition matrix are $\Omega_{x_{i,t}, 1...K}$ in eq. 3. In this formulation, as used in Kéry and Schaub (2011), we assume that a fish is alive in the environment at time t and then moves to the next environment between t and $t + 1$. That is, transitions among states are instantaneous and hence, there is no mortality while moving between environments.

Consider a state-space process with three environments (M: marine, E: estuary, and F: freshwater). Now, the list of states at a given time point is “alive in the marine environment”, “alive in the estuary environment”, “alive in the freshwater environment”, and “dead”. Similarly to the previous case, the process can be represented by a 4×4 transition matrix (Table 3).

Observation model

The second component of the model is the observation model given by

$$(4) \quad y_{i,t} | x_{i,t} \sim \text{multinomial}(1, \Theta_{x_{i,t}, 1...K}), \quad i = 1...n, \text{ and } t \geq e_i$$

where $\Theta_{x_{i,t}, 1...K}$ is also a vector of length K , where the elements are the observation probabilities of a fish at each state

given it’s state at time t (i.e., $x_{i,t}$). Here as well, we assume, given the capture occasion and state, observation probabilities ($\Theta_{x_{i,t}, 1...K}$) to be independent of the fish.

Again, consider a process model with two environments: M and F. Let $p_{s,t}$ be the probability of observing a tagged fish that is alive in environment s at time t . Here, we assume that a fish in environment s can only be observed in environment s but cannot be observed in another environment. Thus the observation process is conditional on the state process and the first capture and this can be represented by a 3×3 matrix (Table 4). The rows of this matrix are $\Theta_{x_{i,t}, 1...K}$ in eq. 4. Similarly, the observation matrix for a state-space process with three environments can be written as in Table 5.

We further assume that the fish are independent of each other, the fish and states are recorded without error, and no tags are lost. The posterior distribution can be written as

$$(5) \quad P(\phi, \psi, \mathbf{p} | \mathbf{y}) = f(\mathbf{y} | \mathbf{x}, \mathbf{p}) \times f(\mathbf{x} | \phi, \psi) \times f(\phi, \psi, \mathbf{p})$$

Here, ϕ , ψ , and \mathbf{p} are the vectors of environment-specific survival probabilities, the vector of transition probabilities, and the vector of observation probabilities, respectively. For all the models, since all the parameters are probabilities with the support $[0,1]$, Beta(α, β) distribution was used as the prior for all parameters. In the model estimation, we used $\alpha = 1$ and $\beta = 1$ so that the priors were noninformative uniform for all parameters.

Data preparation

Since the transmission of an acoustic ping from an individual fish to receiver takes just a few milliseconds, each detection can be considered as an instantaneous sampling point. There were millions of such detection records in our data set. If we consider the time point of each detection to be a sampling point, only one fish will be detected at each point. This will result in the detection matrix (the matrix with detection records in which each row represents a fish and columns are sampling points) having a large number of entries with the unobserved state, which is usually represented by zeroth state. To avoid that, we pooled the detection record over time bins and the initial date of the bin is considered as the sampling point. If the fish was detected at least once during a certain time interval, we recorded the state of the

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Table 2. State transition matrix for a state-space process with two environments.

		True state at time $t + 1$		
		Environment M	Environment F	Dead
True state at time t	Environment M	$\phi_M(1 - \psi_{MF})$	$\phi_M\psi_{MF}$	$1 - \phi_M$
	Environment F	$\phi_F\psi_{FM}$	$\phi_F(1 - \psi_{FM})$	$1 - \phi_F$
	Dead	0	0	1

Note: Here, ϕ_M and ϕ_F are environment-specific survival probabilities for the marine-estuary environment (M) and the freshwater environment (F), while ψ_{MF} and ψ_{FM} are movement probabilities.

Table 3. State transition matrix for a state-space process with three environments.

	Marine	Estuary	Freshwater	Dead
Marine	$\phi_M(1 - \psi_{ME} - \psi_{MF})$	$\phi_M\psi_{ME}$	$\phi_M\psi_{MF}$	$1 - \phi_M$
Estuary	$\phi_E\psi_{EM}$	$\phi_E(1 - \psi_{EF} - \psi_{EM})$	$\phi_E\psi_{EF}$	$1 - \phi_E$
Freshwater	$\phi_F\psi_{FM}$	$\phi_F\psi_{FE}$	$\phi_F(1 - \psi_{FM} - \psi_{FE})$	$1 - \phi_F$
Dead	0	0	0	1

Note: Here, ϕ_M , ϕ_E , and ϕ_F are environment-specific survival probabilities for the marine (M), estuary (E) and freshwater (F) environments, respectively, while ψ_{ME} , ψ_{MF} , ψ_{EM} , ψ_{EF} , ψ_{FM} , and ψ_{FE} are movement probabilities.

