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Influence of dams on population persistence in Atlantic salmon (*Salmo salar*)

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Abstract

Barriers to migration can negatively affect population persistence. To explore how dams can influence the viability of a diadromous fish, we developed an empirically based stochastic model to estimate per capita population growth rate (r) and probability of population decline ($\Pr(r < 0)$). Our simulations incorporated life-history parameters common for many populations of Atlantic salmon (*Salmo salar* L., 1758), particularly in the southern part of the species range. Additionally, we explored the influence of individuals that reproduce more than once, i.e., ‘kelts’, on r and $\Pr(r < 0)$. For the life-history scenarios examined here, dams are forecast to negatively affect persistence, even at the comparatively high per-dam smolt survival rate of 90%. As the number of dams increases from one to four, the probability of negative population growth increases four-fold from 10% to 47%. Kelt survival rate, number of dams, and smolt dam-passage survival were all found to be significant factors in predicting population persistence. The present study suggests two primary conclusions: (i) dams are likely to have a negative influence on Atlantic salmon; and (ii) kelts have considerable and positive influence on population viability. Our work provides compelling support for the hypothesis that mortality attributable to dam facilities can adversely affect survival, persistence, and recovery of depleted migratory fish populations.

Keywords: viability, migration barrier, life history, per capita growth, kelt

Introduction

Threats to species persistence originate primarily as a result of human activity. Among the most prominent of these is anthropogenic habitat destruction or modification. Barriers to migratory species (e.g. dams or roads), whether partial or complete, represent a common form of habitat modification that can negatively affect individual movement and population persistence by increasing mortality rates and (or) by delaying migration (Riley et al. 2006; Acou et al. 2008; Marschall et al. 2011). Migration barriers can also prevent or alter gene flow between subpopulations (Riley et al. 2006; Holderegger and Di Giulio 2010; Crispo et al. 2011), having varying degrees of negative effects on population persistence and survival.

Mitigating the threats responsible for species decline is necessary to effect species recovery. However, it can be difficult to forecast consequences of mitigation measures with respect to persistence in the absence of empirically based, numerical projections of population viability. It was this challenge that motivated the present study on Atlantic salmon (*Salmo salar* L., 1758). The Atlantic salmon is an endangered species throughout its southern North American and European ranges (WWF 2001; Fay et al. 2006; COSEWIC 2011; Horreo et al. 2011; Nieland et al. 2013). At times, salmon in many of the affected rivers must pass by or through dams during their migration from fresh to salt water, an event that can negatively influence their survival (Stier and Kynard 1986; Marschall et al. 2011).

Dams can influence survival during and after dam passage. Short-term consequences during downstream movements have been well documented. Prominent among these are lethal injuries caused by turbine blades which can, in turn, depend on factors such as number of blades, blade speed, type of turbine, and rate of total discharge (NextEra 2011; Nieland et al. 2013). Indirect effects include increased predation due to predator aggregation around dams (Budy et al.

2002; Aarestrup and Koed 2003; Marschall et al. 2011; Nieland et al. 2013), physiological or behavioural stress (Budy et al. 2002), and delays in migration (Lundqvist et al. 2008; Marschall et al. 2011). Although the long-term consequences of dam passage on population viability are not well understood, there is reason to believe that they can be substantive. Budy et al. (2002), for example, attributed delayed mortality after dam passage in Pacific salmon to changes in pressure that smolts experience for periods as brief as 10 seconds when bypassing a hydroelectric dam. Other stressors associated with dam passage that might contribute to delayed dam-related mortality include the depletion of energy reserves required for downstream migration which can lead to decreased survival as well as increased susceptibility to predation and disease (Barton et al. 1986; Barton and Schreck 1987; Rieman et al. 1991; Budy et al. 2002; Marschal et al. 2011; Bailey 2013). The cumulative effects of stressors such as those identified above can, thus, lead to chronic stress and delayed mortality (Budy et al. 2002).

