Predicting how the juvenile life-stages of anadromous Atlantic salmon *Salmo salar* influence their migration phenology and marine survival

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Abstract

Atlantic salmon, *Salmo salar* (hereafter ‘salmon’), is a species of high commercial, recreational, and cultural importance. Native to rivers of both sides on the North Atlantic basin, this species has experienced dramatic population declines since the 1970s. The reasons for this phenomenon are likely to be complex and multifactorial. Thus, striving to understand factors related to salmon survival, as well as other important aspects of their life cycle, such as growth rates and migration phenology, is crucially important.

Salmon are an anadromous species that undertake a marine migration from freshwater to oceanic feeding grounds, returning as mature adults to their natal river to reproduce. Undertaking lengthy migrations represents an evolutionary trade-off, where the risks associated with migration (such as novel environments and predators) are outweighed by the benefits (access to greater resources). For salmon, parts of their migration, such as through estuaries, are often considered a survival bottleneck.

Capture-mark-recapture (‘CMR’) studies have a long history in ecology, particularly for assessing survival patterns between different time periods. A sample of a population of wild animals is captured, marked by some form of tag, released, and subsequently resampled. I used a long-term CMR dataset (2005 to present) of the salmon population from the River Frome, southern England, where approximately 10 000 juvenile salmon (known as ‘parr’) are captured throughout the river each autumn by electric-fishing. The individuals are each measured for their body length and then fitted with a passive integrated transponder (‘PIT’) tag. Each PIT tag has a unique code that allows for each individual fish to later be re-identified on tag detectors and readers. In the spring, the Frome parr metamorphose into ‘smolts’ and commence their emigration downstream to the sea. Previously PIT-tagged individuals are resampled in a trap, remeasured, scanned for their tag code, and then released. PIT-tagged individuals that successfully complete their migration and return to the river as adults are then redetected a final time by PIT-tag reading antennae in the river, enabling the marine return rate, ‘MRR’, to be estimated.

It has been hypothesised that juvenile body size is an important driver of life history events. Body size may be a proxy for overall fitness and can influence, for example, somatic growth rates, migration timing, and survival between different life stages. For salmon, many other factors may also contribute to this, particularly environmental factors, such as temperature. Thus, the aim of this research was to test the hypothesis that juvenile body size achieved in freshwater is an important determinant of individual survival and marine return success.

The hypotheses were tested in in four studies using the long-term CMR dataset of the River Frome. Firstly, I assessed how body size and environmental variables affect overwinter growth rates in the river. I found that smaller individuals grew more during the winter than expected given their initial autumn body size, and that individuals with the fastest winter growth rates were those that experienced warmer winters and more variation in their daily water temperatures. Secondly, I assessed the factors affecting variation in smolt migration timing. I detected that larger smolts migrated earlier than smaller smolts, and that while water temperature and discharge affected migration timing, the importance of these effects varied throughout the migration period. I also found that smolts were more likely to migrate in schools later in the migration period, and during the daytime instead of at night. Thirdly, I assessed factors that affect marine return rates, with an emphasis on conditions experienced by smolts during the early part of their marine migration. I found that smolt body size was the most important determinant of the probability of individual survival and their probability as returning as an adult, although water temperature and the presence of piscine predators may also play a role. Finally, I combined the Frome dataset with smolt tagging data from six other European rivers with PIT-tag programmes to assess whether smolt body size is an important determinant of marine return rates across a substantial portion of the European range of salmon. I found that, as on the Frome, smolt body size was an important determinant of marine return rates across Europe, with larger smolts more likely to return as adults than smaller smolts.

The results of this thesis should be of importance for conservation efforts attempting to bolster population abundances of Atlantic salmon. In lieu of focusing predominantly on increasing the number of juvenile Atlantic salmon in the river to attempt to increase the number that return as adults, efforts should be made to ensure excellent growth conditions in nursey areas to maximise smolt length, given juvenile body size plays an important role in subsequent survival.

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I (OMS) confirm that the research presented within this thesis is my own.

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Chapter 1: Introduction

This first chapter outlines the main themes of the thesis: understanding how the freshwater life-phase of Atlantic salmon *Salmo salar* influences their subsequent growth, migration phenology, and survival at sea to return to their natal river as a mature adult to spawn. The study approaches, aims, objectives and main study sites are introduced at the end of this chapter. The thesis is presented in an integrated format, whereby material is incorporated in a style suitable for submission and publication in a peer-reviewed journal. Thus, the data chapters (Chapters 2 to 5) are each presented as original and complete pieces of research, either as the published paper or as a pre-submission manuscript. This format has been chosen as it provides flexibility around the types and numbers of papers included in the thesis. The final chapter (Chapter 6) discusses the implications of this research and concludes the thesis. A complete list of references is provided at the end of the thesis to avoid their replication in the chapters and to improve readability.

1.1 Anthropogenic environmental change

The impact of human activity on the planet has altered long- term global geological processes to such an extent that scientists have declared we are living in a new geological epoch - the Anthropocene (Foley et al. 2013; Waters et al. 2016). This new era is characterised by deposits of novel human-made materials, such as plastics, concrete, pesticide residues, and phosphorus and nitrogen from fertilisers, as well as the dissemination of chemicals produced from the combustion of fossil fuels, such as black carbon, inorganic ash spheres, and spherical carbonaceous particles worldwide (Foley et al. 2013; Waters et al. 2016). The consequences of these characteristics of the Anthropocene on environmental change and ecosystem stability are potentially severe. Atmospheric changes, resulting from increased levels of greenhouse gases from fossil fuel combustion, have triggered climatic changes, which has seen the average global temperature rise 1.09^{o} Celsius from 1850-1900 to 2011-2020 (IPCC 2021). This has resulted in the rapid retreat of glaciers and Arctic sea ice, the warming and acidification of the upper ocean, a mean 0.2 m rise in sea level, more frequent heatwaves across most land regions, and more frequent and intense heavy precipitation events in recent decades (IPCC 2021). Such climatic alterations have potentially serious consequences for biodiversity and ecosystem functioning.