Table 4. Observation matrix for a state-space process with two environments.

		Observation at time t		
		Environment M	Environment F	Not seen
True state at time t	Environment M	p_M	0	$1 - p_M$
	Environment F	0	p_F	$1 - p_F$
	Dead	0	0	1

Note: Respectively, p_M and p_F are the observation probabilities at marine-estuary environment (M) and freshwater (F) at time t .

Table 5. Observation matrix for a state-space process with three environments.

	Observed at marine	Observed at estuary	Observed at freshwater	Not observed
Marine	p_M	0	0	$1 - p_M$
Estuary	0	p_E	0	$1 - p_E$
Freshwater	0	0	p_F	$1 - p_F$
Dead	0	0	0	1

Note: Respectively, p_M , p_E , and p_F are the observation probabilities at marine (M), estuary (E), and freshwater (E) environments at time t .

fish corresponding to the environment in which the fish was observed. When the fish was detected in multiple environments, the state in which the fish stayed the longest was assigned.

The area is subjected to a long winter where detection probabilities are lower due to inactivity in fresh water (Mulder et al. 2018). This sparseness caused nonconvergence issues in our initial models and, therefore, we pooled the detection records over time intervals under three different scenarios. We used binning intervals with unequal lengths to avoid the effect of overwintering (Table 6). For scenario 1, the detection records were binned into two time intervals for each year: June–September and October–May. June–September would be representative of times when Arctic char would be migrating between freshwater and marine environments and when they would be foraging in marine environments (Moore et al. 2016). October–May, Arctic char in the region would be overwintering. In scenario 2, detection records were binned into three periods annually: June–September, October–December, and January–May. The interval October–December would cap-

ture the spawning and post-spawning period of Arctic char in the region. In scenario 3, annual detections were binned into six periods as June, July, August, September, October–December, and January–May.

Model estimation and evaluation

The models were fitted using the Bayesian Markov chain Monte Carlo (MCMC) approach with "JAGS" (Plummer 2003) in R using the package "R2jags" (Su and Yajima 2015). The models were run on Compute Canada, Graham cluster that mostly used $2 \times$ Intel E5-2683 v4 Broadwell @ 2.1GHz processors with 32 cores in each node. Three parallel chains were run for each model. Thinning is a common practice done to reduce autocorrelation in the MCMC sequence by selecting each k th iteration and discarding the rest. However, thinning is considered to be very inefficient and unnecessary by many researchers (Geyer 1992; Maceachern and Berliner 1994; Link and Eaton 2012). Hence, we performed thinning minimally with $k = 5$ for each model. For each model, the number of MCMC iterations and burn-in (the number of iteration to ig-

Table 6. Binning scenarios that were used to avoid the effect of overwintering.

Scenario	Bins per year	Months
1	2	June–September and October–May
2	3	June–September, October–December, and January–May
3	6	June, July, August, September, October–December, and January–May

nore in the beginning of the chain) were decided based on the number of steps needed for all parameters of the model to converge. The exact number of MCMC iterations and burn-in have been mentioned in the model summary table of each model (see Table 8 and Tables S1–S5). To assess the convergence, in addition to inspecting trace plots and posterior densities, Gelman–Rubin statistics (Gelman and Rubin 1992) and effective sample size (ESS) suggested by Kass et al. (1998) were used.

The Gelman–Rubin statistics that is usually denoted by \hat{R} is widely used to determine whether the MCMC chain has achieved convergence. Calculation of \hat{R} requires multiple MCMC chains (usually 3–5). Then, \hat{R} for a parameter of interest is the variance of the parameter calculated using all the MCMC chains combined, divided by the average of the variances within each chain (Kass et al. 1998). A converged series should result in a $\hat{R} \approx 1$.

