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Predicting how environmental conditions and smolt body length when entering the marine environment impact individual Atlantic salmon *Salmo salar* adult return rates

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Abstract

Populations of Atlantic salmon *Salmo salar* have experienced precipitous declines in abundance since the 1970s. This decline has been associated with reduced numbers of adult salmon returning to freshwater from their marine migration, i.e., their marine return rates (MRR). Thus, understanding the factors that affect MRR is of crucial conservation importance. We used a state-space model with a 13-year time series of individually tagged salmon mark-recapture histories on the River Frome, southern England, to test the effect of smolt body length on their MRR. As well as smolt length, the model tested for the influence of environmental covariates that were representative of the conditions experienced by the smolts in the early stages of their seaward migration, i.e., from the lower river to the estuary exit. The model indicated that, even when accounting for environmental covariates, smolt body length was an important predictor of MRR. While larger smolts have a higher probability of returning to their natal river as adults than smaller smolts, and one-sea-winter salmon have a survival rate twice as high as multi-sea-winter salmon, the actual biological mechanisms underpinning this phenomenon remain uncertain. These results have important applications for salmon conservation, as efforts to bolster salmon populations in the freshwater environment should consider ways to improve smolt quality (i.e., body size) as well as smolt quantity.

Keywords: anadromous salmonid, body size, state space model, survival, temperature, sea bass

Introduction

Diadromous fishes undergo migration as an adaptive strategy to use resources across freshwater and marine habitats (McDowall, 2008). Whilst providing considerable life history advantages, this strategy is proving increasingly problematic in contemporary times, with populations of diadromous fishes declining in abundance across the world, including across the North Atlantic (Limburg & Waldman, 2009; Merg *et al.*, 2020; Tamario *et al.*, 2019). Disentangling the factors responsible for this decline is challenging, leading to uncertainty over optimal conservation management strategies (O'Connor & Cooke, 2015).

Populations of Atlantic salmon *Salmo salar*, an anadromous species native to northern Atlantic and Baltic river basins, have experienced precipitous declines in abundance since the 1970s (Chaput, 2012; ICES, 2020). These declines in salmon abundance have been principally associated with a reduction in return rates after their marine sojourn (Chaput (2012); marine return rate, MRR). The precise mechanisms responsible for this decline are still unknown, but a decline in the marine survival rate is considered to be a highly important factor in this decline (Chaput, 2012; Mills *et al.*, 2013; Olmos *et al.*, 2019). There is growing evidence suggesting these declines could in part be attributable to high mortality rates in the period during and shortly after they migrate to sea as smolts, where migration through lower river reaches and into estuaries and coastal waters is increasingly considered as a critical survival bottleneck, which might be due in part to more intense levels of predation than the fish experienced in their freshwater life-phase (Flávio *et al.*, 2021; Renkawitz *et al.*, 2012; Thorstad *et al.*, 2012).

Smoltification is a physiologically intense process, involving considerable changes in morphology (e.g., gaining silver colouration), physiology (e.g., osmoregulatory changes), and behaviour (e.g., schooling) (Thorpe *et al.*, 1998; Thorstad *et al.*, 2012). Timing of smoltification is also a

determinant for the success of seaward migration, as if smolts arrive at sea too early or too late they might be mismatched with their prey resources (Jonsson & Jonsson, 2014; McLennan *et al.*, 2018; Thorstad *et al.*, 2012). Smoltification is cued by changes in photoperiod and water temperature in the spring, with actual emigration dates also influenced by other factors, including temperature and precipitation levels that determine river discharge (McCormick *et al.*, 1998; Simmons *et al.*, 2021; Thorstad *et al.*, 2012). Smolt body size is also related to the timing of smolt migration, with larger smolts migrating earlier than smaller smolts (Simmons *et al.*, 2021).

Survival during the smolt emigration period ('smolt run') is sensitive to a range of extrinsic factors including river discharge rates that can affect migration speeds and water turbidity (Lothian *et al.*, 2018; Persson *et al.*, 2018), and water temperatures, where warmer river conditions and smaller temperature gradients between freshwater and the marine environment result in higher survival rates (Juttila *et al.*, 2005; Stich *et al.*, 2015). Evidence also suggests smolts tend to migrate through estuaries on an ebbing tide (Lefèvre *et al.*, 2013; Moore *et al.*, 1995, 1998). In the estuary, they are vulnerable to being predated by a wide range of piscivorous animals, including cormorants (*Phalacrocorax* spp.), grey seals (*Halichoerus grypus*), and sea bass (*Dicentrarchus labrax*) (Jepsen *et al.*, 2010; Mantyniemi *et al.*, 2012; Riley *et al.*, 2011).

Smolt survival during their marine migration is, however, also affected by intrinsic factors, such as smolt body size and growth rates. Marine growth rates are known to be closely linked with marine survival, such that faster growing individuals are more likely to survive than smaller conspecifics (Peyronnet *et al.*, 2007). Marine growth rates are autocorrelated with juvenile freshwater growth rates at an individual level (Einum *et al.*, 2002); thus, individual growth rates during the winter before smoltification may also inform subsequent marine survival. Several recent studies have suggested that relatively larger smolts have higher MRR versus smaller smolts

(Armstrong *et al.*, 2018; Chaput *et al.*, 2019; Gregory *et al.*, 2019). This ‘bigger-is-better’ hypothesis has been applied to many juvenile teleost fishes, with size selective processes, such as intolerance of environmental extremes and susceptibility to predation of smaller individuals, thought to be some of the driving factors (Sogard, 1997). However, many studies addressing this ‘bigger-is-better’ paradigm in Atlantic salmon smolts have had inherent issues, including small sample sizes, pseudoreplication in experimental design, and a lack of other explanatory covariates, which potentially limit their conclusions (Gregory *et al.*, 2018). The application of state-space models has been suggested as a robust way to test the effect of smolt size on MRR (Gregory *et al.*, 2018), as these models can separate the observation and process errors (Auger-Methe *et al.*, 2020; Gimenez *et al.*, 2007). While this approach was implemented in Gregory *et al.* (2019) and revealed that larger smolt body sizes did have a positive effect on MRRs, this model only used smolt body length as a covariate. It omitted other potentially important covariates, such as measures of the environmental conditions during the smolt run. As a result, there remain considerable knowledge gaps on how both intrinsic and extrinsic factors during the smolt run influence subsequent MRRs.