1.2 Effects of environmental change on biodiversity

Scientists have proposed that there exists nine ‘planetary boundaries’ comprised of thresholds that are intrinsic features of the Earth system which cannot be transgressed without triggering unacceptable and irreversible global environmental change (Rockström et al. 2009). These include climate change, ocean acidification, stratospheric ozone, biogeochemical nitrogen and phosphorus cycles, global freshwater use, land system change, and the rate of global biodiversity loss (Rockström et al. 2009; Steffen et al. 2015). Declines in biodiversity have been noted across ecosystems and taxa (Wake and Vredenburg 2008; Tollefson 2019; IPCC 2021). Such declines include, but are not limited to, moths, insects, birds, plants, freshwater and marine fishes (Hallmann et al. 2017; Dudgeon 2019; Tollefson 2019; Li et al. 2020; Outhwaite et al. 2020; Pacoureau et al. 2021). The ubiquity of such biodiversity losses is a cause for serious concern (Wake and Vredenburg 2008; Tollefson 2019). Some ecosystems are thought to be at a higher risk from anthropogenic environmental changes than others, with freshwater ecosystems particularly susceptible to the anthropogenic drivers of biodiversity loss, such as climate change (Reid et al. 2018; Dudgeon 2019).

1.3 Effects of environmental change on migratory fish

Some animals migrate to optimise the availability of resources required for different parts of their lifecycle. They might migrate seasonally, migrating to feeding grounds in the summer and then overwintering elsewhere (Milner-Gulland et al. 2011). Alternatively, they might migrate as they develop ontogenetically, such as being born and developing in nursery habitats before heading to other habitats better suited for later life stages. Diadromous fishes take this second approach, with anadromous species, such as species of the genus *Salmo, Alosa, Petromyzon*, born in freshwater but eventually migrating to sea to continue growing, feeding, and maturing, before returning to freshwater habitats to reproduce (Griffiths 2006; Thorstad et al. 2011). There have been marked declines in diadromous fish populations, with such species impacted by factors including climate change and habitat degradation, in both freshwater and marine ecosystems (Reid et al. 2018; Tamario et al. 2019; Merg et al.

2020). Of particular concern to such species is the potential for phenological mismatch during migration. This occurs when the migratory fish is cued to start their migration before the conditions in the habitat to which it is migrating are optimal for survival (Edwards and Richardson 2004; Asch et al. 2019; Wilson et al. 2021). Anadromous fishes that use water temperature as a cue for migration might receive temperature cues earlier in the season as freshwaters warm, but if marine conditions optimal for their survival lag behind, they might enter marine environments in suboptimal conditions, leading to trophic mismatches, with the fish arriving in the marine environment before or after their normal prey peaks in abundance (Edwards and Richardson 2004).

Anadromous salmonid populations, which include culturally and economically valuable species like Atlantic salmon *Salmo salar*, which inhabit freshwater and marine habitats throughout the Northern Hemisphere at different points in their life-cycle, have been in decline for decades (Limburg and Waldman 2009; Chaput 2012; ICES 2020), with declines in some European populations even dating back to the Middle Ages (Lenders et al. 2016). However, these population declines have been substantial since the 1970s, whereby their current catch rates are among the lowest ever recorded (Chaput 2012; ICES 2021). There is increasing evidence that intrinsic factors carried over from their freshwater stages, such as smolt body length (Figure 1.1.A), could be important in determining *S. salar* marine mortality rates (Armstrong et al. 2018; Gregory et al. 2019; Russell et al. 2012). Consequently, an understanding of the factors affecting individual performance, such as juvenile growth in freshwater, seaward migration timings, and alternative environmental factors that might impact survival in estuaries, could have important implications for managers seeking to increase the numbers of adult *S. salar* returning annually to spawn in their natal rivers.

1.4 Atlantic salmon ecology

1.4.1 Atlantic salmon life cycle

Atlantic salmon are native to both sides of the North Atlantic, with a natural range spanning New York State, USA, to northern Quebec, Canada, in the west and Spain to Russia in the east (Thorstad et al. 2011). Born in freshwater, larval salmon, known as 'alevins', hatch from eggs buried in riverbed gravel and feed on their yolk sacs until they have developed enough to emerge as 'fry'. Whilst still in freshwater, the fry develop into ‘parr’, which have characteristic camouflage markings and territorial behaviours. Salmon may spend between one and six years in freshwater feeding and growing prior to heading to sea, though it is most common to spend two to four years (Klemetsen et al. 2003; Thorstad et al. 2011). The amount of time spent in freshwater depends on mean seasonal river temperatures and latitude across their geographic range; in temperate southerly rivers, juvenile salmon, including the fry and parr life stages, will only spend one or two years in freshwater, while in colder northerly rivers, juveniles grow very slowly, spending up to six years in freshwater (Metcalfe and Thorpe 1990; Thorstad et al. 2011). When it becomes time to migrate to sea, the parr undergo ‘smoltification’ (Figure 1.1.B), a physiologically intense process that prepares the fish for saltwater, involving morphological, endocrinological, immune and behavioural changes (McCormick, Hansen, et al. 1998; McCormick et al. 2013). The ‘smolts’ then migrate downstream, predominantly at night, although smolts will also migrate during the day, and will quickly transverse estuaries as they head for the open ocean (Haraldstad et al. 2017; Lothian et al. 2018). As the smoltification process is intense, and the environmental conditions of the estuary and nearshore migration route are novel for the smolts as they move out of their natal river, the early stages of estuarine/marine migration are typically considered a survival bottleneck for the species due to the elevated mortality risk (Thorstad et al. 2012). At sea, the salmon - now termed ‘post-smolts’ - will continue to feed and grow, with some individuals returning as adult salmon to spawn in freshwater after one year (called one-sea-winter fish; 1SW or ‘grilse’) and others returning to spawn after multiple years (2SW for individuals that stay for 2 years, 3SW for individuals that stay for 3 years; generalised to MSW for multi-sea-winter fish; Figure 1.1.A) (Thorstad et al. 2011). The vast majority of Atlantic salmon return to their natal rivers to reproduce, though a small percentage do stray to other rivers (Jonsson et al. 2003). Marine mortality is considered to be high for Atlantic salmon, though factors affecting mortality during this hard-to-study phase of the life cycle remain poorly understood (Russell et al. 2012).

