Original Article

Trends in marine survival of Atlantic salmon populations in eastern Canada

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Declines in wild Atlantic salmon (*Salmo salar*) abundance throughout the north Atlantic are primarily attributed to decreases in survival at sea. However, comparing trends in marine survival among populations is challenging as data on both migrating smolts and returning adults are sparse and models are difficult to parameterize due to their varied life histories. We fit a hierarchical Bayesian maturity schedule model to data from seven populations in eastern Canada to estimate numbers of out-migrating smolts, survival in the first and second year at sea, and the proportion returning after 1 year. Trends in survival at sea were not consistent among populations; we observe positive, negative, and no correlations in these, suggesting that large-scale patterns of changes in marine survival are not necessarily representative for individual populations. Variation in return abundances was mostly explained by marine survival in the first winter at sea in all but one population. However, variation in the other components were not negligible and their relative importance differed among populations. If salmon populations do not respond in a uniform manner to changing environmental conditions throughout their range, future research initiatives should explore why.

Keywords: marine mortality, natural mortality, salmonid, survival at sea

Introduction

Reductions in fishing mortality, albeit necessary, are not always sufficient to facilitate population recovery. Experience with numerous commercially exploited marine fisheries since the early 1990s has shown that not all populations respond as favourably as anticipated to major reductions in exploitation (Hutchings and Kuparinen, 2017). Gradual efforts to close commercial Atlantic salmon (*Salmo salar*) fisheries in eastern Canada culminated in full moratoria in all regions, beginning in the Maritime provinces (1984) and following in Newfoundland (1992), Labrador (1998), and Québec (QC) (2000). Since these closures, many populations have not increased as expected (Dempson *et al.*, 2004; ICES, 2019); some have been assessed as threatened or endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2010), Canada's science advisory body (to the national government) on

species' risk of extinction. While the mechanisms behind population declines are not fully understood, the potential drivers of these are many (see Cairns, 2001, for a detailed discussion of possible causes), including but not limited to: fishing mortality (Dempson *et al.*, 2004); damming of waterways and changes in the freshwater habitat (Dunfield, 1985; Clarke *et al.*, 2014); acidification (particularly in Nova Scotia's [NS] Southern Uplands, see Gibson *et al.*, 2009); predation by seals and birds (Cairns and Reddin, 2000); negative effects of interbreeding or interactions with escaped farmed salmon (Keyser *et al.*, 2018); and climate-driven changes in survival and productivity (Mills *et al.*, 2013).

Several studies suggest that, over broad spatial scales, marine survival of Atlantic salmon has declined throughout the North Atlantic, particularly since the 1980s (Massiot-Granier *et al.*, 2014; ICES, 2019; Olmos *et al.*, 2019). These declines are thought to be driven by oceanic climate effects based on multiple lines of evidence suggesting that climate conditions can directly and indirectly influence the abundance and productivity of Atlantic salmon populations (Mills *et al.*, 2013; Almodóvar *et al.*, 2019; Olmos *et al.*, 2020). Thus, an implicit assumption is that populations sharing a particular oceanic route during seaward migration are likely to show similar trends in marine survival. Put another way, given that salmon from different rivers are hypothesized to share marine habitat during some of their time at sea, it has been presumed that populations would be more likely to experience similar temporal trends in at-sea mortality (Friedland *et al.*, 1993; Friedland, 1998; Russell *et al.*, 2012).

Despite the overall decreases in marine survival, the conservation status of Canadian Atlantic salmon populations differs considerably. In Canada, populations in the southern part of their range are more likely to be assessed as being of conservation concern (i.e. threatened or endangered) than those in more northerly regions (COSEWIC, 2010). This latitudinal disparity suggests that if marine survival has been, or is, a key factor responsible for most population declines, these changes are not uniformly distributed across all populations.

Given the logistical challenges associated with estimating at-sea survival for individual populations, it is not surprising that the number of studies that have estimated temporal trends has been limited. The evidence for widespread declines in marine survival mostly comes from studies over broad spatial scales that do not include empirical smolt abundance data, and rely on highly variable stock-recruitment relationships. An additional limitation has been the derivation of proxies (e.g. return rates), rather than direct model-based estimates, of marine survival. For example, Chaput (2012) examined return rates (i.e. ratio of adult salmon to outgoing smolts) as a metric of marine survival, finding that most Canadian populations had experienced declining return rates. However, with the exception of one-sea-winter (1SW) dominated populations (such as most populations in Newfoundland) where return rates closely approximate marine survival, return rates cannot directly be interpreted as marine survival rates and examination of trends in return rates alone can mask changes in differential survival during different years at sea, as well as changes in the proportion of adults returning after 1 or 2 years at sea (Hubley and Gibson, 2011).

In the present study, we compile data on the number of migrating smolts and number of returning adults for seven wild Canadian populations of Atlantic salmon to model population-level trends in marine survival and assess their among-population variation. While some studies have previously used maturity-schedule models

to estimate marine survival for a limited number of salmon populations (Chaput *et al.*, 2003; Hubley and Gibson, 2011), none have incorporated data extending over multiple decades, nor have they examined trends among more than two or three populations. Accordingly, we develop a hierarchical Bayesian model that uses Murphy's maturity schedule method (Murphy, 1952), in conjunction with informative priors, to estimate yearly marine survival in salmon. In addition to accounting for observation error in smolt and return estimates, we estimate the proportion of salmon returning after one winter hierarchically.

Methods

Data

We obtained time series data of out-migrating smolt and returning adult abundances for seven Atlantic salmon populations in eastern Canada, encompassing a wide range of the species' westerly distribution. Populations included the LaHave River in NS Southern Uplands, Nashwaak River in New Brunswick (NB), Rivière de la Trinité (Trinité) and Rivière Saint-Jean in QC, and Western Arm Brook (WAB), Campbellton, and Conne River, in Newfoundland and Labrador (NL) (Figure 1). Data were collected in NS, NB, and NL by Fisheries and Oceans Canada (DFO) and in QC by the Ministère des Forêts, de la Faune et des Parcs, QC.

Smolt and adult return abundance data

Smolt and adult return abundance estimates originate from a variety of sources. Smolt estimates from the Trinité, Saint-Jean, LaHave, Nashwaak, and Conne populations were obtained using a mark-recapture approach, while estimates from the WAB and Campbellton populations were obtained by direct counts using fish counting fences. For further details on the data collection methodologies refer to Dempson and Stansbury (1991), Schwarz and Dempson (1994), and Venoitt *et al.* (2018) for NL populations, April and Cauchon (2018) for QC populations, Jones *et al.* (2014) for the NB population, and Gibson *et al.* (2009) for the NS population.

