Chapter 5: Adult return rates of the anadromous Atlantic salmon: influences of smolt length across a latitudinal gradient

5.1 Abstract

Populations of anadromous Atlantic salmon *Salmo salar* ('salmon') have decreased dramatically across much of their geographic range in recent decades. It is posited this is being driven by low marine survival, resulting in reduced adult return rates to natal rivers. We hypothesised that marine return rates (MRR) of adult salmon are positively influenced by their body lengths as seaward-migrating juveniles ('smolts'), so larger smolts will be more likely to survive at sea and return as spawning adults to the natal river. We also suggest that the magnitude of this effect decreases with latitude, with its effect being weaker in more northerly populations. These were tested using individual capture-mark-recapture data from seven salmon populations in Western Europe spanning 13 degrees of latitude and 12 years of smolt cohorts. We used a multi-state state-space model to test whether MRR was influenced by smolt body length and latitude, and their interaction. Across the seven populations, smolt length had a significant positive effect on the probability of adult return, which was stronger in southern versus northern populations. Atlantic salmon smolt body length is thus an important indicator of their MRR, especially among populations in the warmer, southern part of their geographic range, with this having important implications for conserving declining salmon stocks. It suggests that management in their freshwater juvenile stages can increase MRR and should focus not only on the numbers of seaward-migrating juveniles, but also their individual quality, as indicated by their body length.

5.2 Introduction

Populations of diadromous fishes, which spend different parts of their life cycle in freshwater and marine habitats, have generally decreased around the North Atlantic over the recent past (Limburg and Waldman 2009; Tamario et al. 2019; Merg et al. 2020). One such species, the anadromous Atlantic salmon *Salmo salar* ('salmon' hereafter), has experienced steep population abundance declines since the 1970s (Chaput 2012; Dadswell et al. 2021; ICES 2021) with populations from southern rivers appearing to be declining faster than more northerly populations (Parrish et al. 1998; Lehnert et al. 2019). The mechanisms underlying this pattern are likely to be

multifaceted and potentially span both the freshwater and marine phases of their life cycle (Dadswell et al. 2021; Thorstad et al. 2021). However, it is often considered that the early part of their marine migration is a particular survival bottleneck for the species (Thorstad et al. 2012).

Anadromous salmon are born in freshwater. They undergo a springtime metamorphosis, called 'smoltification,' to become 'smolts' prior to their seaward emigration from freshwater, which is driven by reaching a growth-dependent size threshold that occurs between age 1 and 6 years old (Thorstad et al. 2011). Many factors can affect body size at smoltification. Freshwater growth rate and age are closely related, with individuals that have a higher growth rate more likely to smoltify at a younger age and, thus, a smaller body size (Metcalfe and Thorpe 1990; Letcher and Gries 2003). Growth rate itself is linked to various factors, including prey abundance, inter- and intra-specific density, genetics, and body length, to name a few (Grant and Imre 2005; Garcia de Leaniz et al. 2007; Simmons et al. 2020). There may be latitudinal trends in size at smoltification, as juvenile salmon are known to grow faster and smoltify younger, in southern populations relative to northern populations. The size at smoltification of sea trout *Salmo trutta*, a closely related species, has been shown to vary from north to south, with northern populations producing larger (and older) smolts (L'Abee-Lund et al. 1989).

Juvenile body length is an important trait linked to selective mortality processes for many teleost fishes (Sogard 1997). This is thought to be largely driven by size-selective mortality caused by a lower tolerance to environmental extremes and/or a greater probability of being preyed upon by piscivores (Ellis and Gibson 1995; Oldham et al. 2019; Simmons, Britton, et al. 2021). Since the 1970s, the inverse-weight hypothesis has postulated that larger smolts of Pacific salmon species experience lower marine mortality than smaller conspecifics (Ricker 1976). Many studies have attempted to associate the body size of Atlantic salmon smolts with their subsequent marine survival (Jonsson et al. 2017; e.g., Saloniemi et al. 2004; and see Table 1 in Gregory et al. 2018). Conclusions from these studies have, however, been weakened by issues with their data and/or analyses, such as small sample sizes, pseudoreplication, and using population rather than individual-level data (Gregory et al. 2018). In particular, imperfect detection when using capture-mark-recapture data to estimate adult returns is rarely considered

(Gregory et al. 2018). Imperfect detection occurs when the efficiency of the devices used to record the return of marked salmon is below 100% (Simmons, Britton, et al. 2021). Recent work using a large long-term dataset of individually marked salmon from the River Frome, southern England, together with a state-space model that accounted for imperfect detection, demonstrated that longer smolts were indeed more likely to return as adults to their natal rivers (Gregory et al. 2019; Simmons, Britton, et al. 2021). While successful in demonstrating the hypothesised positive association between smolt length and their MRR, these studies were only carried out in one river and thus uncertainty remains as to whether this represents a more widespread pattern.

Extrapolating effects of smolt length on their MRR derived from one river in southern England to rivers elsewhere in the salmon's geographic range would be highly speculative and could result in misdirected and potentially harmful management actions to encourage better quality or longer smolts. Rather, studies suggest that relationships between freshwater and marine aspects of the salmon lifecycle vary between populations, and potentially along latitudinal gradients. For Pacific sockeye salmon *Oncorhynchus nerka*, smolts from more northerly rivers appear to have higher marine return rates than those from more southerly rivers (Koenings et al. 1993). In coho salmon *O. kisutch*, Zimmerman et al. (2015) found that wild smolts from northern populations have a 1.1-30.8% probability of surviving to adulthood, whilst those from southern populations have a 0.2-10.4% probability. They discuss that this trend could relate to the local environmental conditions experienced by the smolts as they enter the marine environment.