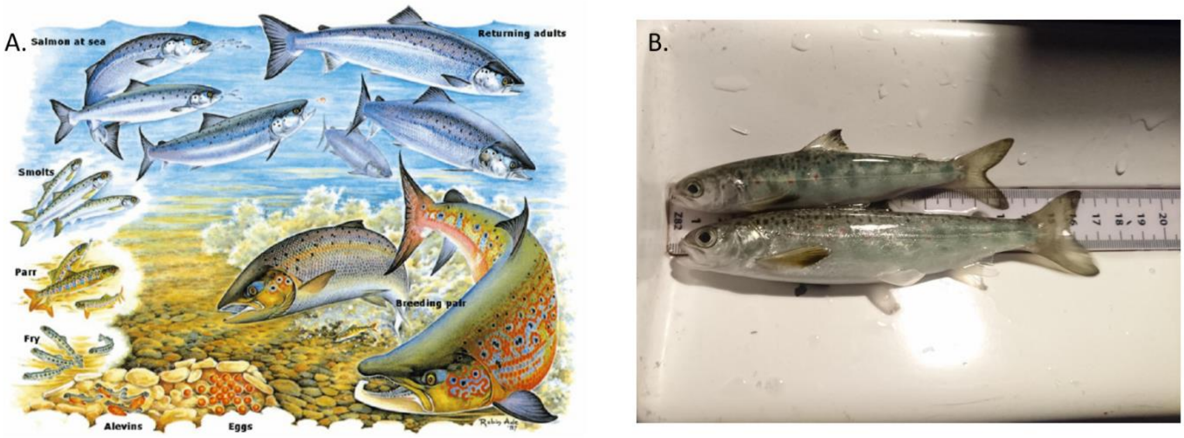

Figure 1.1. Simple diagram of the Atlantic salmon life cycle from Atlantic salmon lifecycle, Atlantic Salmon Trust and Robin Ade, available online at http://ness.dsfb.org.uk/salmon-lifecycle/ (A); Two Atlantic salmon smolts captured on the River Frome showing individuals that are the same age but have different body lengths, courtesy of Stephen Gregory (B).

The effects of climate change on salmon are an increasing concern and are likely affecting Atlantic salmon in both the freshwater and marine phases of their life cycle (Walsh and Kilsby 2007; Mills et al. 2013; Dempson et al. 2017; Rooke et al. 2019; Thorstad et al. 2021). In freshwater, unusually warm water temperatures coupled with high discharge rates at the time of spawning and alevin emergence lead to poor recruitment (Gregory et al. 2020; Marsh et al. 2021). However, for fry and parr, warmer water temperatures might extend the growth season, particularly in northern populations (Jonsson et al. 2001; Jonsson and Jonsson 2009). The outcome of this is likely to be nuanced and varied, with higher parr growth rates potentially leading to larger springtime smolts in populations where salmon smoltify at age 1+, though in other populations with older parr it could lead to parr smoltifying at younger ages, ultimately resulting in smaller smolts (Jonsson and Jonsson 2009). Increased water temperatures and altered discharge regimes may also cause changes in smolt emigration timing, with these important emigration cues triggering migratory behaviours earlier in the year across the range (Kennedy and Crozier 2010; Otero et al. 2014). Changes in migratory timing might lead to phenological mismatches between the arrival of smolts in the marine environment and the availability of prey resources and optimal environmental conditions (Jonsson and Jonsson 2009; Teichert et al. 2020). At sea, climate change-induced shifts in plankton communities and prey abundance have been postulated as drivers in reductions in Atlantic salmon abundance (Beaugrand and Reid 2012; Mills et al. 2013; Thorstad et al. 2021). In addition to effects on growth, phenology and mortality, climate change might alter the range of Atlantic salmon, with Arctic rivers currently ill-suited for Atlantic salmon potentially becoming habitable in future (Bilous and Dunmall 2020).

1.4.2 Atlantic salmon freshwater phase and implications for marine survival

It has long been hypothesized that events that occur during the freshwater portion of the Atlantic salmon’s early life cycle will shape each individual’s likelihood of later marine survival and return to freshwater to spawn (see review by Gregory et al. 2018). There is emerging evidence that body length and condition (the relationship between body length and weight) attained by the time a parr transitions to a smolt has major implications for marine survival (Russell et al. 2012; Armstrong et al. 2018). As such, the amount a parr can grow prior to smoltification is potentially a key predictor of future survival.

Most *S. salar* smoltify in the spring, as ice melts and rivers begin to warm (Thorstad et al. 2012). In more southerly and temperate rivers, parr may grow well all year round, whilst further north, growth can be severely reduced or inhibited entirely during the winter (Murphy et al. 2006; French et al. 2017). Many environmental and biological factors are thought to contribute to parr growth rates. Environmental factors such as temperature and flow rates have been shown to affect growth. As ectotherms, juvenile salmon have a specific thermal range (6 °C – 22 °C) that promotes somatic growth (Jonsson et al. 2001; Elliott and Elliott 2010). Above or below this thermal range, growth rates are reduced, while temperatures above 28 °C or below 0 °C can incur mortality (Elliott and Elliott 2010). Likewise, juvenile salmonids grow is optimal when flow rates are sufficiently high to ensure adequate supplies of prey are moved downstream to them, but not so high as to cause exertion from the fish maintaining station or even by flushing them downstream away from their preferred habitats (Parrish et al. 2004; Warren et al. 2015). Density-induced intra- and inter-specific competition plays an important role in determining fry and parr growth rates (Bal et al. 2011; Cunjak et al. 2013). In areas with high densities of juveniles, competition for food resources can be intense (Grant and Imre 2005). With the overwinter period prior to smoltification potentially quite important for determining smolt length, particularly in the southern extent of their natural range where the juvenile phase generally only takes one year, a greater understanding of factors affecting growth during this time is important.

The timing of the smolt emigration, known colloquially as the ‘smolt run’, varies by latitude. For example, in northern Iceland the smolt run might last from mid-June to early August (Antonsson and Gudjonsson 2002), while further south in the warmer latitudes of southern England the smolt run might start in early April (Riley et al. 2002). Photoperiod and water temperature are believed to cue smoltification, while water discharge and temperature are the main environmental cues that initiate emigration (McCormick, Hansen, et al. 1998; Thorstad et al. 2012; Aldvén et al. 2015). Annual variation in mean water temperatures is highly correlated to variations in the timing of smolt migration (Jonsson and Ruud-Hansen 1985; Jonsson and Jonsson 2009). At the beginning of the smolt run, most smolts migrate at night, but towards the end of the smolt run larger smolts begin to migrate more frequently during the day (Haraldstad et al. 2017). The timing of the smolt run is crucial, as the smolt ‘migration window’ encapsulates the ideal marine conditions for facilitating smolt survival (McCormick, Hansen, et al. 1998). As winters and springs are anticipated to become warmer due to climate change, smolt migrations are expected to shift earlier each spring; however, this could lead to increased mortality for post-smolts as freshwater warms more rapidly than seawater, causing smolts to enter marine conditions that are too cold (Jonsson and Jonsson 2009).

1.4.3 Marine factors affecting Atlantic salmon survival

Much of the mortality experienced by *S. salar* occurs at sea (Chaput 2012; ICES 2021). With populations in decline, increasing the proportion of salmon leaving their natal rivers as smolts and surviving at sea to return to freshwater to reproduce is particularly interesting to managers (Thorstad et al. 2021). There are many challenges faced by smolts as they leave freshwater and enter new saline habitats, such as physiological changes, and novel predators and environmental conditions. (Thorstad et al. 2012). Survival rates during the smolt migration can be very influential on later adult return rates (Stich et al. 2016).