Annual return data are often recorded in terms of two size groups: small ($<$63 cm FL) and large ($\geq$63 cm FL) salmon, as these closely represent different life-history strategies (i.e. 1SW and two-sea-winter [2SW]), but can be confounded with repeat spawners of different sizes. To correct for this in returns reported as small and large salmon, rather than 1SW and 2SW fish, we estimated the abundance of 1SW and 2SW returns using yearly scale age data of a subsample of returns:

$$p_{r,t,a} = \frac{\sum_s \left(\frac{n_{r,t,s,a}}{n_{r,t,s}} * N_{r,t,s} \right)}{\sum_s N_{r,t,s}}, \tag{1}$$

where $p_{r,t,a}$ is the proportion of annual returns in river r, year t, and of spawning history a (either 1SW or 2SW returns); $n_{r,t,s,a}$ is the number of samples in river r, year t, of returning age a, and of size group s; $n_{r,t,s}$ is the total number of samples in river r, year t, and of size group s; and $N_{r,t,s}$ is the returns of salmon in river r, year t, and of size group s. For years where scale data of a given size group is lacking, we averaged the proportions of annual returns for the closest 10 years for which there were data. We incorporated the uncertainty in the conversion between size group and returning age in the model indirectly as an estimate of the variance of annual log-1SW and 2SW return abundance (see Supplementary Materials).
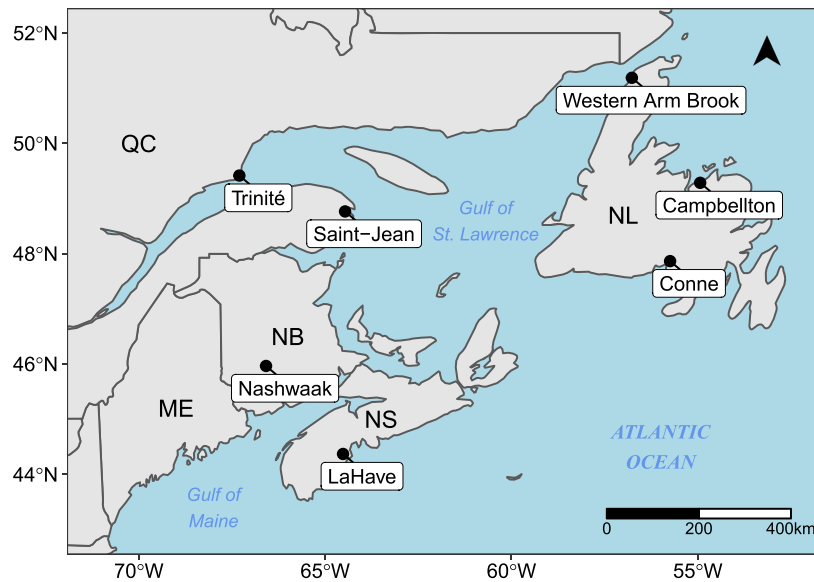
Figure 1. Locations of the seven rivers in eastern Canada with time series abundance data of out-migrating smolts and returning adult Atlantic salmon.

Bayesian model

We developed a hierarchical Bayesian model that uses Murphy's maturity schedule method, in conjunction with informative priors, to estimate annual marine survival. We account for observation error in smolt and return estimates, as well as estimating the proportion returning after one winter (i.e. P_g) hierarchically. There is an identifiability problem in the maturity schedule equations where the parameter estimates cannot be optimally solved (Chaput, 2003). However, this issue can be mathematically overcome by using informative priors for the two marine survival parameters and the maturation parameter in a Bayesian framework. This method requires abundance estimates of smolts as well as abundance estimates of returning 1SW and 2SW adults. With these data, it estimates three parameters: survival in the first year at sea (S_1), survival in the second year at sea (S_2), and the proportion of fish returning after 1 year at sea (P_g).

Our model does not include repeat spawners and assumes that no fish spend three or more winters at sea before returning to spawn for the first time. Assuming that there are no age 3+ maiden spawners is likely to result in slightly lower S_1 and S_2 estimates as these older maiden spawners that would be returning in later years are assumed to have died. Nonetheless, in the populations examined, these fish comprise a very small fraction of maiden spawners, and we do not expect these to substantially affect our results. The model also assumes that mortality in the second winter at sea (S_2) for 2SW returns is additive to mortality in the first winter at sea in the previous year, and therefore does not account for differences in environmental conditions experienced between 1SW and 2SW fish of the same smolt cohort during their overlapping first year at sea. In other words, our model assumes that the decision of returning occurs just before actually being counted as returns and that S_2 is additional mortality in the subsequent year.

Observed smolt estimates were modelled hierarchically and included observation error:

$$log(smolts_{obs,r,t}) = log(smolts_{true,r,t}) + \epsilon_{r,t}, \qquad (2)$$

where $smolts_{true,r,t}$ are the true smolt abundances for river r and year t, and $\epsilon_{r,t}$ is the error term, which is calculated from the yearly coefficient of variation in the empirically derived smolt estimates (see Supplementary Tables S4–S6). Where available, we used population-specific measurement error estimates for smolt abundances; if not available, we set the measurement error at 5 or 10%, depending on whether the smolt abundance estimates originated from direct counts or mark-recapture studies, respectively (see Supplementary Table S5). The log-transformed true smolt abundances are normally distributed around a population-level mean and standard deviation:

$$log(smolts_{true,r,t}) \sim Normal(\mu_{smolts,r}, \sigma_{smolts,r}), \qquad (3)$$

where $\mu_{smolts,r}$ and $\sigma_{smolts,r}$ are the mean and standard deviation of the hierarchical population-level log-smolt abundances estimated by the model for each population r.

Once we have yearly estimates of smolt, 1SW, and 2SW abundances, we estimate marine survival parameters using Murphy's maturity schedule method (Murphy, 1952; Ricker, 1975):

$$R_{r,1,t} = smolts_{true,r,t-1} * S_{1,r,t} * P_{g,r,t}, \qquad (4)$$

$$R_{r,2,t+1} = smolts_{true,r,t-1} * S_{1,r,t} * (1 - P_{g,r,t}) * S_{2,r,t+1}, \qquad (5)$$

where $R_{1,r,t}$ and $R_{2,r,t+1}$ are the estimated abundances of 1SW and 2SW salmon returning for river r in years t and $t+1$, respectively, $smolts_{true,r,t-1}$ is the estimated number of out-migrating smolts for river r in year $t-1$, $S_{1,r,t}$ is the proportion of salmon surviving in their first year (t) at sea for river r, $P_{g,t}$ is the proportion of salmon that return to spawn at year t for river r, and $S_{2,r,t+1}$ is the survival in their second year at sea of the same cohort of salmon who did not return to spawn at year t for river r.

We log-transform Equations (4) and (5) so the model is linear on the log-scale:

$$log(R_{1,r,t}) = log(smolts_{r,t-1}) + log(P_{g,r,t}) - Z_{1,r,t}, \qquad (6)$$

$$log(R_{2,r,t+1}) = log(smolts_{r,t-1}) - Z_{1,r,t} + log(1 - P_{g,r,t}) - Z_{2,r,t+1},$$
(7)

where $Z_{1,r,t}$ and $Z_{2,r,t+1}$ are the instantaneous mortality rates and $R_{1,r,t}$ and $R_{2,r,t+1}$ are the estimated 1SW and 2SW returns in consecutive years, respectively. Observation error was included as the standard deviation of the log-transformed return estimates from Equation (7):

$$log(R_{obs,1,r,t}) \sim Normal(log(R_{1,r,t}), \epsilon_{1,r,t}),$$
(8)

$$log(R_{obs,2,r,t}) \sim Normal(log(R_{2,r,t}), \epsilon_{2,r,t}),$$
(9)

where $R_{obs,1,r,t}$ and $R_{obs,2,r,t}$ are the observed return estimates for year t and river r of 1SW and 2SW fish, respectively, and $\epsilon_{1,r,t}$ and $\epsilon_{2,r,t}$ are the process error terms. These error terms are estimated by approximating the abundance of 1SW and 2SW returns from hypergeometric distributions based on the scale sample data. We assume that the error in the total number of returns is zero; the error in the total number of returns is likely minor compared to the error in the number of outmigrating smolts and the error due to a small scale sample size. Hence, ignoring the error in the returns is unlikely to change our results significantly. We were able to obtain scale data for all but two of the populations (LaHave and Nashwaak), and we bootstrapped a distribution of abundances of annual 1SW and 2SW returns for each population from hypergeometric distributions, from which we estimated the variance in log-space. See the Supplementary Materials for a description of the methodology and the resulting estimates.