ESS is calculated as

$$(6) \quad \text{ESS} = \frac{B}{1 + 2 \sum_{k=1}^{\infty} \rho_k}$$

where B is the length of the MCMC chain after burn-in and ρ_k is the autocorrelation of the sequence at lag k . In practice, the infinite sum in the formula is cutoff at a finite k when the ρ_k is sufficiently small ($\rho_k < 0.05$; Kruschke 2014). ESS can be used to measure the amount of independent information in MCMC chain.

To evaluate how well each model fits the data, posterior predictive checks were performed (King 2012; Gelman et al. 2013). First, we drew a sample of 1500 parameter vectors from the joint posterior distribution (obtained from the converged MCMC chains) along with the unobserved states corresponding to each parameter vector (eq. 3). Then, we predicted a dataset using each sampled set of values and compared the predicted data with the observed data. In our case, since the predicted values are categorical, instead of calculating the Bayesian p value, we explored the probability of accurately predicting the observed state of a fish in different environments of the study area.

Model identifiability was accessed by inspecting Bayesian MCMC outputs (posterior density and trace plots) and pairwise correlations between the model parameters obtained using MCMC chains. A posterior density that is not unimodal and extends over a large fraction of the parameter space, and the trace plot with multiple chains that do not converge/mix indicate nonidentifiable models (Siekmann et al. 2012; Simpson et al. 2020). Furthermore, nonidentifiable models also result in strong correlations between model parameters (Gimenez et al. 2009; Hines et al. 2014).

Model selection

In this study, the fitted models were compared using the deviance information criterion (DIC) proposed by Spiegelhalter et al. (2002) that measures both the fit and the complexity of a model and DIC is described as the predictive measure of choice in Bayesian model selection (Gelman et al. 2013). DIC can be written as

$$(7) \quad \text{DIC} = D(\bar{\theta}) + 2p_D$$

where $\bar{\theta}$ is the posterior mean and p_D is the effective number of parameters given by

$$(8) \quad p_D = \overline{D(\theta)} - D(\bar{\theta})$$

where

$$(9) \quad D(\theta) = -2 \log p(y|\hat{\theta}) + 2 \log f(y)$$

Here, $f(y)$ is the standardizing term that is a function of data (Spiegelhalter et al. 2002). DIC is “a somewhat Bayesian version” of the well-known Akaike information criterion, which measures both the model fit and the complexity (Gelman et al. 2013, 2014). In this work, we used a version of DIC that uses an alternative formulation to p_D suggested by Gelman et al. (2004), which is given below

$$(10) \quad p_V = \text{Var}(D(\theta)) / 2$$

A model with lower DIC is preferred over a model with larger DIC. One of the reasons for the popularity of DIC is the computational convenience, since it has been incorporated into the Bayesian programming languages such as “BUGS” and “JAGS” (Plummer 2003; Spiegelhalter et al. 2003).

Results

There were 2.34 million records of detection of the selected 188 fish from 1 July 2014 to 1 July 2018 by 30 receivers. The majority of the detections were recorded by the receivers in fresh water (1.76 million). The receivers in the estuary environment recorded 0.15 million detections, and the receivers in the marine environment recorded 0.42 million detections. Among the 188 selected fish, 158 fish were detected at least once after the initial release.

For all models, the trace plots showed a good mixing and the Gelman–Rubin statistics was very close to 1 for all the parameter estimates ($\hat{R} < 1.01$). Also, the posterior distributions were unimodal and the bivariate correlation among most parameters was weak with a few pairs having moderately strong correlations indicating no convergence or identifiability issues. ESS estimates were large for all parameters showing that the MCMC chains contain a sufficient amount of independent information. The posterior predictive check

Table 7. Prediction probabilities for the models under different binning scenarios.

	Scenario 1	Scenario 2	Scenario 3
Model 1	65.9%	69.0%	77.2%
Model 2	75.5%	65.6%	84.7%

Note: Models 1 and 2 refer to the model with two environments and the model with three environments, respectively. Scenarios 1, 2, and 3 refer to the binning scenarios in Table 6.

Table 8. Deviance information criterion (DIC) (Δ DIC) values for the models under different binning scenarios.