Predation is an important mortality risk to emigrating smolts that move through the lower reaches of the rivers and out through estuaries. Saithe (*Pollachius* virens) and cod (*Gadus morhua*) predate smolts in estuaries, with cod known to cause substantial mortality (for example, 10-25% of smolts leaving Norwegian rivers) (Hvidsten and Mokkelgjerd 1987; Hvidsten and Lund 1988). European bass are also known to predate smolts, with as many as eight individual smolts found in the stomachs of individual bass in an English estuary (Riley et al. 2011). Avian predators also hunt migrating smolts, with herring gulls (*Laris argentatus*) and cormorants (*Phalacrocorax* spp.) known to predate smolts heavily during their migration through lower river reaches, the estuary, and their first day at sea (Dieperink et al. 2002; Flávio et al. 2019; Jepsen et al. 2019).

At sea, post-smolts that experience optimal growth conditions should have marine survival rates and attain body sizes that enables their sexually maturity and return to freshwater to spawn (Friedland 2000; Peyronnet et al. 2007; Friedland et al. 2009). Marine growth and survival are linked to both sea surface temperature and primary productivity (Friedland 2000; Friedland et al. 2009; Beaugrand and Reid 2012), and these trends appear to be synchronous for populations across the North Atlantic (Olmos et al. 2019, 2020). Marine growth can inform maturation schedules, with faster marine growth increasing the likelihood of an individual maturing after one year at sea, though female salmon might require higher growth rates than males to reach their maturation threshold (Tréhin et al. 2021). Climatic indices, such as North Atlantic Oscillation (NAO), impact the temperature regimes in the North Atlantic, which in turn has a profound impact on the abundance and composition of plankton communities, which form the basis of all marine food webs (Beaugrand and Reid 2012). For example, temperature-related decreases in euphausiids and the copepod *C. finmarchicus* is associated with declines in the annual salmon commercial catch at sea (Beaugrand and Reid 2012).

1.5 Body size as a proxy for fitness and probability of marine survival

With many challenges facing migrating smolts and post-smolts, an important predictor of salmon survival and the likelihood of returning to freshwater as an adult could be the size of the smolt as it leaves freshwater (Kallio-Nyberg et al. 2004; Russell et al. 2012; Armstrong et al. 2018; Gregory et al. 2018). It has been posited that among juvenile teleost fishes, larger individuals experience lower mortality rates than smaller conspecifics (Ricker 1976), with this often attributed to larger juvenile fish being predated less frequently by gape-limited predators than their smaller conspecifics (Sogard 1997). Until relatively recently, evidence supporting this hypothesis among salmon smolts had been equivocal (see review by Gregory et al. 2018); while many studies have shown some evidence supporting the hypothesis (i.e., Henderson and Cass 1991; Saloniemi et al. 2004; Armstrong et al. 2018), others suggested that medium-sized smolts have higher marine survival rates (Jonsson et al. 2017).

The uncertainty regarding whether larger smolts fare better than smaller individuals may in part be due to studies addressing this question often have inherent issues, such as small sample sizes, population-level data instead of individual-level data, pseudo-replication, and imperfect detection of returning adults (Gregory et al. 2018). Using population-level data means ignoring the natural individual heterogeneity in body sizes that occurs in populations and is potentially an important fitness-related trait (Gimenez et al. 2018). Studies that use individual-level data often use body length data derived from fish scales, as opposed to measurements taken directly from the fish, where annual growth markings on scales are measured and used to estimate body lengths associated with each annulus (Pierce et al. 1996). However, using this method to estimate body length involves an unquantifiable amount of uncertainty and can be biased if the scale collection method is biased (for example, scales collected from anglers who preferentially target fish of particular body sizes and during specific periods of the adult riverine migration) (Francis 1990; Henderson and Cass 1991). Imperfect detection of returning adults is an issue that has long affected studies that utilise capture-mark-recapture data (‘CMR’) to assess marine survival rates. This occurs when some individuals survive but are not captured/detected and are considered as not having survived. These issues can be overcome by using large datasets with individual-level body measurements and robust statistical techniques (Gimenez et al. 2007, 2018; Gregory et al. 2018). For example, Gregory et al. (2019) implemented a multi-state capture-mark-recapture (CMR) state-space model (SSM) in a case study that tested the effect of individual smolt length on their probability to return as an adult. Their study was, however, limited to a single river and the only explanatory variable included was body length; more work is needed to determine how generalized the bigger-is-better pattern is across Europe.

1.6 Aim and objectives

The overarching aim of this thesis is to examine how biological variables, with an emphasis on body size and environmental conditions experienced by *S. salar* as juveniles, affects their later life stages through carry-over effects. Specifically, factors affecting freshwater growth, migration timing, and marine survival will be evaluated. Much of this work focussed primarily on the River Frome population of *S. salar*. However, the work was also expanded via collaboration with other study groups to a general predictive model developed to generalise the effect of smolt length on adult returns rates across rivers spanning the western coasts of Europe. Correspondingly, the objectives for each data chapter are as follows:

1. Assess the environmental and biological factors determining the variability in the overwinter growth rates of juvenile *S. salar* (Chapter 2).
2. Test the influence of biological and environmental variables on migration timing of *S. salar* smolts (Chapter 3).
3. Test the effect of *S. salar* smolt body length versus environmental factors on their subsequent marine return rates using a CMR state-space model (Chapter 4).
4. Test the effect of *S. salar* smolt body length on marine return rates for populations of anadromous *S. salar* across Western Europe by generalising the CMR state-space model to populations in multiple rivers (Chapter 5).

Then, a final discussion chapter (Chapter 6) brings together the main results from Chapters 2 to 5 and provides more global context for these findings.

1.7 Study sites

1.7.1 The River Frome

The River Frome is a lowland chalk stream in Southern England (Figures 1.2 and 1.3). Chalk streams are unique ecosystems, with 85% of the world’s chalk streams being in Britain. With an underlying geology of chalk, such streams are mostly groundwater-fed because chalk is very porous; thus, aquifers form in the chalk which then feed the streams (Westlake et al. 1972; Berrie 1992). This provides them with relatively stable thermal regimes and discharge rates (Berrie 1992). They also tend to be quite nutrient-rich (Westlake et al. 1972; Berrie 1992; Clarke and Wharton 2001). These conditions lead to them being relatively productive systems that are rich in invertebrates and vegetation (Armitage and Cannan 2000). In particular, *Ranunculus sp.* Are found throughout the River Frome and are important aquatic vegetation that can structure the local habitat, with their leafy fronds helping to accumulate nutrient-rich sediment and with their canopy helping to provide cover for juvenile salmonids and their invertebrate prey (Cotton et al. 2006; Marsh 2019; Marsh et al. 2021). Chalk streams are also important habitats for Atlantic salmon, with chalk stream subpopulations being genetically distinct from all other European populations (Ikediashi et al. 2018).