Our primary objective is to forecast population persistence of Atlantic salmon inhabiting rivers where dams are present. We develop a universally applicable model to estimate salmon per capita population growth rate (r) and probability of population decline in the presence and absence of dams, accounting for demographic stochasticity associated with population dynamics. While population persistence models (often in the form of population viability analyses) have been developed previously (e.g. Legault 2004), such models were population specific and a broadly applicable model has not yet been developed to estimate salmon population persistence across the species range. Additionally, the inclusion of dams within such a model has not been previously undertaken.

A secondary objective of the present study is to investigate the contribution of kelts (i.e. an individual who has previously spawned) to population persistence. Kelts have been shown to

have low or variable return rates (ranging from <1% to 40-60%; Ducharme 1969; Niemela et al. 2006; Hubley et al. 2008; USASAC 2011), varying levels of survival (Hubley et al. 2008), and it is uncertain exactly how their contribution to spawning might affect population persistence. The present study investigates the magnitude of kelt survival required to effectively influence population persistence.

Methods

Life history framework

The life history framework used here, including the associated parameter estimates, is intended to reflect, to the best extent possible, populations of Atlantic salmon within a considerable part of their southern North American range (Hutchings and Jones 1998). To achieve this, we utilize data on salmon inhabiting rivers flowing into the Gulf of Maine (GOM), U.S.A. There are two reasons for this. Firstly, the survival estimates quantified for dams in GOM rivers are among the very few currently available for Atlantic salmon dam passage. Secondly, the probabilities of population growth produced by the present simulations are intended to inform, in the general sense, persistence forecasts of endangered salmon that encounter dams during migration. The GOM Distinct Population Segment (GOMDPS) offers the best available data to inform such forecasts. Thus, the present study is intended to illustrate a general means of predicting how dams might affect population viability. The results should not be interpreted as providing comprehensive population viability analyses for GOM salmon.

Age-specific fecundity (m_x) and survival (l_x) were estimated for four developmental periods characteristic of the life history of salmon that spawn after spending two sea winters (2SW) in the ocean: 'egg to smolt'; 'smolt to 2SW adult'; '2SW adult to kelt'; and 'kelt to

return spawner' (Figure 1). For the purposes of our study, we have defined a smolt as an individual undergoing its initial downstream migration at 2.5 years of age. A kelt is an individual who has survived one spawning season and has migrated back to sea. A return spawner is a kelt who has survived to reproduce in a second spawning season. To introduce stochasticity into the life-history parameters, trait frequency distributions were created for each stage, based on empirical survival and fecundity data. A distribution was also created for the survival probability of fish passing through dams during downstream migration. All distributions were created with a Monte Carlo approach for which the generation of random deviates about a mean (using the R functions *rbeta* and *rnorm*) constitutes the basis for the life history distributions. For simplicity, the model is intended to explore the effects of dams on wild salmon for which survival is constant among generations. If desired, complexities such as temporal variability in marine and freshwater survival rates, or contributions by hatchery fish, could be incorporated in future analyses.

Life history parameter estimates

All parameter distributions were generated with 5000 draws of random deviates about a mean, regardless of the type of distribution (e.g. *rbeta* or *rnorm*). The resultant frequency distributions encompass parameter values that are empirically defensible for Atlantic salmon in the southern limit of their range (e.g., Hutchings and Jones, 1998). The fecundity parameter was represented by a lognormal distribution (Figure 2A). Utilizing a distribution for fecundity as opposed to a single value, and employing random sampling, helps to account for the natural variability in this parameter. To create the distribution, a normal distribution was first generated using the natural logarithm of the desired mean, 8500, the number of eggs per female reported by

USASAC (2011), and validated by work from Nieland et al. (2013). The standard deviation was calculated by setting the natural logarithm of 45000 (a maximum number of eggs for Atlantic salmon reported by Heinimaa and Heinimaa (2004)) as being two standard deviation units from the mean. The resulting difference, divided by two, of $\ln(45000)$ and $\ln(8500)$ was 0.8335, and was therefore the standard deviation. To create the lognormal distribution, we back-transformed the normal distribution using $\exp(x)$. The distribution was then limited to be between a minimum fecundity of 1500 and a maximum of 45000.