	Scenario 1	Scenario 2	Scenario 3
Model 1	1942.6*	2811.2 (868.6)	6789.7 (4847.1)
Model 2	2626.9 (684.3)	2603.3 (660.7)	9691.9 (7749.3)

Note: The best model is the model with lowest DIC (marked by an asterisk, *). Δ DIC is the difference in the DIC scores from best model. Models 1 and 2 refer to the model with two environments and the model with three environments, respectively. Scenarios 1, 2, and 3 refer to the binning scenarios in Table 6.

shows all models satisfactory fit to observed data, where the model fitted with three environments under binning scenario 3 showed the best fit (Table 7). Parameter estimates of all models had small standard errors. All the models and convergence evaluation results can be found in the supplementary material (Fig. 2, 3, Figs. S1–S10; Tables 9, 10, and Tables S1–S10). The model with two environments under scenario 1 showed the minimum DIC value, while the model with three environments under scenario 3 resulted in the highest DIC (Table 8). Hence, for making conclusions, we used the model that resulted in the lowest DIC.

The survival probability in the freshwater environment (0.95 ± 0.02) was higher than the survival probability in the marine and estuary environments (0.87 ± 0.02). The recapture probability was also higher in the freshwater environment than in the marine and estuary environments (Table 9). The standard errors of all parameter estimates were small. Furthermore, we observed a difference between the freshwater to marine and marine to freshwater transition probabilities.

Discussion

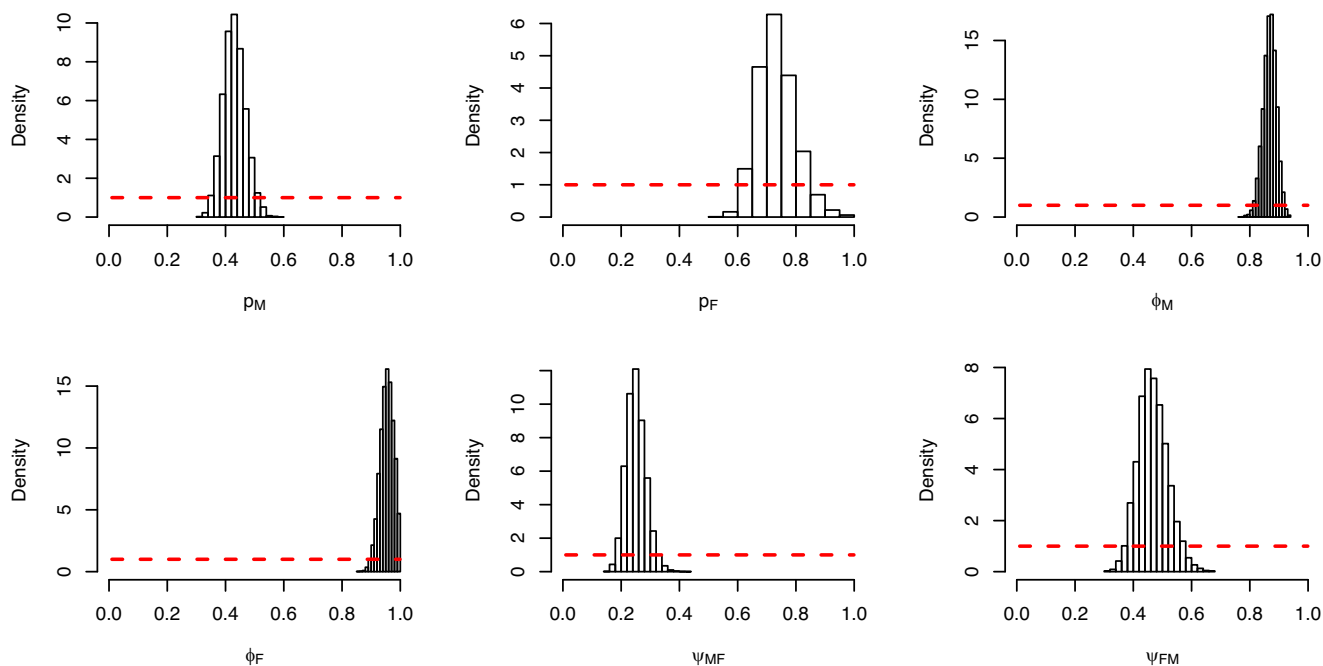
Acoustic telemetry is a powerful tool in fisheries research for studying movement and habitat use (Donaldson et al. 2014; Kraus et al. 2018). More recently, acoustic data have been used in novel ways for estimating and inferring demographic parameters such as survival and population size (Donaldson et al. 2014; Crossin et al. 2017; Lees et al. 2021). In this study, we estimated the survival and recapture probabilities of Arctic char in marine-estuary and freshwater environments using Bayesian multistate mark–recapture models and acoustic telemetry data. We found that the survival probability was generally high (>0.87) and survival estimates were typically higher in the freshwater compared to that estimated for marine and estuary environments. We also found that the recapture probability was higher in the freshwater compared to marine and estuary environments. To the best of our knowledge, this is the first time a Bayesian multistate