Furthermore, we use instantaneous mortality rates in the model instead of survival probabilities as the model is more efficient in its parameter search in log-space. Instantaneous rates are easily converted to survival probabilities by

$$S_{1,r,t} = e^{-Z_{1,r,t}},$$
(10)

$$S_{2,r,t} = e^{-Z_{2,r,t}}.$$
(11)

The priors for Z_1 and Z_2 are specified as log-normal distributions:

$$Z_{1,r,t} \sim logNormal(1, 0.22),$$
(12)

$$Z_{2,r,t} \sim logNormal(0.2, 0.3).$$
(13)

These priors, when converted to yearly survival, are roughly constrained between 0 and 0.2 for S_1 and between 0.2 and 0.5 for S_2 (Figure 2a). They are informative only to the extent that they limit the estimates of marine survival to what we considered to be biologically realistic based on previous studies on return rates of 1SW-dominated populations in NL, as well as the few studies that have explored survival in the second winter at sea of Atlantic salmon in eastern Canada. Although two published values are higher than 0.8 (Chaput *et al.*, 2003; Hubley and Gibson, 2011), most estimates of S2 encompass a range between 0.1 and 0.6; this is the empirical basis for our prior. While there is circularity in setting priors based on data for the same rivers and is far from ideal, these are the only data we have available to set priors and the models used previously are considerably different to the one in the present study.

We estimate population-level mean probit P_g values around which the yearly P_g values are normally distributed. We specify different informative hyperpriors for $\mu_{P_g,r}$ and $\sigma_{P_g,r}$ based on whether
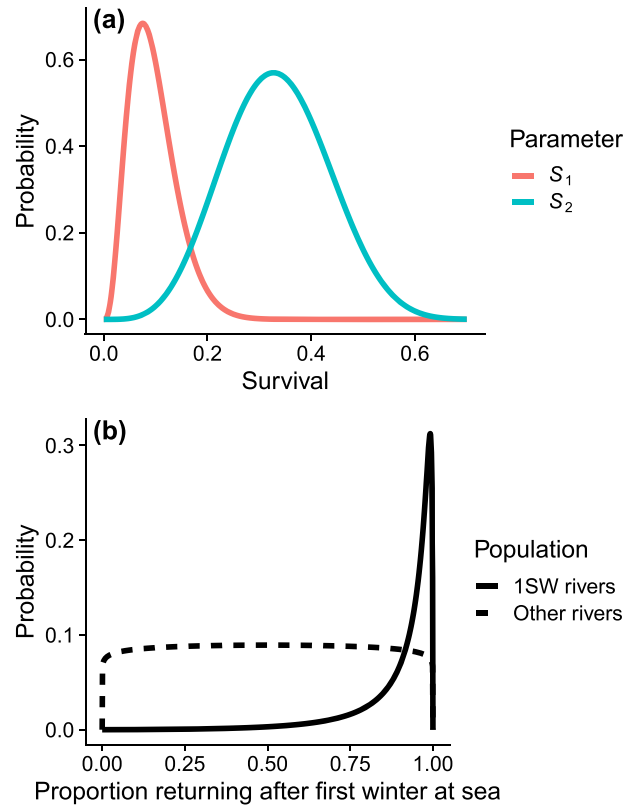

Figure 2. Priors for (a) marine survival of one sea-winter (S_1) and two sea-winter (S_2) returns, and (b) probability of returning as 1SW for 1SW-dominated populations (proportion 1SW > 0.9) and other populations.

the population is 1SW-dominated (i.e. with a proportion of 1SW fish in the total returns greater than 0.9) or not:

$$probit(P_{g,t}) \sim Normal(\mu_{P_g,r}, \sigma_{P_g,r}),$$
(14)

$$\mu_{P_g,r} \sim \begin{cases} Normal(2.3, 0.4), & \text{for 1SW-dominated populations} \\ Normal(0, 2.8), & \text{for non-1SW-dominated} \\ & \text{populations,} \end{cases}$$
(15)

$$\sigma_{P_g,r} \sim halfNormal(0, 1).$$
(16)

The three Newfoundland populations (WAB, Campbellton, and Conne) are 1SW-dominated, while the other four have the more generic priors for $probit(P_{g,t})$. These priors, when converted back to a proportion, are narrowly constrained for 1SW-dominated populations, but relatively wide for all other populations (Figure 2b).

We explored the effect of using weaker priors for Z_1, Z_2, and P_g, and found that the posteriors of Z_1 were not sensitive to the choice of prior, while the posteriors Z_2 and P_g became more uncertain with weaker priors while maintaining the same temporal trends observed when using stronger priors. See Supplementary Figures S2–S7.

Correlations among trends in survival and parameters

We looked at the correlation among trends in S_1 between populations by directly estimating the error-corrected correlation for each posterior iteration and then calculating the distribution of correla-
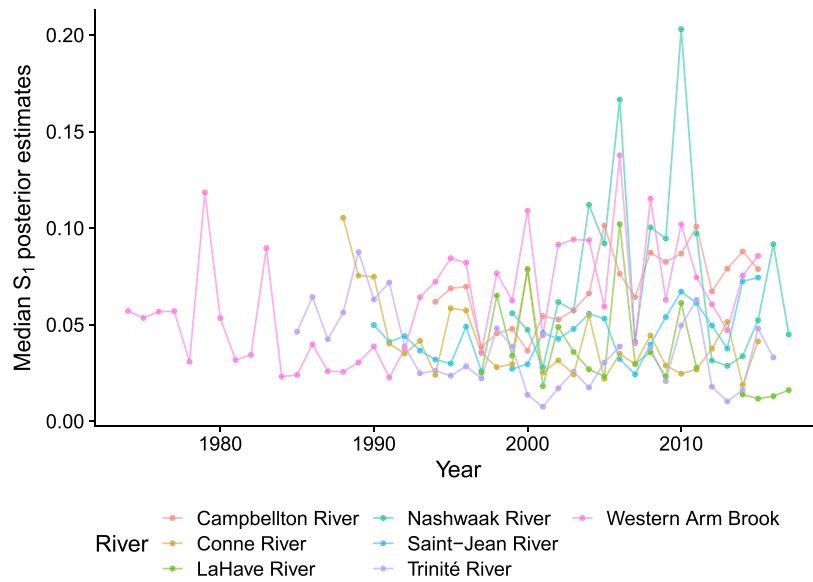
Figure 3. Median posterior estimates of survival in the first year at sea (S_1) for the seven populations examined.

tion values:

$$cor_{corrected}(Z_{1,r=1}, Z_{1,r=2})$$

$$= \frac{cov(Z_{1,r=1}, Z_{1,r=2}) - cov_{error}(Z_{1,r=1}, Z_{1,r=2})}{\sqrt{var(Z_{1,r=1}) - var_{error}(Z_{1,r=1})} * \sqrt{var(Z_{1,r=2}) - var_{error}(Z_{1,r=2})}},$$
(17)

where $Z_{1,r=1}$ and $Z_{1,r=2}$ are the Z_1 estimates, across years, for a single posterior iteration for populations 1 and 2, $cov(Z_{1,r=1}, Z_{1,r=2})$ is the covariance between these overlapping Z_1 estimates, $cov_{error}(Z_{1,r=1}, Z_{1,r=2})$ is the error covariance term, $var(Z_{1,r=1})$ and $var(Z_{1,r=2})$ are the variances, while $var_{error}(Z_{1,r=1})$ and $var_{error}(Z_{1,r=2})$ are error variance estimates. Estimates of the error covariance (cov_{error}) and error variances (var_{error}) are obtained by estimating the covariance of two parameters across all values in the posterior for a given year (rather than across years for each posterior iteration), which results in one covariance estimate for each year in each river, which then are averaged across years for each river. Likewise, the error variance of a parameter is estimated across all values in the posterior for a given year and then are averaged across years for each river. Given that the time series do not cover the same years, and that some populations have missing years in the middle of the time series, only years with overlapping Z_1 estimates were used for the pairwise correlation estimates, and thus each pairwise correlation is specific for those years and does not include sample uncertainty due to sample size.