Figure 1.2. The catchment area of the River Frome, available online at *https://environment.data.gov.uk/catchment-planning/OperationalCatchment/3367*.

Figure 1.3. River Frome, approximately 8 km upstream from the tidal limit, showing the bubble screen used to deflect smolts down the millstream towards the rotary screw trap.

The River Frome rises at Evershot (50.50.24°N; 02.36.12°W) and flows for approximately 70 km to the mean high-water mark, near the town of Wareham (50.40.38°N; 02.07.30°W) (Ibbotson et al. 2013). From this point, the lower Frome is tidal, but still carries freshwater, and passes Wareham Quay, Redcliff, and Ridge to join Poole Harbour a further 3.5 km downstream. The mouth of the harbour is a further 10.5 km (50.40.04°N;56.48.51°W). The River Frome is a low-gradient river with a distinct main channel, although many sections are braided with smaller channels (Figure 1.2). It is the site of ongoing long-term salmon monitoring, which has been taking place in various forms for nearly 50 years (Game and Wildlife Conservation Trust 2018). This monitoring was primarily for returning adult Atlantic salmon; however, since the early 2000s, the parr and smolt populations have also been monitored. To do so, every autumn approximately 10000 parr are captured by electric fishing from sites throughout the river (Figure 1.4.A). Each parr is measured (fork length, nearest mm) and implanted internally with a passive integrated transponder tag (‘PIT’ tag, see Chapter 2 for details; Figure 1.4.D). Upon recovery, they are released to the same river reach from which they were captured. In the spring, migrating smolts are directed down a small side channel to a rotary screw trap (‘RST’) by a bioacoustics fence (Figures 1.3, 1.4.B, and 1.4C). These smolts are checked for PIT tags, with tagged individuals re-measured again before release. Any salmon that survive at sea and return to the River Frome are then redetected by PIT tag readers in the river (see Chapter 4 for details).

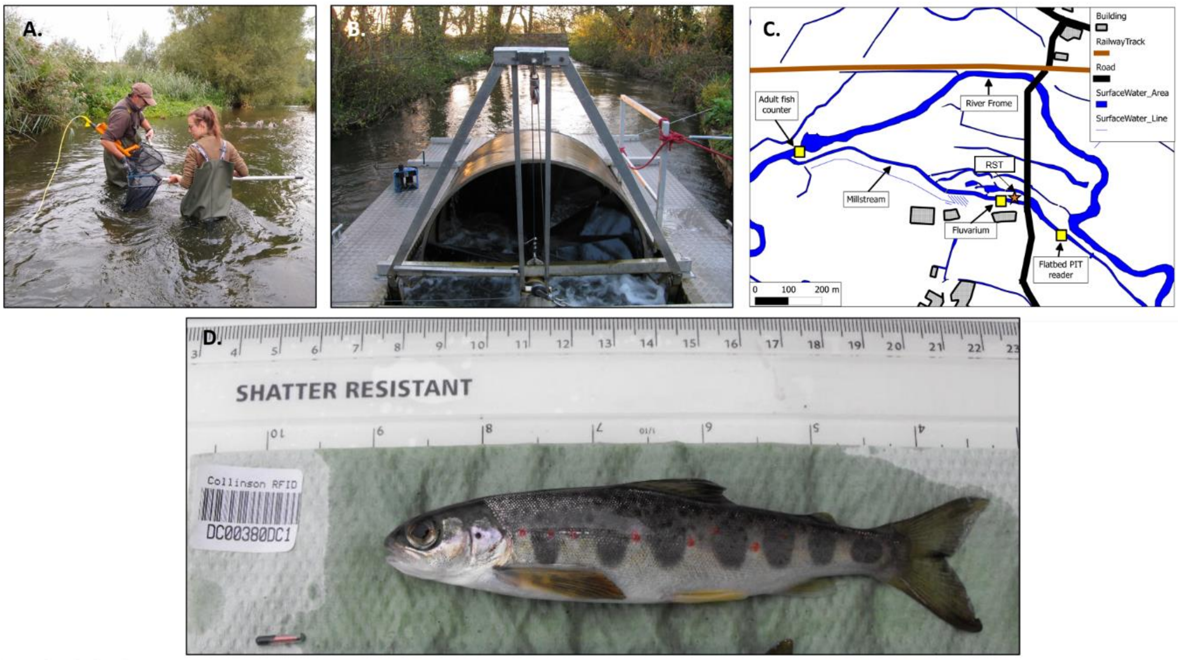

Figure 1.4. Capturing salmon parr on the River Frome for PIT-tagging (A); Rotary screw trap used top resample PIT-tagged salmon as they migrate to sea as parr (B); Map showing location of RST in the 'Millstream', a small channel adjacent to the main river (C); A salmon parr with a PIT-tag (D). Panels 1.4.A and 1.4.D are courtesy of GWCT; Panel 1.4.C is adapted with permission from [*https://stephendavidgregory.github.io/blog/2017-04-01-smolt-run-2017/*](https://stephendavidgregory.github.io/blog/2017-04-01-smolt-run-2017/)*.*

1.7.2 Other study sites

In the final data chapter (Chapter 5), data from six other rivers in Western Europe are used in conjunction with data from the River Frome. These rivers are the rivers Scorff (France), Corrib and Erriff (Ireland), Connon (Scotland), and Storelva and Etne (Norway).

Characteristics of these rivers and the *S. salar* populations therein are described in greater detail in that data chapter. These rivers were selected as there was data available from them that had been sampled using similar methods to the methods used on the Frome, including the use of PIT-tags to track salmon, and because they were thought to embody a representative latitudinal range of *S. salar* in Western Europe.

Chapter 2: Influence of environmental and biological factors on the over-winter growth rate of Atlantic salmon *Salmo salar* parr in a UK chalk stream

2.1 Abstract

Smolt lengths are increasingly recognised as an important determinant of salmonid marine survival rates. Overwintering growth rates could thus strongly influence adult return rates. In Atlantic salmon *Salmo salar*, most overwintering studies focus on rivers in harsh climates with minimal growth, yet in more southerly rivers, overwintering growth rates can be relatively high. Here, the factors influencing annual overwinter growth rates were tested for juvenile *S. salar* in a temperate chalk stream in southern England over 13 years, where over 10,000 salmon parr were tagged annually in autumn and a proportion recaptured the following spring during smolt emigration. Winters of higher and more variable water temperatures, with longer periods of high flows, showed increased overwintering growth rates. Faster growth rates were recorded from sites further upstream and that had lower parr densities; smaller individuals also grew more than expected for their initial size. These results suggest that a range of factors influence overwintering salmonid growth rates and can be used to inform management decisions to maximize the quality of emigrating smolts.