capture–recapture framework has been used to estimate the survival of an Arctic anadromous salmonid. The results of the study further our understanding of survival in Arctic char from Canada’s largest commercial fishery for this species, the results of which may inform fisheries management in the region. The Cambridge Bay commercial fishery is the largest in Canada, employing dozens of Nunavummiut annually (DFO 2014) and having information on annual survival will be valuable in understanding the viability of these populations and potential responses to warming Arctic conditions.

Demographic parameter estimation using hierarchical Bayesian models is becoming more common and has now been used across a variety of taxa (Clark 2005). For example, Calvert et al. (2009) applied a hierarchical Bayesian multistate mark–recapture model with three states to estimate daily transience and departure of migratory birds. They found that the parameter estimation can be improved by using the hierarchical Bayesian approach compared to frequentist nonhierarchical models. Wu and Holan (2017) also used a Bayesian hierarchical multipopulation multistate Jolly–Seber model to estimate the abundance of pallid sturgeon (*Scaphirhynchus albus*) in the Lower Missouri River. These authors also incorporated covariates (sampling efforts for different gear types) to further improve the model in terms of reducing computational burden and precision. These studies highlight that the Bayesian framework when combined with acoustic telemetry data can be an effective method for estimating demographic parameters when traditional methods/data are not available.

Similar to our study, Jensen et al. (2019) also presented evidence for higher annual mortality rates for the Arctic char in the marine environment (Arctic region of Norway) than in fresh water for fish that were captured using permanent fish traps during the ice-free period between 1987 and 2012. These authors suspected that mortality was higher in the marine environment due to osmoregulation difficulties in the salt water and higher number of predators in the marine habitats. Recently, Caza-Allard et al. (2021), also using a CJS framework, estimated high annual survival probabilities (varying between 0.79 and 0.88) for Cambridge Bay Arctic char in the marine environment, with recapture probabilities varying between 0.64 and 0.90. However, the standard errors of survival estimates in our study were much lower than those reported in Caza-Allard et al. (2021), which were estimated using ordinary CJS models. The lower error resolved in this study is likely because the Bayesian multistate mark–recapture models borrow information through all environments to estimate the parameters, highlighting the utility of the Bayesian framework used here. Finally, recent stock assessments completed on stocks of commercially harvested Arctic char in the region also suggest that overall natural mortality is low with values between 0.15 and 0.18 (Zhu et al. 2021). However, these authors estimated mortality for every age class while in this study, we only considered adult Arctic char in parameter estimation. Including all age classes would likely inflate mortality estimates as younger age classes (e.g., juvenile) would be expected to have much higher mortality. Therefore, mortality for adults alone should be even lower than what Zhu et al. (2021) reported in their assessment. Thus, our results corroborate previous findings for

Fig. 2. Posterior plots of parameter estimates for the model with two environments under binning scenario 1. Here, ϕ_M and ϕ_F are environment-specific survival probabilities for the marine-estuary environment (M) and freshwater environment (F) while ψ_{MF} and ψ_{FM} are movement probabilities; p_M and p_F are the corresponding detection probabilities. Dashed horizontal lines represent the prior distributions.



Arctic char in that survival is generally high in this species once they are adults.

Adult Arctic char in the study area inhabit fresh water during the long winter (September–June/July) and migrate to forage in the marine environment in late June or early July before returning to fresh water in August or September for spawning and (or) overwintering purposes (Moore et al. 2016; Harris et al. 2020a). High survival in both environments is not surprising, given that Arctic char are a top predator with few competitors. During the winter months while in fresh water, the survival probability is likely higher since there are fewer risks of mortality compared to the marine environment. For example, there are likely no predators for adult Arctic char in the freshwater environment, and most fisheries (subsistence and commercial) are executed in marine and estuarine habitats (Day and Harris 2013). The activity level of Arctic char is also greatly reduced when overwintering in fresh water (Mulder et al. 2018) possibly reducing their chances of encountering potential threats to survival. In the marine environment, the mortality can be expected to be higher due to these fishing activities and possibly due to predators such as seals, which are known to predate on char in other regions (Moore 1975; Jensen et al. 2019). The difference in the detection probability between the two environments can be accounted for by the difference in the receiver cover. In fresh water, there is a higher probability that the receiver would detect a fish than in the marine and estuary environments. One reason for the higher detection probability in fresh water is that the river funnels the fish that migrate to estuary and marine environments. Also, once there is ice on the lake surface,

