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Original Article

Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic

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The migration dynamics and inter-annual variation in early at-sea survival of Atlantic salmon (*Salmo salar*) smolts over 14 years of study are reported for four river populations located in the Gulf of St. Lawrence (Canada). Acoustically tagged smolts were monitored at three points along their migration from freshwater to the Labrador Sea, a migration extending more than 800 km at sea and a period of 2 months. A hierarchical state-space version of the Cormack–Jolly–Seber model was used to estimate apparent survival rates from incomplete acoustic detections at key points. There was a positive size-dependent probability of survival through the freshwater and estuary areas; the odds of survival of a 16 cm smolt were 1.5–1.7 times higher than for a 13.5 cm smolt, length at tagging. Length adjusted (centred to the mean fork length of smolts during the study of 14.6 cm) survivals through the estuary and nearshore waters were estimated to range between 67 and 90% for the two river populations migrating through Chaleur Bay in contrast to lower survival estimates of 28–82% for the two populations from the neighbouring Miramichi Bay. Across the 14 years of study, survival estimates varied without trend for the populations of Chaleur Bay, but declined for the populations migrating through Miramichi Bay. Survival through the Gulf of St. Lawrence was variable but generally high among years and rivers, ranging from 96% day^{-1} to 99% day^{-1}. Long term, replicated studies at multiple sites using acoustically tagged smolts can provide empirical data to examine hypotheses of the location and timing of factors contributing to smolt and post-smolt mortality of salmon at sea.

Keywords: acoustic telemetry, Atlantic salmon, hierarchical CJS model, smolt survival.

Introduction

Many Atlantic salmon (*Salmo salar*) populations in the western North Atlantic portion of the species' range are currently at or near record low abundances (ICES, 2017). Since the 1990s, sharp declines in population abundance estimates or fisheries landings, as proxies for abundance, have been noted (Beaugrand and Reid, 2003, 2012; Chaput *et al.*, 2005). Historically, multiple causes in fresh water (dams, poor land-use patterns, etc.) diminished the

salmon's natural range and reduced population productivity (Parrish *et al.*, 1998) but declines in the past two decades cannot be directly or exclusively attributed to freshwater factors. In the past decade, return rates of smolts to one-sea-winter salmon for populations in the North Atlantic have been low, averaging less than 3.5% (an instantaneous mortality rate >3.35) across monitored rivers (ICES, 2017). Favourable oceanographic conditions have been associated with higher abundances of Atlantic salmon in some populations and in some years, but the same factors do not appear to be acting on all populations equally (Friedland *et al.*, 2000; Peyronnet *et al.*, 2007).

Anadromous salmonid population abundances are most sensitive to factors affecting marine survival (Otero *et al.*, 2011; Kilduff *et al.*, 2015; Nieland *et al.*, 2015), suggesting that the causes of the most recent declines of Atlantic salmon are due to increased mortality at sea. Increasingly variable inter-year marine survival for several Pacific salmon species is correlated with changes in oceanographic conditions (Kilduff *et al.*, 2015). Local effects, such as fish passage and the nearshore ecosystem, and offshore factors including variations in the physical, chemical, and biological components of the ecosystem are involved in the mortality of Atlantic salmon but the location, timing, and the proportional contribution of various factors to total mortality remain elusive (Thorstad *et al.*, 2012). If an important component of the annual marine mortality of anadromous salmon takes place in the initial phase of seaward migration and can be documented, then further studies can be defined to understand the causal mechanisms and advise on mitigation options. However, if the early marine phase is not an important survival period/area, then local mitigation may not be useful and factors further afield need to be studied.

It is now possible to implant electronic (acoustic) transmitters in small fish and track their movements over increasingly long periods of time. Such studies can provide information on individual fish distribution, migration rates, marine residency patterns, as well as population-level survival rates and to identify critical marine habitats and periods (Lacroix, 2008; Drenner *et al.*, 2012; Thorstad *et al.*, 2012; Goulette *et al.*, 2014; Hussey *et al.*, 2015). In eastern North America, acoustic tracking studies have been undertaken on a geographically diverse number of wild Atlantic salmon populations ranging from the southern areas in Maine (USA; Lat. 44.67°N; Kocik *et al.*, 2009) to northeastern populations in Newfoundland (Lat. 47.9°N; Dempson *et al.*, 2011) and mid-latitude populations in the Gulf of St. Lawrence (Lat. 50.28°N; Lefèvre *et al.*, 2013; Daniels *et al.*, 2018). With few exceptions (Lacroix, 2008; Kocik *et al.*, 2009; Stich *et al.*, 2015), the studies reported on movements and survival of Atlantic salmon smolts in the home river estuary within 50 km from the head of tide or to nearshore environments in the vicinity of the river's confluence with the sea, and rarely included more than 2 years of smolt tagging from the same river. At many sites, predation on smolts during the initial period and area of migration is considered to be important, and local conditions that either enhance or reduce predation risk may determine initial survival (Kocik *et al.*, 2009; Halfyard *et al.*, 2013; Daniels *et al.*, 2018). Few of the published studies provide sufficient annual replication to characterize the annual variation in survival rates thus precluding the testing of hypotheses of factors which may be responsible for the early marine-phase mortality of salmon smolts.

We report on data collected from a 14-year and multi-population acoustic telemetry study to quantify survival rates of acoustically tagged wild Atlantic salmon at pre-defined geographic locations during the freshwater (smolt stage), estuarine (smolt stage), and open ocean (post-smolt stage) migratory phases. The study considers populations of Atlantic salmon from four unimpacted (free fish passage) rivers from the southern Gulf of St. Lawrence (Canada) over the period 2003–2016. Acoustically tagged salmon smolts are tracked over a period extending approximately 2 months at sea and over 800 km offshore.

Material and methods

Description of study area

The Miramichi River (47.2°N 65.0°W) has a basin area of approximately 14 000 km^2 with two major tributaries that converge in tidal waters; the Southwest Miramichi River and the Northwest Miramichi River (Chiasson, 1995). Salmon from the Miramichi River pass through Miramichi Bay on their migration to the Gulf of St. Lawrence. Miramichi Bay, a shallow natural barrier-built estuary, is seasonally stratified with average salinities in the outer portion of less than 25 parts per thousand (ppt) and a maximum depth that rarely exceeds 10 m (Chiasson, 1995; St-Hilaire *et al.*, 1995). The Restigouche River (48.0°N 66.3°W; basin area of 12 820 km^2) and the Cascapedia River (48.2°N 65.9°W; basin area of 3 147 km^2) both flow into Chaleur Bay, an open bay that enters directly into the Gulf of St. Lawrence. It is deep compared to Miramichi Bay, with a central trough of maximum depth of approximately 100 m and surface salinities generally less than 27 ppt during the open water period (Koutitonsky and Bugden, 1991). The Chaleur and Miramichi Bays are located in the southwest portion of the Gulf of St. Lawrence (GSL), a stratified semi-enclosed sea with an approximate surface area of 226 000 km^2 (Koutitonsky and Bugden, 1991). Surface layers (<30 m) are of low salinity (27–32 ppt) and sea surface temperatures generally approximate or exceed 20°C in summer (DFO, 2017). The Gulf of St. Lawrence has two connections to the North Atlantic Ocean; Cabot Strait to the east at a width of 104 km and a maximum depth of 480 m and the Strait of Belle Isle to the north at a width of 15 km and depth less than 60 m (Koutitonsky and Bugden, 1991) (Figure 1). The head of tide locations of the four study rivers are approximately 900 km from the Strait of Belle Isle (Figure 1).

Smolt collection and tagging

Atlantic salmon smolts were captured in rotary screw traps (Chaput and Jones, 2004) set at the same locations over the study period for the Southwest Miramichi (127 km above the head of tide), Restigouche River (115 km above the head of tide), and the Cascapedia River (8 km above the head of tide) (Figure 1). For the Northwest Miramichi, smolts were captured in the Little Southwest Miramichi River (30 km above the head of tide) during 2003–2008 and in the Northwest Miramichi River (24 km above the head of tide) during 2013–2016. The distances from the head of tide to the outer bays ranged from just under 70 km for the Miramichi River locations to between 47 and 106 km for the two rivers in Chaleur Bay. The outlets of the two bays are approximately 800 km south of the Strait of Belle Isle (Figure 1).

The dates of tagging and release of Atlantic salmon smolts varied by river and year (Supplementary Figure S1). Generally, smolts were first captured and tagged in the Southwest Miramichi, then the Northwest Miramichi, followed by the Restigouche and finally the Cascapedia. Among years, the dates of release varied by as much

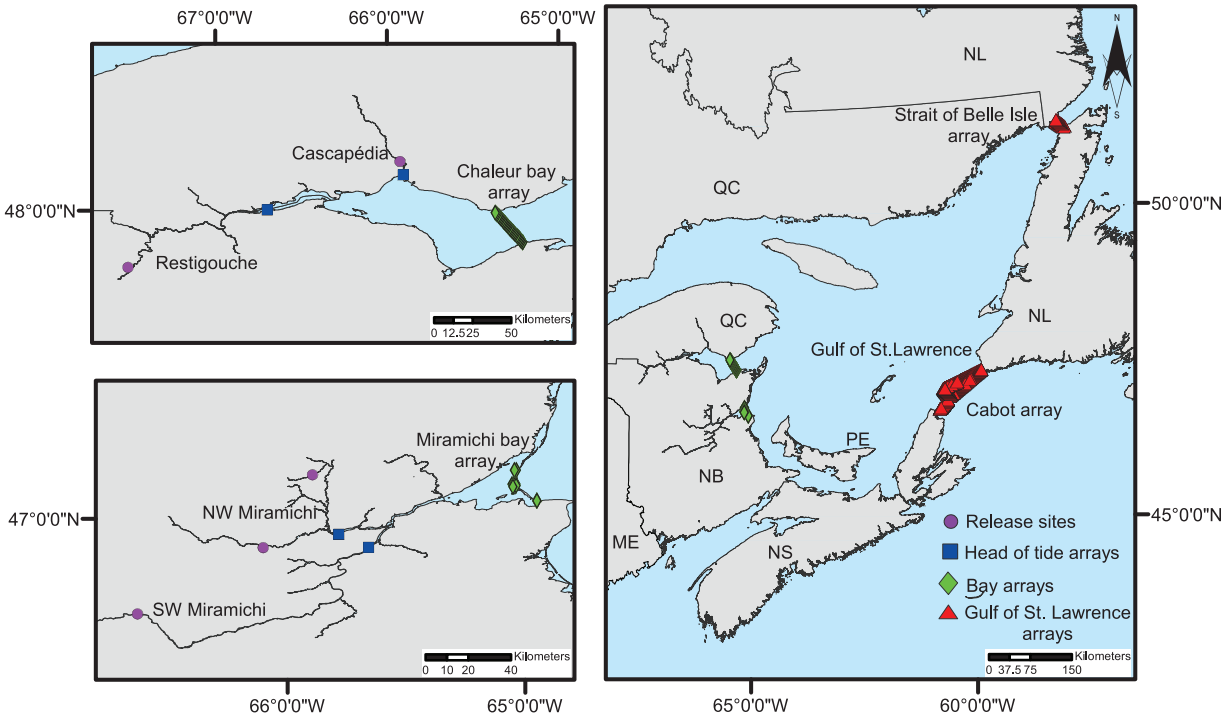

Figure 1. Map of study area. Left sub-panels show the release locations by study river, the head of tide receiver locations, and the respective bay receiver lines. Right panel depicts bay receiver lines as well as the receiver line locations at exits from the Gulf of St. Lawrence.