There is less evidence of an effect of latitude of the natal river on MRR for Atlantic salmon populations, although there is evidence that smolt emigration phenology and lipid stores do vary by latitude, with northern populations tending to migrate later and having higher lipid stores than southern populations, and both factors could play a role in subsequent survival (Berg et al. 2009; Otero et al. 2014; Vollset et al. 2021). Furthermore, the distance and time taken to reach marine feeding areas are higher for southern salmon populations, which may increase the risks of predation and energy requirements (Rikardsen et al. 2021). Understanding the influence of latitude on later marine return rates could also be important given climate change projections, as

patterns in MRR currently observed in the south might become more common in northern rivers as conditions become warmer (Liu et al. 2020) if the underlying mechanism is related to emigration phenology and lipid stores, which themselves are likely linked to environmental conditions including water temperature (Teichert et al. 2020).

Our aim was to test whether the positive effect of smolt lengths on salmon MRR was widespread across the Western European part of their geographical range and whether the effect varied systematically with latitude. We compiled and analysed a large dataset of individually marked salmon smolts from seven rivers spanning more 13 degrees of latitude and covering 12 years of smolt cohorts. Individual fish were marked with passive integrated transponder ('PIT') tags inserted into their coelomic cavity of the fish either prior to (as juvenile salmon known as 'parr'), or during (as smolts), their seaward migration. Each tagged smolt was measured at a capture site in the lower river and then released to continue their migration and, subsequently, marked adults were recaptured (detected) in the river upon their return from sea. We tested the hypotheses that: (1) larger smolts would have higher MRR than smaller individuals, (2) MRR would be higher for individuals from northern populations compared to southern populations, and (3) the effect of smolt length on the MRR would be weaker among individuals from northern populations compared to those among southern populations.

5.3 Methods

5.3.1 Site descriptions

Data were collated from seven rivers in Western Europe: the River Scorff (France), the River Frome (England), the River Corrib (Ireland), the River Erriff (Ireland), the River Conon (Scotland), the River Storelva (Norway), and the River Etne (Norway) (Figure 5.1; Table 5.1). Each of these has a scientific salmon population monitoring program in which juvenile salmon are tagged with PIT tags either prior to (as parr) or during (as smolts) their seaward migration. The tagged smolts are measured (fork length) during their seaward migration. Smolt age and smolt sex were not considered here as this data was too sparsely available; thus smolt of all ages and both sexes were pooled for all analyses. Returning adults were detected by a range of methods in each river. Some rivers had only a primary detection device, whilst others had a secondary device that could be used

to calculate the detection efficiency of the primary device (Table 5.1). For rivers without a secondary detection device, there was no way to assess detection efficiency; therefore, this was assumed to be 100%.
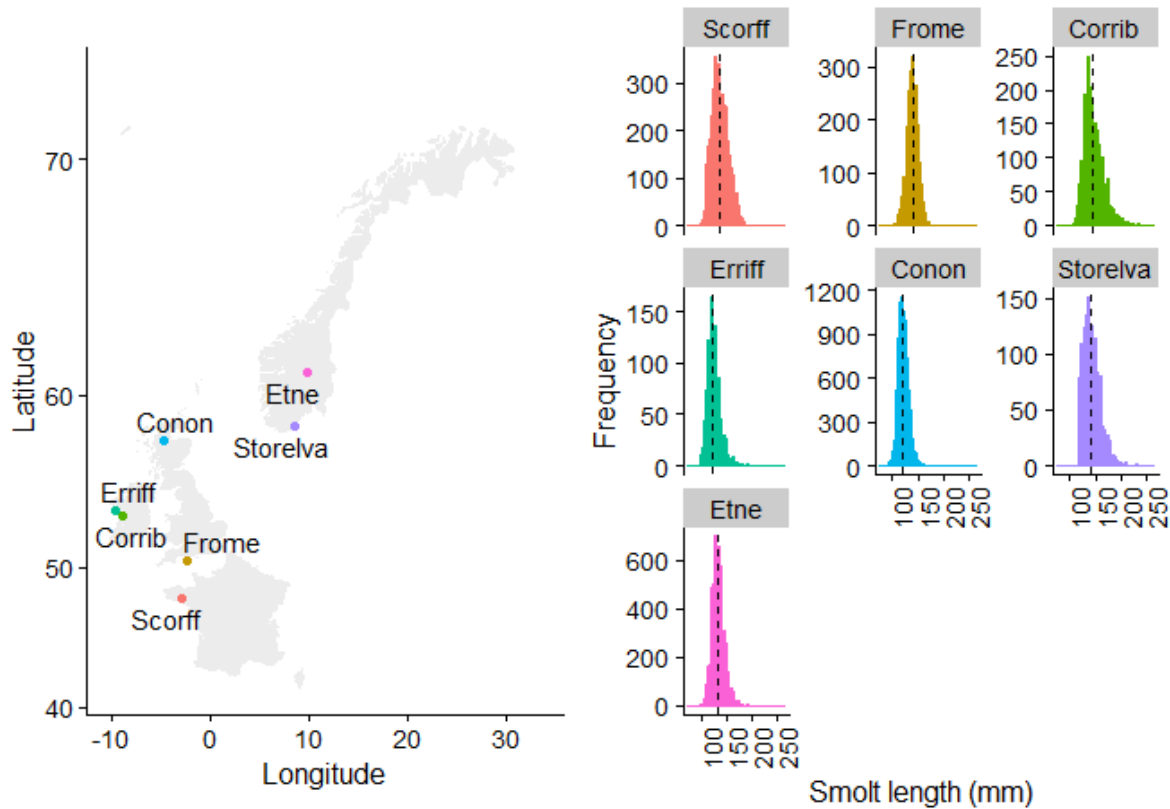

Figure 5.1. Map showing the locations of the seven rivers used in the study and histograms of the smolt body lengths across all study years, regardless of smolt sex and age. The dashed line shows the median smolt length per river.