the detection range of the tags improves resulting in a higher probability of detection (Moore et al. 2016; Munaweera et al. 2021).

The model we developed in this study is directly applicable for analyzing acoustic telemetry data from other studies incorporating a fixed array of receivers and where the study species is monitored in multiple habitats (i.e., anadromous and catadromous fishes) for which survival estimates are wanted. However, for long-term studies (>5 years) it is possible that the acoustic array may not be static throughout the study period due to a variety of reasons (e.g., lost receivers, changed objectives, etc.). In these cases, we recommend the reader maintain an approximately fixed receiver array throughout the duration of the study in order to improve parameter estimates. In our study, we filtered the data set by removing some receivers and some fish tagged before 2014 so that the receiver array was fixed throughout the study period. Even though we had to remove a significant amount of data, this allowed us to assume that the detection probabilities for each environment were fixed over time allowing us to use a simpler model with lower number of parameters. Using a simpler model allowed us to avoid issues such as nonconvergence and large computational burden. All the models we attempted in this study were completed in less than 2 hours except for the model with three environments under scenario 3, which required about 4 hours to complete. Furthermore, users of this model must take into consideration varying detection probability among environments. A reference tag experiment conducted in different environments under different conditions (e.g., ice on/off) would be ideal in this situa-

Fig. 3. Trace plots of parameter estimates for the model with two environments under binning scenario 1. Here, ϕ_M and ϕ_F are environment-specific survival probabilities for the marine-estuary environment (M) and freshwater environment (F) while ψ_{MF} and ψ_{FM} are movement probabilities; p_M and p_F are the corresponding detection probabilities. [Colour online.]