The aim of this study is to overcome these important knowledge gaps by implementing a multi-state capture-mark-recapture state-space model that evaluates the effect of *S. salar* smolt body length versus other factors on their subsequent MRR. We test the main hypothesis (Table 1) that smolt body length retains a strong positive effect on MRR when extrinsic factors are accounted for, as well as a series of secondary hypotheses about the expected influences of environmental conditions on MRR (see hypotheses in Table 1; Gregory *et al.* (2019)). For measures of extrinsic conditions, we focused on those likely experienced by the smolts in the lower river, estuary, and just outside the estuary, as this earliest phase of migration is typically considered an important survival bottleneck (Thorstad *et al.*, 2012). To do so, we use a 13-year dataset of individually

tagged *S. salar* from the River Frome, southern England, which comprises individual smolt body length and growth rate records and their recapture history (from tag detections) as returning adults, providing a strong dataset for hypothesis testing.

Methods

Smolt and adult data collection

The River Frome is a lowland, low-gradient, chalk stream in southern England. Since 2005, approximately 10 000 *S. salar* parr (generally age 0+ due to fast growth rates; Simmons *et al.* (2020)) have been captured and tagged each August and September at sites throughout the River Frome catchment by electric-fishing (pulsed DC with a square-wave waveform fished at 50 Hertz, ~200 volts and 25–30% duty cycle). In this sampling, captured individuals are anaesthetised (2-phenoxy-ethanol), measured (fork length, nearest mm), marked by the removal of their adipose fin, and then tagged with a passive integrated transponder (PIT) tag in their coelomic cavity (2005-2013: 12.0 x 2.12 mm full duplex PIT tag [Wyre Micro Design Ltd, Lancashire, UK]; 2014-2019: 12.5 x 2.03 mm full duplex PIT tag [Biomark, USA]). The following spring (between March and May), the emigrating age 1+ smolts are then re-sampled in the lower river to estimate the abundance of seaward emigrating smolt. This involves diverting the smolts into a small side-channel of the lower river at East Stoke (50.40.47°N; 02.11.2°W) using a bioacoustic fence. A rotary screw trap (RST), positioned within the side channel, then captures a sample of the smolts (Figure 1; Ibbotson *et al.* (2013)). From 2006 to 2013, the RST operated continuously over most of the duration of the smolt run (for dates, see Riley *et al.* (2018)). From 2014 onward, it only operated during periods when previous data suggested the *S. salar* smolts were most likely to be migrating, accounting for more than 12 hours a day for at least 35 days of each annual smolt run. During operation, the RST was checked for trapped fish every 30 minutes. All captured fish were removed from the trap, anaesthetised, checked for the presence of a PIT tag and measured (fork length, nearest mm). From 2006 to 2012, PIT-tagged smolts were also marked with a coded wire tag. They were then placed in a fresh container of water to recover normal behaviour before being

released downstream. Emigrating smolts typically spent 1 or 2 years at sea before returning as adults to the River Frome to spawn (although a small and therefore inestimable proportion is thought to stay for 3+ years).

The returning adults were detected on a continuously operating PIT antenna array located 8 km upstream of the tidal limit (hereafter, the first PIT antenna). A second continuously operating PIT antenna array was located 3.5 km further upstream (hereafter, the second antenna). The two successive detection devices allowed estimation of the returning adult detection probability (or detection inefficiency; Gregory *et al.* (2018); Gimenez *et al.* (2018)). The second antenna was not operational for the first 7 years of monitoring, during which time the probability of detecting a returning adult could not be estimated and was inferred in the model from the later years.

Model description

The model developed here was based on that originally developed by Gregory *et al.* (2019). It is a capture-mark-recapture state-space model, built at an individual level, which distinguishes the state (ecological) processes from the observation (detection) processes. The core assumptions of this model were:

1. The inter-annual and inter-individual variability of MRR results from the variability of fish survival during their first year at sea, and the survival of multi-sea-winter ('MSW') fish during their second year at sea will be constant, i.e., MSW MRR is equal to the 1-sea-winter ('1SW') survival, and MSW MRR is equal to the 1SW return rate times an additional constant term (constant between years and individuals) that captures the additional mortality caused by additional time spent at sea. Imposing a strong relationship between 1SW and MSW returns rates is needed because the sample size of observed adult returns was deemed too low to treat them separately (Gregory *et al.*, 2019).
2. All explanatory variables affect smolt survival in the early part of their migration to the sea, i.e., from the lower river to the estuary exit, and influence subsequent survival during the first year at sea.
3. The usual capture-mark-recapture assumptions apply, including that tags are not lost or damaged, that individuals represent an independent and random sample, and that individuals do not emigrate from the population (Cooch & White, 2011).

State process

The survival of smolt i during its first year y at sea, $\phi_{i,y}^{1sw}$, is modelled on the logit scale as a linear function of the MRR explanatory variables (Table 1):

Equation 1

$$\begin{aligned}\text{logit}(\varphi_{i,y}^{1sw}) &= \eta_{i,y} \\ \eta_{i,y} &= \alpha + \beta_y + \gamma \times X_i\end{aligned}$$

where $\gamma = \gamma_1, \gamma_2, \dots, \gamma_k$ is a vector of k parameters (fixed effects) relating the effects of a matrix of individual-specific explanatory variables $X_i = x_{i,1}, x_{i,2}, \dots, x_{i,k}$ on $\varphi_{i,y}^{1sw}$, while accounting for their year y of out-migration as a random effect, β_y .

