Could bigger be better? Longer Atlantic salmon smolts seem more likely to return as adults

Stephen D. Gregory[1]

[1] Salmon & Trout Research Centre, Game and Wildlife Conservation Trust, UK

E-mail for correspondence: `sgregory@gwct.org.uk`

Abstract: Atlantic salmon stock declines are thought to be due to climate-driven changes in the marine environment that have rendered it hostile to migrating smolts. Recently, there has been a growing sense that factors affecting smolts during their development, i.e., in the freshwater environment, might play a larger role than previously judged. It has been hypothesised that smolt size is related to their marine survival, i.e., that larger smolts are better able to survive at sea than their smaller counterparts. With a large database of individual smolt capture histories and characteristics, I test the "bigger is better" hypothesis for Atlantic salmon smolts inhabiting the river Frome in Dorset, UK. By fitting and comparing multi-state mark-recapture state-space models with different covariates, I show support for the "bigger is better" hypothesis in these data, i.e., that longer smolts are more likely to return as adults compared to smaller smolts. This suggests that freshwater environments could be managed to maximise smolt quality (e.g., length) and thereby the numbers of returning adults.

Keywords: multi-state mark-recapture state-space model; smolt length; individual covariates; group covariates.

1 Introduction

Atlantic salmon *Salmo salar* stocks are declining (ICES, 2017). For a long time, the finger of blame has been pointed at the marine environment, where climate change and the processes it influences, such as spatial and temporal variation in algal blooms (Beaugrand and Reid, 2012), are thought to have rendered the environment hostile to seaward-migrating juveniles, known as smolts. More recently, however, there has been a growing sense that factors affecting juveniles during their development, i.e., in the fresh-

This paper was published as a part of the proceedings of the 33rd International Workshop on Statistical Modelling (IWSM), University of Bristol, UK, 16-20 July 2018.

water environment, might play a larger role than previously judged (Russell et al., 2012).

Myriad extrinsic and intrinsic factors, such as water temperature and body length (respectively), are thought to affect juvenile salmon development (for a review, see Russell et al., 2012). Among intrinsic factors, it has been long postulated that smolt mortality is inversely related to their body size, i.e., the inverse-weight hypothesis (Ricker, 1976). Many studies have provided some empirical evidence testing this "bigger is better" paradigm, which are reviewed in Gregory et al., (2018). For example, Armstrong et al. (2018) used individual-level data, together with covariates and their interactions, to show that the probability of adult salmon return was related to smolt size. However, in a review of studies that assessed the effect of salmonid smolt length on their subsequent survival, Gregory et al. (2018) found limited support for the "bigger is better" hypothesis.

In this paper, I use capture histories and characteristics of over 1500 smolts to parameterise multi-state mark-recapture state-space models, admitting individual- and group-level covariates, and compare their fits using model selection to measure the support for an effect of Atlantic salmon smolt length on their probability to return as an adult.

2 Methods

Since 2011, the Game and Wildlife Conservation Trust has been monitoring the seaward migration and adult return of a large sample of Atlantic salmon smolts on the river Frome in Dorset, UK, using Passive Integrated Transponders (PIT), an array of PIT detection antennae and a rotary screw trap (RST) (Figure 1). Each autumn, approximately 10,000 juvenile salmon are marked with a PIT tag and returned to their place of capture. Throughout the following spring, an RST is operated 24h per day to capture and measure a sample of emigrating smolts and monitor changes in their lengths. All smolts are processed within 30mins of capture and returned to the river $\approx$ 50m downstream of the RST within an hour of capture. All of the aforementioned procedures are carried out under a UK Home Office project license. Adult returns are collected passively on two PIT antenna approximately 3km apart, which are used as primary detection and secondary re-detection devices in a mark-recapture experiment to estimate the probability of adult return while accounting for imperfect detection. Approximately 97% of river Frome smolts emigrate one year after emerging from their gravel nests, and I limited samples to these individuals to reduce any potential effect of different life strategies of older (and larger) smolts.