Estimates of survival between the egg and smolt stages are uncommon for salmon, based on the reviews undertaken by Bley and Moring (1988) and by Hutchings and Jones (1998). The only study cited by either for GOM salmon is the work of Meister (1962) who provided an estimate of 1.1% for salmon in Cove Brook, Maine. Based on egg-smolt survival data compiled for 12 rivers worldwide, Hutchings and Jones (1998) reported a median probability of surviving between the egg and smolt stages of 0.0137. However, here we considered only those estimates for the six populations nearest to the Gulf of Maine populations (Big Salmon River, Miramichi River, Pollett River, Rivière Bec-Scie, Rivière Saint-Jean, Rivière Trinité). The median ‘egg-to-smolt’ survival for these populations, as reported by Hutchings and Jones (1998), is 0.0177 and is the value used in our analysis. This value is very similar to other survival estimates for this stage (e.g. 1.31%; Nieland et al. 2013). Although egg-smolt survival can differ spatially and temporally, the published range in estimates is usually no greater than 5% (e.g. 0.38% to 3.20%; Bley and Moring 1988).

Survival during the ‘egg-to-smolt’ stage was defined by the median of a lognormal distribution (Figure 2B), which was chosen because the survival distribution for this stage is not uniform and approximates log-normality (Legault 2004). The remaining life stages were defined

by a beta distribution (Figure 2C-F), similar to that used by Hutchings (1999) in a study of life-history variability in Atlantic cod (*Gadus morhua* L., 1758):

$$(1) \quad f(x) = \frac{(x/s)^{(a-1)}(1-(x/s))^{(b-1)}}{\Gamma(a)\Gamma(b)/\Gamma(a+b)}$$

where $\Gamma(b)$ is the Gamma function and the scale parameter, s , establishes the upper bound of the distribution at 1.0. The means of the distribution were set to age-specific survival probabilities (i.e. values of l_x) by $mean=a/(a+b)$, where a and b are shape parameters for beta distributions. This distribution appropriately constrains the survival parameter estimates between 0 and 1. The mean survival for each life stage before encountering dams (i.e. values of s_x) was based on stage-specific values either estimated from or reported in the literature. The ‘smolt to 2SW adult’ stage survival (expressed as a proportion) was set at 0.0083, based upon the average annual estimate for wild salmon smolts emigrating from the Narraguagus River, USA during the years 1999 to 2008 (see Figure 1.1.3 in USASAC 2011). Given a general paucity of survival data for the ‘smolt to 2SW adult’ stage, the use of 0.0083 in our analyses has a defensible empirical basis.

Survival estimates for the kelt stage (i.e. ‘2SW to kelt’ stage) and beyond are exceedingly limited. Given this empirical reality, we set the mean overwinter survival of post-spawning one sea-winter (2SW) fish to the kelt stage at 0.63, as reported by Chadwick et al. (1978). Once kelts have re-entered the ocean, they are assumed to experience an 80% survival rate (i.e., the ‘kelt to return spawner’ stage) prior to their return to the river to spawn for a second time. Although there are no published data on survival during the at-sea phase for kelts, we feel our value of 0.8 can be justified. For example, multiplying 0.63 (see above) by 0.8 yields a survival value of 50% for individuals from the time that they spawn until they return to the river the following year.

This percentage is encompassed by the upper range of return rates reported by Atlantic salmon kelts which range overall from <1% to 40-60% (Ducharme 1969; Niemela et al. 2006; Hubley et al. 2008; USASAC 2011). In addition, given the absence of empirical data, we vary kelt survival in a sensitivity analysis, the results of which are reported below. A summary of all life stage survival rates can be found in Table 1.