To account for the additional mortality experienced by adults returning to the River Frome as MSW, the survival of smolt i to a MSW fish $\varphi_{i,y}^{msw}$ was directly calculated from $\eta_{i,y}$ by adding an additional mortality term δ :

Equation 2

$$\text{logit}(\varphi_{i,y}^{msw}) = \eta_{i,y} + \delta$$

All parameters in equations (1) and (2) were set uninformative priors:

$$\begin{aligned}\alpha &\sim \text{Normal}(\mu = 0, \sigma = 0.001^{-1/2}) \\ \beta_y &\sim \text{Normal}(\mu = 0, \sigma = \tau) \\ \delta &\sim \text{Student-t}(\mu = 0, \tau = 1, k = 2.5) \\ \tau &\sim \text{Gamma}(r = 0.001, \lambda = 0.001) \\ \text{for all } j \text{ in } j = 1, \dots, k, \gamma_j &\sim \text{Student-t}(\mu = 0, \tau = 1, k = 2.5)\end{aligned}$$

Any smolt i tagged and released in year y will return as 1SW or MSW fish and reach the first antenna, or will die at sea. This transition is modelled as a Categorical distribution with probability $\varphi_{i,y}^{1SW}$ (returns as 1SW and reached first antenna), $\varphi_{i,y}^{MSW}$ (returns as MSW and reached the first antenna) or $1 - (\varphi_{i,y}^{1SW} + \varphi_{i,y}^{MSW})$ (dies at sea).

Then, any returning fish, (1SW or MSW) that reached the first antenna will have the opportunity to survive and transit up to the second antenna, with probability ψ , considered constant over time and homogeneous among all individuals. This transition from the first to the second antenna is modelled as Bernoulli distribution with probability ψ , all fish being considered independent. ψ was given a Uniform prior distribution between 0 and 1.

Observation process

The observation process is only modelled at the return stage. All fish have the potential to be detected at the first antenna only, at the second antenna only, or successively at both antennas. All detection events at the first and second antenna are modelled as independent Bernoulli distribution with detection probability p , assumed to be the same for the two antennas, and considered constant in time and homogeneous among all individual. p was given a Uniform prior distribution between 0 and 1.

Explanatory variables

A literature review was used to identify variables potentially impacting smolt survival during and immediately after they emigrate to sea, and thus affect MRR (Table 1). To test their effects on MRR, explanatory variables were derived to represent these effects in three distinct areas, namely in the lower reaches of the River Frome (hereafter *River*), the River Frome estuary of Poole Harbour (hereafter *Estuary*) and the 1° by 1° area in the English Channel immediately outside Poole Harbour (hereafter *Nearshore*) (Table 1; Figure 1).

Several explanatory variables measured in the river were hypothesised to influence smolt MRR (Table 1). Individual springtime smolt body lengths were available, as described above. All smolt lengths were measured at their time of release following capture in the RST. It was assumed that smolts suffered no mortality between the point of release and their arrival in the estuary.

Individual overwinter growth rate of fish i was calculated as the difference between smolt and parr body lengths divided by the number of days between its recapture (the date when the smolt was captured in the spring in the RST) and capture (the date the same fish was captured as a parr during the autumn electric-fishing):

Because of the potential mismatch between the date of migration and favourable environmental conditions at sea, we tested the effect of the smolt migration timing on adult marine return rates. To complete this, the day of year (DoY) that each smolt was captured in the RST at East Stoke (Figure 1) was used as a proxy for migration timing. DoY was defined using the function `yday` from R package `lubridate` (Grolemund & Wickham, 2011).

As river discharge could affect migration speed and turbidity, and in turn survival rate, then discharge ($\text{m}^3\text{sec}^{-1}$) was recorded by the Environmental Agency every 15 minutes at two locations

on the River Frome (Figure 1) throughout the 13-year period and used to calculate a daily mean discharge for each DoY of the smolt run each year (National River Flow Archive, 2020).

As low dissolved oxygen is expected to have a negative effect on marine survival (Friedland *et al.*, 2017), it was used in the model from dissolved oxygen (mg l^{-1}) data from sporadic recordings taken in Poole Harbour (Figure 1), with monthly recordings for much of the study period. For months with more than one record, the monthly mean was calculated. For six months when there was no dissolved oxygen record, the data were imputed via the `impSeqRob` function of R package `rrcovNA`, which successively estimates the missing data in an incomplete dataset (Todorov *et al.*, 2011).

As studies have shown smolts to prefer to migrate through estuaries at an ebbing tide (Lefèvre *et al.*, 2013; Moore *et al.*, 1995, 1998), the time of each high and low tide throughout the study period in Poole Harbour was used in the model. These data were provided by the UK Hydrographic Office (UK Hydrographic Office). It was assumed that a smolt took 36 hours to migrate from the location of the RST to the tidal limit (C. Artero, unpublished data). Thus, it was determined whether the tide was ebbing or flooding 36 hours following the release of each smolt. This was included in the model as a binary fixed effect, where 0 = the smolt arrived at the tidal limit during an ebb tide and 1 = the smolt arrived during a flood tide.

In the nearshore, daily sea surface temperature SST data were extracted for a 1° by 1° grid from COBE-SST2 data provided by the NOAA/OAR/ESRL PSL (Hirahara *et al.*, 2014; NOAA, 2019) and formatted using the R package `raster` (Hijmans *et al.*, 2020). We included nearshore SST as a fixed effect in the model, as colder SST might negatively impact survival rates (Jutila *et al.*, 2005). We also used nearshore SST to calculate the temperature gradient between the river and

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nearshore area, as a smaller gradient might result in higher survival rates (Jutilla *et al.*, 2005). To do so, the river water temperature was recorded every 30 minutes just upstream of the RST (see Simmons *et al.* (2020) for details). These data were used to calculate a mean daily water temperature, and then the temperature gradient was calculated by subtracting the SST from the river water temperature for each smolt on the DoY of the smolt's capture in the RST.

To account for predation pressure, bass abundance was represented by annual September surveys of age 2+, 3+, and 4+ fish in the Solent, undertaken by the Centre for Environment, Fisheries, and Aquaculture Sciences. Annual abundances for the three age classes were summed to provide a single abundance index. While the Solent is located east of Poole Harbour on the south coast of England, we assumed that the population dynamics of sea bass in the Solent are related to sea bass in and immediately outside Poole Harbour, such that a year with a low sea bass abundance in the Solent would be reflected as a year of low abundance in and immediately outside Poole Harbour (Figure 1). We also assumed that the abundance of bass calculated from September surveys would reflect the abundance of bass during the previous spring when smolts were emigrating. There were two years when data was not collected for the sea bass survey, thus, data for these years were imputed via the `impSeqRob` function of R package `rrcovNA` (Todorov *et al.*, 2011).