Using these data, I parameterised multi-state mark-recapture state-space models (SSM) to explore the effect of smolt length on the probability to return as an adult. State-space models have the advantages of separating

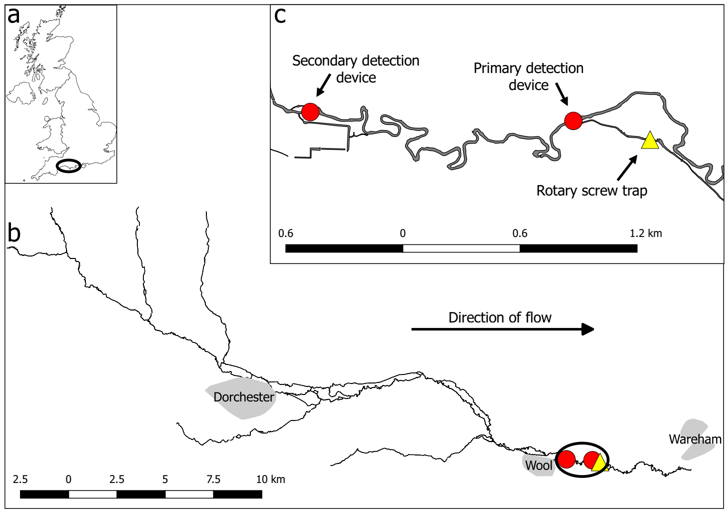

FIGURE 1. A map showing (a) the location of the river Frome in the UK, and the locations of the detection devices and the trap (b) in the catchment and (c) on the river.

the ecological process from the observation process. In this way, I could investigate the effect of length on the ecological process, i.e., survival, while making no assumptions about the observation process, i.e., detection. Moreover, when specified in a Bayesian language, such as BUGS or stan, SSMs are highly flexible and admit many types of covariates as fixed or random effects.

In the simple case of estimating the effect of individual smolt length on its probability to return as an adult, then:

$$\begin{aligned} y_{(i,t)}|z_{(i,t)} &\sim \text{Bernoulli}(z_{(i,t)}p) \\ z_{(i,t+1)}|z_{(i,t)} &\sim \text{Bernoulli}(z_{(i,t)}\varphi_i) \end{aligned} \tag{1}$$

where $t > 0$, z is a latent variable describing the state of smolt i at time t, φ_i is the survival rate of smolt i from state $z_{(i,t)}$ to state $z_{(i,t+1)}$ and y is the observation of smolt i given the probability p of detecting it. From these equations, it can be noted that φ_i and p are time-invariant and p does not vary for individuals. To estimate the effect of smolt i length l_i on its survival, φ_i is specified as a deterministic function of logistic regression parameters:

$$\text{logit}(\varphi_i) = \alpha + \beta \mathrm{l}_i \tag{2}$$

where α is the estimated probability to return as an adult for any smolt returning to the river and β is the effect of smolt i length on α while accounting for imperfect detection, i.e., $1 - p$.

I parameterised three SSMs: (1) a *null* model equivalent to Equation 1 with no effect of year or length on the probability to return as an adult; (2) a *year* model that included an effect of year, represented as annual deviations from the overall probability to return as an adult; and (3) a *length* model including both an effect of year and an overall effect of length on the probability to return as an adult.

Parameter values were estimated using `Stan` (http://mc-stan.org/) through the `R` interface in package `rstan`. Parameter values for each SSM were estimated using 3 parallel chains run for 2000 iterations including a 1000 iteration warmup that was discarded. All parameters were assigned weakly informative priors, i.e., Gaussian$(0, 1)$ or Uniform$(0, 100)$. For more details on estimation using `Stan`, see Stan Development Team (2017).

3 Results

Comparison of the SSM fits revealed the best support for the *length* model including a length effect and fixed year deviations (scaled approximate leave-one-out cross-validation estimate [looic]: 496.57), followed by the *year* model including fixed year deviations only (looic: 501.42) and then the *null* model omitting both terms (looic: 504.98). Moreover, the estimated parameter values and their lower and upper credible intervals were comparable between models (Table 1). Examination of fit diagnostics, include trace and autocorrelation plots, confirmed that all SSM fits were well-behaved.

TABLE 1. Table of estimated parameter values. The *null* model omits year and length terms; the *year* model includes the fixed year deviations; and the *length* model includes both fixed year deviations and an effect of individual length. Median estimated parameter values are presented with lower and upper credible intervals, respectively.

parameter	*null*	*year*	*length*
ϕ	0.034 (0.025 - 0.048)	0.029 (0.013 - 0.067)	0.026 (0.011 - 0.060)
ψ	0.730 (0.526 - 0.953)	0.717 (0.524 - 0.934)	0.725 (0.512 - 0.944)
p	0.714 (0.530 - 0.862)	0.720 (0.537 - 0.863)	0.721 (0.542 - 0.852)
β			0.449 (0.117 - 0.792)

My results suggest that an individual smolt's probability to return as an adult is a function of its length; the *length* model received substantially higher empirical support compared to the alternative models examined that omitted a length effect, and the 97.5% credible interval of the length effect parameter β that did not intercept 0 (Figure 2a).