Each of the stage-specific estimates of survival (s_x) was used to calculate l_x , the probability of surviving from birth until the beginning of age x (e.g. for the '2SW adult to kelt' stage: $0.00015 \times 0.63 = 9.26 \times 10^{-5}$; Table 1). Thus, the survival means were set to 0.0015 for the 'smolt to adult' stage, 9.26×10^{-5} for the 'adult to kelt' stage, and 7.40×10^{-5} for the 'kelt to return spawner' stage (Table 1).

Influence of dams on survival

Mark-recapture estimates of survival for smolts as they pass by and (or) through dam facilities are available for salmon inhabiting the Kennebec and Androscoggin GOM rivers (NextEra 2011). The average whole station survival (that is, the total survival experienced at an individual dam) was estimated to be 87%, based on an initial injury rate model (where survival is based on one-hour empirical injury data and one-hour empirical turbine survival data). These 'initial' injuries include scale loss, gill damage, severed body/backbone, and bruised head or body (NextEra 2011), all of which can be expected to result in an increased likelihood of death. In addition to this average value, the high (90%) and low (83%) estimates (represented by Brunswick and Weston dam projects, respectively) of survival documented by NextEra (2011) were also used in our simulations. The DPS values estimated from NextEra (2011) and used here are based on hydroelectric dams that utilized spillways and downstream bypasses for radio-

tagged fish passage, and also incorporated turbine damage in the estimation. Their models were constructed with a spill rate of 50% and a 50% flow exceedance value (i.e. the percentage of time flow through the dam is exceeded). The means of the beta distributions in our simulations ($n=5000$) for the survival of smolts and post-spawning kelts during their downstream passage by dams were, thus, set to 0.90, 0.87 and 0.83. There is some concern that kelts may experience a lower DPS than smolts. Although comparable data are not available for Atlantic salmon, Wertheimer and Evans (2005) found that steelhead (*Oncorhynchus mykiss* Walbaum, 1792) kelts experience a similar dam passing efficiency through hydroelectric dams as smolts. Comparing our values with absolute estimates for steelhead, Colotelo et al. (2013) have reported DPS rates for steelhead kelts in the Columbia River ranging between 0.895 and 0.996. Based on these limited comparative data, our range of survival estimates should ensure an empirically reasonable representation and allow for uncertainty regarding actual dam-passage survival probabilities (which can vary between dams and with rates of water flow; Nieland et al. 2013). One of the three survival frequency distributions is presented here for illustration (Figure 2F).

Population growth rate estimation

To estimate the per capita population growth rate, r , frequency distributions were created by randomly drawing a value from the life stage survival (l_x) and fecundity (m_x) distributions as well as the DPS distributions (which were incorporated as another l_x value) where applicable (Figure 2) according to the equation:

$$(2) \quad r = \ln(R_0)/G$$

where R_0 is the net reproductive rate and G is generation time. This in turn corresponds to (Gotelli 2008):

$$(3) \quad r = \frac{\ln(\sum l_x m_x)}{(\sum l_x m_x x) / (\sum l_x m_x)}$$

This calculation was repeated 10,000 times to produce frequency distributions of r for each dam scenario. The net reproductive rate, R_0 , was also calculated, but due to similarity between these outcomes and those for r , only the results for the latter parameter are presented here.

Effect of dams on probability of population decline

To incorporate the effects of dams on r , the DPS distribution was added as a separate l_x variable in the calculation of $l_x * m_x$ (see Table A1 for example calculation). We assumed DPS varied only for the life stages that encounter dams during downstream migration (i.e. ‘smolt to 2SW adult’ and ‘2SW adult to kelt’); other life stages were assumed to experience a DPS of 1. We also assumed that dam survival is constant and independent of the number of dams passed by a fish, that is, the passing of one dam does not influence the survival of passing a second, or third dam. This assumption is supported by work in the Columbia River which showed no difference in smolt survival between rivers with numerous dams and rivers with very few or no dams (Welch et al. 2008; Rechisky et al. 2013). Note that the fish released in Rechisky et al.(2013) were larger in order to accommodate acoustic tags and there is debate surrounding the interpretation of these results (Welch et al. 2008; Haeseker 2013; Hilborn 2013; Rechisky et al. 2013). This addresses another of our assumptions: that the age and size of salmon passing dams had no effect on their survival. There is contrasting evidence surrounding this topic; however there is a positive relationship between survival to adulthood and juvenile length in steelhead salmonids (Evans et al. 2014) and thus the survival of larger fish (e.g. kelts) is likely to be higher than that of smaller fish (e.g. smolts) when passing dams.