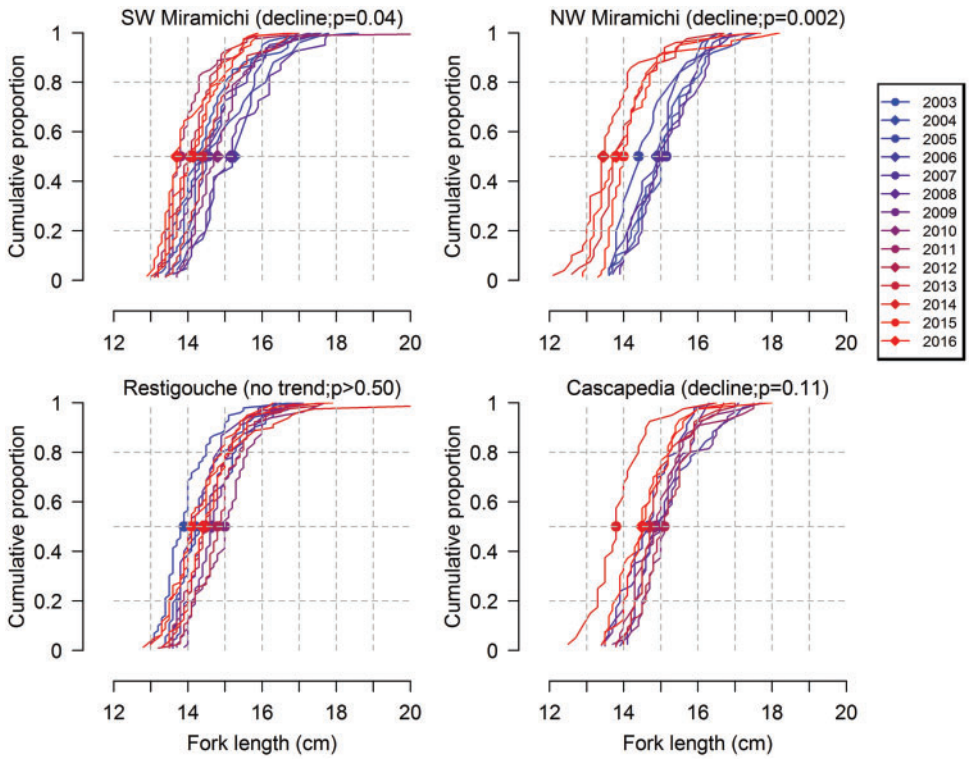

Figure 2. Cumulative frequency distributions by fork length (cm) of Atlantic salmon smolts tagged and released in the four rivers over the period 2003–2016. Also shown in each river panel is the trend and associated *p*-value of the linear regression of median length vs. year.

as 3 weeks, the earliest dates of tagging were in 2010, 2012, and 2013 while the latest dates of tagging occurred in 2008 and 2014.

Smolts were selected for tagging on the basis of length with efforts to select smolts generally greater than 13 cm fork length (FL). The realized length range was 12.1–23.3 cm FL with median lengths among rivers and years ranging from 13.5 to 15.0 cm FL (Figure 2). Size distributions of tagged smolts in 2014 in three of the four rivers were among the smallest of the time series (Figure 2).

Acoustic transmitters, models V8SC and V9 (9 mm diameter, 2.9–3.3 g in air, hereafter referred to as V9) and the smaller V8 (8 mm diameter, 2.0 g in air) pinging at 69 kHz (Innovasea Marine Systems Canada, Inc., Halifax, NS) with a unique identification code, were surgically implanted into the peritoneal cavity of selected smolts (Daniels *et al.*, 2018). Smolts were generally tagged and released at the site of capture. The exception was in 2014–2016, when smolts from the Northwest Miramichi River were released upstream of their capture location, approximately 52 km above the head of tide. Fish recovered post-surgery in a holding pen in the river for a few hours prior to being released. Each tag was programmed to ping at random delays of either 20–60 s or 25–55 s and had an estimated minimum battery life of 74 days (Supplementary Table S1). The whole weight of tagged smolts was not reliably measured. The tag burden, expressed as the ratio of tag length to fork length of fish, ranged from 9.0 to 16.9%, with a mean of 14.2%. Based on general length to weight relationships of smolts from these rivers (Fisheries and Oceans Canada, unpublished data), the tag burden ratio in terms of weight was estimated to be very similar to the tag burden ratio based on length.

Receiver deployments and monitoring

Lines, in some cases staggered, of acoustic receivers (VR2, VR2W, VR2AR, or VR4 models, Innovasea Marine Systems Canada, Inc.) were deployed at the head of tide of each of the four rivers and at the outer bay exits to the Gulf of St. Lawrence (Miramichi Bay and Chaleur Bay) (Figure 1). Effective detection range of the receivers is considered to encompass a radius of 0.5 km. Since 2007, a receiver line has been installed annually at the Strait of Belle Isle (Figure 1). A second receiver line was installed 3.5 km north of the primary Strait of Belle Isle line during 2015 and 2016 to provide empirical data for estimating the detection efficiency of the primary Strait of Belle Isle line. A partial receiver line was installed across the Cabot Strait beginning in 2010 and complete coverage closing off the strait was established in 2012 (Figure 1). Spacing distance among receivers at the Strait of Belle Isle line was a maximum of 800 m. All receiver lines were seasonally deployed in spring and removed in the fall, with the exception of Cabot Strait receiver line which operates year-round. The structure (number of receivers, placement) of each receiver line was generally similar among years, however, the physical environment and other anthropogenic factors affected the detection range of the individual receivers and the overall array.

Description of data

There are 14 years of tracking data for the Southwest Miramichi River (2003–2016), 10 years for the Northwest Miramichi River (2003–2008; 2013–2016), 13 years for the Restigouche River (2004–2016), and 11 years for the Cascapedia River (2006–2016) (Figure 3; Supplementary Table S2). A total of 2 862 Atlantic salmon smolts had complete tagging and release information over the 48 years and river combinations. The number of smolts tagged and released annually by river ranged from 25 to 105 fish. When presented, migration characteristics are based on the times and dates of the first detections of individual smolts at any receiver in each array.

Modelling detection and survival probabilities

A Bayesian state-space implementation of the Cormack–Jolly–Seber (CJS) model (Gimenez *et al.*, 2007; Royle, 2008) is used to disentangle the imperfect detection (p) of tagged smolts on the receiver arrays from apparent survival (ϕ) during their out migration from freshwater to the Gulf of St. Lawrence and to the Strait of Belle Isle. The state-space parameterization of the CJS model constructs distinct models for the unobserved survival (ϕ) process and the observed detection process (p). For simplification, we refer to apparent survival or simply survival as the joint probability of a tagged fish surviving to pass a receiver array and of the tag being detected at that array (see discussion for implications on estimates of apparent survival of tagged smolts).

The unobserved survival process model (Equation 1) assumes that if a fish (i) carrying an acoustic tag is alive at the observation point j-1 then its survival state at point j is a realization from a Bernoulli process with parameter ϕ_j. The state process (survival) is represented by a binary variable $z(i, j)$, which takes the value 1 if individual i is alive at the detection point j and 0 otherwise. This process is modelled as random draws from a Bernoulli distribution where $z(i, j)$ is conditional on $z(i, j\text{-}1)$, whether fish i is alive (1) or dead (0) at the previous detection point:

$$z(i,j) \mid z(i,j-1),\ \emptyset_j \ \sim\ \text{Bernoulli}(z(i,j-1)\emptyset_j) \qquad (1)$$

with $j = 1$–4 corresponding to the three to four post-release detection points where a fish, which is alive may be observed after initial tagging and release ($j = 0$). If a fish is not alive at j-1 then $z(i, j) = 0$ with probability 1. The initial state at release, i.e. $z(i, 0)$, is set equal to 1.

The re-observations $y(i, j)$ are modelled as independent Bernoulli random variables, conditional on the $z(i, j)$'s and the probability of detection (p):

$$y(i,j) \mid z(i,j),\ p_j \ \sim\ \text{Bernoulli}(z(i,j)p_j), \qquad (2)$$

where $y(i, j) = 0$ with probability 1 if $z(i, j) = 0$, otherwise $y(i, j)$ is a Bernoulli random variable with parameter p_j the probability of detection at array j.

The parameters p and ϕ are proportions bounded on the range [0, 1] but are logit-transformed to improve the model's convergence properties. A hierarchical structure assuming exchangeability is considered for the detection and survival parameters, conditional on individual effects of tag type and smolt size, reflecting the multi-year (t) and multi-population (r) design of the study (Gelman *et al.*, 2004; Bonner and Schwarz, 2006). The exchangeability assumption considers that the year and population specific parameters at the arrays ($p_{r,t,j}$; $\phi_{r,t,j}$) are drawn from common prior distributions with unknown hyperparameters for the corresponding groups (river r and array j) (Gelman *et al.*, 2004).