Table 5.1. Description of data collected for the analysis. The rivers are listed by latitude, from south to north. 1SW stands for one-sea-winter adult salmon and MSW stands for multi-sea-winter, which includes both two-sea-winter and three-sea-winter adults.

River	Latitude	Brief description	Smolt cohorts	PIT tag	Life stage tagged	Total smolts tagged	Smolt length measurements	Primary adult detection occasion	Secondary adult detection occasion	Total 1SW adult recaptures	Total MSW adult recaptures
Scorff, France	47.44 N	Rain-fed. Length: 75km, incl 15 km estuarine. Catchment area: 480 km²	2008 - 2019	12 x 2.12 mm duplex	Juveniles >= 6 cm and smolts (since 2015)	6360	Captured in two traps in lower river and measured to mm	Captured in trap in lower river	Captured on redds during spawning	128	8
Frome, England	50.50 N	Aquifer-fed; Length: 70 km, incl 15 km estuarine. Catchment area: 463.7 km²	2008 - 2019	12 x 2.12 mm duplex	Juveniles >= 6 cm	2997	Captured in rotary screw trap (RST) in lower river and measured to mm	Detected at PIT antenna array 8 km from tidal limit	Detected at PIT antenna array 11 km from tidal limit since 2011	49	23
Corrib, Ireland	53.27 N	Lake & rain-fed. Length: 7 km, incl 1.4 km estuarine. Catchment area: 3139 km²	2018-2019	12.5 x 2.03 mm duplex	Smolts >= 10 cm	4043	Captured in smolt trap and measured to mm	Detected at PIT antenna 0.2 km from tidal limit	Detected at a submersible PIT antenna at tidal limit	188	0
Erriff, Ireland	53.62 N	Rain-fed. Length: 33 km, incl 500 m estuarine. Catchment area: 166 km²	2018-2019	12.5 x 2.03 mm duplex	Smolts >= 10 cm	1802	Captured in wolf trap in Tawnyard subcatchment or RST in lower river and measured to mm	Detected at PIT antenna 0.05 km from tidal limit	None	58	0
Conon, Scotland	57.61 N	Loch-fed. Length: 23.5 km. Catchment area: 1100 km²	2008-2014	12 x 2.12 mm duplex	Smolts	6858	Captured in trap in lower river and measured to mm	Detected at PIT antenna array upstream of tidal limit	None	217	48
Storelva, Norway	58.40 N	Lake and rain-fed. Length: 30 km, incl 5.5 km estuarine. Catchment area: 409 km²	2010, 2012, 2015	23 x 3.65 mm, half duplex	Juveniles and smolts	2437	Captured in RST at river mouth or two RSTs in lower river and measured to mm	Detected at PIT antenna array 100 m from tidal limit	None	38	74
Etne, Norway	61.14 N	Rain-fed. Length: 13 km, incl 300 m estuarine. Catchment area: 0.29 km²	2016-2019	12 x 2.12 mm, full duplex	Smolts	7747	Captured in fyke net in lower river and measured to mm	Captured by resistance board weir upstream from tidal limit	None	59	52

5.3.2 Marine return rate estimation

A multi-state capture-mark-recapture ('CMR') state-space model was used to assess the effect of smolt body length and river latitude on their MRR. The model has two components: the state process, which estimates the true MRR of adult salmon, and the observation process, which estimates the efficiency of the river-specific observation models to detect returning adults. Only rivers with both a primary and secondary detection device have an observation process.

The state process represents the survival (or not) at sea of salmon *i*, tagged as a juvenile or smolt, to return to its natal river as an adult after one winter at sea ('1SW') or two or more winters at sea ('MSW'). This was modelled as a Categorical prior distribution with the probability of individual *i* emigrating from river *r* in year *y* returning as a 1SW fish ($\varphi_{i,r,y}^{1sw}$), a MSW fish ($\varphi_{i,r,y}^{msw}$), or not returning ($1 - \varphi_{i,r,y}^{1sw} - \varphi_{i,r,y}^{msw}$), presuming it has died at sea.

The survival of smolt *i* during its first year at sea ($\varphi_{i,r,y}^{1sw}$) was modelled on the logit scale as a linear function of the explanatory variable and random effects. The full model included the fixed effects of two covariates, smolt body length and river latitude, the fixed effect of their interaction, and random effects of smolt river of origin and migration year. Specifically, $\varphi_{i,r,y}^{1sw}$ was given by:

$$\text{logit}(\varphi_{i,r,y}^{1sw}) = \eta_{i,r,y}$$
$$\eta_{i,r,y} = \alpha + \beta 0_r + \beta 1_y + \beta 2 \times \text{Length}_i$$

where priors are listed in Table 5.2. It was possible to include latitude and river together in the same model because latitude was treated as a continuous covariate and river was treated as a categorical covariate with seven levels. Both length and latitude were *z*-standardised.