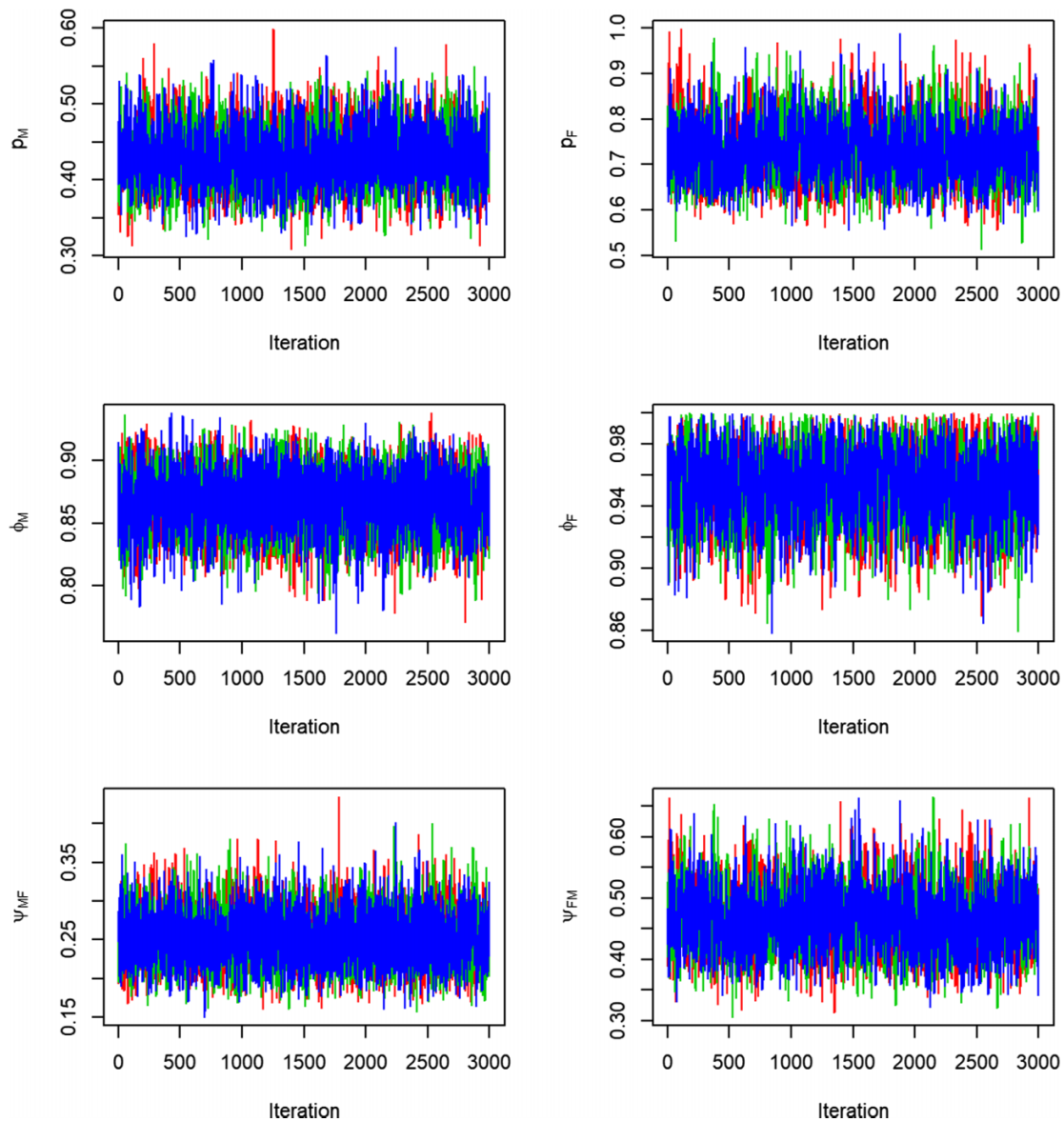


Table 9. Parameter estimates for the model with two environments under binning scenario 1.

Parameter	Mean	Standard error	95% credible interval		\hat{R}	ESS
			Lower	Upper		
p_M	0.43	0.04	0.36	0.51	1.001	9000
p_F	0.73	0.07	0.62	0.88	1.001	9000
ϕ_M	0.87	0.02	0.82	0.91	1.001	9000
ϕ_F	0.95	0.02	0.91	0.99	1.002	2700
ψ_{MF}	0.25	0.03	0.19	0.32	1.001	9000
ψ_{FM}	0.47	0.05	0.38	0.57	1.001	5900
Deviance	1489.13	30.12	1426.87	1543.83	1.002	2700

Note: Here, ϕ_M and ϕ_F are environment-specific survival probabilities for the marine-estuary environment (M) and freshwater environment (F), while ψ_{MF} and ψ_{FM} are movement probabilities, and p_M and p_F are the corresponding detection probabilities. \hat{R} denotes Gelman–Rubin statistics and ESS is the effective sample size. The model was estimated using three MCMC chains each with 20 000 iterations, 5000 burn-in with thinning by selecting each fifth iteration.

Table 10. Bivariate correlations between parameters for the model with two environments under binning scenario 1.

	p_M	p_F	ϕ_M	ϕ_F	ψ_{MF}	ψ_{FM}
p_M	1.00	—	—	—	—	—
p_F	-0.53	1.00	—	—	—	—
ϕ_M	-0.11	0.13	1.00	—	—	—
ϕ_F	-0.31	0.01	-0.27	1.00	—	—
ψ_{MF}	0.33	-0.31	-0.12	-0.11	1.00	—
ψ_{FM}	-0.52	0.61	0.02	0.23	-0.04	1.00

Note: Here, ϕ_M and ϕ_F are environment-specific survival probabilities for the marine-estuary environment (M) and freshwater environment (F) while ψ_{MF} and ψ_{FM} are movement probabilities; p_M and p_F are the corresponding detection probabilities.

tion to support the constant detection probabilities assumption over time (Munaweera et al. 2021). However, such data do not exist for the study region at this point. As a consequence of model violation due to temporal varying detection probabilities, we can expect the estimated parameter to be biased and hence, less accurate. Another alternative is to account for the annual changes in the receiver array by adding temporally varying detection probabilities to the model. Even though this would allow us to use all the detection records from all receivers, this will significantly increase the number of parameters in the model and the computational burden that can result in nonconvergence. However, as more data become available, this will be a natural extension of the model presented here. The framework we used in this study can be easily generalized for a larger number of states. Even though we did not use the three-environment model (model 2) to draw conclusions, the model still converged and the standard errors of the parameter estimates under all three binning scenarios were also satisfactory for obtaining separate estimates of survival for marine, estuary and freshwater environments.