All explanatory variables were *z*-standardised and assessed for collinearity (Pearson's correlation) before analysis (Figure S1). All variables were found to have $r < 0.7$, so were considered not collinear, and thus could be tested in the model together.

The effect of each covariate was assessed through the posterior distribution of its associated parameter γ . In lieu of performing model selection, we opted to interpret the full model to maximise biological realism while still testing support for our different hypotheses. Some model

simplification was trialed and confirmed that none of the effects crossing the no effect (0) line would be important when tested with different combinations of other variables.

MCMC simulations

The JAGS sampler (<http://mcmc-jags.sourceforge.net/>), run using R package rjags (Plummer, 2017), was used to estimate parameter values via MCMC. For data collected before the installation of the second PIT antenna (2006-2011), the log likelihood was estimated using only the state transition matrix by conditioning the observation transition matrix on a binary variable indicating which data were missing. There were 150 000 iterations of MCMC chains run, of which the first 50 000 were discarded as the burnin period. Parameter values at every 100th iteration were saved for inferences to limit auto-correlation in the MCMC samples. There were three parallel MCMC chains run for each analysis. The 95% Bayesian credible intervals were calculated for each parameter estimate. To assess convergence, MCMC trace plots were examined and the Gelman-Rubin convergence statistic was calculated for each parameter (Brooks & Gelman, 1998). These were considered stable if the chains were mixing and non-convergent, i.e., R ratio of the Gelman-Rubin test < 1.1 for all parameters. The effective sample size for each parameter was determined using the `effectiveSize` function from the R package `coda`.

Ethics Statement

Animal handling and processing procedures were reviewed by GWCT Animal Welfare & Ethical Review Body and were carried out by personnel working under the authority of U.K. Home Office A(SP)A Licences (current Project Licence: PPL 30/3277).

Results

There were 3922 PIT-tagged *S. salar* smolts captured in the RST between 2006 and 2018. Of these, 88 were re-detected as returning adults in the river, of which 59 were 1SW and 29 were MSW fish.

There was a temporal decline in the number of PIT-tagged salmon captured in the RST, with the maximum number captured in 2007 (602 smolts, of which 7 were detected returning as adults; Table 2) and the minimum in 2018 (137 smolts, of which 2 were detected returning as adults; Table 2). However, at least some of this decrease is likely related to the reduced trapping effort from 2014 (see Methods). The highest proportion of smolts detected as returning adults was 8.4% in 2016, whilst the lowest was 0.3% in 2008 (Figure 2).

The MCMC chains mixed well and converged, and the Gelman-Rubin convergence statistics and effective sample sizes for all parameters were less than 1.1 and more than 1000, respectively (Figure S2 and S3). Pairwise scatterplots of the posterior distributions of the fixed effects were examined and it was deemed that there were no strong correlations between the distributions (Figure S4). The 1SW survival rate parameter was almost twice that of the MSW survival rate parameter (Figure 3). The posteriors of both p (the probability of an adult being detected on the first PIT antenna) and ψ (the probability of an adult transitioning from first PIT antenna to the second PIT antenna) were different to their Uniform(0,1) priors (Figure 3) with posterior medians of 0.926 and 0.587, respectively. Of the explanatory variables in the model, only smolt body length had a non-negligible effect on MRR (Figure 3), and its effect on both 1SW and MSW return rate was positive, while accounting for the effects of all other hypothesised variables (Figure 4). Of the other explanatory variables, temperature gradient and SST had the largest effect sizes (although no effect [0] was within their credible effect sizes), where smaller temperature gradients and higher SSTs were associated with increased MRR (Figure 3). The year random effect estimates showed

no trend, were a mixture of positive and negative estimates, and most intercepted the no effect (0) line, except for 2016 that had a positive effect on MRR (Figure S5).

Discussion

This analysis of a 13-year capture-mark-recapture dataset of individually tagged River Frome *S. salar* smolts revealed a strong positive and significant effect of smolt body length on adult MRR, while accounting for the effects of other variables hypothesised to impact MRR and imperfect detection. These results add to the growing body of literature supporting the ‘bigger-is-better’ hypothesis, but unlike previous studies, the model used was also able to test this hypothesis while including a range of other explanatory variables (Armstrong *et al.*, 2018; Chaput *et al.*, 2019; Gregory *et al.*, 2019). All of these other explanatory variables had negligible effects on MRR for these years on the River Frome.

The early stages of estuarine and marine migration are typically considered to be a survival bottleneck for *S. salar* smolts (Thorstad *et al.*, 2012) and the results here suggest their survival in these environments is enhanced when their body sizes are relatively large (e.g. Gregory *et al.* (2019); Chaput *et al.* (2019); Armstrong *et al.* (2018)). The advantages of larger body sizes for smolt survival might be direct, such as providing them with advantages over smaller smolts through faster swimming speeds that facilitate their survival in the early migration (Remen *et al.*, 2016). Faster swimmers might, for example, be better able to avoid predators, as predation in early migration contributes to this survival bottleneck (Jepsen *et al.*, 2010; Riley *et al.*, 2011), or they might simply be able to move through dangerous areas more quickly (Thorstad *et al.*, 2012). Additionally, larger body sizes may be advantageous when predators are gape-limited, such as sea bass (Andrews *et al.*, 2019; Thorstad *et al.*, 2012). However, the advantages of large body sizes might be more complex, with larger sizes being a proxy of other biological differences between individuals, such as higher condition factors and lipid content in larger individuals that indicate a generally superior level of fitness (Armstrong *et al.*, 2018). Body size has also been linked to

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metabolic rates, whereby smaller individuals typically have higher metabolic rates. For example, in three different Finnish stocks of hatchery-reared *S. salar* post-smolts, individuals from one stock were shown to have higher metabolic rates, but lower condition factors than those from the other stocks (Seppänen *et al.*, 2009). This is potentially important, as not only could having a lower condition factor (indicating, perhaps, a lower overall fitness) be problematic for survival but it has also been shown experimentally that the higher metabolic rates of smaller salmon may increase susceptibility to adverse environmental conditions, such as hypoxia (Oldham *et al.*, 2019). Conversely, metabolic rate may be linked to their behavioural traits. In juvenile masu salmon *Oncorhynchus masu*, individuals with higher metabolic rates were more likely to display ‘dominant’ behaviours (Yamamoto *et al.*, 1998). Indeed, Yamamoto *et al.* (1998) found that in juvenile salmonids, juvenile body size was partially a consequence of dominance status, with dominance status being linked to metabolism. Perhaps, if smaller smolts have higher metabolic rates, and thus might be more likely to engage in more aggressive behaviours, they might be more likely to be ‘risk-takers’ (Grand, 1999), which could affect their probability of marine survival. However, in the River Frome, evidence suggests that smolts migrating at night are smaller (Simmons *et al.*, 2021), which is believed to be a predator avoidance tactic, so the link between body size and risk-taking behaviours may be nuanced.