MSW salmon experience additional mortality from spending longer at sea. To account for this, the MRR of MSW salmon $\varphi_{i,r,y}^{msw}$ was calculated by adding δ, a parameter

representing the additional mortality, directly to the linear function of $\varphi_{i,r,y}^{1sw}$. Specifically, $\varphi_{i,r,y}^{msw}$ was given by:

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

where the prior δ is assumed to be spatially and temporally invariant and homogenous among all individuals spending two or more winter at sea (Table 5.2).

The rivers Scorff, Frome, and Corrib all have a secondary device, to which the salmon might survive and transit. The probability of surviving and transitioning to the secondary device in river r (ψ_r) is considered constant and homogenous among all individuals. Similarly, the detection probability for river r (p_r), estimated from adult salmon detected on the second device that were also detected on the first device, is considered constant and homogenous among all individuals.

Table 5.2. List of parameters and their prior distributions.

Process	Parameter	Prior
Survival	α	Normal($\mu = 0, \sigma = 0.001$)
	$\beta 0$	Normal($\mu = 0, \sigma = \tau 0$)
	$\beta 1$	Normal($\mu = 0, \sigma = \tau 1$)
	$\beta 2$	Normal($\mu = 0, \sigma = 0.001$)
	$\tau 0$	InvGamma($r = 0.001, \lambda = 0.001$)
	$\tau 1$	InvGamma($r = 0.001, \lambda = 0.001$)
	δ	Student-t($\mu = 0, \tau = 1, k = 2.5$)
Observation	p_r	Uniform(min = 0, max = 1)
	ψ_r	Uniform(min = 0, max = 1)

5.3.3 Parameter estimation

Parameter values were estimated via MCMC using the JAGS sampler implemented in R package `rjags` (Plummer 2003). There were 130 000 iterations of MCMC chains run, of which the first 50 000 were discarded as the burn-in period. Parameter values at every 100th iteration were saved for inferences to limit auto-correlation in the MCMC samples. There were six 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 and 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 models were fit inside a Docker container (Merkel 2014).

5.3.4 Model selection

Our candidate model set contained four models. The full model included length, latitude, and the interaction between length and latitude, the subsequent models contained length and latitude, just length, and just latitude (Table 5.1). The candidate model set was compared using the approximate leave-one-out cross-validation (LOO) procedure in R package `loo` (Vehtari et al. 2017). The best model was the model with the lowest LOOIC (Vehtari et al. 2017).

5.4 Results

There were 32244 smolts included in the analysis. Of these, 935 (2.9%) were detected as returned to the rivers as adults, with 729 (78.2%) of these adults age 1SW fish and 206 (21.8%) as MSW fish. There were no MSW fish detected in the River Corrib, and only two MSW fish detected in the River Erriff, with the latter considered too small a sample size to include in further analysis. River Corrib smolts were on average the largest smolts (mean length ($\pm$ SD) = 147 mm ($\pm$ 19 mm) and those from the River Conon were the smallest (mean length ($\pm$ SD) = 121 mm ($\pm$ 10 mm) (Figure 5.1).

There were no convergence issues with the models as the chains were well-mixed (Figure A4.1). The Gelman-Rubin convergence statistic was <1.10 for all models (Figure A4.2). The best model was the 'Full' model, with a LOOIC value 9.6 points less than the next best model (Table 3; LOOIC differences of >2 was considered a substantial improvement). In this model, smolt length had a positive effect on MRR, latitude had a negative effect on MRR, and the interaction term had a negative effect (Figure 5.2). Thus, while longer smolts are more likely to return as adults than shorter smolts, this pattern weakens as latitude increases.

The predicted probability of return conditioned on age at maturation for a 1SW salmon increases with increasing smolt size in all the rivers (Figure 5.3). The effect of the interaction between smolt length and latitude was positive, indicating that longer smolts from southern rivers had a higher probability of returning as 1SW adults than smaller northern smolts (Figure 5.4). This pattern might be driven, in part, by the data from the Rivers Scorff and Corrib. Examination of the parameter estimates from the random effect river suggests that the Corrib is particularly unusual, with a relatively high effect, while the Frome is relatively low (Figure 5.5). Additionally, the random effect of year suggests that the years 2015-2017 are unusual (Figure 5.5).

Observation equations were only evaluated for rivers with two detection devices (Rivers Scorff, Frome, and Corrib). The probability of surviving and transitioning between the first and secondary detection devices was low for the Scorff and Corrib but high for the Frome (Figure 5.2), while the detection efficiency of the primary detection devices was also low for the Scorff and Corrib, but high for the Frome (Figure 5.2). With relatively low estimates for the Rivers Scorff and Corrib, it is possible there is some confusion between the survival and detection parameters, particularly for the River Scorff (sup mat).

Table 5.3. Comparison of the candidate models using an approximate leave-one-out (LOO) predictive performance measure (expected log pointwise predictive density (elpd)) presented as the LOO information criterion (looic) on the deviance scale. The effective number of parameters is also displayed (np).