We also estimated the correlation between the model parameters for each population using the same approach as in Equation (17), by including the error in the variance and covariance estimates:

$$cor_{corrected}(P_{g,r}, -Z_{1,r})$$

$$= \frac{cov(P_{g,r}, -Z_{1,r}) - cov_{error}(P_{g,r}, -Z_{1,r})}{\sqrt{var(P_{g,r}) - var_{error}(P_{g,r})} * \sqrt{var(-Z_{1,r}) - var_{error}(-Z_{1,r})}}.$$
(18)

Lastly, to determine which parameters best explain the number of returns in the model (including the model uncertainty), we estimated the variance in returns explained by each parameter by calculating the squared correlation between the estimated parameters and the estimated 1SW and 2SW returns [$R_{1,r,t}$ and $R_{2,r,t+1}$ in Equations (6) and (7)].

The model was written in Stan (Carpenter *et al.*, 2017) and all analyses were run in R version 3.6.1 (R Core Team, 2019) using the rstan package version 2.19.2 (Stan Development Team, 2019). The model was run with 3 chains and 3000 iterations, with the first 1500 discarded as a burn-in. The models were considered to have converged when the $\hat{R}$ of all parameters were lower than 1.03 and the effective sample sizes were higher than 500. The data and code are available at https://github.com/sebpardo/salmon-marine-survival.

Results

Trends in marine survival parameters

Estimates of marine survival probabilities in the first winter at sea (S_1) were highly variable within and among populations (Figure 3). The highest median posterior estimates of S_1 were for the Nashwaak River in 2006 and 2008, with values of 0.18 and 0.21, respectively. The lowest median S_1 estimate was in the Trinité in 2001, with an estimate of S_1 of 0.007, while the Conne, LaHave, and Trinité had years where the lowest estimates of S_1 varied between 0.01 and 0.02 (Figure 4).

Visual inspection of long-term trends among populations also varied: Campbellton, Saint-Jean, and WAB populations showed increases in S_1 over time, Trinité, Conne, and LaHave populations showed decreases, while at Nashwaak there was an increase in median S_1 during the early 2000s but a decrease since 2010. Annual estimates of S_1 had little uncertainty for one sea-winter dominated populations (Conne, Campbellton, and WAB), with the exception of the 2004–2011 period in the Campbellton where there were very few scale samples, and hence high process error; but in general, uncertainty was higher (i.e. wider credible intervals) in the other populations.

Estimates of survival in the second year at sea (S_2) were highly uncertain in all populations, and trends were not apparent in most populations given the large range of the credible intervals in the
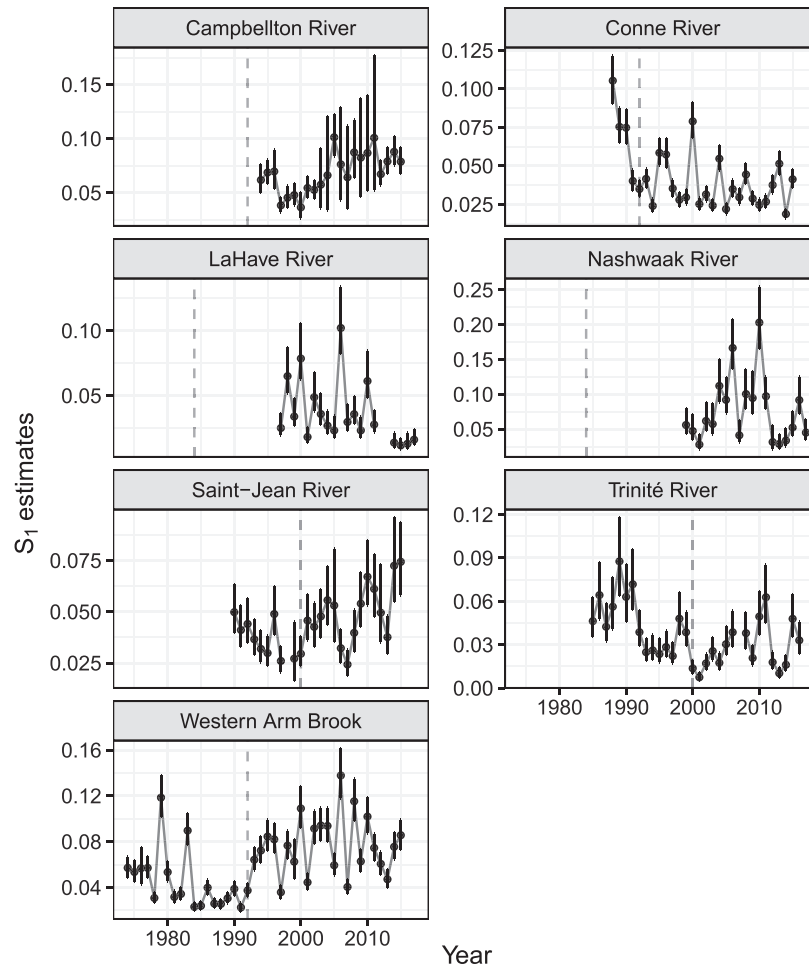
Figure 4. Posterior estimates of survival probabilities in the first year at sea (S_1). Dots indicate median estimates and error bars indicate the 90% credible intervals. Dashed vertical lines reflect the year the commercial fishing moratoria were enacted in each province.

yearly estimates (Figure 5). The estimates of S_2 for the Saint-Jean and Trinité were considerably less uncertain than for the other populations, with the latter showing an increase with a peak in the mid-1990s followed by a decrease.

Estimates of P_g were mostly stable across time, except for the La-Have and Nashwaak populations; for the La Have, the estimates of P_g were slightly lower in the last 4 years than in the previous ones, while in the Nashwaak, the posterior estimates of P_g in 2012 were much lower than in all other years (Figure 6). Variation in yearly estimates was highest in the LaHave, Nashwaak, and Trinité, and lowest in the 1SW-dominated populations.

Estimates of the population-level mean ($\mu_{Pg, r}$) and standard deviation ($\sigma_{Pg, r}$) of proportion returning after 1 year at sea varied considerably among populations. For all three 1SW-dominated populations (Campbellton, Conne, and WAB), estimates of $\mu_{Pg, r}$ were very close to 1.0 and had little variation in $\sigma_{Pg, r}$ (Figure 7; Supplementary Table S10). Estimates of $\mu_{Pg, r}$ were the lowest for the two QC populations, particularly the Saint-Jean (median $\mu_{Pg, r} = 0.11$). Estimates of $\mu_{Pg, r}$ for the Nashwaak and the LaHave populations were close to 0.5, with these two populations having the highest estimated values of $\sigma_{Pg, r}$, particularly the Nashwaak (Figure 7; Supplementary Table S11).