Several of the extrinsic explanatory variables had relatively large effect sizes, even though the ranges of their 95% credible effect sizes overlapped no effect (0). Two of these, the temperature gradient between the river and nearshore and the sea surface temperature, had negative effects on MRR, where larger temperature gradients and colder nearshore conditions appeared sub-optimal for emigrating smolts. This could be caused by additional physiological stress caused by a greater difference in marine temperatures and riverine temperatures (Juttila *et al.*, 2005). Another extrinsic

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variable with a relatively large effect size was sea bass abundance, a species known to predate on *S. salar* smolts (Riley *et al.*, 2011) and that can be dietary specialists at an individual level, despite being generalists at population levels (Cobain *et al.*, 2019). Riley *et al.* (2011) found that sea bass stomach contents from the tidal River Frome included salmonid smolts, though whether the prey were *S. salar* or *S. trutta* was difficult to determine. However, the bass predated on salmonid smolts from that study were age 10+, so it is likely that bass older than those for which abundance data was available in the current investigation are also important predators of salmonid smolts. Abundance data from these older age classes would, therefore, make a useful addition to this model. Data on predator abundance of different species, particularly cormorants (Jepsen *et al.*, 2019; Ovegård *et al.*, 2021), would also be a useful future addition. The effect of overwinter growth rate on MRR was negative with a similar magnitude as the effect of bass abundance. Previous work on *S. salar* has suggested freshwater growth prior to smoltification is correlated with marine growth, with slower growing juveniles exhibiting faster marine growth rates, which suggests that the traits that encourage fast growth in freshwater may not encourage fast growth at sea (Einum *et al.*, 2002). With faster marine growth rates linked to better marine survival in *S. salar* (Peyronnet *et al.*, 2007), our results suggest individuals that grow more slowly prior to smoltification then grow more rapidly at sea, as they are more likely to survive their marine migration. However, as the 95% credible intervals of this parameter estimate cross the no effect line (0), the relationship between freshwater growth, marine growth, and marine survival may be more nuanced. Indeed, in other salmonid species (*Oncorhynchus kisutch*, *O. mykiss*, and *O. tshawytscha*) weak positive relationships have been observed between freshwater and marine growth rates (Johnsson *et al.*, 1997; Ruggerone *et al.*, 2009). Therefore, more work is required to better understand this relationship for *S. salar*.

The explanatory variables used in the model were selected following the design of hypotheses following a review of literature on *S. salar* survival in estuaries and nearshore areas. Despite this, none of the explanatory variables, other than smolt body length, had a strong effect on MRR. This might be because the values of these variables in the years of this study were not extreme enough to impact MRR. Alternatively, the effect of body length demonstrated here could have been particularly strong under the specific environmental conditions observed during the years of this study. It was also apparent that the mean smolt body length of detected returners was highest in 2008 and 2013, the two years for which the proportion of smolts returning as adults was lowest, suggesting that in these two cohorts, only the largest smolts survived, whereas, in other years, the mean smolt body length of detected returning adults was smaller.

A further reason why some of the extrinsic variables had weak effects on MRR could be due to having only monthly (dissolved oxygen) or annual (sea bass abundance) measurements available. Having data at a finer temporal resolution (e.g., daily records) might capture higher variability in the conditions experienced by the migrating *S. salar* smolts and thus better reveal their impacts on MRR. Thus, the importance of maintaining long-term environmental datasets with high-resolution data should not be underestimated (Lindenmayer *et al.*, 2012). In addition, future work could explore interactions between fixed effects. As the hypotheses were based on available literature, interactions were not included in this work, as there did not seem to be strong evidence in the literature supporting interactions between the covariates assessed.

The MRR of a 1SW *S. salar* was approximately twice that of a MSW fish, indicating that there is some non-negligible additional mortality associated with spending longer at sea (Chaput, 2012). The survival rate of MSW fish is the product of two components: survival during the first year at sea (which depends on the covariates, like smolt body length) and the survival during the second

year at sea (which is fixed). As the covariates only modify the first component, their effect is quantitatively less important for MSW fish; thus, the slope of the predicted probability curve is more gradual for MSW fish than 1SW fish. However, the relative effect of the covariates on 1SW survival is the same as on MSW survival. The finding that the MRR of 1SW is nearly twice that of MSW does not account for confusion between mortality and maturation schedules (Chaput, 2012). Because there were very few MSW returns detected, assumptions had to be made to limit the number of parameters to be estimated. Therefore, it was not possible to know whether an individual *S. salar* died at sea during its first year or if it stayed for an additional second year and died during that period. Future work should attempt to overcome this, perhaps by further developing a method to explicitly separate out the different phases (e.g., Pardo & Hutchings (2020)). To solve for statistical identifiability between the different phases, additional data could be introduced, e.g. more years to increase the number of MSW returns, or genetic data (e.g., Barson *et al.* (2015)) where available to help identify the probability of an individual being a 1SW or MSW regardless of whether they get detected as a returning adult.

In conclusion, this study presents strong evidence of a significant positive effect of *S. salar* smolt body size on MRR. This is potentially concerning for the conservation management of the species given there is evidence that smolt body size has decreased over time (e.g. Jutila *et al.* (2006)). Thus, these findings have important implications for populations of *S. salar*, should this trend continue. Managers seeking to improve the return rates on *S. salar* to their rivers should consider ways to improve growing conditions in the river (Simmons *et al.*, 2020), to try and enhance smolt body size and thus their quality, not just their quantity.