Five scenarios (presence of zero, one, two, three or four dams) were examined by incorporating the influence of dams on the l_x parameter estimates. For example, in a river containing a single dam, the survival for the smolt to 2SW stage would include a value obtained from the l_x survival distribution and a value obtained from the DPS distribution. Similarly, the 2SW adult to kelt stage would include two DPS values multiplied by the l_x survival value because at this life stage the salmon would have encountered the same dam twice, once during its migration downstream as a smolt and again when it migrates downstream following spawning. (Note that DPS is only incorporated at these life stages because it is assumed that upstream migration survival is not affected by dams because of the common inclusion of measures to mitigate upstream passage, such as fish ladders or the relocation of migrating stock by humans.)

Based on the r frequency distributions, the probability of population decline, $P(r < 0)$, was estimated by calculating the ratio of r values less than zero divided by the total number of r values (i.e. 10 000).

Influence of kelts

The influence of kelts on population persistence was examined to evaluate the importance of kelts as population contributors. The probability of $r < 0$ was estimated as described above for a model including kelts, however no DPS values were included in this model. The 'kelt to return spawner' stage was then removed from the model by setting survival for this stage to zero, and $P(r < 0)$ was estimated again to compare probabilities of decline in the presence or absence of kelts.

To acknowledge the lack of empirical basis for setting our kelt survival at 0.80, we performed a sensitivity analysis to determine how the model responded to varying levels of kelt

survival. The probability of population decline was calculated for 24 scenarios where kelt survival was set at one of eight values: 1.0, 0.8, 0.5, 0.3, 0.2, 0.1, 0.05, or 0.01. Dam-passage survival for dams (ranging from 0 to 4) was also included and was set at 0.90, 0.87, or 0.83. To test for significant differences among kelt survival scenarios, a one-way ANOVA test was used, followed by Tukey's HSD post-hoc test.

Stochasticity

In order to address the concern that the results might be dependent on the levels of stochasticity chosen, the expected values of r were compared between stochastic and deterministic models. To create the deterministic model, the same life table approach was taken. However, instead of using a distribution set around a mean for survival and fecundity, a single l_x or m_x value was used to calculate r (i.e. Table A1). The results were not significantly different between deterministic and stochastic models and thus this comparison will not be discussed further; a table of the results for the deterministic model is presented in Table A2.

Results

Effect of dams on probability of population decline

The presence of dams is predicted to have a considerable and negative influence on Atlantic salmon population persistence (Table 2, Table 3). Three of twelve scenarios that included kelts in the model produced a probability of decline greater than 50%; 6 of 12 produced probabilities greater than 40%. When kelts were excluded from the model, 11 of 12 scenarios produced probabilities of decline greater than 50%. The presence of kelts always improved the likelihood of persistence, reducing probability of decline by 8-27% (Table 2). However, their positive influence weakened as the number of dams increased or DPS decreased. Interestingly,

for scenarios in which the kelt stage was included and dams were absent, the probability of population decline was very low (14%).