Individual effects

Individual effects on p and ϕ are examined for the acoustic tag type used and the size of smolts at tagging (Royle, 2008). The V9

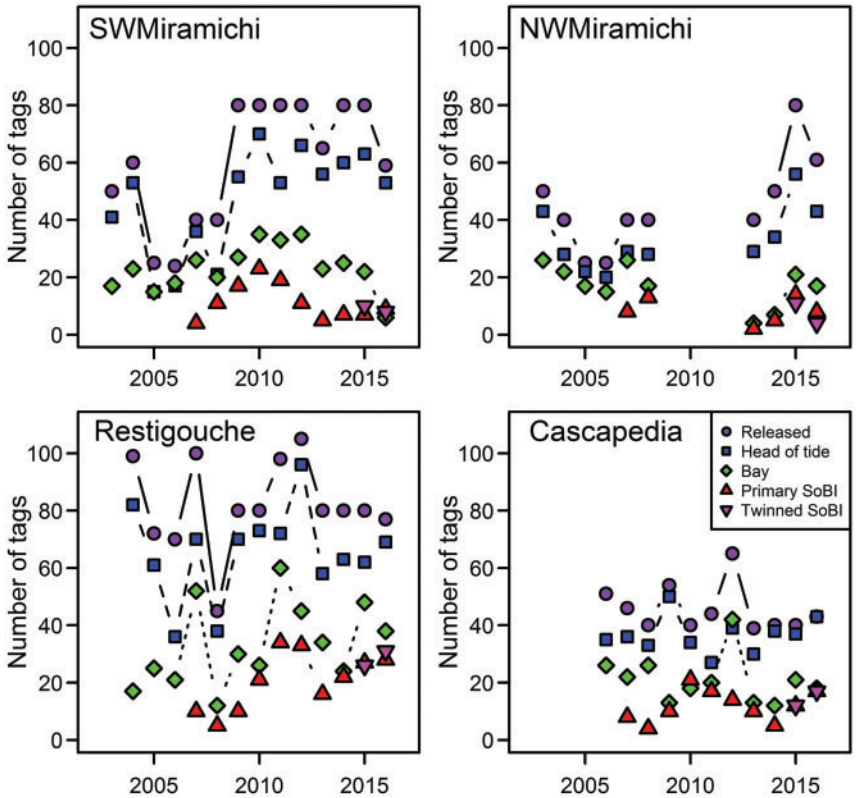

Figure 3. Summary of number of tagged fish released and number of tags detected at the respective receiver lines for four rivers during 2003–2016, for tag types (V9, V8) combined.

version of the tag was used during 2003–2015. The V8 version was used in 2014–2016 (Supplementary Table S2). The tag model is considered to have potential effects on both the probability of detection, due to differences in output, and on the probability of survival, due to differences in relative tag burden.

Tag type (V9; V8) is modelled as an offset on the logit scale of the average probability of detection at the arrays:

$$y(i[r,t],j) \mid z(i[r,t],j),\ p(i[r,t],j) \sim \text{Bernoulli}(z(i[r,t],j)p(i[r,t],j)) \quad (3)$$

with

$$\text{logit}\Big(p(i[r,t],j)\Big) = \mu^p(r,t,j) + \beta_p * v9_i - \beta_p * v8_i \quad (4)$$

for $j = 1{:}3$; $r = 1{:}4$; $t = 2003{:}2016$; $i =$ individual fish 1:2 862; $p(i[r,t],j)$ the probability of detecting fish i within river r and year t at array j; $\mu^p(r,t,j)$ the mean logit probability of detection within river r, year t, at array j; β_p the offset in the probability of detection for tag type; $v9_i = 1$ if tag type was V9 for fish i, 0 otherwise; $v8_i = 1$ if tag type was V8 for fish i, 0 otherwise.

Preliminary analyses of the proportions of tags detected at the arrays suggested a positive association with the fork length of the fish at tagging (Figure 4). There is also a decreasing temporal trend (linear regression of median length vs. year) in the size distributions of smolts tagged in the Southwest Miramichi and Northwest Miramichi rivers over the period of study (Figure 2). Survival probabilities relative to the length of fish at tagging by river and tag type overall are modelled as linear effects on the logit scale with tag type included as an interaction term with fork length (i.e. differing slopes for tag type) as:

$$z(i[r,t],j) \mid z(i[r,t],j-1),\ \varnothing(i[r,t],j) \sim \text{Bernoulli}(z(i[r,t],j-1)\varnothing(i[r,t],j)) \quad (5)$$

With

$$\text{logit}\Big(\varnothing(i[r,t],j)\Big) = \mu^{\varnothing}(r,t,j) + (\alpha_{fl} + \beta_{\varnothing} * v9_i - \beta_{\varnothing} * v8_i) * fl_i' \quad (6)$$

for $j = 1{:}2$; $r = 1{:}4$; $t = 2003{:}2016$; $i = 1{:}\ 2\ 862$; $\varnothing(i[r,t],j)$ the probability of survival of fish i within river r and year t through transition zone j; $\mu^{\varnothing}(r,t,j)$ the mean logit probability of survival within river r, year t through transition zone j; α_{fl} the average slope over tag type to fish length relationship, logit scale; $\beta_{\varnothing}$ the offset in the slope of fork length due to tag type; $v9_i = 1$ if tag type was V9 for fish i, 0 otherwise; $v8_i = 1$ if tag type was V8 for fish i, 0 otherwise; $fl_i' = fl_i - \overline{fl}_{.}$ the centred fork length (cm) of individual i; $\overline{fl}_{.}$ the mean fork length (cm) of smolts across all rivers and years.

The effects for smolt length and tag type on the probabilities of survival are considered for the release to head of tide transition and the head of tide to bay array transitions ($j = 1, 2$) but not for the Gulf of St. Lawrence transition ($j = 3$). It is assumed that the tagging and handling effects associated with the size of smolt tagged and tag type are negligible for the surviving smolts migrating through the Gulf of St. Lawrence given the time required for the tagged smolts to reach the Gulf and the increased body size of the surviving smolts which would result in reduced tag burdens on the survivors.

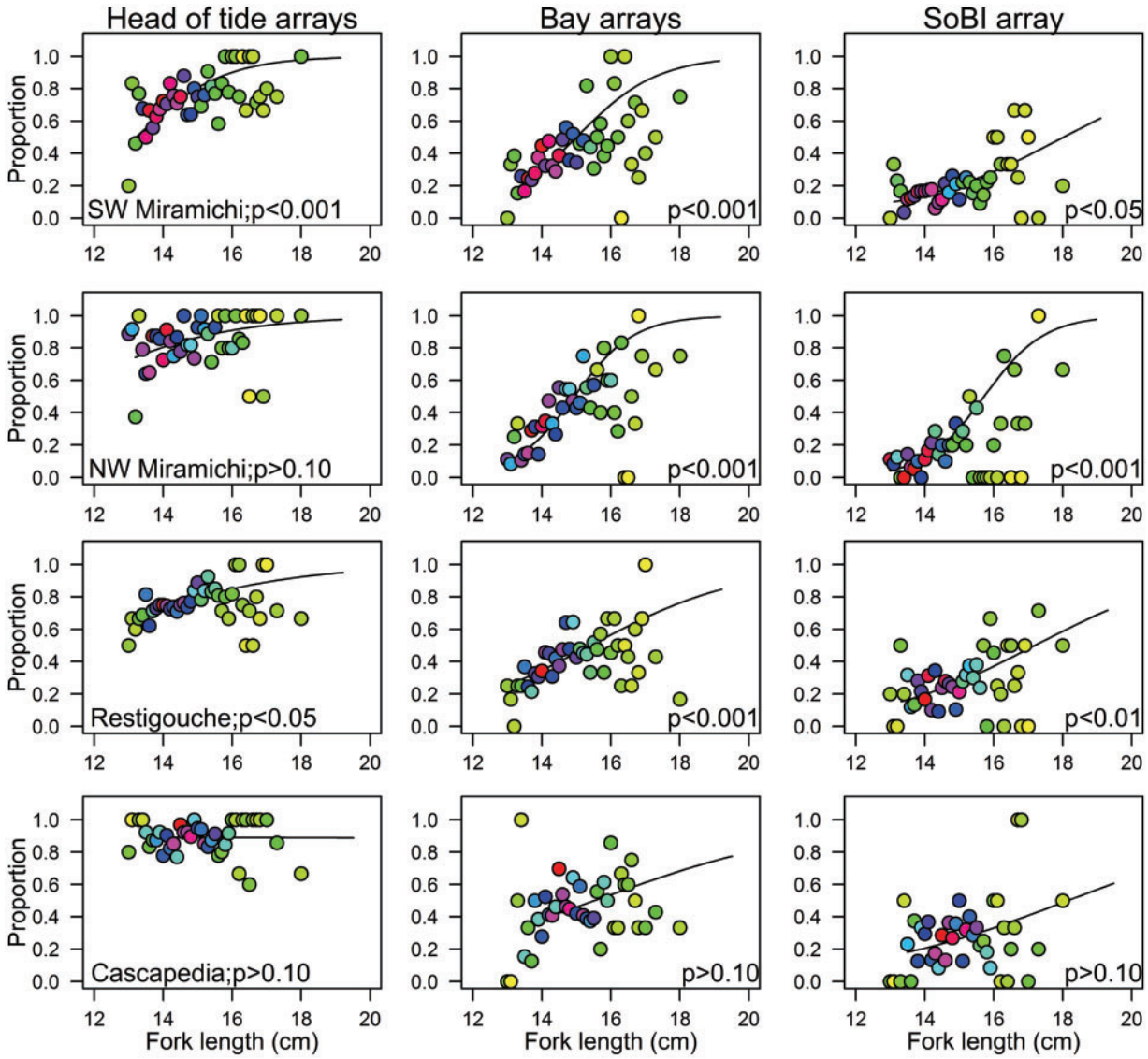

Figure 4. Proportion by fork length bin (0.1 cm) of tagged smolts detected at the head of tide lines (left column), at the bay lines (middle column), and at the primary Strait of Belle Isle line (right column) by river over all years 2003–2016. The colour of the symbol represents the relative sample size by year for each length bin with yellow (light grey) lowest and magenta (dark grey) the largest. Fork length bin 13.0 cm includes all fish of length <= 13.0 cm. Fork length bin 17.3 includes lengths of 17.1–17.5, and fork length bin 18.0 includes fish of lengths >17.5 cm. The *p*-values for the null hypothesis (Ho: slope = 0) of the logistic regressions of detected tag (binary 0, 1) vs. fork length (centred to the mean fork length of 14.6 cm over all years) are also shown in each panel.

Hierarchical structure for probability of detection (*p*)

For the head of tide arrays (p_1), the number of receivers and their placement was annually similar (exchangeable) for a location but differed among locations. The annual probabilities of detection [$\mu^p(r,t,j)$ in Equation (3)] are modelled conditional on a prior hyperdistribution for each array ($r = 1{:}4$) (Table 1). For the two bay receiver arrays (p_2), the number of receivers and their placement was annually similar but differed between the deployments at the outlet of Miramichi Bay and the outlet of Chaleur Bay to the Gulf of St. Lawrence. The annual river-specific probabilities of detection at the bay arrays are modelled as exchangeable among years and rivers within each bay; Miramichi Bay array ($b = 1$) for the Southwest Miramichi ($r = 1$) and Northwest Miramichi ($r = 2$) rivers and Chaleur Bay array ($b = 2$) for the Restigouche River ($r = 3$) and Cascapedia River ($r = 4$) (Table 1). During 2003–2006, the primary Strait of Belle Isle array was not operational and the bay arrays were the last detection point. For those years, the prior distribution for the probability of detection at each bay array is set at the respective bay-specific hyper-distribution of the probability of detections inferred from the 2007 to 2016 monitoring years.