Uniquely for the Saint-Jean population, yearly variation in S_2 is being estimated by the model but there is almost no variation in P_g estimates (Figure 6) and a very low estimate of $\sigma_{Pg, r}$ (Supplementary Table S11). In other words, the variation in the relative proportion of 1SW and 2SW returns for Saint-Jean is being manifested as variation in S_1 and S_2 but not in P_g rather than being manifested in S_1 and P_g but not S_2, which is the case for the other six populations. This difference is likely a result of the identifiability issue with the maturity schedule method, which for the Saint-Jean population data, combined with the priors used, results in the model estimating variation in P_g rather than S_2.

Correlations
Roughly half (11) out of the 21 pairwise correlations were significant (*p*-value below 0.05) (Figure 8). When looking at the direction of the correlations, these spanned both positive and negative coefficients. All seven populations had both positive and negative correlations among them. The corrected pairwise correlations in Z_1 were almost identical to the uncorrected ones as the error variance and covariance terms were very small. The correlations between populations in the region were positive between Nashwaak and
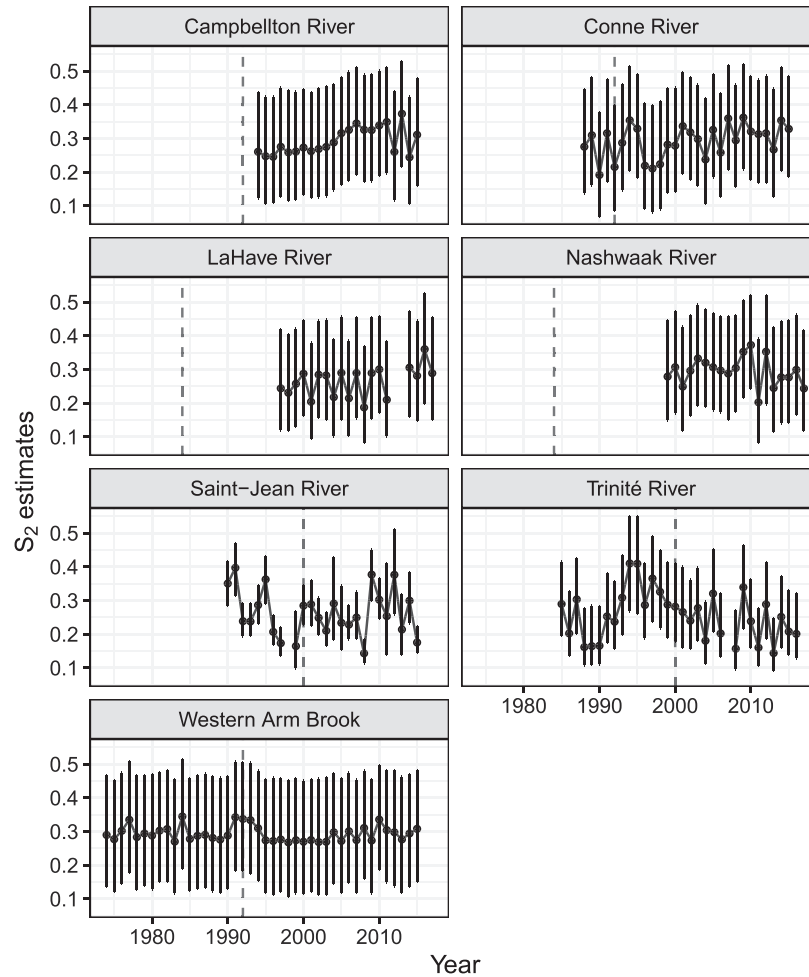
Figure 5. Posterior estimates of survival in the second year at sea (S_2). Dots indicate median estimates and error bars indicate the 90% credible intervals. Dashed vertical lines reflect the year the commercial fishing moratoria were enacted in each province.

LaHave (Scotia-Fundy region), non-significant between the Trinité and Saint-Jean (QC), non-significant between WAB and Campbellton but negative between Conne and WAB (NL). Campbellton had mostly non-significant pairwise correlations with other populations, even though there are both positive and negative correlation coefficients, except with the Saint-Jean where the correlation between Z_1 trends is positive and significant. Note that the uncertainty in these correlations reflects the uncertainty in the measurements, but not in the process (in this respect they are equivalent to population variance and not sample variance). Our choice of priors affected these correlations: using weaker priors for S_1 and S_2 resulted in slightly different coefficients and significance thresholds (see Supplementary Figure S7).

As is expected from Murphy's method, there are strong negative, yet highly uncertain, correlations between survival in the second year at sea (i.e. $-Z_2$) and proportion returning as 1SW ($log(P_g)$, Figure 9). Some populations (Campbellton, LaHave, Nashwaak, and Saint-Jean) show a negative correlation between the estimated number of smolts and survival in the first year at sea, while the others fluctuate around zero. There is overall a positive correlation between survival in the first year (i.e. $-Z_1$) and proportion returning

as 1SW, except for the Campbellton population, where this correlation is negative.

Overall, variation in return abundances was mostly explained by marine survival in the first winter at sea, with R^2 estimates between 0.5 and 0.75 for all populations with the exception of the Saint-Jean (Figure 10). The low R^2 for the Saint-Jean is likely due to the negative correlation between survival (i.e. $-Z_1$) and number of outmigrating smolts (see Figure 9). There are also moderately negative correlations between survival and smolts in the Campbellton, LaHave, and Nashwaak populations. These negative correlations could be indicative of density-dependent mortality at sea; however, this is generally thought to be unlikely. Populations with a lower proportion of 1SW in their returns (e.g. Trinité and Saint-Jean) have a higher R^2 with estimated number of smolts than those that are 1SW-dominated, but overall, smolts estimates had low R^2 values in all populations except the Saint-Jean (Figure 10). The proportion returning as 1SW explained a moderate amount of the variance in estimated 1SW returns in the Conne, LaHave, and Nashwaak, and much less in the other four populations. Values of R^2 were overall low for all parameters with regards to explaining the variance of estimated 2SW returns. Estimates of mortality in the second winter at
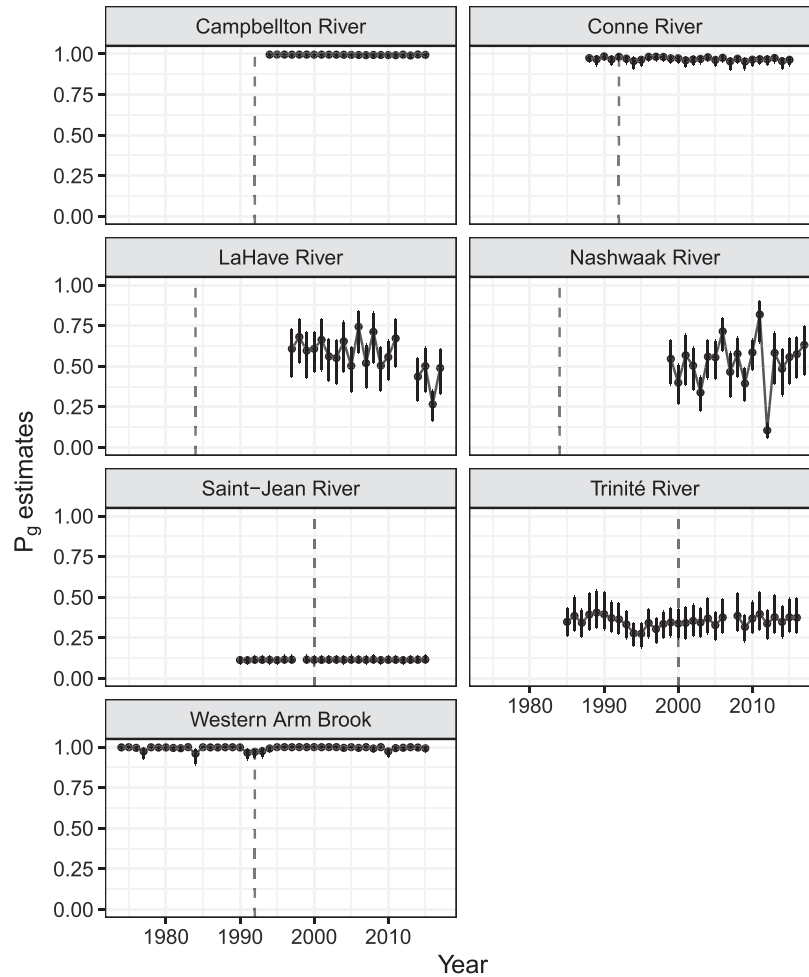
Figure 6. Posterior estimates of proportion returning after one winter at sea (P_g). Dots indicate median estimates and error bars indicate the 90% credible intervals. Dashed vertical lines reflect the year the commercial fishing moratoria were enacted in each province.
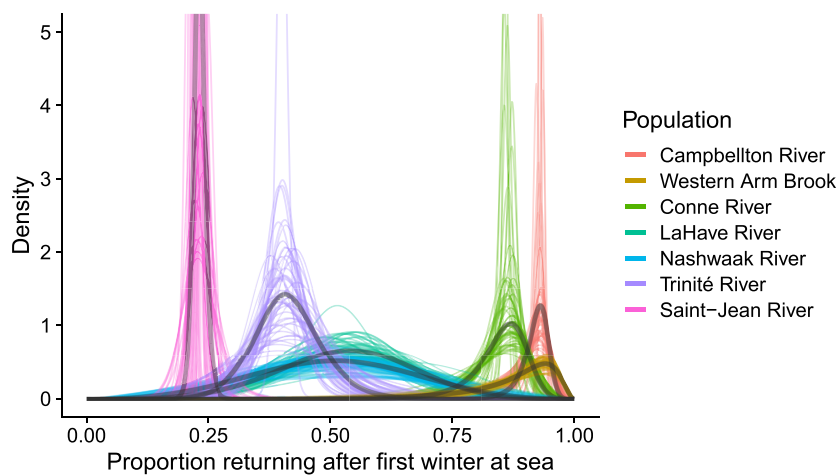