The frequency distributions of r shifted 'left' to lower values as the number of dams increased from one to four and DPS probabilities decreased from 0.90 to 0.83 (Table 2, Table 3, Figure 3), corresponding to an increased frequency of negative population growth. The distributions also become increasingly wider and skewed as the number of dams increases (Figure 3). The mode of the distributions are either zero or positive, with the exception of two scenarios for which the mode is negative (DPS of 0.87 and 0.83 with four dams). Similarly, the medians are all positive with the exception of three scenarios for which DPS is 0.87 and there are four dams, and where there is a DPS of 0.83 with three and four dams (medians range from 0.160 to -0.092). This suggests not only an increase in the probability of population decline in the presence of multiple dams, but also an increase in the likelihood of rapid population decline.

The one-dam scenario with the highest dam survival (i.e. 0.90) was associated with a probability of population decline that increased from 22% to 47% when the number of dams increased to four (Table 2). The probability of decline for the intermediate dam survival scenario (i.e. 0.87) increased from 24% in a river with one dam to 55% in a river containing four dams. In the scenario with the lowest dam survival (i.e. 0.83), the probability of population decline increased from 28% in a river containing one dam to 68% in a river containing four dams.

Influence of kelts

Model results were sensitive to inclusion of the kelt stage in the salmon life history. The removal of kelts from the 'no-dam' scenario caused a greater than three-fold increase in the probability of decline (14% to 43%; Table 2), underscoring the contribution of post-spawning

salmon to population viability. The removal of kelts from scenarios including dams also caused large increases in probability of decline, particularly for the one- and two-dam scenarios. As the number of dams increased from 0 to 4, the exclusion of kelts appeared to have a consistent but decreased effect on probability of decline. For example, in a four-dam scenario with 0.90 DPS, the probability of decline increased from 0.47 when kelts were included to 0.69 when kelts were excluded. In a one-dam scenario with 0.90 DPS, the probability of decline increased much more drastically – from 0.10 with kelts included to 0.44 without kelts.

Given the model output reported in Table 2, it is perhaps not surprising that the probability of population decline was somewhat sensitive to kelt survival (Table 4). $P(r < 0)$ increases with increases in kelt mortality (Figure 4). For example, in a one-dam scenario with DPS of 0.90 and 100% kelt survival, the probability of decline is only 0.18. This probability increases to 0.49 when kelt survival drops to 0.01. At moderate levels of kelt survival (i.e. 0.50 to 0.20), probability of decline ranges from 0.30 to 0.41. A one-way ANOVA test was used to compare across levels of kelt survival and significant differences were found ($p\text{-value}=0.01e-6$). Results from Tukey's HSD test (Figure 5) showed that eight comparisons were significantly different from zero: kelt survival of 0.01-0.8, 0.01-1, 0.05-0.8, 0.05-1, 0.1-0.8, 0.1-1, 0.2-1, and 0.3-1. However all comparisons have overlapping confidence intervals, suggesting that probability of decline may not change significantly as kelt survival varies.

Discussion

The stochastic simulations presented here support the hypothesis that dams can negatively influence population persistence. For Atlantic salmon having life-history parameters similar to those in our simulations, the presence of a single dam is predicted to increase the

probability of population decline by nearly one order of magnitude when compared to a no-dam scenario (Table 2). In the presence of 3 or 4 dams – experienced by some endangered salmon at the southern edge of the species' North American range (NMFS 2009) – the probability of population decline exceeded 30% for all scenarios considered here. Our simulations also underscore the very considerable importance that the kelt stage can have on population viability.

The parameter values used in our simulations have substantive empirical support. The life history considered here is typical of Atlantic salmon near the southern limit of the species' North American range (Hutchings and Jones 1998; USASAC 2011; Nieland et al. 2013). Our range in dam-passage survival probabilities (0.83-0.90) encompasses the range for the injury-rate model reported by NextEra (2011). In a related species (steelhead), Colotelo et al. (2013) has reported DPS values ranging between 0.895 and 0.996.