The number of receivers and their placement at the primary Strait of Belle Isle line ($j = 3$) was generally similar during 2007–2016. The probability of detection at the primary Strait of Belle Isle is assumed to be identical among rivers ($r = 4$) and exchangeable across years (t) (Table 2). An informative prior for the mean probability of detection of the primary array is derived from an analysis of a sentinel tagging experiment conducted at the primary Strait of

Table 1. Variables, likelihoods, and priors for the observation (p; probability of detection) and the process (ϕ; probability of survival) dynamics of the hierarchical state space formulation of the Cormack–Jolly–Seber capture and recapture model.⊗ ⊗ ⊗ ⊗ ⊗

Parameter	Likelihood	Priors
Probability of detection (p)	Head of tide lines ($j=1$) $\text{logit}(p_{1,\ r,\ t}) \sim N(\mu.p_{1,r},\ \tau.p_{1,r})$ $r=1:\ 4;\ t=2003:\ 2016$	$\mu.p_{1,r} \sim N(0,\ \tau.\varepsilon_{p;\ 1,r})$ $\tau.\varepsilon_{p;\ 1,r} = 1/(\sigma.\varepsilon^2_{p;\ 1,r});\ \sigma.\varepsilon_{p;\ 1,r} = 10$ $\tau.p_{1,r} = 1/(\sigma.p_{1,r})^2;\ \sigma.p_{1,r} \sim \text{Uniform}(0,\ 10)$
	Bay lines ($j=2$) $\text{logit}(p_{2,r\|b,\ t}) \sim N(\mu.p_{2,b},\ \tau.p_{2,b})$ $r=1:\ 4;\ b=1:\ 2;\ t=2003:\ 2016$	$\mu.p_{2,b} \sim N(0,\ \tau.\varepsilon_{p;\ 2,b})$ $\tau.\varepsilon_{p;\ 2,b} = 1/(\sigma.\varepsilon^2_{p;\ 2,b})\ ;\ \sigma.\varepsilon_{p;\ 2,b} = 10$ $\tau.p_{2,b} = 1/(\sigma.p_{2,b})^2;\ \sigma.p_{2,b} \sim \text{Uniform}(0,\ 10)$
	At primary Strait of Belle Isle line ($j=3$) $\text{logit}(p_{3,\ t}) \sim N(\mu.p_3,\ \tau.p_3)$ $t=2007:\ 2016$	$\mu.p_3 = \log\left(\frac{p'_3}{1-\ p'_3}\right);\ p'_3 \sim \text{Beta}(4.4,\ 5.6)$ $\tau.p_3 = 1/(\sigma.p_3)^2;\ \sigma.p_3 \sim \text{Uniform}(0,\ 10)$
	Tag type $\beta_p \sim N(\mu.\beta_p,\ \tau.\beta_p)$	$\beta_p = 0$ $\tau.\beta_p = 1/(\sigma.\beta_p)^2;\ \sigma.\beta_p \sim \text{Uniform}(0,\ 10)$
Product (δ_4)	At secondary Strait of Belle Isle line ($j=4$) $\delta_{4,y} \sim \text{Beta}(a,b)$	$a=b=1$
Probability of survival ($\varnothing$)	To head of tide line ($j=1$) $\text{logit}(\varnothing_{1,\ r,t}) \sim N(\mu.\varnothing_{1,r},\ \tau.\varnothing_{1,r})$ $r=1:4;\ t=2003:\ 2016$	$\mu.\varnothing_{1,r} \sim N(0,\ \tau.\varepsilon_{\varnothing;\ 1,r})$ $\tau.\varepsilon_{\varnothing;\ 1,r} = 1/(\sigma.\varepsilon^2_{\varnothing;\ 1,r});\ \sigma.\varepsilon_{\varnothing;\ 1,r} = 10$ $\tau.\varnothing_{1,r} = 1/(\sigma_{1,r})^2;\ \sigma_{1,r} \sim \text{Uniform}(0,\ 10)$
	From head of tide to bay line ($j=2$) $\text{logit}(\varnothing_{2,r,\ t}) \sim N(\mu.\varnothing_{2,r},\ \tau.\varnothing_{2,r})$ $r=1:4;\ t=2003:\ 2016$	$\mu.\varnothing_{2,r} \sim N(0,\ \tau.\varepsilon_{\varnothing;\ 2,r})$ $\tau.\varepsilon_{\varnothing;\ 2,r} = 1/(\sigma.\varepsilon^2_{\varnothing;\ 2,r});\ \sigma.\varepsilon_{\varnothing;\ 2,r} = 10$ $\tau.\varnothing_{2,r} = 1/(\sigma_{2,r})^2;\ \sigma_{2,r} \sim \text{Uniform}(0,\ 10)$
	From bay line to primary Strait of Belle Isle line ($j=3$) $\text{logit}(\varnothing_{3,\ r\|b,t}) \sim N(\mu.\varnothing_{3,b},\ \tau.\varnothing_3)$ $r=1:4;\ b=1:2;\ t=2007:\ 2016$	$\mu.\varnothing_{3,b} \sim N(0,\ \tau.\varepsilon_{\varnothing;\ 3})$ $\tau.\varepsilon_{\varnothing;\ 3} = 1/(\sigma.\varepsilon^2_{\varnothing;\ 3});\ \sigma.\varepsilon_{\varnothing;\ 3} = 10$ $\tau.\varnothing_3 = 1/(\sigma_3)^2;\ \sigma_3 \sim \text{Uniform}(0,\ 10)$
	Fork length $\alpha_r \sim N(\mu.\alpha_r,\ \tau.\alpha)$ $r=1:4$	$\mu.\alpha_r = 0$ $\tau.\alpha = 1/(\sigma.\alpha)^2;\ \sigma.\alpha \sim \text{Uniform}(0,\ 10)$
	Tag type $\beta_\varnothing \sim N(\mu.\beta_\varnothing,\ \tau.\beta_\varnothing)$	$\mu.\beta_\varnothing = 0$ $\tau.\beta_\varnothing = 1/(\sigma.\beta_\varnothing)^2;\ \sigma.\beta_\varnothing \sim \text{Uniform}(0,\ 10)$

The superscript $r|b$ refers to the river (r) within a bay (b) with 1|1 the Southwest Miramichi within Miramichi Bay, 2|1 the Northwest Miramichi within Miramichi Bay, 3|2 the Restigouche River within Chaleur Bay, and 4|2 the Cascapedia River within Chaleur Bay. In all cases, σ refers to the standard deviation. For all normal distributions, the variance is expressed as precision (inverse of variance).

Belle Isle array to provide independent information on detection probabilities (Supplementary). The average detection probability to a radius of 0.5 km was estimated to be 44% and this is used to parameterize an informative but uncertain prior for the mean detection probability of the primary Strait of Belle Isle array (Table 1).

The secondary Strait of Belle Isle line ($j=4$) was installed in 2015 and 2016 to provide empirical data to estimate the detection efficiency of the primary Strait of Belle Isle array. This is the last point of detection and there is no auxiliary information on the expected value of the probability of detection. The detections at this array are modelled as conditional on the product of p_4 and ϕ_4 (δ; on the logit scale) and on a fish being alive at the primary Strait of Belle Isle array ($z(i,3)$);

$$y(i,\ 4)\ |\ z(i,\ 3), \delta_4 \sim \text{Bernoulli}(z(i,\ 3), \delta_4). \qquad (7)$$

It is assumed that δ_4 differs between years but is similar for the river origins of the smolts and an annually uninformative prior for the product is used (Table 1).

Hierarchical structure for probability of survival (ϕ)

The first transition stage (ϕ_1) encompasses the point of release ($j=0$) to the head of tide array ($j=1$) and the distance as well as the physical and biological environment of this zone differs among the four rivers. Thus, the $\mu^{\phi}(r,t,1)$ [Equation (6)] are modelled exchangeably among years (t) for each river group ($r=1{:}4$) (Table 1). The second transition stage (ϕ_2) encompasses the geographic region from the head of tide array ($j=1$) to the bay arrays ($j=2$) in Miramichi Bay and Chaleur Bay. The distance from the head of tide arrays and the physical and biological characteristics of the estuary zones also differ among the four rivers and the survival probabilities are modelled exchangeably among years (t) for each river group (r) (Table 1).

The third transition stage (Gulf of St. Lawrence) encompasses the geographic region from the exit of Miramichi and Chaleur Bays ($j=2$) to the Strait of Belle Isle array ($j=3$). There is a minimal difference in the straight-line migration distances between the bay arrays and the Strait of Belle Isle array but there are important differences in the observed migration durations with tagged smolts from

Table 2. Summary of migration characteristics (median and 5th to 95th percentile range for all smolts and years) and survival rates (range of median values as % and based on median migration days expressed as % day^{-1}) of acoustically tagged Atlantic salmon smolts from four rivers in the Gulf of St. Lawrence.

Transition	River	Distance	Migration (days)	Migration (km day^{-1})	Survival (%)	Survival (% day^{-1})
Release to head of tide array	Southwest Miramichi	127	5.2; 2.1–11.3	27; 12–65	62–92	93–98
	Northwest Miramichi	30; 52	2.9; 0.8–7.7	10; 4–37	90–91	93–98
	Restigouche	115	4.4; 2.3–10.6	26; 11–50	73–93	96–98
	Cascapedia	8	1.2; 0.2–4.2	6; 2–36	93–97	82–97
Head of tide to bay array	Southwest Miramichi	68	3.6; 2.2–7.9	19; 9–31	42–82	83–97
	Northwest Miramichi	67	4.6; 2.6–10.2	15; 7–26	28–74	78–93
	Restigouche	106	7.4; 4.2–13.7	14; 8–25	67–95	96–99
	Cascapedia	47	8.0; 3.7–18.5	6; 3–13	68–90	93–99
Bay array to primary Strait of Belle Isle array	Southwest Miramichi	~800	48.4; 31.7–53.7	17; 15–25	54–64	98–99
	Northwest Miramichi		46.2; 35.2–51.5	17; 16–23	60–68	99–99
	Restigouche		40.2; 29.8–49.3	20; 16–27	35–74	96–99
	Cascapedia		36.1; 21.9–47.9	22; 17–37	27–78	97–99

the Miramichi River locations taking longer to transit the Gulf of St. Lawrence than smolts from the Chaleur Bay rivers (Table 2; Supplementary Table S3). The probabilities of survival are modelled exchangeably among years by bay specific group, Miramichi Bay rivers and Chaleur Bay rivers (Table 1).

Odds ratios of survival probabilities associated with the size of smolt at tagging are calculated as the predicted survival of a 16 cm smolt relative to the predicted survival of a 13.5 cm smolt. Survival rates by transition zone for a smolt of fork length corresponding to the mean length smolts in the study (14.6 cm), are presented as well as the survival rates per median day at large in each zone ($\phi^{1/d}$). Uncertainties in the estimates of the probabilities of detection and survival are described by the coefficient of variation, corrected for the logit transformation.