Figure 7. Posterior probability distributions resulting from the population-level estimates of the proportion returning after one winter at sea based on the parameters $\mu_{P_g,r}$ and $\sigma_{P_g,r}$. Gray lines denote population-specific median estimates of $P_{g,r}$, while the colored lines represent a sample of 20 posterior iteration draws for each population.
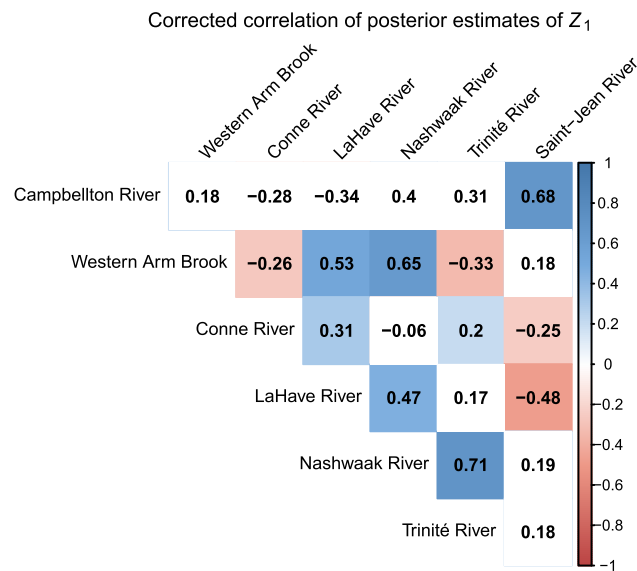
Corrected correlation of posterior estimates of Z_1

Figure 8. Correlations of estimated trends in instantaneous natural mortality in the first winter at sea, Z_1, among populations. Correlation coefficients are shown in each square, while colouring denotes significance of the correlation ($p \leq 0.05$) as well as the direction and magnitude.

sea (Z_2) explained little variance in estimates for 2SW returns, with the Saint-Jean again being the exception.

Discussion

Our results show that trends in marine survival among monitored Atlantic salmon populations in eastern Canada are highly variable, both temporally and spatially. Over the time periods for which data were available, some populations show positive trends in survival in the first winter at sea (S_1) while others exhibit highly variable yet stationary trends, and some show declines. Variation in survival at the population level can be large even within a region. With one possible exception (LaHave River), consistent declines in marine survival within populations are not evident since the onset of fishing moratoria.

While correlations in marine survival trends among rivers are highly variable (Figure 8), there are some years in which the populations appear to behave in concert: years 1997, 2007, and to some extent 2001 have consistently low survival across all populations (i.e. <5%, Figure 3) and little variation across populations. Our results also show that variation of survival in the first year at sea is the most important factor determining variation in number of returns, suggesting that changes in abundance are primarily driven by changes in early marine survival. Nonetheless, variation in number of out-migrating smolts and, for some populations, variation in probability of returning after one winter at sea, also explain variation in returns, thus contributing to the observed variation in return abundances. Furthermore, the negative correlation between marine survival and smolt abundances in some populations is suggestive of density-dependent processes. We could not assess trends for survival in the second winter at sea (S_2) or proportion returning as grilse (P_g), as these parameter estimates were highly uncertain and in most cases the posteriors encompassed the entire range of the prior (suggesting that S_2 were strongly influenced by the prior).

At first glance, the large variation in marine survival trends among the seven populations examined seems to be at odds with the synchronous trends of declining marine survival detected at broad regional scales (Olmos *et al.*, 2019). However, these two observations are not necessarily mutually exclusive: our study represents a subsample of the populations in the region, and, with one exception, encompasses a shorter period of time; highly variable trends in marine survival among populations can still add up to overall negative trends at a regional scale. Aside from the overarching difference in the spatial scale of data sources (i.e. river vs. province scales), the divergence in local vs. regional trends could be further confounded by differences in model structure (e.g. methods used for estimating covariance), use of stock-recruitment relationships (Olmos *et al.*, 2019) rather than empirical smolt count estimates (present study) to estimate marine survival, and separation between fishing mortality and natural mortality, which was not done in our study. Our results suggest that trends from broader geographical areas (i.e. province, state, or country-wide estimates) might not be representative of individual populations, and concomitantly, trends of individual populations might also not be representative of region-wide trends.

Trends in marine survival among populations were compared by Chaput (2012) using adult return rates. He found that for four of six populations examined, return rates in the 1990s were lower than those during the 1970s. Gibson *et al.* (2016) calculated higher return rates of 2SW for Nashwaak River salmon in the 1970s than in the period since, with return rates of 1SW in the 1970s being comparable to those in the late 2000s. Friedland *et al.* (1993) compared return rates for a number of populations in eastern North America between 1973 and 1988, and suggested there are similar trends among these. However, the similarity in these trends was driven primarily by two years, 1977 and 1978, which show concurrent low and high relative return rates across populations, respectively. Other years are much more variable relative to each other. The time series in Friedland *et al.* (1993) end in 1988; thus there are only a few years that overlap with the time series in our study. While declines in return rates since the 1970s seem to be consistent among populations, we were unable to assess if marine survival estimates were also higher in the 1970s because smolt count data from this decade are not available. Dempson *et al.* (2003) described a general declining trend in marine survival for Newfoundland populations (except WAB). We drew the same conclusion for Conne River, but not Campbellton River nor WAB. It is not possible to draw broader conclusions with data from only three Newfoundland populations, but it seems that among index rivers, those in northern Newfoundland are among those with the highest marine survival rates.