There is reason to believe that our estimates of the effects of dams on population viability might be conservative. We assumed that individuals experience 100% survival during upstream migration past dams because of mitigative measures (e.g., fishways, transportation of fish). There is evidence that this might not always be the case. Roscoe et al. (2010) found that about half of the upstream-migrating sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) released upstream of a dam did not reach spawning grounds. Lundqvist et al. (2008) documented a 70% average loss of potential Atlantic salmon spawners during upstream passage by dams in Sweden. In addition, several studies (Wilson et al. 1991; Gowans et al. 1999; Naughton et al. 2007; Hartvich et al. 2008; Lundqvist et al. 2008; Roscoe et al. 2010) have indicated that fishways and spillways vary in their efficiency for allowing dam passage, and have associated survival costs for fish (e.g. energy depletion, migration delays). The movement of fish past a dam by trucking can also have impacts on migrating species because of handling and (or)

transport stress in addition to premature entry into the environment (Budy et al. 2002; Roscoe et al. 2010). It is, therefore, likely that the results presented in the present study would show a left shift in the per capita population growth distributions (Figure 3) and an increase in the probabilities of population decline.

The modelling undertaken here would be strengthened by further research that more accurately estimates the survival of Atlantic salmon at each life stage, particularly marine survival stages which may contain many more factors than the scope that this study addresses (e.g. changes to seawater, predation, fishing mortality, etc.), and the survival associated with dam passage. Survival correlates in one river need not be applicable to another river (Bley and Moring 1988). The dam survival estimates used here were based on an injury-rate model for whole station survival and did not take into consideration delayed mortality associated with dam-passage. The inclusion of delayed dam-associated mortality in the model would be beneficial and offer further insight into the effects of dams on salmon population persistence.

Atlantic salmon are at historically low levels of abundance throughout the southern part of the species' North American distribution. This renders the depleted populations extremely vulnerable to any anthropogenic or natural factor that negatively affects survival. As a consequence of this demographic fragility, and based on the results of the stochastic modelling presented here, it seems clear that dam-related mortality experienced by downstream migrating smolts and kelts, as well as mortality of returning adults, can adversely affect the survival and the prospects for population recovery. Given that dam removal is not always a feasible option, we recommend efforts to increase survival rates for early life stages by incorporating modifications to dams such as bypass systems and spillways (Muir et al. 2001; Wertheimer 2007) or by altering dam discharge timing (Harnish et al. 2013).

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Table 1. Stage-specific survival (s_x) and survivorship from birth to each life stage (l_x) for the Atlantic salmon (*Salmo salar* L., 1758) life history examined here. All survival values are presented as proportions.

Stage	Age (x)	s_x	Source	l_x
Egg to smolt	2.5	0.0177	(see text; Hutchings and Jones 1998)	0.0177
Smolt to 2SW	4	0.0083	(see text; USASAC 2011)	0.00015
2SW to kelt	4.5	0.63	(Chadwick et al.1978)	9.26E-5
Kelt to 2S*	5	0.8	(see text)	7.40E-5
Passage by dam	4 & 4.5	0.90, 0.87, or 0.83	(Next Era 2011)	--

* 2S = return spawner

Table 2. Probability of population decline ($P(r < 0)$) for Atlantic salmon (*Salmo salar* L., 1758) inhabiting rivers having 1 to 4 dams for a range of dam-passage survival rates. A no-dam scenario is also presented along with the inclusion or exclusion of kelts.

Kelt stage part of life history	Number of dams in river	Dam-passage survival probability			
		1.00	0.90	0.87	0.83
Yes	0	0.14	--	--	--
	1	--	0.22	.24	0.28
	2	--	0.30	.35	0.42
	3	--	0.39	.46	0.56
	4	--	0.47	.55	0.68
No	0	0.43	--	--	--
	1	--	0.49	0.51	0.53
	2	--	0.53	0.57	0.62
	3	--	0.58	0.63	0.69
	4	--	0.63	0.69	0.76

Table 3. The mean value of r for Atlantic salmon (*Salmo salar* L., 1758) inhabiting rivers having 0 to 4 dams for a range of dam-passage survival rates under a stochastic model..