Model fitting and assessing convergence

The hierarchical state-space CJS model was fit to smolt tagging data from the four rivers for the years 2003–2016, representing 2 862 observations, using the freely available software package OpenBUGS (Lunn *et al.*, 2013). A total of 60 000 Markov chain Monte Carlo (MCMC) simulations with two chains was used, the first 50 000 were discarded and the remaining 10 000 samples were thinned by 10 to produce 2 000 MCMC values to summarize the posterior distributions. We assessed whether there was evidence of non-convergence by examining trace plots of the MCMC chains, by checking that the Gelman–Rubin r-hat statistics were < 1.1, and by examining for unimodal distributions of the model parameters (Brooks and Gelman, 1998). The diagnostics examined did not suggest any non-convergence.

We examined a number but not all possible combinations of parameters and model structures for detection and survival. Adequacy of the model was assessed by predicting detections at the three array locations based on the posterior distributions of p and ϕ (Supplementary Table S4 and Figures 3S–S10). By design, we favoured a hierarchical structure for the probabilities of detection to make use of the data from the entire time series of the study. The alternative of assuming a constant probability of detection over years at each of the arrays was not realistic given the empirical observations to the contrary, and all the model variants that assumed a constant probability of detection over years resulted in higher residual deviances and poor fits. Independent and hierarchical structures were examined for the probability of survival with and without individual effects associated with size of smolts and tag type (Supplementary Table S4).

When discussed, statistical significance corresponds to a p-value $<= 0.05$. For the individual effects parameters, the p-values are calculated as the smallest proportion of the MCMC values drawn from the marginal posterior distribution that overlap zero.

Results

During 2003–2016, a total of 2 862 Atlantic salmon smolts from four rivers were tagged with acoustic transmitters. A total of 2 243 of these tags, 78% of releases, were subsequently detected at receiver arrays located at or near the head of tide (Figure 3; Supplementary Table S2). A total of 1 160 tags, 41% of released fish, were subsequently detected at the bay receiver arrays. Finally, 487 tags, 17% of released fish for the corresponding years, were detected at the primary Strait of Belle Isle array, almost 2 months and more than 800 km away from their release locations. In 2015 and 2016, 119 tags were detected at the secondary Strait of Belle Isle array, representing 23% of the tagged smolts released, similar to 122 tags detected at the primary Strait of Belle Isle array for the same years. During 2010–2016, only two tags placed in smolts were detected at the Cabot Strait line (Ocean Tracking Network, unpublished data) suggesting that the Strait of Belle Isle is the primary migration route for smolts from the rivers in this study leaving the Gulf of St. Lawrence.

Migration summaries

Tagged smolts from the Cascapedia River had the shortest freshwater distance from release to the head of tide (8 km) and were generally detected within 2 days post-release (Table 2; Supplementary Table S3). In contrast, smolts from the Southwest Miramichi had the longest migration distance to the head of tide (127 km) and most fish were detected at the head of tide 2–11 days post release. Tagged smolts from the Southwest Miramichi River and the Restigouche River had the fastest migration rates in freshwater at a median over years of 27 km day^{-1} and 26 km day^{-1}, respectively (Table 2). The median migration rate of tagged smolts in the Northwest Miramichi was 10 km day^{-1} and the slowest migration rate was estimated for the Cascapedia smolts at 6 km day^{-1} (Table 2).

Migration rates of tagged smolts through the bays were highest for the Southwest Miramichi (19 km day^{-1}), relatively similar for

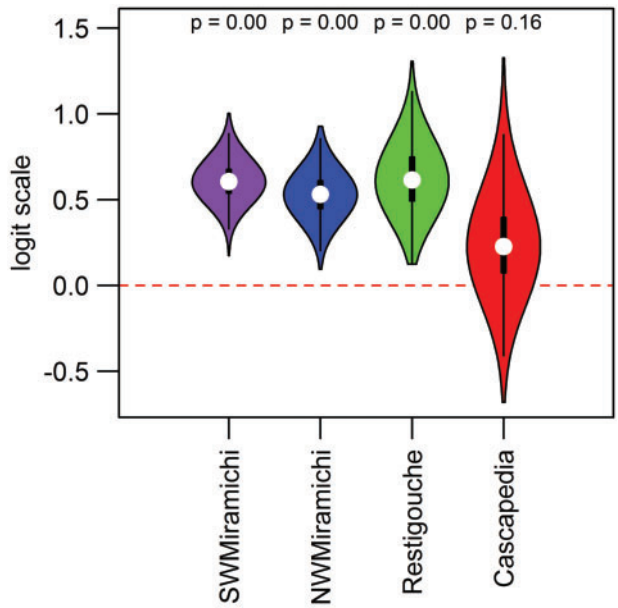

Figure 5. Posterior distributions of the fork length individual effects (logit scale) on the probability of survival through the freshwater and bay zones for each river. Violin plots summarize the kernel densities of the distributions and show the median (open symbol), interquartile range (thick line), and the range of 95% of the observations (thin line).

the Northwest Miramichi and Restigouche River groups (15 km day^{-1} and 14 km day^{-1}, respectively), and slowest for the Cascapedia River smolts (6 km day^{-1}; Table 2). In contrast to the differences in migration rates through Chaleur Bay, the days from release to detection at the Chaleur Bay arrays were more similar for the Restigouche (7 days) and Cascapedia (8 days) smolts, indicating that the Cascapedia smolts which had a very short freshwater phase post-release lingered longer in brackish and saltwater compared to the Restigouche smolts before exiting the bay (Table 2). These differences in migration duration between rivers within the same bay may reflect an acclimation period associated with tagging and handling.

The migration duration through the Gulf of St. Lawrence varied from just over 20 days to just under 65 days (Table 2; Supplementary Table S3). Migration duration was generally the longest for the Southwest Miramichi smolts at 48 days (median), and the shortest but most variable for the Cascapedia smolts at 36 days (Table 2). Detections of acoustic tags at the Strait of Belle Isle from the four rivers were synchronized among the four rivers with detections across all years (2007–2016) and rivers occurring during a relatively narrow 4-week period of late June to late July (Supplementary Figure S2). Migration rates through the Gulf of St. Lawrence were in the range of 17–22 km day^{-1} (median over all rivers and years) with the fastest median migration rate for the Cascapedia and Restigouche smolts (22 and 20 km day^{-1}, respectively) and the slower rates for the Northwest Miramichi and Southwest Miramichi smolts (17 km day^{-1}; Table 2).

Individual—tag type and fork length

There was no statistically significant ($p = 0.36$) difference in the probabilities of detection associated with the tag type used. Tag type was also not a statistically significant covariate ($p = 0.12$) for survival when included as an interaction term with fork length (Supplementary Figure S8c). Statistically significant ($p < 0.05$) positive associations of fork length on probability of survival were estimated for three of the four rivers; the exception being the Cascapedia River ($p = 0.16$) (Figure 5). Based on the median of the marginal posterior distribution of the fork length coefficient, the odds ratio of survival for a smolt of 16 cm fork relative to a smolt of 13.5 fork length was in the range of 1.51–1.74.

Estimated probabilities of detection

The estimated probabilities of detection at the head of tide receiver lines were generally high (often >90%) with few exceptions such as for the Northwest Miramichi in 2006 (<40%) and for the Restigouche in 2011 (~50%) (Figure 6). The uncertainties (coefficient of variation on the inverse logit scale) in the annual probabilities of detection at the head of tide array were most consistent for the Southwest Miramichi, Cascapedia, and Restigouche Rivers (0.1–11.1%) and most variable for the Northwest Miramichi River (0.1–32.4%).

The estimated probabilities of detection were higher at the Miramichi Bay line compared to the Chaleur Bay line, with median posterior values across years of 83 vs. 56%, respectively (Figure 6). The uncertainties in the annual probabilities of detection were higher at the bay arrays compared to the head of tide arrays, with annual CVs by river ranging from 7.3 to 31.9%.

The probabilities of detection of the primary Strait of Belle Isle line varied annually from a low of 42% in 2006 (median value; very similar to the prior) to a high of just over 67% in 2010 and in 2015 (Figure 6). The median of the estimates for 2015 and 2016 derived from the detections at the twinned line were 67 and 64%, respectively. The uncertainties in the annual estimates of the probability of detection ranged from 8.6 to 30.4% with CV values in 2015 and 2016 of 8.7 and 8.6%, respectively.

Estimated probabilities of survival

The posterior distributions of the estimated probabilities of survival in freshwater, in the estuary, and in the Gulf of St. Lawrence, standardized to the mean fork length (14.6 cm) of smolts from all rivers and years, are shown in Figure 7. The probabilities of survival in freshwater were highest (median 96%) and relatively similar (median range 93–97%) over years for the Cascapedia River, slightly lower (90%) for the Northwest Miramichi River and lowest for the Restigouche (median values 73–93%) and Southwest Miramichi (range of medians 62–92%) rivers which had the longest distance and migration duration to head of tide (Figure 7; Table 2). Survival estimates from release to the head of tide were generally high and greater than 90% day^{-1} for all rivers and years (Table 2). The uncertainties in the annual estimates of survival were lowest for the Cascapedia and the Northwest Miramichi Rivers (annual CV range of 2.3–4.4%), in contrast to the Southwest Miramichi and Restigouche rivers with annual CV ranges of 2.7–10.6%, respectively.