2.2 Introduction

Populations of anadromous fishes have declined drastically in recent decades due to pressures including climate change, overexploitation, and habitat loss (Limburg and Waldman 2009). This is the case for anadromous Atlantic salmon *Salmo salar* which have experienced declines since the 1970s (Parrish et al. 1998; Limburg and Waldman 2009; Mills et al. 2013). Evidence increasingly suggests that intrinsic factors from their freshwater stages, such as smolt body size, are important in determining *S. salar* marine mortality rates (Russell et al. 2012; Armstrong et al. 2018; Gregory et al. 2019). Consequently, understanding the factors affecting individual performance, such as growth during their freshwater stage, could inform management decisions that aim to increase marine survival rates and their probability of returning as a spawning adult (Gregory et al. 2019).

The overwinter period can act as a natural bottleneck for *S. salar* juveniles (Heggenes et al. 2018), because growth rates decrease and mortality rates increase as individuals succumb to the more severe abiotic conditions and increased competition for resources (Cunjak and Therrien 1998). For example, juvenile salmon survival in a Canadian stream was lower prior to ice formation compared to after, due to highly variable water temperatures and flows during the early winter acclimatization period (Linnansaari and Cunjak 2010). Harwood et al. (2001) experimentally demonstrated that overwintering juvenile salmon prefer deep waters but will use areas of shallow water or switch to higher diurnal activity to avoid the negative effects on their growth and survival from competition with brown trout *Salmo trutta*. Whilst these studies suggest the importance of variability in temperature, flow, and competitor density for overwinter growth and survival, other factors have also been suggested as important, including habitat characteristics and juvenile body length (Achord et al. 2007; Hurst 2007; Jonsson and Jonsson 2009; Elliott and Elliott 2010; Nunn et al. 2012; Warren et al. 2015).

The consequences of differences in individual over-wintering performance of salmonids are increasingly understood, including on the phenology of their spring migration, with colder winters sometimes delaying migration (Cunjak and Therrien 1998; Huusko et al. 2007; Munsch et al. 2019). Nevertheless, there is limited understanding on how winter growth contributes to their overall body length at smoltification, despite smolt length being an important determinant of marine survival (Kallio-Nyberg et al. 2004; Armstrong et al. 2018; Chaput et al. 2019; Gregory et al. 2019). This could be because most over-wintering studies have focused on populations experiencing sufficiently harsh conditions to inhibit growth (e.g. Koskela et al. 1997; Murphy et al. 2006). However, salmon in more stable environments, such as temperate rivers and chalk streams, rarely experience the low temperatures and high flows that inhibit juvenile *S. salar* growth. Overwintering growth rates in these rivers could have an important influence on smolt body lengths and marine survival (Berrie 1992; Elliott and Elliott 2010; Kemp et al. 2017). In recent years, winters have been getting warmer, especially regarding minimum winter temperatures (Davy et al. 2017), so studying populations in temperate rivers could help understand systems that are currently cold and harsh but may become less so in the future.

Long-term data are crucial for studying population dynamics and their drivers by allowing the decoupling of the abiotic and biotic drivers of fish growth rates (Reinke et al. 2019). Unfortunately, many long-term fish population studies have issues with the availability of long-term robust environmental data as, for example, flow gauges and temperature sensors can be out of operation at key times (Nakagawa and Freckleton 2008). How these periods of missing data are handled within analyses is important, such as whether biological data for these periods are also removed from analyses or whether the missing environmental data are inferred from surrogate data or via statistical methods (Nakagawa and Freckleton 2008). For the latter, multivariate imputation by chained equations (MICE) enable the data to be imputed using a method that accounts for uncertainty in the estimated values (Buuren & (Buuren and Groothuis-Oudshoorn 2011; Penone et al. 2014). Unlike single imputation methods, it imputes several estimates for the missing values before pooling the parameter estimates for subsequent analyses. While it provides a robust method for handling missing data (Buuren and Groothuis-Oudshoorn 2011), it has rarely been applied in ecological contexts.

The aim of this study was to assess the environmental and biological factors determining the variability in the overwinter growth rates of juvenile *S. salar*. We analysed a 13-year time-series of data in which over 10,000 juveniles were individually Passive Integrated Transponder (PIT) tagged in the autumn of each year in the River Frome and then recaptured the following spring during their smolt migration. The primary objective was to develop statistical models to test the contribution of environmental and biological factors to the annual variability in *S. salar* overwinter growth. The models tested the hypotheses that variation in temperature, flow and population abundance affected juvenile salmon overwinter growth rates in accordance with expectations (Table 2.1). In the River Frome, the majority of smolts emigrate at age one year, unlike northernly rivers where smolts grow slower and emigrate at age two or more years. Consequently, their overwinter growth rate could strongly affect their smolt length. As with most long-term datasets, data were missing in the environmental explanatory variables, so MICE was used to inform the modelling process of the possible effects of environmental variables on overwinter growth rates for periods with missing environmental data.

2.3 Methods

2.3.1 Sampling

The River Frome is a lowland, aquifer-fed chalk stream located in Southern England whose salmon population has been monitored for almost 50 years (Game and Wildlife Conservation Trust 2018). For this study, data were used from annual standardised juvenile *S. salar* surveys that were undertaken between 2005 and 2017. These surveys involved sampling in August and September when, at multiple sites across the catchment (Fig. 2.1), salmon parr were captured during a single run by electric fishing survey (pulsed DC with a square-wave waveform fished at 50 Hertz, ~200 volts and 25-30% duty cycle). Captured parr were anaesthetized, measured (fork length, nearest mm) and weighed (to 0.1 g), and tagged with a uniquely identifying PIT tag. The following spring, a proportion of these fish were recaptured as they moved downstream during their smolt migration. A rotary screw trap (RST) at a fixed location was used each spring between 2006 and 2018 to recapture the salmon (Fig. 2.1). For more detail about the sampling methodology, refer to Riley et al. (2018). Consequently, this study focuses on the overwinter periods between 2005-2006 and 2017-2018. All captured smolts were removed from the trap, anaesthetized, and scanned for the presence of a PIT tag. Where a tag was identified, its code was recorded, and the smolt was remeasured and reweighed as described previously. They were released within one hour of their capture, once their behaviour was judged to have returned to normal. A total of 3899 smolts that had been tagged as parr in autumn were recaptured as migrating smolts the following spring across the 13-year time series. Animal handling and processing procedures were approved by GWCT Animal Welfare Ethical Review Body and were carried out by licenced personnel under a UK Home Office A(SP)A licence (PPL 30/3277).