Kelt stage	Number of dams	Per capita population growth (r)			
		1.00	0.90	0.87	0.83
Yes	0	0.16			
	1		0.12	0.11	0.09
	2		0.08	0.07	0.03
	3		0.05	0.02	-0.03
	4		-0.01	-0.03	-0.09
No	0	0.04			
	1		0.00	-0.01	-0.03
	2	-	-0.03	-0.06	-0.08
	3		-0.07	-0.09	-0.14
	4	-	-0.10	-0.13	-0.20

Table 4. Probability of population decline ($P(r < 0)$) at range of values for kelt survival and dam-passage survival by Atlantic salmon (*Salmo salar* L., 1758).

Kelt survival	Dam-passage survival & number of dams												
	1.0	0.90				0.87				0.83			
	0	1	2	3	4	1	2	3	4	1	2	3	4
1.0	0.11	0.18	0.26	0.34	0.42	0.20	0.31	0.41	0.52	0.24	0.37	0.52	0.64
0.8	0.14	0.22	0.3	0.39	0.47	0.24	0.35	0.46	0.55	0.28	0.42	0.56	0.68
0.5	0.22	0.30	0.37	0.46	0.52	0.33	0.42	0.53	0.61	0.35	0.49	0.61	0.71
0.3	0.30	0.38	0.45	0.51	0.57	0.39	0.48	0.57	0.64	0.43	0.54	0.64	0.73
0.2	0.33	0.41	0.47	0.54	0.58	0.43	0.52	0.58	0.65	0.46	0.57	0.67	0.74
0.1	0.45	0.45	0.51	0.57	0.63	0.47	0.54	0.61	0.68	0.50	0.59	0.67	0.75
0.05	0.40	0.48	0.52	0.57	0.62	0.49	0.55	0.62	0.67	0.52	0.61	0.68	0.75
0.01	0.42	0.49	0.54	0.60	0.63	0.49	0.57	0.63	0.69	0.52	0.61	0.69	0.76

Figure 1. Timeline of Atlantic salmon's (*Salmo salar* L., 1758) life cycle; the presence of dams are indicated where they would be encountered in the life cycle during migration downstream. Age in years is indicated for each life stage and correlate with the age-at-stage indicated in Table 1. Adapted from the Atlantic Salmon Federation (2012). *2S = return spawner.

Figure 2. The survival parameter distributions. A: Lognormal distribution for Atlantic salmon (*Salmo salar* L., 1758) fecundity; median = 8500, CV of 15%; $n=5000$. B: Lognormal distribution for Atlantic salmon survival estimates for the egg to smolt stage; $n = 5000$, median = 0.0177. C: Beta distribution for survival estimates for the smolt to 2SW stage; mean = 0.00146, $n = 5000$. D: Beta distribution for survival estimates for the 2SW to kelt stage; mean = 0.0000926, $n=5000$. E: Beta distribution for survival estimates for the kelt to return spawner stage; mean = 0.0000740, $n=5000$. F: Beta distribution for survival estimates of fish travelling through dams; median = 0.90, $n=5000$. Note that distributions were also created for dams with survival probability means of 0.87 and 0.83 but are not shown here.

Figure 3. Frequency distributions for the per capita population growth rate (r) of an Atlantic salmon (*Salmo salar* L., 1758) life history that includes kelts for different dam scenarios (0, 1, 2, 3, or 4 dams; indicated on the left), and dam-passage survival probabilities (0.90, 0.87 or 0.83). The distributions represent the outcomes produced from 10,000 runs of the stochastic model described in the text. The red vertical line corresponds to $r=0$.

Figure 4. A) Boxplot of the probability of decline ($P(r<0)$) as kelt survival decreases across all dam scenarios. B) Plot of the mean probability of decline under different kelt survival

scenarios and number of dams. Each colour represents a different DPS scenario, and point shapes represent different numbers of dams.

Figure 5. Plot of Tukey's HSD test results for differences between mean r produced from various levels of kelt survival ("KELT").

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FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4

FIGURE 5