The estimated probabilities of survival of tagged smolts transiting Chaleur Bay were higher (annual medians ranging from 67 to 95%, 93 to 99% day^{-1}) than for smolts transiting Miramichi Bay (annual medians ranging from 28 to 82%, 78 to 97% day^{-1}) (Figure 7; Table 2). The lowest estimated survivals of any rivers and years were for smolts from the Northwest Miramichi River during 2013–2016 (medians ranging from 28 to 45%; Figure 7). Survival rates of smolts migrating through Miramichi Bay were higher during 2006–2008

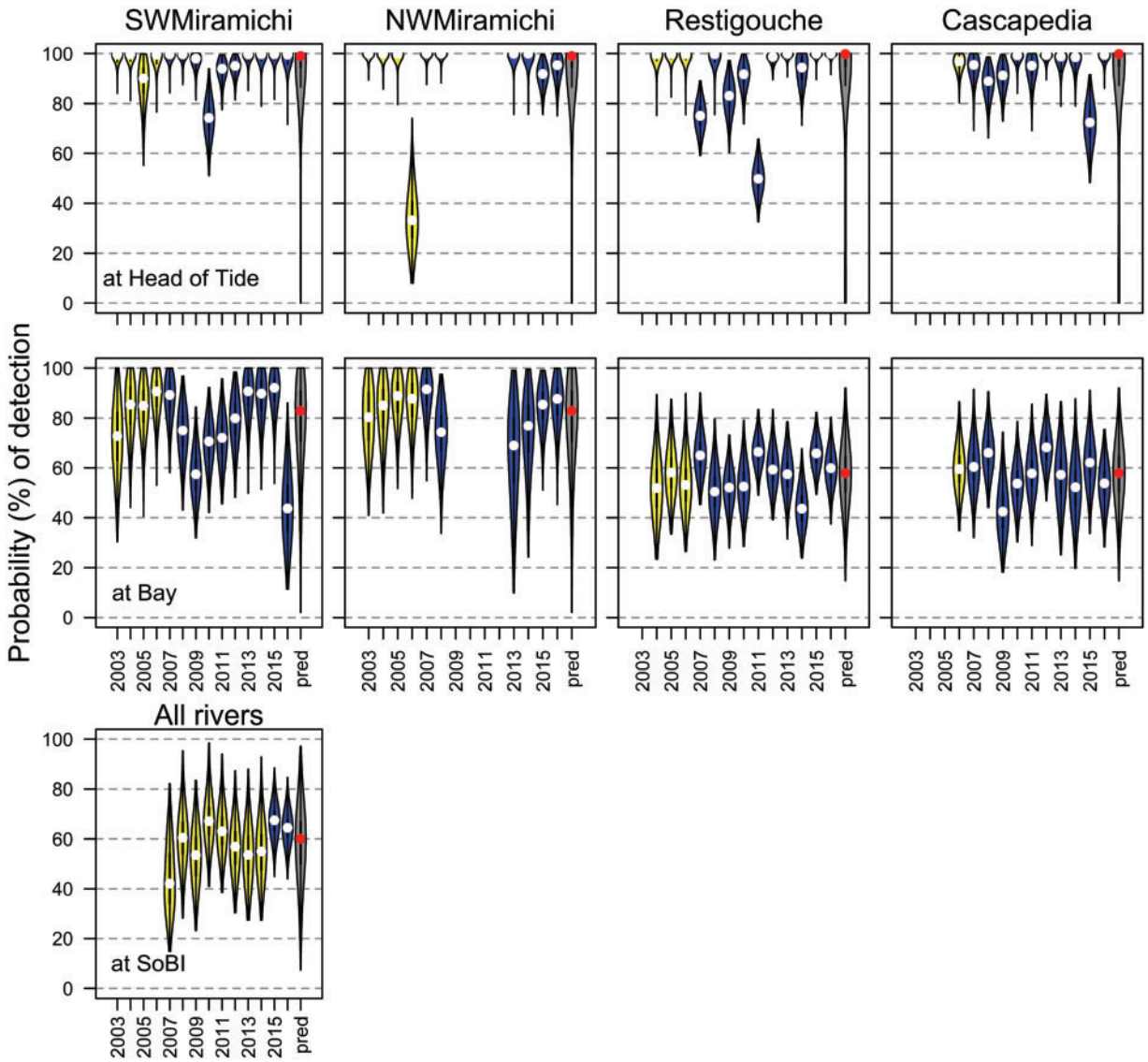

Figure 6. Violin plots of posterior distributions of the probability of detection by river at the head of tide lines (upper row), at the bay lines (middle row), and by year (all rivers) at the primary Strait of Belle Isle line (lower row), 2003–2016. The open symbol is the median of the posterior distribution. For the bay lines, the violin plots in blue are for the years (2007–2016) when the primary Strait of Belle Isle line was operational. For the Strait of Belle Isle line, the violin plots in blue correspond to the years when the secondary twinned line was operational (2015 and 2016). The results are for Model variant 11 g in Supplementary. In all panels, the grey shadings are the posterior distributions of the predicted probabilities of detection over all years for the corresponding spatial hierarchical structure (Table 1).

(91–94% day^{-1} for Southwest Miramichi; 90–91% day^{-1} for Northwest Miramichi) than during the last 4 years of the study (2013–2016; 83–90% day^{-1} for Southwest Miramichi; 78–91% day^{-1} for Northwest Miramichi). This contrasts with survival rates through Chaleur Bay that remained high with no evidence of declines over the same periods (Figure 7). Uncertainties (CV) in the annual estimated probabilities of survival were greatest for the Northwest Miramichi River, ranging from 17 to 43%.

With few exceptions (Restigouche River in 2007–2009, Cascapedia River in 2008), the median estimated survival rates of tagged smolts through the Gulf of St. Lawrence were between 45 and 78% (Figure 7), 96–99% day^{-1} (Table 2). Estimates of survival rates through the Gulf of St. Lawrence were the most uncertain of all the transition zones, with annual CVs ranging from 13 to 45%.

Discussion

The objectives of this study were to characterize the early phase migration and to gain insights into the location and timing of smolt and post-smolt mortality of wild Atlantic salmon smolts and post-smolts from unimpacted (free fish passage) rivers in eastern Canada. Atlantic salmon smolts and post-smolts were successfully detected using acoustic telemetry during the initial 50+ days post migration from freshwater, through estuaries and nearshore bays and to distances exceeding 900 km at sea from the point of release in freshwater.

In this study, we refer for convenience to the estimation of survival of smolts and post-smolts when what is in fact being estimated is the probability of detecting a tag that has been deployed

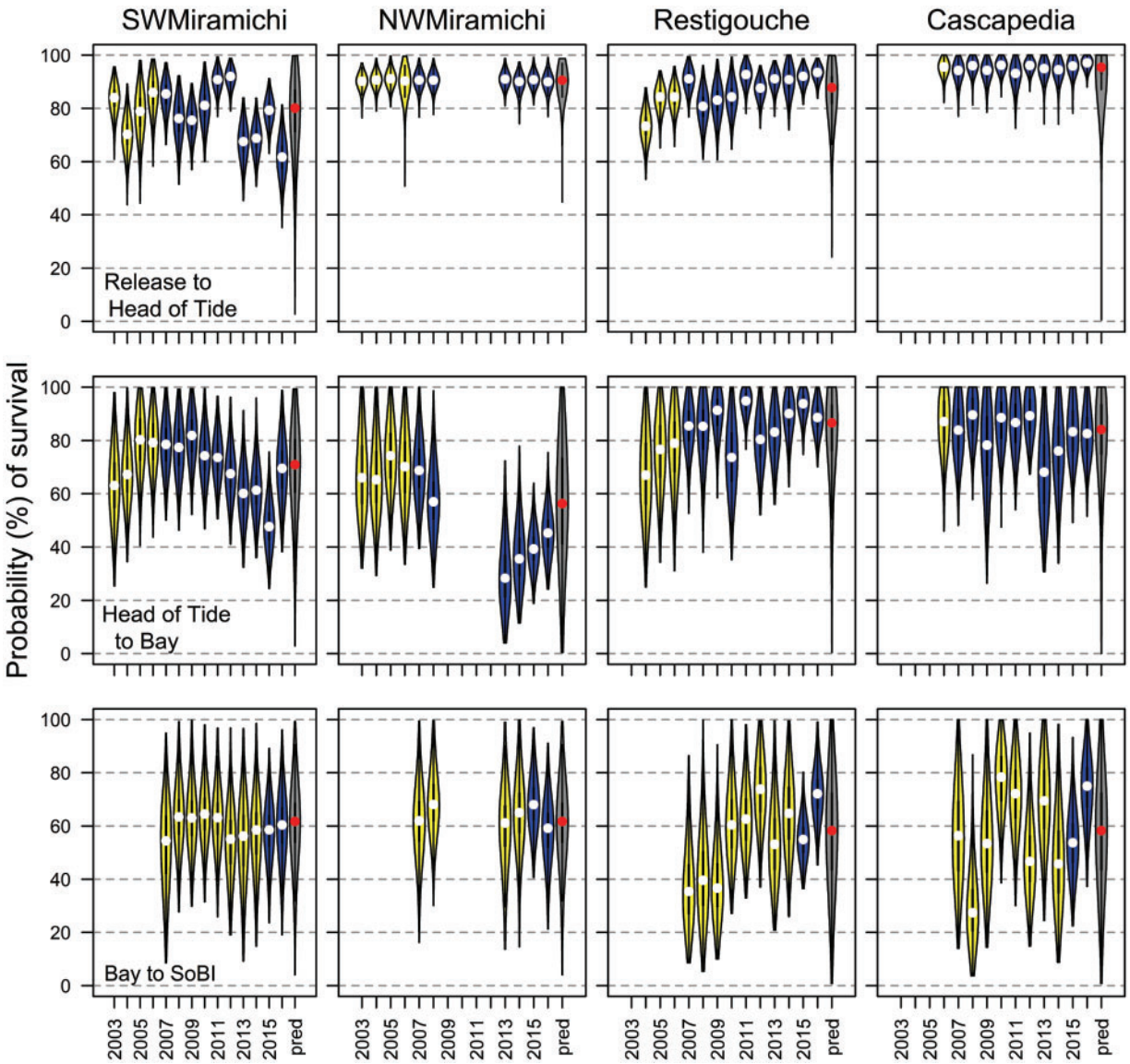

Figure 7. Violin plots of posterior distributions of probability of survival for a smolt of centred length 14.6 cm to the head of tide lines (upper row), from the head of tide to the bay lines (middle row), and from the bay lines to the primary Strait of Belle Isle line (lower row), for the four rivers, 2003–2016. For the survivals through the bays, the violin plots in blue are the probabilities of survival estimated for the years when the primary Strait of Belle Isle line was operational (2007–2016). For the survivals through the Gulf of St. Lawrence, the violin plots in blue are the years when the secondary twinned line was operational (2015 and 2016). In all panels, the grey shadings are the posterior distributions of the predicted probabilities of survival over all years for the corresponding spatial hierarchical structure (Table 1).

in a fish, conditional on the tag being retained in the fish, the fish with the tag moving within range of the receivers and a tag transmission being detected by a receiver. Within the model in this study, the observations represent the last component of this dynamic (probability of a tag transmission being detected by a receiver) whereas what we referred to as survival represents the other components; that an implanted tag is retained in a fish and the tag within the fish migrates downstream within the range of receivers, more correctly termed apparent survival.

Location and timing of mortality

The main interest of this study was to estimate population level smolt and post-smolt survivals. Survival rates through the freshwater stage were generally high (>90%) for the fish released less than 30 km from the head of tide but lower (60–90%), annually variable and negatively associated with the migration distance or the time from release to detection for the two rivers (Southwest Miramichi and Restigouche) with a longer freshwater migration distance. Variable but generally high survival rates (ranging from 70 to 100%) of acoustically tagged smolts over variable migration distances in freshwater zones (2–53 km) have been reported in other studies (Lacroix, 2008; Halfyard *et al.*, 2012; Lefèvre *et al.*, 2013; Gibson *et al.*, 2015; Crossin *et al.*, 2016; Hawkes *et al.*, 2017). The exception to this was reported for smolts in the Penobscot River for which survival rates through freshwater zones were much lower (mean cumulative survival of 47%) and attributed to the effects of passage at hydro facilities (Stich *et al.*, 2015).