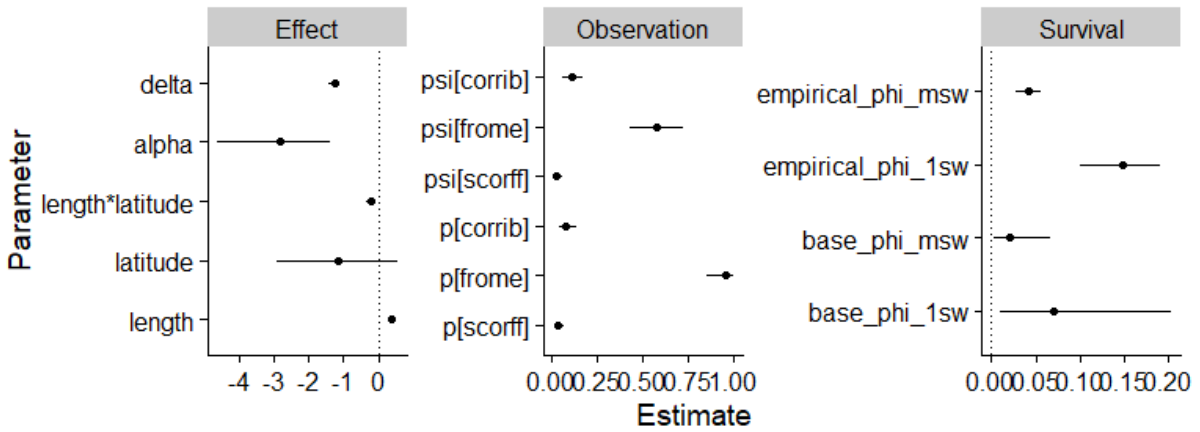| Model name	Parameters	elpd	np	looic
Full model	length + latitude + length*latitude	-4645.2	24.9	9290.4
Length + Latitude model	length + latitude	-4650.0	24.6	9300.0
Length model	length	-4651.5	26.0	9303.0
Latitude model	latitude	-4660.2	21.6	9320.4

Figure 5.2. Coefficient estimates for the 'Full' model showing point estimate and 95% credible intervals.
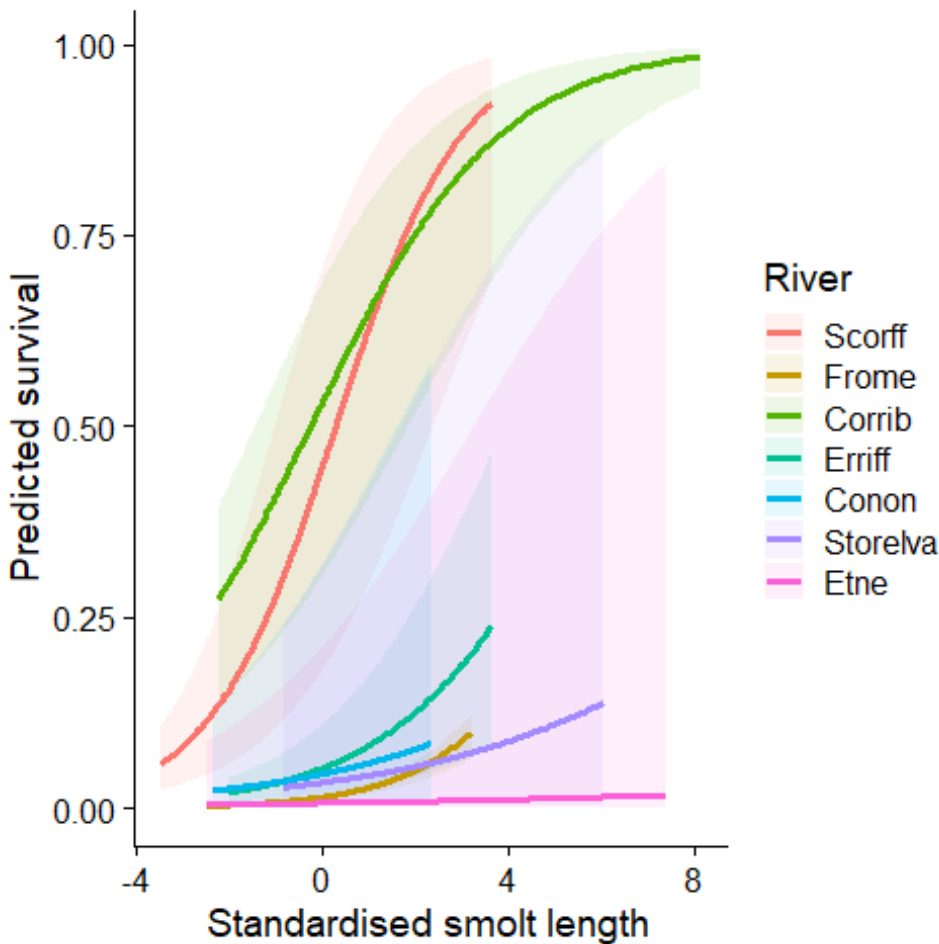