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Contributions

OMS, JRB, PKG, and SDG conceived of the study. OMS and SDG analysed the data. OMS wrote the paper. JRB, PKG, MN, WDR, ER, and SDG revised the paper and helped prepare it for submission.

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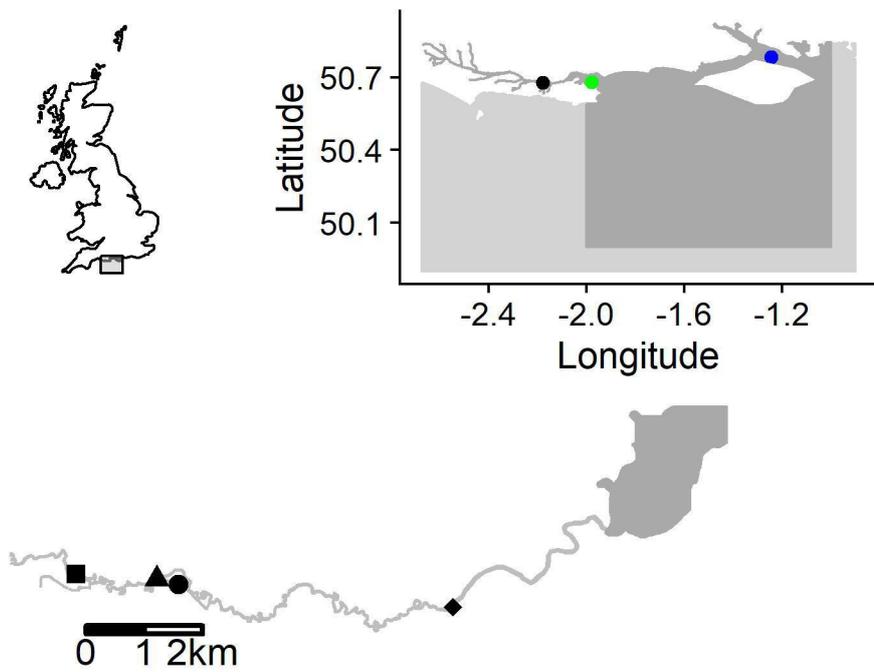
Figure Captions

Figure 1. A map showing the UK in the top left panel with the study area in a grey box. The study area is shown in the top right panel, with the area that the SST data covers shown in dark gray, the location from which the bass data were collected as a blue dot, the location of the DO logger in Poole Harbour as a green dot, and the location of the RST in the River Frome as the black dot. The bottom panel shows the part of the River Frome where the tidal limit is the diamond, the RST is the circle, the first PIT detection antenna is the triangle, and the second PIT detection antenna is the square.

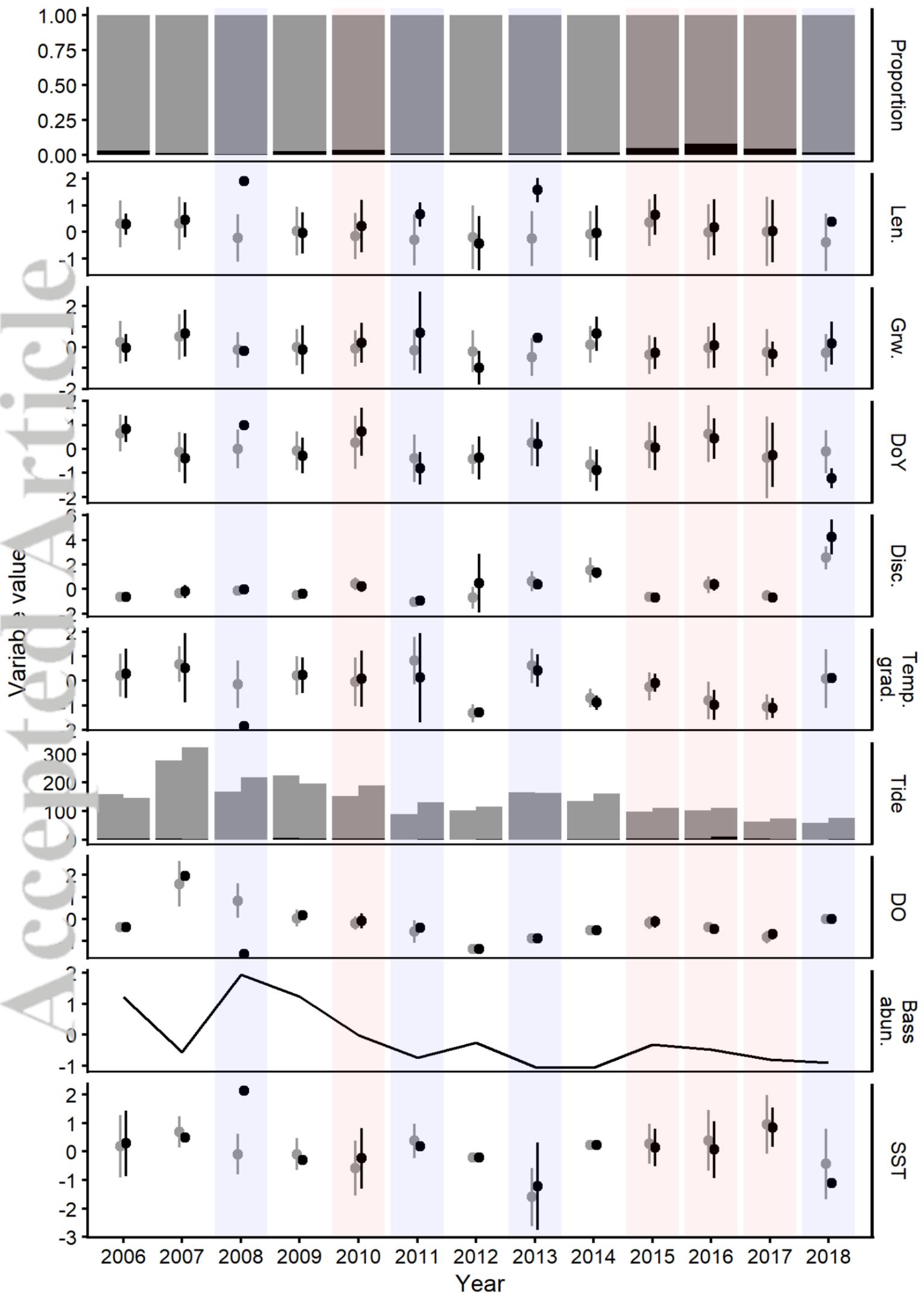
Figure 2. Plots of empirical data used in the River Frome *Salmo salar* survival model, where grey points and bars represent smolts that were not detected returning as an adult and black points and bars represent smolts that were detected returning as an adult. ‘Year’ on the x-axis refers to the smolt cohort. The ‘proportion’ plot shows the proportion of smolts from each year that were or were not detected returning as an adult. The point plots for all the continuous fixed effects show the mean value of various explanatory variables experienced by emigrating smolts each year, with vertical lines indicating 1 standard deviation above and below the mean. The tide plot shows the number of returners/non-returners for each year, split between those that arrived as smolts to the estuary during an ebbing tide (the bar on the left) and those that arrived during a flooding tide (the bar on the right). Because bass abundance was recorded annually, the bass plot shows the bass abundance for each year, which does not vary between returners/non-returners. All explanatory variables, except tide, have been z-standardised. Blue boxes are a visual aid to distinguish years with a low proportion of returners; red boxes are for years with a high proportion of returners.