Survival rates through estuaries and coastal bays were lower than in freshwater areas, highly variable among years and contrasted among bays. Comparisons across studies of survival estimates through estuaries, bays, or nearshore coastal environments are more difficult in large part because of physical differences in the dynamic and geographically diverse habitats transited by salmon in the species range in eastern North America. In this study, the two areas monitored differ in coastal structure, water chemistry and passage routes, with the Miramichi being a semi-enclosed bay with constrained passage into the Gulf of St. Lawrence in contrast to the wide and open Chaleur Bay. Dempson *et al.* (2011) monitored tagged smolt movements in a geographically complex fjord, island and channel habitat, similar to the complex nearshore area traversed by tagged smolts in the study by Stich *et al.* (2015) and Hawkes *et al.* (2017). The study area in Halfyard *et al.* (2013) consisted of geographically complex areas with diverse estuaries and bays and extended estuary areas whereas in the study area of Lefèvre *et al.* (2013) the river opened almost directly into the Gulf of St. Lawrence with no estuary or inner bay component. Survival rates through these diverse areas are highly variable, with values of 54–87% for the Conne River study (Dempson *et al.*, 2011), 39–74% for smolts for the Atlantic coast of Nova Scotia (Halfyard *et al.*, 2012), and much lower survivals, <50%, for two southern stocks (Kocik *et al.*, 2009; Hawkes *et al.*, 2017). Survival rates per day in these near coastal areas are highly variable but compared to the freshwater phase of the migration, the survival rates are lower in the estuary/bay areas (see studies above).

Once the smolts leave the coastal bays, inferred apparent survival rates as post-smolts through the Gulf of St. Lawrence were in the range of 28–78% with survivals rates exceeding 96–99% day^{-1} for all rivers and years. Survival rates of tagged smolts, expressed as rates per day, are lowest in the estuary portions and highest during the migration through the Gulf of St. Lawrence, which is consistent with mortality being highest on small fish at first entry to the sea and declining as fish grow and move offshore (Thorstad *et al.*, 2012).

The spatial and temporal differences in apparent survival rates from our study in two neighbouring coastal areas, and between two rivers within one basin over two time periods, may in part be related to both physico-chemical and biotic differences. Although we present the temporal trend in survival rates of Northwest Miramichi smolts as a contiguous series, the fish tagged during 2003–2008 were taken from a different branch of the Northwest Miramichi than those tagged in 2013–2016 with the smolts from the latter period captured downstream and released again above a tributary (Tomogonops River) impacted by acid and metal runoff from a decommissioned base metal mine (St-Hilaire and Caissie, 2001). There are concerns for Atlantic salmon smolt vulnerability to episodic acidification and elevated concentrations of bioavailable aluminum during spring snow melt and increased runoff (Kroglund *et al.*, 2008; Kelly *et al.*, 2015). Thorstad *et al.* (2013) reported on delayed mortality in the early period of marine migration of smolts exposed to aluminum and moderate acidification in freshwater. This cannot be excluded as a factor contributing to the lower apparent survival rates in the Northwest Miramichi smolts in the latter part of the time series as well as a factor contributing to differences between the Miramichi Bay and the Chaleur Bay rivers.

There is also an important biotic difference in the estuarine environments of Miramichi Bay and Chaleur Bay. The upper portion of the Northwest Miramichi estuary is the only confirmed spawning location of striped bass (*Morone saxatilis*) in the southern Gulf of St. Lawrence and the spawning period overlaps in timing with the downstream smolt migration. Atlantic salmon smolts have been identified in stomachs of striped bass sampled from the Miramichi (DFO, 2016). Furthermore, Daniels *et al.* (2018) report on inferred predation rates of striped bass on salmon smolts from the Miramichi based on contrasting movement patterns of acoustically tagged animals. The inferred predation rates ranged from 2 to 18%, between stocks and years, with annual variations in the spatial and temporal overlap of the two species likely contributing to the differences in the inferred predation rates.

Finally, we cannot exclude the possibility that the differences in estimated survival rates between bays and over years in this study are also in part due to differences in the size distributions of acoustically tagged smolts among years and rivers. A weight of evidence analysis of factors contributing to variations in apparent survival rates is beyond the scope of this paper however the data from this 14-year study would be appropriate for testing these hypotheses.

Limitations of study and results

Modelled estimates of apparent survival of acoustically tagged and tracked smolts can be biased. Survival estimates can be biased downward if the tag is not retained by the fish and the fish survives and migrates past the receiver arrays. There is evidence from literature that implanted tags can be expelled from the body cavity without resulting in death of the fish, and the probability of expulsion was related to the ratio of tag size to fish size (Lacroix *et al.*, 2004; Welch *et al.*, 2007; Sandstrom *et al.*, 2013). Expulsion of larger tags (24 mm length by 8 mm diameter) was noted but Lacroix *et al.* (2004) indicated that the 24 mm tags were the only tags, which were retained by some fish during the 316-day duration of the experiment. In the study by Welch *et al.* (2007), tag expulsion of 24 mm by 8 mm tags generally occurred after 4 weeks post-surgery. Based on these studies, tag shedding in this study was not considered to be a factor that would bias the estimation of apparent survivals since the smolts had migrated through the bays within 2 weeks or less in most cases.

However, it is assumed that a tag detection at a receiver line is from a tag in a salmon smolt rather than in the stomach of a predator swimming by the receiver. If the predation event occurred upstream of the bay array, then some of the detections at the bay arrays could be of tags in predator stomachs rather than smolts and in such cases, the inferred survival rate of tagged smolts to the bay arrays would be overestimated; consequently the survival rate through the Gulf of St. Lawrence would be underestimated.

One important factor that can affect the exchangeability assumption of survival in the hierarchical model used in this study is the size of the smolts tagged. Sizes of smolts used in the experiments varied annually and differed among rivers. Other studies have reported on correlations between tagging effects (survival) and smolt size (Lacroix *et al.*, 2004; Welch *et al.*, 2007; Halfyard *et al.*, 2013). Lacroix *et al.* (2004) recommended a transmitter length of 16% or less of fish length for telemetry studies. The V9 tags used in this study measured 21 mm in length, and based on criteria of Lacroix *et al.* (2004) could be placed in smolts 13.1 cm or longer. There were very few smolts in this study that did not meet this minimum size, representing <2% of smolts over all rivers and years and less than 6% of smolts from the Northwest Miramichi.

Relevance of inferences from tagged smolts to untagged smolts

An important concern regarding the use of marked animals to make inferences on behaviour and survival of unmarked/unhandled animals is the consequence of tagging and handling effects on the estimates of survival or migration dynamics. It is extremely difficult to make the case that a tagged smolt would behave and have the same mean probability of survival as an untagged smolt. In terms of absolute levels, it is unlikely that the estimates derived from marked animals correspond to those of unmarked animals (Riley *et al.*, 2018). There can be important growth and survival effects of handling and tagging even when animals are held in captivity post tagging (Moore *et al.*, 1990; Lacroix *et al.*, 2004; Welch *et al.*, 2007; Ammann *et al.*, 2013) and monitoring tagged fish in captivity does not provide much insight into the conditions encountered by fish released to the wild. The capture, handling, tagging procedures in addition to introducing stress and injury to individual animals (Ammann *et al.*, 2013) also interrupt the migration phenology of wild smolts during a particularly sensitive period (Riley *et al.*, 2007). Removal from schooling with conspecifics, release back to the river during the day or even near dusk when wild conspecifics are sheltering and not in active migration phase, can result in increased vulnerability to predation (Furey *et al.*, 2016). There is evidence from this study that acoustically tagged Atlantic salmon smolts less than 14 cm fork length suffered a higher mortality than smolts of greater size and this could be an effect of stress from tagging and handling and correlated with the tag/body size ratio. In two rivers (Southwest Miramichi, Restigouche), estimated apparent survival rates to the head of tide receivers after correcting for size, are negatively associated with the migration duration, which can be interpreted as a delayed mortality from handling and tagging and an increased vulnerability to predation. For the Cascapedia smolts for which there is a very short freshwater migration distance and time from release to the head of tide, the smolts had a prolonged migration duration through Chaleur Bay compared to Restigouche River smolts suggesting that there may have been a period of acclimation in the bay specifically for the Cascapedia smolts.

Estimating apparent survival rates at the further migration points and times is also challenging. As fish die over time, there are fewer tagged fish available with which to estimate detection and survival probabilities. This has consequences on the uncertainty of the estimates, as evidenced from the higher coefficient of variations of the estimates of the detection and apparent survival probabilities at the bay and the Strait of Belle Isle arrays. Increased sample sizes of tagged fish from a single stock could be considered, as was the case for the Restigouche River, by tagging multiple stocks that share a common bay exit, or multiple stocks that share a common exit to the Labrador Sea. The probability of detection at receiver lines can only be inferred if there are tags, which are detected at a "downstream" array (along the migration route, or temporally). At the last detection array only the product of the survival and detection can be inferred (Gimenez *et al.*, 2007; Royle, 2008). The use of auxiliary data such as sentinel tags to independently inform on detection rates is required if survival rates to the last array are to be estimated. Auxiliary data from sentinel tags are best incorporated in the model as prior information. When the last array is twinned, as was done for the Strait of Belle Isle line in 2015 and 2016, the detection probabilities of the next to last array can be estimated from observations, i.e. the prior for the primary Strait of Belle Isle line is updated with observations. In this study, the prior probability of detection based on sentinel tags was strongly updated by the empirical observations of the secondary twinned line at the exit to the Labrador Sea.

Insights into the factors that modify the variation in survival rates within particular areas of the smolt and post-smolt migration require experiments to be conducted over multiple years and populations (Thorstad *et al.*, 2012). The multi-year and multi-river aspects of this study provided particular advantages to describing and modelling smolt migrations and estimating survival rates that otherwise would not be possible from single year and single river experiments. The observations in this study can be effectively modelled using a hierarchical structure and such a model provides a means of using all the information even in years when the full monitoring infrastructure is not in place.

In long-term studies, it is imperative that the methods and experimental design be standardized to ensure that the empirical observations reflect to the extent possible, the variations in the phenomenon of interest, rather than a consequence of differences in methodologies, experimental design, or technologies. In the study reported here on estimating survival rates of Atlantic salmon smolts from four rivers over 14 years, factors that could be standardized include the tag type, the size distribution of smolts being tagged, the tag implantation procedures and the placement of the receiver arrays. By standardizing these elements of the study, the individual river experiments are more likely to be exchangeable and by using hierarchical models, the inferences on the parameters of interest less uncertain.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

References

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

Beaugrand, G., and Reid, P. C. 2003. Long term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology, 9: 801–817.

Beaugrand, G., and Reid, P. C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. ICES Journal of Marine Science, 69: 1549–1562.