Figure 5.3. Predicted probability of marine survival for 1SW salmon from each river, over the range of smolt lengths observed at each river. The solid lines represent the estimated effect and the bands represent the 95% credible interval. Wide bands can be due to small and uncertain effects, small sample sizes, and both.
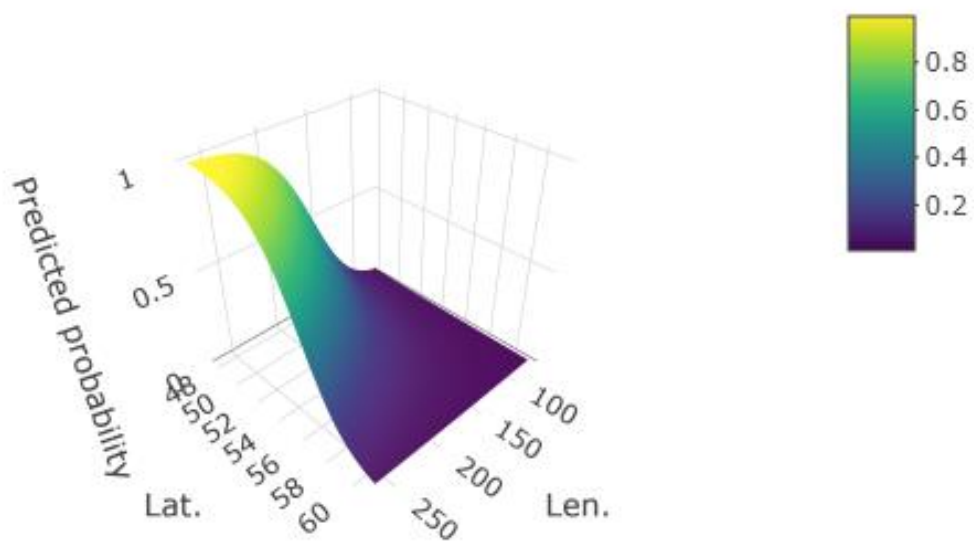
Figure 5.4. 3D surface plot showing the effect of the interaction between smolt body length ('len.' on x-axis) and latitude ('lat.' on y-axis) on the predicted probability of marine survival for a 1SW adult salmon. The colour legend denotes probability, with the probability increasing from the dark to the light colours.
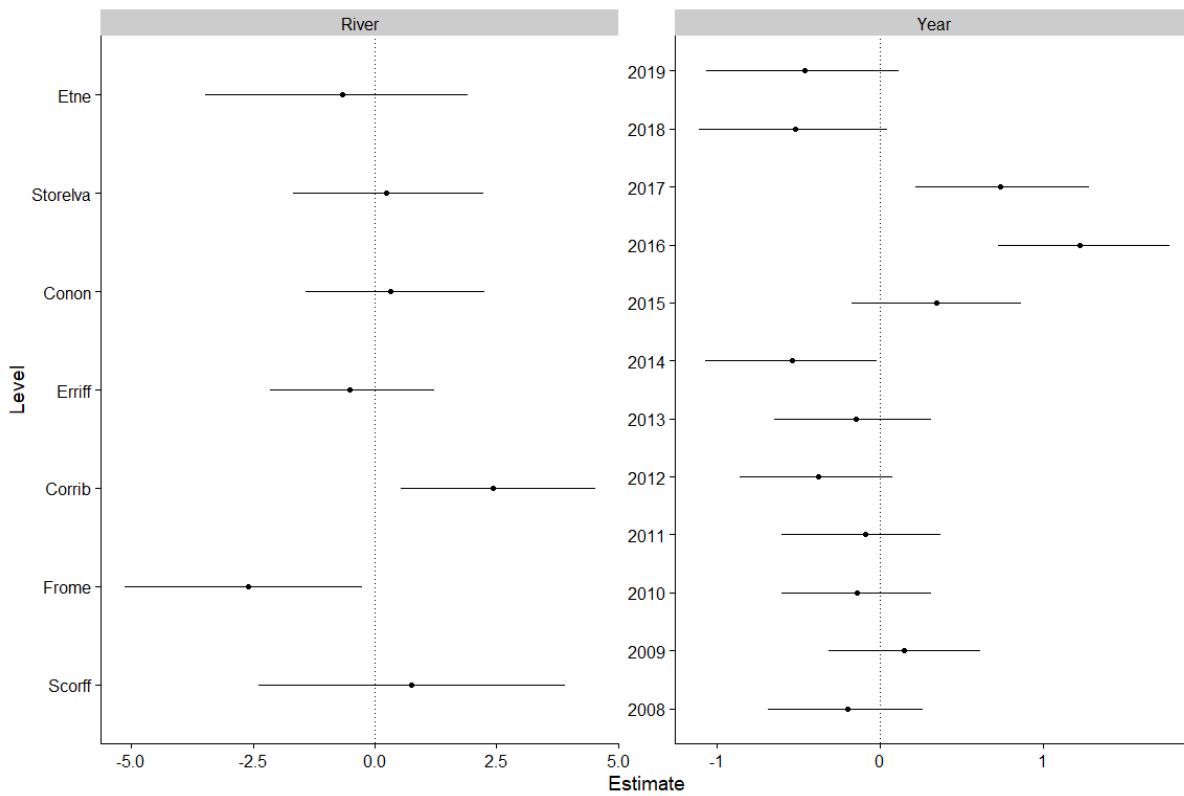
Figure 5.5. Parameter estimates for the random effect of river and year. The point represents the estimate and the lines represent the 95% credible intervals. The dashed lines show the no effect (0) line.

5.5 Discussion

Through careful statistical analysis of a large long-term dataset of individual salmon mark-recapture records, we have provided compelling evidence that 'bigger-is-better' for marine return rates among seaward-migrating Atlantic salmon smolts, and that this finding can be generalised across salmon populations spanning much of Western Europe. Additionally, we have shown that the effect of smolt length on MRR varies systematically by latitude, with smolt length having a stronger effect on MRR for individuals from southern populations compared with those from northern populations. This finding has potentially important consequences in the context of climate change, as populations in more northerly rivers of might start to experience freshwater growth conditions (which determine smolt length) that are more similar to conditions currently experienced in the south (Jonsson and Jonsson 2009).