2.3.2 Response and explanatory variables

The metric used to measure overwinter growth was mass specific growth rate ($MSGR$), (Ostrovsky 1995):

$$MSGR = \frac{L_{sm}^{b} - L_{pr}^{b}}{b * (T_{recap} - T_{cap})}$$

where L_{sm} is the fork length (mm) of the individual as a smolt when recaptured in the RST in spring, L_{pr} is the fork length (mm) of the same individual when it was first captured and marked as a parr the previous autumn, b is the allometric mass exponent for the relation between growth rate and body mass, T_{cap} is the day of year that the individual was first captured that autumn and T_{recap} is the day of year that the individual was recaptured as a smolt in the RST. The coefficient b was set to 0.31, as determined previously for Atlantic salmon parr by Elliot and Hurley (1997). Using $MSGR$, which allows for the relation between body growth and initial size, enabled us to determine whether smaller individuals grew more overwinter than would be expected for their size.

Environmental data were recorded using a combination of methods and were used to calculate environmental explanatory variables for the overwinter period experienced by each individual fish, defined as the number of days between their T_{cap} and T_{recap}. Water temperature was recorded every 15 minutes from January 2005 to January 2009 at a fixed location using a temperature logger (Fig. 2.1). Since then, water temperature has been recorded every 30 minutes by two temperature loggers from January 2009 to 2018 located in the main river close to the RST (River Lab Long Term Monitoring Project, unpublished data). All three loggers (one for 2005-2009 and two from 2009 onwards) were located within 200 m of each other at East Stoke, Wareham (Fig. 2.1). These two datasets were combined to provide the full temperature record over the study period and were applied across the catchment. The temperature measurements were used to calculate degree days ('DD'), the sum of the daily mean water temperature ≥ 6 ^{o}C for each overwinter period (as *S. salar* parr are considered not to grow at water temperatures below this in Britain (Elliott and Elliott 2010), and the coefficient of variation of water temperature ('CV temp'), determined by the standard deviation of the water temperature divided by the mean water temperature for the overwinter period (Table 1). River flow data (m^3s^{-1}) were recorded every 15 minutes at two locations on the river at East Stoke (Fig. 2.1) and used to calculate a daily mean flow (UK Centre for Ecology & Hydrology 2021). The flow measurements were also used to calculate the coefficient of variation of water flow ('CV flow'), determined by the standard deviation of the water flow divided by the mean water flow for the overwinter period. The duration of the high flow events ≥ Q10 (‘DurHF’) were also determined for each overwinter period (Table 2.1).

The distance upstream (km) from the tidal limit of each electrofishing site was also included as an explanatory variable and calculated using the ‘riverdistance’ function in the R package `riverdist` (Tyers 2017). All other explanatory variables were from data collected during the sampling period and were derived after literature review suggested their potential importance to overwinter juvenile salmon growth (Table 2.1). We hypothesised the effect of each explanatory variable on the response variable $MSGR$ from evidence in the literature (Table 2.1), with a candidate model then formulated to explore the form and strength of evidence for these hypothesised effects in the dataset.

In the candidate models, two variables were included as random effects: site of capture of each parr during sampling and year of recapture of the smolt in the RST. There were 50 sites from which parr had been sampled. Eight of these sites were excluded from the analysis because there were too few parr captured at each of them during the 13 years of parr sampling (n ≤ 7).

2.3.3 Missing data and multivariate imputation

A total of 47 days of water temperature data required for calculating DD and CV temp were missing from the long-term data due to equipment failure. These missing data were from across three of the 13 overwinter periods. DD and CV temp were set to ‘NA’, (i.e. missing) for all fish observed during these overwinter growth periods, resulting in 1124 individuals (28.8% of all recaptured fish) without these water temperature data variables (Table 2.2). These years were assumed to be missing at random, but this assumption was explored by examining air temperature data downloaded from a weather station in Dorset (Met Office 2019). None of the three overwinter periods with missing temperature data (Table 2.2) had the warmest or coldest mean winter air temperatures. Monthly means were plotted using the `ggplot` function from the R package `ggplot2` (Wickham 2011) and were visually assessed to determine whether any of the years between 2005–2018 had anomalous temperature patterns. Once satisfied that there were no such anomalies, it was assumed that the missing water temperature measurements were random (Figure A1.1).

The proportion of the total number of cases with missing data were deemed to be non-negligible. Consequently, the missing data were imputed using multivariate imputation by chained equations (MICE), implemented in the R package `mice` (Buuren and Groothuis-Oudshoorn 2011). Unlike other methods of imputation that assume no uncertainty in the imputation model, MICE imputes missing data for several replicate datasets that are then analysed and summarised so as to incorporate uncertainty in the imputation model. The `2l.lmer` method was used from the R function `mice` that uses an iterative algorithm requiring far fewer iterations than other Gibbs sampling methods. Five iterations were used to impute 10 datasets. Density plots of the distributions of the 10 imputed datasets and the observed values for both degree days and CV temperature were inspected to ensure the distributions of the imputed datasets were similar to the distributions of the observed values (Figure A1.4). Trace plots of the five iterations showed that the algorithm converged for both variables (Figure A1.5). The R function `with` was used to fit the model to each of the imputed datasets. These results were combined so that there was a single estimate and standard error for each model parameter using the R function `pool`.

2.3.4 Statistical analysis

Prior to analysis, all explanatory variables (Table 2.1) were standardised by subtracting the mean value and dividing by the standard deviation using the R function `scale`. The variables were then tested for collinearity (Pearson's correlation; Figure A1.3); variables that had $r \leq 0.70$ were retained; variables with r > 0.71 were considered collinear, with only the most ecologically interesting collinear variable retained (based on variables other researchers have investigated and found to be important) (Table 2.1).

The statistical models took the form:

$$MSGR \sim \mathrm{Normal}(\mu, \sigma^2)$$

$$\mu = \alpha + \beta X + \nu_{\mathrm{Y}} + \upsilon_{\mathrm{S}}$$

where α is a constant, $\beta = \beta_1, \beta_2, \ldots \beta_k$ is a vector of k parameters relating the matrix (X) of explanatory variables $x_1, x_2, \ldots x_k$ to $MSGR$, assuming a Normal and i.i.d. error term, while treating years and sites as random effects, ν_Y and υ_S respectively, i.e., representative samples of a longer period and a larger area.