Acoustic telemetry data are more commonly being incorporated into fishery and habitat management decision-making processes (Crossin et al. 2017; Lees et al. 2021), for example in determining protected areas to preserve critical fish habitats (Halpern 2003; Goodchild 2004; Lea et al. 2016) and fisheries stock assessments aimed at resolving sustainable removal levels (Kneebone et al. 2014; Sippel et al. 2015; Cooke et al. 2016). Acoustic telemetry results in higher recapture rates than conventional capture–mark–recapture studies, and therefore, the analysis of acoustic telemetry data often results in more precise estimates of demographic parameters, including survival, mortality, and abundance compared to conventional capture–mark–recapture studies (Pollock et al. 2004; Dudgeon et al. 2015; Kraus et al. 2018). Hence, the management decisions based on acoustic telemetry information can be developed with less uncertainty (Lees et al. 2021). Our data have provided a multiyear perspective on the annual survival of adult Arctic char highlighting differences among environments (freshwater vs. estuary/marine). It is not clear what mortality rates would be detrimental to Arctic char population persistence in the region but Johnson (1980) suggested that an 11% harvest rate would be excessive. This would suggest that our estimates of survival leave the

possibility that the mortality rate is above the level considered safe, which might be concerning from a fisheries management perspective. However, our estimates are for annual survival, which would include other mortality-related factors such as predation and senescence. Furthermore, others have estimated mortality rates (Harris et al. 2021) and exploitation rates (Day and Harris 2013) in excess of 11% for fisheries in the region that have still been deemed sustainable. As mentioned above, it is unclear as to what harvest rates would be considered detrimental to stock health, and further work is required in order to shed light on this important knowledge gap in the region and for Arctic char in general. Overall, the relatively high survival rate for adult Arctic char for all the environments in the region, combined with recent assessments that have suggested at least some stocks are considered healthy (Day and Harris 2013; Zhu et al. 2021; Harris et al. 2021), suggests that the contemporary fishery management strategies in the region are likely effective.

In this study, we used acoustic telemetry data to estimate the survival and recapture probabilities of adult Arctic char in different environments. The parameter estimates in this study generated using Bayesian multistate mark–recapture models were more precise than those reported in previous studies in the region using the traditional CJS models. The models we used did not suffer from convergence issues and convergence was achieved quickly. Hence, Bayesian multistate mark–recapture models incorporating acoustic telemetry data can be recommended as a suitable alternative for estimating demographic parameters such as survival compared to the conventional CJS models. Anadromous fishes that migrate between marine and freshwater environments throughout their lives are common across the Canadian Arctic. These fishes, including the Arctic char studied here but also Dolly Varden char (*Salvelinus malma malma*), anadromous lake trout (*Salvelinus namaycush*), and multiple whitefishes and ciscoes (*Coregonus* spp.), all share a relatively similar life history in that they forage in marine habitats in the summer before migrating back to fresh water to spawn and (or) overwinter. This group of fishes is also highly sought after in subsistence and commercial fisheries throughout the Canadian Arctic where they are important for local economies, food security, health, and maintaining traditional cultures (e.g., Government of Nunavut 2016). The results of our study are relevant for future telemetry projects on Arctic anadromous fishes, and the Bayesian multistate capture–recapture models we employed here could inform survival and mortality in other regions on other important species with similar life histories. Furthermore, there are currently multiple projects across the Canadian Arctic that are using, or have recently used, acoustic telemetry for inferring spatiotemporal aspects of migrations and habitat use in anadromous Arctic char (Smith 2020; Hammer et al. 2022; Hollins et al. 2022). Therefore, our results are widely applicable to these other studies that have already generated acoustic telemetry data for anadromous Arctic char and the model proposed here may prove valuable for shedding additional light on the mortality and survival of this species, which will be useful in developing future fishery conservation and management plans effectively. This will be valuable in ensuring the long-

term sustainability of this culturally and commercially important resource to Inuit across the Canadian Arctic.

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Data availability statement

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2021-0262>.

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