It seems that the larger you are, the higher your probability to return as an adult. Moreover, the effect is not small: a smolt of approximately 16 cm is between 3 and 4 times more likely to return as an adult compared to 12 cm smolt (Figure 2b).

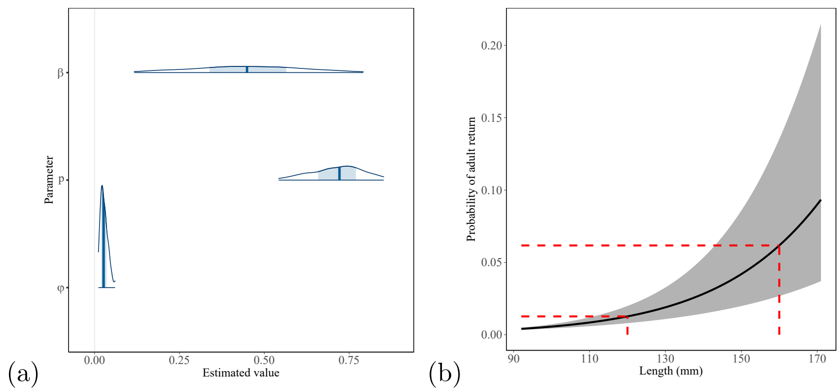

FIGURE 2. (a) Posterior density plots computed from posterior draws with all chains merged. The shaded areas under the curves highlight the 50% uncertainty range and the distributions are trimmed to the 95% uncertainty range. (b) Fitted effect of length on probability that an individual smolt will return as an adult. Grey ribbon represents the 50% uncertainty range of the fit. Note that length is standardised by subtracting the mean and dividing by 1 standard deviation. Dashed red lines highlight the probability that a 12 and 16 cm smolt will return as an adult.

4 Discussion

A long-standing prevailing hypothesis is that "bigger is better" among Atlantic salmon smolts, i.e., that larger smolts will have a higher marine survival and therefore a higher probability to return to their natal river as an adult to spawn. This hypothesis has, however, been untested, in large part because of insufficent or inadequate data to test it robustly.

Here, I show that smolt length is indeed related to the probability to return as an adult in these data. It seems that longer smolts are between two and three times more likely to return as an adult than shorter smolts. Aside from suggesting that bigger is indeed better among Atlantic salmon smolts, this finding has potentially important implications for their management; it is far easier to manage their freshwater habitats, i.e., rivers, than it is to manage their marine habitat, i.e., the nearshore coast or high sea. Accordingly, these findings suggest that we might manage smolt freshwater habitats to maximise their condition, here represented as length, to maximise the probability to return as an adult, i.e., to bolster declining adult salmon stocks.

An ability to improve the probability that an individual smolt will return as an adult could be particularly important in light of the observation

that Frome smolts (and possibly smolts elsewhere), like Atlantic salmon juveniles (Gregory et al., 2017) appear to be getting shorter.
We must, however, be cognisant of alternative factors; it is unlikely that their length at emigration is the only factor influencing their probability of adult return: marine conditions are undoubtedly deteriorating and the timing of salmon migrations are changing.

Acknowledgments: Special thanks to all the people who helped collect the data used in this study, including present and past members of the GWCT Fisheries Department, Cefas and the many volunteers who have given up their time to help the imperiled salmon population of the river Frome.

References

Armstrong, J. D., Mckelvy, S., Smith, G. W., Rycroft, P. and Fryer, R. J. (2018). Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon smolts. *Journal of Fish Biology*, **92**, 569 – 578.

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.

Gregory, S. D., Armstrong, J. D. and Britton, J. R. (2018). Is bigger really better? Towards improved models for testing how Atlantic salmon Salmo salar smolt size impacts marine survival. *Journal of Fish Biology*, **92**, 579 – 592.

Gregory, S. D. et al. (2017). Patterns on a parr: Drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. *Freshwater Biology*, **62**, 1117 – 1129.

ICES. (2017). *Report of the Working Group on North Atlantic Salmon (WGNAS), 29 March7 April 2017*, Copenhagen, Denmark. ICES CM 2017/ACOM:20. 296 pp.

Russell, I. et al. (2012). The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science*, **69**, 1563 – 1573.

Stan Development Team (2017). *Stan Modeling Language: Users Guide and Reference Manual*. Version 2.15.0.