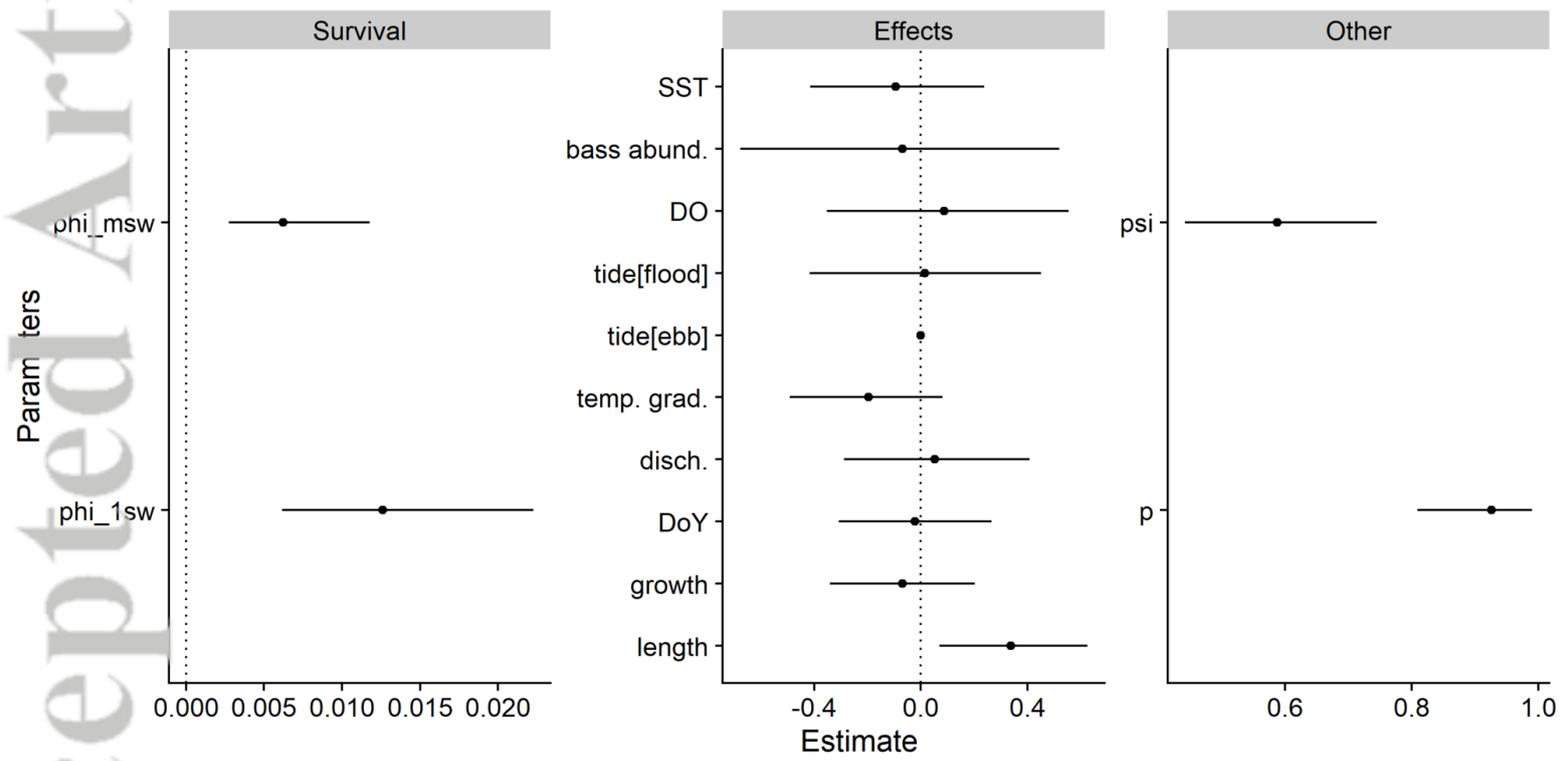
Figure 3. MCMC parameter estimates for 1SW and MSW survival (“Survival”), explanatory variable effects on 1SW survival (“Effects”) and the remaining parameters (“Other”) from the state-space model of River Frome *Salmo salar* survival. The dashed line indicates zero on the x axis. The points represent the mean estimate and the horizontal bars represent the 95% credible intervals.

Figure 4. The predicted probability of survival for *Salmo salar* on the River Frome after spending 1 year at sea (1SW) and after spending multiple years at sea (MSW) as a function of its body length as a smolt. The dashed lines show the marine return rate for a 12 cm and 16 cm smolt, respectively. These are two body lengths within the normal range of smolt body lengths commonly observed on the River Frome (Gregory et al., 2019). The grey area represents the 95% credible interval.