In any event, we caution that the pooling of adult return rates (Chaput, 2012; Friedland *et al.*, 1993; Gibson *et al.*, 2016) can mask inter-annual variation in marine survival (Hubley and Gibson, 2011), and hence might not produce an accurate depiction of marine survival trends. While river-specific return rate estimates are available for the populations used in this study (ICES, 2019), these estimates are only an approximation of marine survival with varying degrees of similarity depending on each population's life history.

The estimates of return rates of one sea-winter salmon approximate marine survival in the first year at sea for one sea-winter-dominated populations, particularly for years in which directed marine fisheries are largely non-existent, and we see this by comparing S_1 in the three NL populations with the return rates presented in ICES (2019). However, as the proportion of fish that return as one sea-winter decreases, marine survival in the first year at sea can
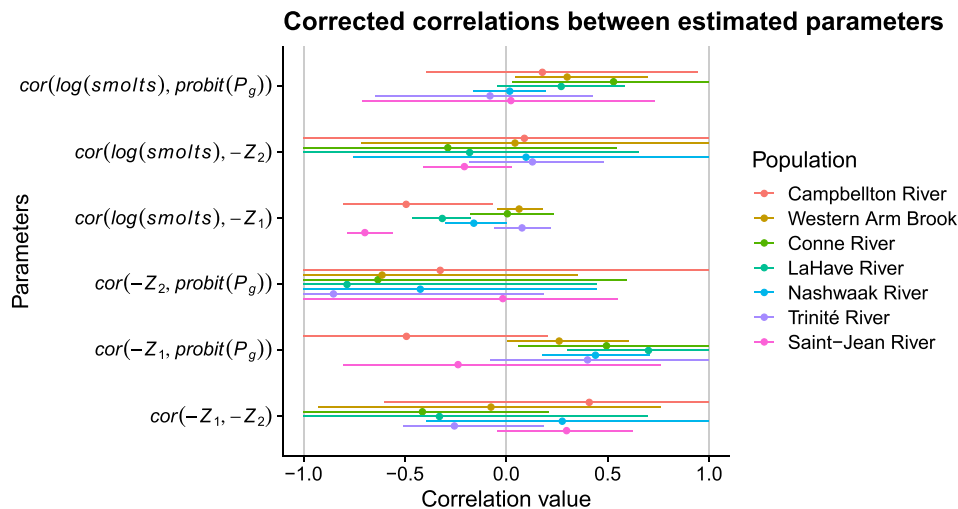
Corrected correlations between estimated parameters

Figure 9. Correlations among estimated model parameters. $log(smolts)$ = estimated smolt abundances in log-space, $probit(P_g)$ = probit-transformed probability of returning after one year at sea, $-Z_1$ = marine survival in the first year at sea, and $-Z_2$ = marine survival in the second year at sea. Note the correlations derived from negative instantaneous total mortalities $-Z_1$ and $-Z_2$ are representative to those of marine survival S_1 and S_2.
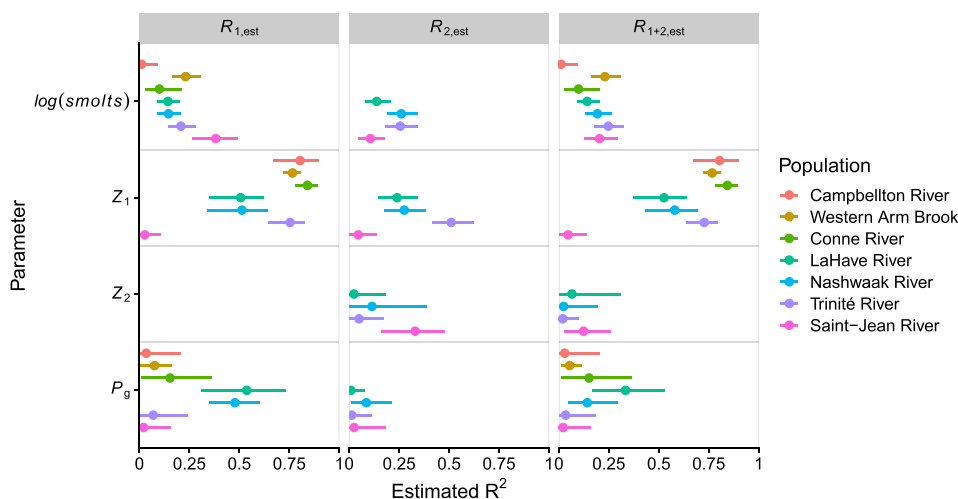

Figure 10. Estimated R^2 values for the correlation between estimated returns ($R_{1,r,t}$ and $R_{2,r,t+1}$) and the model parameters used for their estimation (i.e. estimated smolts, mortality in the first year at sea Z_1, mortality in the second year at sea Z_2, and proportion returning as 1SW, P_g). Note we did not estimate R^2 values between $R_{1,est}$ and Z_2 as the latter is not used to estimate the former, and that only the non-1SW dominated populations are shown in the R^2 values of the model parameters and $R_{2,est}$.

increasingly diverge from return rates. Thus, trends in return rate would be particularly misleading if the proportion returning as one sea-winter varies in time; proportion returning as one sea-winter was an important factor driving the number of 1SW returns in three of the populations examined (Figure 10). Furthermore, return rates of two sea-winter fish also include survival in the first winter at sea and the proportion returning as two sea-winter, thus providing a very coarse estimate of marine survival in the second year at sea. Given that changes in return rates of two sea-winter fish are a result of a combination of changes in survival in the first year at sea in the year prior, survival in the second year at sea, and in the proportion returning as two sea-winter, an increase in any of those parameters while the others remain the same will result in an increase in return

rates. Our model attempts to improve some of the shortcomings of using return rates as a proxy of marine survival by directly estimating marine survival in the first and second years at sea, as well as the proportion returning as 1SW.

Interestingly, our estimates of survival in both first and second years at sea for the Trinité population are very similar to those produced by Chaput *et al.* (2003), who applied a two-sex model, and our trends are almost identical for the overlapping time period that marine survival was estimated for in their study (1984–1998). While Chaput *et al.* (2003) separated abundance data for males and females based on sex ratio information and assumed their survival rates were the same (to be able to reach an analytical solution), our study reached almost the same results (albeit with slightly higher

uncertainty), using a Bayesian approach with informative priors. These overlapping trends obtained with two different methods suggest that our method is indeed a viable alternative approach for estimating marine survival.

There are a variety of potential explanations for the highly variable trends in estimates of marine survival in the first winter at sea. Environmental drivers of survival (e.g. temperature, predation, prey abundance, and interactions with farmed salmon) could be highly localized relative to broader-scale, even ocean-wide, drivers. A large fraction of total marine mortality occurs as post-smolts in the early part of their outmigration through estuarine and coastal areas (Halfyard *et al.*, 2012; Chaput *et al.*, 2019). These differences in migration routes and resulting early survival could be one of the main drivers of the marine survival variation observed in the present study. Concomitantly, correlations between oceanic temperature, primary productivity, and post-smolt survival in the North Atlantic are better explained by broad-scale environmental trends than regional ones (Olmos *et al.*, 2020), suggesting that ocean-wide changes also impact overall marine survival. It is important to consider that local drivers are potentially much more difficult to quantify than broader ones, which could impact our ability to detect local effects on post-smolt survival. There is some evidence of a correlation between return rate and growth (as indicated by inter-circuli spacing on scales), where years of poor growth tended to also be years of poor survival (Friedland *et al.*, 1993), supporting the idea that marine survival is mediated by environmentally-driven changes in growth. Furthermore, among European salmon, there is evidence of a positive correlation between spring temperature in the Norwegian and North Seas and population abundance, suggesting warmer conditions favor post-smolts (Friedland, 1998), based on mapping the extent of area of suitable temperature (7–13°C).