This study provides strong evidence that smolt body size is a predictor of MRR across 13 degrees of latitude in Europe. There may be various mechanisms that underlie this pattern. Larger smolts may be stronger swimmers, better able to avoid predation and move through dangerous parts of their migratory route more quickly (Thorstad et al. 2012; Remen et al. 2016). Body size is also linked to metabolic rate and lipid content, with smaller individuals generally having lower lipid stores and higher metabolic rates (Seppänen et al. 2009), which can reduce overall fitness and increase susceptibility to adverse environmental conditions. At sea, foraging behaviours may vary between large and small post-smolts, with individuals having to attain a critical size to shift to piscivory (Salminen et al. 1994, 2001). Such a shift in prey selectivity would result in larger salmon acquiring more nutrient-rich foods sooner, which might increase their probability of marine survival through attaining larger body sizes more rapidly via faster growth rates (Peyronnet et al. 2007). Susceptibility to parasites and disease also varies with body size, with the negative pathological effects of parasites like sea lice *Lepeophtheirus salmonis* and *Caligus spp.* higher in smaller migrating smolts and post-smolts than larger conspecifics (Vollset 2019). Smaller individuals have also been shown to have higher lice settlement rates, meaning they are more likely to be infected (Tucker et al. 2002). Migration timing is also correlated to smolt body size, with larger smolts migrating earlier than smaller smolts (Kennedy and Crozier 2010; Simmons, Gregory, et al. 2021). Any negative effect arising from poor migration timing on subsequent MRR could be

related to body length, and indirectly to previous freshwater growth. Thus, variation in swimming ability, lipid stores, metabolism, foraging ability, parasite susceptibility, and migratory timing might be some of the factors that explain higher MRR in larger versus smaller smolts.

A novel finding in this study is that the effect of smolt body length varies systematically by latitude. Though the fixed effect of latitude had a CI that crossed the no effect line, suggesting that on its own it did not impact MRR, the interaction between smolt body length and latitude was significant. Thus, while it is ubiquitous that longer smolts are more likely to return as adults, it is more important to be a larger smolt in a more southerly river than in a more northerly one. The mechanisms underlying this pattern are likely to be interacting and varying in nature. They could relate to the routes taken by migrating post-smolts to their marine feeding grounds, with individuals from southern populations spending longer migrating than those from northern populations, and thus facing higher mortality risks (Jonsson and Jonsson 2005, 2009; Rikardsen et al. 2021). Differences in migration routes, timing of marine entry, and time spent at sea could expose the salmon to different risks, for which the advantage of larger body size is more important when migrating further. There are also differences in migratory timing from south to north, with northern smolts leaving their rivers later in the year than southern smolts (Otero et al. 2014).

Smolts that migrate earlier could also face more challenging environmental conditions, such as colder sea surface temperatures and larger differences between river and sea temperatures, which mean larger 'fitter' individuals would fare better (Jutila et al. 2005). Other studies have observed that longer smolts tend to migrate earlier in the migration window than smaller smolts (Kennedy and Crozier 2010; Simmons, Gregory, et al. 2021), which supports the idea that there might be an advantage to a larger body size when entering the marine environment earlier in the spring. In addition, there could be physiological differences between the populations. For example, Berg et al. (2009) found that over a 13° range of latitude in Norway, the size-controlled lipid content in juvenile salmon from the northernmost study rivers was nearly three times higher than those from the southernmost rivers at the end of the winter. If this trend were pervasive throughout the European range of Atlantic salmon, it could be expected that salmon of

the same body length might have different lipid stores prior to smoltification depending on river latitude. This could explain why it is more important to be a larger smolt in the south than the north, as northern smolts may have better lipid stores regardless of body length than southern conspecifics.

An unstudied aspect in the current work is the effect of smolt age on MRR. Generally, juvenile growth is slower in the north than in the south, leading to smoltification occurring at older ages in northern populations (Metcalfe and Thorpe 1990). Thus, there is potential for differences in age-at-smoltification to explain some of this pattern, where older smolts may be more experienced at avoiding danger and predators than younger smolts. Alternatively, perhaps only the fittest individuals in the older cohorts migrate to sea, as weaker individuals will have already died in freshwater. There may be underlying physiological differences, such as metabolic differences, between relatively young and old smolts. These differences may explain why large body size is more advantageous to southern smolts than smolts from the north but require further research on the mechanisms if the pattern is to be understood.

The marine return rate is a combination of survival at sea, maturation schedule, and dispersal. To return to its natal river, a salmon must not only survive at sea, but also 'decide' whether to mature as a 1SW fish or a MSW fish, and then migrate. The effect of body length on MRR could be explained if any one of these processes is size-dependent. For example, if maturation schedule is size-dependant, with larger smolts more likely to mature as 1SW adults (Salminen 1997; Jonsson and Jonsson 2007), and there are additional mortality risks associated with staying at sea for longer to become a MSW fish, then this size-dependent 'decision' around maturation could explain the positive effect of smolt length on MRR. Additionally, the observation process could be size-dependent. On the River Scorff, adult salmon are detected when captured in a trap, with such traps possibly being more efficient for larger fish. Thus, with 1SW salmon generally migrating upstream later in the year than MSW salmon (Jonsson et al. 1990), if river conditions (such as discharge) vary across the year, then trap efficiency might differ between periods when 1SW and MSW fish are prevalent in the run.