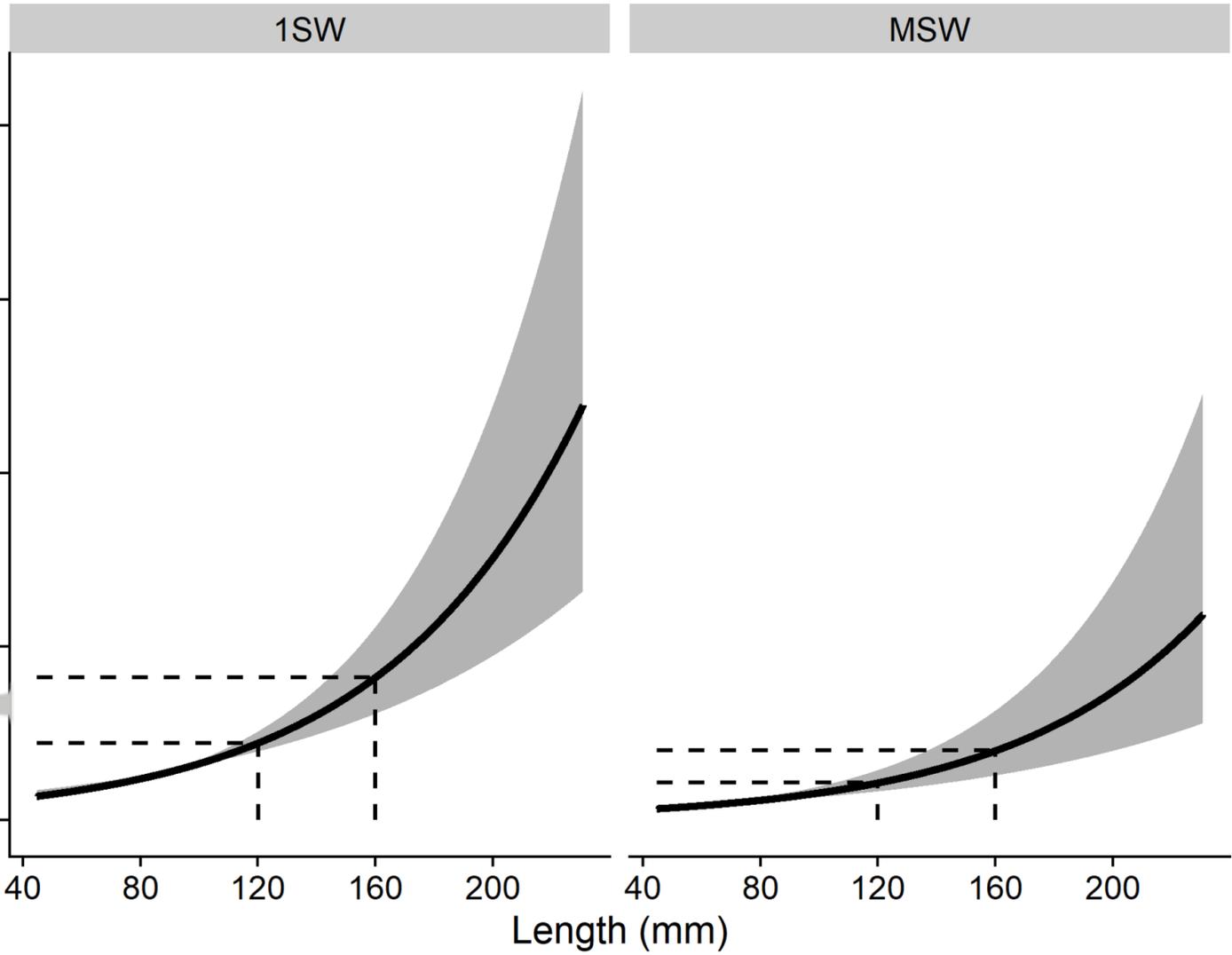


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Table 1. List of explanatory variables and their hypothesised effect on adult River Frome *Salmo salar* marine return rates (MRR)

Term	Description	Abbreviation	Hypothesis	Reference(s)
Smolt length	Fork length (mm) of smolts when captured in the RST	Len.	Bigger smolts are more likely to return as adults	Armstrong et al., 2018; Chaput et al., 2019; Gregory et al., 2019
Growth rate	Daily overwinter growth rate	Grw.	Smolts with slower freshwater growth rates compensate with higher growth rates at sea, leading to higher marine return rates	Einum et al., 2002; Peyronnet et al., 2007
Day of year	The day of year that the smolt was captured in the RST	DoY	Later migrating individuals are more likely to return as adults than earlier migrating individuals	Jonsson & Jonsson, 2014; Antonsson et al., 2010
River discharge	River discharge (m^3/s^{-1})	Disc.	Smolts emigrating under higher river discharge will be able to migrate (swim) faster in more turbid water,	Lothian et al., 2018; Persson et al., 2018

			and thus better avoid predators in the lower river, and are more likely to return as adults	
Water temperature gradient between river and estuary	The difference between the water temperature in the lower river and the near shore SST	Temp. grad.	A smaller temperature gradient will be less physiologically stressful, increasing survival during estuary migration, and so smolts are more likely to return as adults	Juttila, Jokikokko, & Julkunen, 2005
Tide state	Whether the tide is ebbing or flooding	Tide	Smolts that enter the estuary during the ebb tide are more likely to return as adults	Martin et al., 2009; Lefevre et al., 2013
Dissolved oxygen	Dissolved oxygen (mg/L) in Poole Harbour	DO	Higher levels of oxygen in water will increase their survival and so smolts are more likely to return as adults	Kevin D. Friedland et al., 2017
Predators in Poole Harbour	Sea bass population data	Bass abun.	Higher numbers of sea bass in Poole Harbour will lead to higher	Riley et al., 2011

Sea surface Degrees SST
temperature Celsius

predation and so smolts
are less likely to return
as adults

Warmer SST outside Jutila,
Poole Harbour will lead Jokikokko, &
to increased survival Julkunen, 2005
and so smolts are more
likely to return as adults

Table 2. The number of River Frome *Salmo salar* smolts from each cohort that were subsequently detected as adults.

Smolt cohort	PIT-tagged smolts captured in the RST and measured in length	Those subsequently detected returning as adults
2006	307	9
2007	602	7
2008	388	1
2009	422	11
2010	344	12
2011	222	2
2012	220	3
2013	330	2
2014	298	5
2015	210	10
2016	215	18
2017	139	6
2018	137	2