Nonetheless, the causal mechanisms for why warming should affect post-smolt survival almost certainly differ depending on the difference between temperature experienced by the post-smolts and their respective population-specific thermal optimum. This difference could explain why populations in eastern North America are declining in the southern part of their range but potentially increasing, or remaining stable, further north, and also why some studies find positive correlations between temperature and abundance (Friedland, 1998; Friedland *et al.*, 1998; Jonsson and Jonsson, 2004) while others find negative associations (Friedland *et al.*, 1993; Todd *et al.*, 2008). Olmos *et al.* (2020) documented a positive relationship between temperature and marine survival in northern regions and a negative one in southern regions, providing evidence of differing mechanisms across latitudes. Putative associations between temperature and direct estimates of marine survival warrant further study at the population level.

Oceanic conditions have been correlated with abundance trends, growth, and marine survival in Atlantic salmon, which are thought to be mediated by bottom-up effects driving ocean productivity and food availability (Todd *et al.*, 2008; Renkawitz *et al.*, 2015; Olmos *et al.*, 2020). However, the mechanism by which such bottom-up effects, mediated by changes in food availability, affect population dynamics beyond marine survival needs to be considered further. There are potential carry-on effects of oceanic conditions that manifest with regards to freshwater production for individuals that survive the marine phase of their life cycle. For example, adults that return to their natal streams after spending suboptimal conditions at sea might be less likely to make it to the spawning grounds or secure a mate, and might also produce fewer eggs or eggs with a lower ener-

getic content than those produced by adults which grew in optimal oceanic conditions. As larger females tend to be more productive, in terms of fecundity and total reproductive energy, than the same weight's worth of smaller females (Barneche *et al.*, 2018), a small decrease in body condition resulting from bottom-up impacts on food availability and quality could potentially have disproportionate effects on fecundity and fitness of the offspring.

Egg-to-smolt survival in Atlantic salmon is also highly variable, and perhaps more so than marine survival (Klemetsen *et al.*, 2003; Chaput *et al.*, 2015). While this variation is attributable to changes in freshwater conditions (e.g. discharge, temperature, and water quality) and uncertainty in spawner and smolt estimates, changes in the oceanic conditions that spawners experience could also be contributing to this variation through, for example, decreases in body condition, fecundity, and hence fitness. However, while variation in number of smolts was important for number of returns, it was considerably less important than survival during the first year at sea, suggesting that return abundances are mostly influenced by the marine phase of their life cycle. While there would be a generational lag in how climate-driven freshwater effects might manifest at the subsequent adult stages, a correlation between freshwater effects and adult abundances might be expected as most climate–salmon abundance correlations are between relatively monotonic declines in abundance coupled with monotonic increases in climatic indices over decadal time scales (e.g. Friedland, 1998; Todd *et al.*, 2008; Beaugrand and Reid, 2012). There is little evidence that marine survival is density-dependent in Atlantic salmon (Jonsson *et al.*, 1998; Gibson, 2006), but these density-dependent processes could occurr during parts of the marine phase, particularly for populations that are near historically low levels of abundance. One potential mechanism might be a "predator pit": when prey populations are very small, predator-induced mortality can also be low because the prey are simply not abundant enough to be generally consumed by an optimal forager (for example, search costs may be too high relative to the fitness benefits of consuming the prey). But as prey abundance increases from very low levels, predator-induced mortality might also increase as preference for the prey increases. Another potential mechanism is if smolt quantity and quality are negatively correlated; abundant smolt cohorts likely experience high competition in rivers and thus attain smaller size or reduced body condition than less abundant cohorts. Correlations between return estimates and survival were negative for some populations (Figure 9), indicating that there may be some compensatory density dependent effects during the marine phase. Exploring relationships between survival and population size could potentially shed light on the processes that have caused many of the population declines that have been documented.

As with all novel modelling approaches, there are caveats to acknowledge. The seven populations examined in the present study represent a small subset of the total number of salmon rivers in eastern Canada and hence might not be representative of the overall regional trends in marine survival. However, there are no other long-term time series of smolts and adult returns from which to draw inferences from. While there are analytical issues associated with the estimation of S_1, S_2, and P_g, the assumption that survival in the second year at sea is multiplicative to survival in the first year at sea could produce unrealistic results. We know there is a period of a few months where 1SW returns are subject to a different environment than those salmon that will return as 2SW the next year. While this is not ideal, overcoming this assumption would require an additional parameter to be estimated, or an additional

assumption as to what proportion of S_1 is not multiplicative to S_2 (as the returning 1SW adults do not experience the same environment when they return to their natal streams as those fish who stayed at sea for an additional winter before returning to spawn).

Secondly, our error estimates of 1SW and 2SW returns might not approximate the underlying uncertainty. Nonetheless, our approach likely overestimates uncertainty as we did not model error in annual 1SW and 2SW returns hierarchically within each population (see Supplementary Materials for details), which should produce conservative results.

Thirdly, the accuracy and precision of the model's output is different for different populations. Survival in the first year at sea is the variable that explains most of the variance in estimates of 1SW returns, except for the Saint-Jean; it seems the model does not provide reliable parameter estimates for this population, which is the population with the highest proportion of 2SW returns. Furthermore, estimates of S_2 and P_g in all populations are negatively correlated and highly uncertain, and this must be considered when making any inferences based on these parameters for any of the populations examined, at least for those population appreciable contributions of 2SW salmon.

Lastly, our model does not differentiate mortality resulting from natural causes (e.g. predation) or from anthropogenic factors such as fishing or interactions with aquaculture. Fishing mortality has decreased significantly due to the sequential moratoria enacted across eastern Canada, and aquaculture, which has grown over recent decades, can negatively impact salmon survival through sea lice (Shephard and Gargan, 2021; Bøhn et al., 2020) or genetic introgression (Glover et al., 2017; Vollset et al., 2021). Thus, estimated trends in marine survival are confounded because we know marine survival will be reduced in years where commercial fishing occurred (i.e. pre-2000s), while the trends in aquaculture-related mortality are unknown. In other words, any increasing trends in marine survival are confounded by the additional fishing mortality before the turn of the century.

Perhaps a reframing of the issue of marine survival is key to furthering our understanding of Atlantic salmon population dynamics. Marine survival has not declined consistently, and over the same time periods, across all populations, even if the overall trend has been one of decline. But the fact that, for most of the populations examined, present-day survival fluctuates around levels similar to those that have occurred in the past, *despite* reduced commercial fishing mortalities, suggests that there may well be an interaction between small population size (small relative to unfished population size or carrying capacity), recovery potential, and environmental stochasticity that has not been fully explored in Atlantic salmon. All else being equal, relatively small populations are more vulnerable to demographic, environmental, and genetic stochasticity than large populations (Lande, 1993; Hutchings, 2015). Interactions between population size and the demographic consequences of environmental stochasticity appear to have affected recovery in many marine fishes that have exhibited impaired recovery since mitigation of the threat posed by fishing mortality (Hutchings and Kuparinen, 2017, 2020). The possibility that similar interactions may be impairing the recovery of wild Atlantic salmon merits study.

SUPPORTING INFORMATION

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

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