Some studies have noted a decrease in average smolt size in long-term datasets (e.g. Jutila et al. 2006), which may be linked to climate change. Ultimately, smolt size is determined by a combination of juvenile growth rate and the age at smoltification. Warmer water temperatures have been shown to lead to higher growth rates for fry and parr (Jonsson and Jonsson 2005; Simmons et al. 2020) with faster freshwater growth resulting in smoltification at a younger age and at smaller body sizes, particularly in southern populations (Økland et al. 1993; Strothotte et al. 2005). In northern populations, complex interactions between physiological and ecological mechanisms (i.e., the effect of water temperature on growth rates and age at smoltification) might limit the ability to predict the effect of temperature changes under climate change on smolt body length. Smaller smolts are a predicted outcome of climate warming in other salmonids species as well, such as Pacific sockeye salmon *O. nerka* (Ulaski et al. 2021). Faster freshwater growth, caused by increasing river water temperatures, is more likely to become a problem in northern Atlantic salmon populations where parr smoltify at older ages, as they may begin to smoltify at younger ages and smaller body sizes, relative to smolts in southern populations, such as the River Frome, that already primarily emigrate at age 1+ (the youngest age a wild salmon can undergo smoltification) (Jonsson and Jonsson 2009; Simmons et al. 2020). In the River Frome, there has been no observable significant trend in overwinter growth rate of parr prior to smoltification, though warm winters have been shown to increase growth rates (Simmons et al. 2020) and decrease recruitment (Marsh, Lauridsen, Riley, et al. 2021) during that period. However, in that system, the timing of the smolt emigration has advanced over the years, with a clear pattern of warmer winters resulting in an earlier entry into the marine environment (Simmons, Gregory, et al. 2021). Thus, while smolts in southern populations may not be getting younger, they may be experiencing a shorter period for in-river growth and, thus, smaller body sizes. Growth rate is likely also have a genetic basis (Garcia de Leaniz et al. 2007), so for populations that predominantly smoltify at age 1+ years, there might be strong selection for fast growing individuals.

As body size appears to impact the probability of survival at sea, managers seeking to bolster salmon populations in their rivers ought to try and improve conditions to allow juvenile salmon to attain large body sizes prior to smoltification. Such measures could include improving growth conditions in the river by planting riparian vegetation,

particularly trees, along riverbanks to help maintain water temperatures within the optimal range for growth, particularly as the climate changes (Broadmeadow et al. 2011). Flow regimes are also an important factor related to growth, as they relate to foraging success (Nislow et al. 1998). Preferences for different flow regimes changes as the juveniles grow, such that smaller individuals prefer habitats with lower flows while larger individuals prefer higher flows (Nislow et al. 1999). Thus, ensuring rivers have different microhabitats with a range of flow characteristics could be very important. Aquatic vegetation, such as *Ranunculus spp.* are important for providing refugia and foraging areas for juvenile salmon (Marsh, Lauridsen, Gregory, et al. 2021); thus, encouraging instream macrophyte growth could benefit juvenile salmon. Furthermore, interspecific density and the competition for resources that can arise in densely inhabited reaches, can lead to reduced foraging opportunities and thus reduced growth rates (Imre et al. 2005). Ensuring that adult salmon have favourable spawning habitat across much of the catchment could ensure the distribution of redd numbers are widely spaced, so helping to avoid intense density dependent competition between the offspring of different spawning adults in their post-emergence period. To do so, ensuring important habitat characteristics, like substrate type, are available by undertaking practices such as gravel rehabilitation, could be helpful (Meyer et al. 2008). Furthermore, in rivers with anthropogenic barriers, such as weirs and dams, barrier removal can help adult salmon access spawning habitats that were previously unavailable (Pess et al. 2014; Koed et al. 2020). However, it should be noted that improving growth conditions might not be the best solution for populations where juveniles remain in the rivers for several years before smoltifying, as faster growth might encourage earlier migrations of smaller smolts (Metcalfe and Thorpe 1990; Letcher and Gries 2003). Thus, a nuanced and river-specific approach for attempting to encourage larger smolts is recommended that works in conjunction with the dynamics and ecology of the salmon population.

There are some limitations to this study that mean the results should be treated a little cautiously. While the datasets from the Scorff, Frome, and Conon span the full study period, there are only two years of data from the Irish rivers (Corrib and Errirff). Additionally, the distance between the smolt traps and tidal limit varied on each river. Flávio et al. (2019) found that a substantial amount of smolt predation occurs in the

lower river, a few kilometres upstream of its confluence with the sea, so the location of the smolt traps and adult PIT-tag readers may affect the MRR estimates. Additionally, there were differences in the data collection for each river, with no consistent method of capture, recapture, and detection of salmon. Some rivers had primary and secondary detection devices, allowing parameterisation of an observation model for these rivers, while others had only a single device. Beyond differences in data collection methods, the models were limited to using latitude as a proxy for the abiotic characteristics of each river. Other abiotic variables, such as water temperature, discharge, and biotic variables, such as predator abundance, might be more important determinants of MRR at a local level. The effects of PIT tagging on mortality can also be more harmful for smaller fish (Vollset et al. 2020). However, it could not be assessed whether any mortality of fish tagged as smolts occurred in this study, and whether it was related to smolt body length. Furthermore, this study does not address processes that affect post-smolt and adult survival at sea. Future work studying marine survival should incorporate CMR data with chemical methods, like stable isotopes and genetics, to better understand migratory routes undertaken by salmon at sea (MacKenzie et al. 2011; Almodóvar, Leal, et al. 2020; Bradbury et al. 2021). By better understanding the migration routes and main foraging areas, other potential marine survival bottlenecks might be identified, and future modelling might incorporate abiotic factors, such as sea surface temperature and measures of marine productivity, that influence conditions during their marine lifestages (Mills et al. 2013).

To conclude, this study provides strong compelling evidence that smolt body size influences the probability of marine survival and their successful return to freshwater as an adult, although the effect of smolt size does vary with latitude. For conservationists interested in increasing adult salmon returns, it is imperative to try to improve freshwater growth conditions, so that emigrating smolts have larger body sizes.