Bonner, S. J., and Schwarz, C. J. 2006. An extension of the Cormack–Jolly–Seber model for continuous covariates with application to *Microtus pennsylvanicus*. Biometrics, 62: 142–149.

Brooks, S. P., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics, 7: 434–455.

Chaput, G. J., and Jones, R. A. 2004. Catches of downstream migrating fish in fast-flowing rivers using rotary screw traps. Canadian Manuscript Report of Fisheries and Aquatic Sciences, 2688: v + 14 pp.

Chaput, G., Legault, C. M., Reddin, D. G., Caron, F., and Amiro, P. G. 2005. Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. ICES Journal of Marine Science, 62: 131–143.

Chiasson, A. 1995. The Miramichi bay and estuary: an overview. *In* Water, Science and the Public: The Miramichi Ecosystem, pp. 11–28. Ed. by E. M. P. Chadwick. Canadian Special Publication of Fisheries and Aquatic Sciences, 123: 300.

Crossin, G. T., Hatcher, B. G., Denny, S., Whoriskey, K., Orr, M., Penney, A., and Whoriskey, F. G. 2016. Condition-dependent migratory behaviour of endangered Atlantic salmon smolts moving through an inland sea. Conservation Physiology, 4: cow018.

Daniels, J., Chaput, G., and Carr, J. 2018. Estimating consumption rate of Atlantic Salmon smolts (*Salmo salar*) by Striped Bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. Canadian Journal of Fisheries and Aquatic Sciences, 1. https://doi.org/10.1139/cjfas-2017–0373.

Dempson, J. B., Robertson, M. J., Pennell, C. J., Furey, G., Bloom, M., Shears, M., Ollerhead, L. M. N., *et al.* 2011. Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. Journal of Fish Biology, 78: 1976–1992.

DFO. 2016. Spawner abundance and biological characteristics of Striped Bass (*Morone saxatilis*) in the southern Gulf of St. Lawrence in 2015. DFO Canadian Science Advisory Secretariat Science Response, 2016/017.

DFO. 2017. Oceanographic conditions in the Atlantic zone in 2016. DFO Canadian Science Advisory Secretariat Science Advisory Report, 2017/031.

Drenner, S. M., Clark, T. D., Whitney, C. K., Martins, E., Cooke, S. J., and Hinch, S. G. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLoS One, 7: e31311.

Friedland, K. D., Hansen, L. P., Dunkley, D. A., and MacLean, J. C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. ICES Journal of Marine Science, 57: 419–429.

Furey, N. B., Hinch, S. G., Bass, A. L., Middleton, C. T., Minke-Martin, V., and Lotto, A. G. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. Journal of Animal Ecology, 85: 948–959.

Gelman, A., Carlin, J. B., Stern, H. S., and Rubin, D. B. 2004. Bayesian Data Analysis, 2nd edn. Chapman & Hall/CRC, Boca Raton, Florida. 668 pp.

Gibson, A. J. F., Halfyard, E. A., Bradford, R. G., Stokesbury, M. J. W., and Redden, A. M. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. Canadian Journal of Fisheries and Aquatic Sciences, 72: 728–741.

Gimenez, O., Rossi, V., Choquet, R., Dehais, C., Doris, B., Varella, H., Vila, J.-P., *et al.* 2007. State-space modelling of data on marked individuals. Ecological Modelling, 206: 431–438.

Goulette, G. S., Hawkes, J. P., Kocik, J. K., Manning, J. P., Music, P. A., Walling, J. P., and Zydlewski, G. B. 2014. Opportunistic acoustic telemetry platforms: benefits of Collaboration in the Gulf of Maine. Fisheries, 39: 441–450.

Halfyard, E. A., Gibson, A. J. F., Ruzzante, D. E., Stokesbury, M. J. W., and Whoriskey, F. W. 2012. Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. Journal of Fish Biology, 81: 1626–1645.

Halfyard, E. A., Gibson, A. J. F., Stokesbury, M. J. W., Ruzzante, D. E., and Whoriskey, F. W. 2013. Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland, Nova Scotia, Canada. Canadian Journal of Fisheries and Aquatic Sciences, 70: 452–460.

Hawkes, J. P., Sheehan, T. F., and Stich, D. S. 2017. Assessment of early migration dynamics of river-specific hatchery Atlantic salmon smolts. Transactions of the American Fisheries Society, 146: 1279–1290.

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., *et al.* 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science, 348: 1255642.

ICES. 2017. Report of the Working Group on North Atlantic Salmon (WGNAS), 29 March–7 April 2017, Copenhagen, Denmark. ICES CM 2017/ACOM: 20: 296 pp.

Kelly, J. T., Lerner, D. T., O'Dea, M. F., Regish, A. M., Monette, M. Y., Hawkes, J. P., Nislow, K. H., *et al.* 2015. Evidence for episodic acidification effects on migrating Atlantic salmon *Salmo salar* smolts. Journal of Fish Biology, 87: 1129–1146.

Kilduff, D. P., Di Lorenzo, E., Botsford, L. W., and Teo, S. L. H. 2015. Changing central Pacific El Niños reduce stability of North American salmon survival rates. Proceedings of the National Academy of Sciences of the United States of America, 112: 10962–10966.

Kocik, J. F., Hawkes, J. P., Sheehan, T. F., Music, P. A., and Beland, K. F. 2009. Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the Narraguagus River, Maine using ultrasonic telemetry. American Fisheries Society Symposium, 69: 293–310.

Koutitonsky, V. G., and Bugden, G. L. 1991. The physical oceanography of the Gulf of St. Lawrence: a review with emphasis on the synoptic variability of the motion, *In* The Gulf of St. Lawrence: Small Ocean or Big Estuary? pp. 57–90. Ed. by J.-C. Therriault. Canadian Special Publication of Fisheries and Aquatic Sciences, 113: 359.

Kroglund, F., Rosseland, B. O., Teien, H.-C., Salbu, B., Kristensen, T., and Finstad, B. 2008. Water quality limits for Atlantic salmon (*Salmo salar* L.) exposed to short term reductions in pH and increased aluminum simulating episodes. Hydrology and Earth System Sciences, 12: 491–507.

Lacroix, G. L., Knox, D., and McCurdy, P. 2004. Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Transactions of the American Fisheries Society, 133: 211–220.

Lacroix, G. L. 2008. Influence of origin on migration and survival of Atlantic Salmon (*Salmo salar*) in the Bay of Fundy, Canada. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2063–2079.

Lefèvre, M. A., Stokesbury, M. J. W., Whoriskey, F. G., and Dadswell, M. J. 2013. Migration of Atlantic salmon smolts and post-smolts in the Rivière Saint-Jean, QC north shore from riverine to marine ecosystems. Environmental Biology of Fishes, 96: 1017–1028.

Lunn, D., Jackson, C., Best, N., Thomas, A., and Spiegelhalter, D. 2013. The BUGS Book a Practical Introduction to Bayesian Analysis. CRC Press Taylor & Francis Group, LLC, Boca Raton, Florida. 381 pp.

Moore, A., Russell, I. C., and Potter, E. C. E. 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, *Salmo salar* L. Journal of Fish Biology, 37: 713–721.

Nieland, J. L., Sheehan, T. F., and Saunders, R. 2015. Assessing demographic effects of dams on diadromous dish: a case study for Atlantic salmon in the Penobscot River. ICES Journal of Marine Science, 72: 2423–2437.

Otero, J., Jensen, A. J., L'Abée-Lund, J. H., Stenseth, N. C., Storvik, G. O., and Vøllestad, L. A. 2011. Quantifying the ocean, freshwater and human effects on year-to-year variability of one-sea-winter Atlantic salmon angled in multiple Norwegian rivers. PLoS One, 6: e24005.

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., and Reeves, G. H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic Sciences, 55: 281–287.

Peyronnet, A., Friedland, K. D., Poole, R., OMaoiléidigh, N., and Manning, M. 2007. Links between marine growth and survival of Irish Atlantic salmon (*Salmo salar*, L.) Journal of Fish Biology, 71: 691–700.

Riley, W. D., Moore, A., Russell, I. C., Davidson, I. C., Cove, R. J., and Ives, M. J. 2007. Impact of trapping and tagging on the timing of continued seaward migration of wild salmon, *Salmo salar*, smolts. Fisheries Management and Ecology, 14: 287–290.

Riley, W. D., Ibbotson, A. T., Gregory, S. D., Russell, I. C., Lauridsen, R. B., Beaumont, W. R. C., Cook, A. C. , *et al.* 2018. Under what circumstances does the capture and tagging of wild Atlantic salmon *Salmo salar* smolts impact return probability as adults? Journal of Fish Biology, 93: 477–489.

Royle, J. A. 2008. Modeling individual effects in the Cormack–Jolly–Seber model: a state-space formulation. Biometrics, 64: 364–370.

Sandstrom, P. T., Ammann, A. J., Michel, C., Singer, G., Chapman, E. D., Lindley, S., MacFarlane, R. B., *et al.* 2013. Growth, survival, and tag retention of steelhead trout (*Oncorhynchus mykiss*) and its application to survival estimates. Environmental Biology of Fishes, 96: 145–164.

St-Hilaire, A., Booth, D., Bettignies, C., Chadwick, E. M. P., and Courtenay, S. C. 1995. Is the Miramichi a stratified estuary? *In* Water, Science and the Public: The Miramichi Ecosystem, pp. 73–82. Ed. by E. M. P. Chadwick. Canadian Special Publication of Fisheries and Aquatic Sciences, 123: 300.

St-Hilaire, A., and Caissie, D. 2001. River mixing characteristics in the Northwest Miramichi River (NB) and associated metal concentration following a discharge by Heath Steele Mines in 1991. Canadian Technical Report of Fisheries Aquatic Sciences, 2367: vi + 23 pp.

Stich, D. S., Bailey, M. M., Holbrook, C. M., Kinnison, M. T., and Zydlewski, J. D. 2015. Catchment-wide survival of wild- and hatchery-reared Atlantic salmon smolts in a changing system. Canadian Journal of Fisheries and Aquatic Sciences, 72: 1352–1365.

Thorstad, E. B., Whoriskey, F. W., Uglem, I., Moore, A., Rikardsen, A., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. Journal of Fish Biology, 81: 500–542.

Thorstad, E. B., Uglem, I., Finstad, B., Kroglund, B., Einarsdottir, I. E., Kristensen, T., Diserud, O. , *et al.* 2013. Reduced marine survival of hatchery-reared Atlantic salmon post-smolts exposed to aluminium and moderate acidification in freshwater. Estuarine, Coastal and Shelf Science, 124: 34–43.

Welch, D. W., Batten, S. D., and Ward, B. R. 2007. Growth, survival and tag retention of steelhead trout (*O. mykiss*) surgically implanted with dummy acoustic tags. Hydrobiologia, 582: 289–299.

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