The model parameters were then estimated using the `lmer` function in the R package `lme4` via restricted maximum likelihood (Bates et al. 2014). Candidate models were compared by their goodness of fit using information criterion and R^2 values. The candidate model set included 31 models. Before fitting models to test hypotheses about the environmental variables (Table 2.1), the different combinations of spatial and temporal variables that best captured the sampling protocol underlying our data were explored. To do this, models were built and compared using only the variables ‘distance upstream’ (fixed effect), ‘year’ (fixed trend effect), ‘site’ (random effect), and ‘year’ (random effect). The combination of these variables included in the most parsimonious model was taken forward for the remaining analyses. This was indicated by the lowest Akaike information criterion (AIC) value from the median imputed dataset. Next, the shape of the relationship of variables CV temp and CV flow with $MSGR$ were determined by building models including them as linear and quadratic fixed effects and taking forward the most parsimonious model for the remaining analyses. Again, the model with the lowest AIC from the median imputed dataset was used to decide whether each term should be included as a linear or quadratic term. Finally, the other explanatory variables were added to the model as fixed effects. The final, best model was taken to be the most parsimonious model as indicated by the lowest median AIC across the multiple models. The marginal and conditional R^2 values were calculated using the R function `rsquared` in the R package `piecewiseSEM` (Lefcheck 2016). The marginal effects of the parameter estimates were plotted via the `ggplot` function in R package `ggplot2` (Wickham 2011).

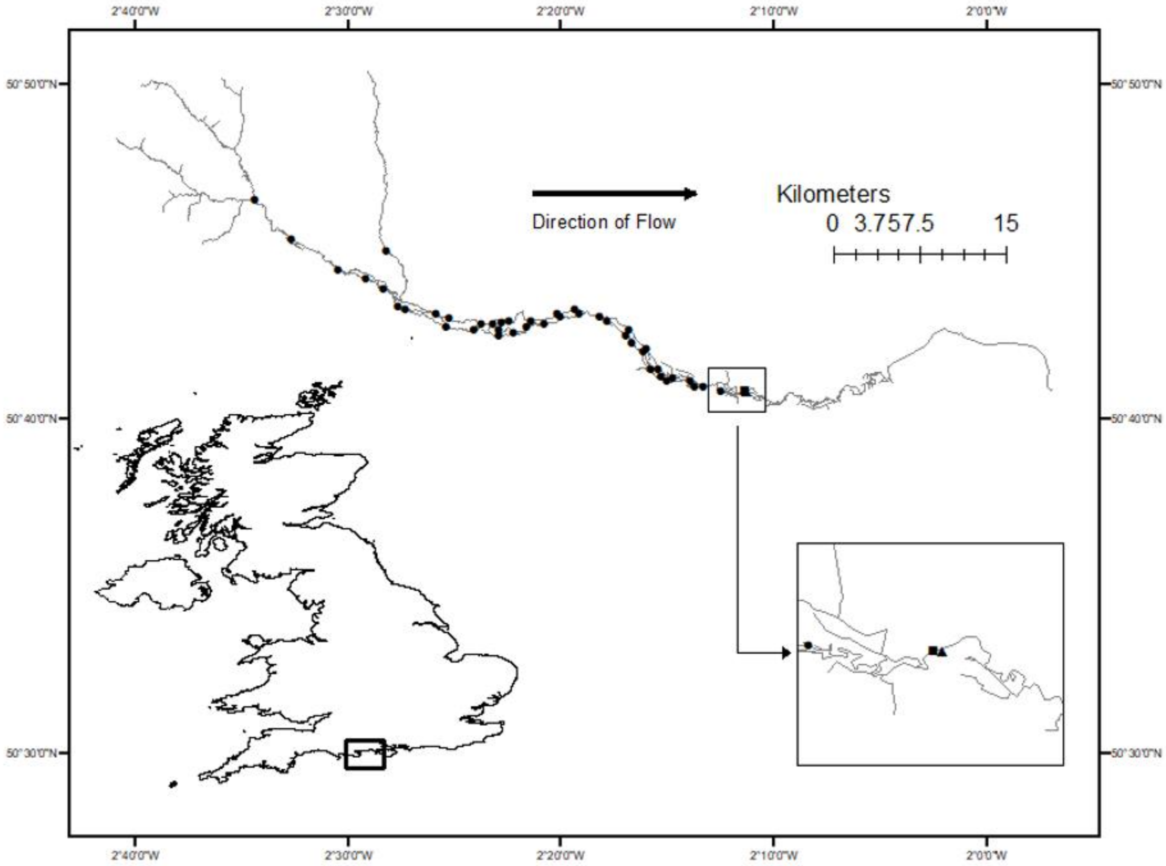

Figure 2.1. Map of the study river. On the main plot of the river, each black circle is a site sampled by electric fishing. On all maps, the square represents the location of the flow meter throughout the study period and the temperature logger from 2005 to 2009, and the triangle shows the location of the temperature loggers from 2009 to 2018, as well as the location of the RST each spring.

Table 2.1. List of explanatory variables used to describe overwinter mass specific growth rate (MSGR) of juvenile Atlantic salmon on the River Frome between 2005 and 2018. The range of values provided is for the unstandardized observed values at the study site over this time period.

	Variable	**Abbreviation**	**Definition**	**Hypothesized effect on $MSGR$**	**Range of observed values**	**Mean ± Standard Deviation**	**References**
Environmental Variables	Degree days over 6 °C	DD	Sum of daily temperatures between date of parr capture and smolt recapture	+	223.3 - 1449.8	890.75 ± 178.619	(Harstad et al. 2018; Jonsson et al. 2005)
	Coefficient of variation of temperature	CV temp	Coefficient of variation in water temperature between date of capture and recapture for each fish	-	0.125 - 0.330	0.240 ± 0.040	(French et al. 2017)
	Coefficient of variation of flow	CV flow	Coefficient of variation in water flow between date of capture and recapture for each fish	-	0.256 - 0.720	0.460 ± 0.095	(Arnekleiv et al. 2006)
	Duration of high flow events in the autumn	DurHFT1	Length of high flow events ≥ Q10 from date of parr capture to December 31	-	7.125 - 122.000	38.491 ± 25.729	(Arndt et al. 2002)
	Duration of high flow events in the winter	DurHFT2	Length of high flow events ≥ Q10 from January 1 to date of smolt recapture	-	22.467 - 122.500	51.373 ± 29.305	(Arndt et al. 2002)

Other Variables	Distance upstream	Distance	Distance upstream from East Stoke of parr sampling site (km)	+	1.897 - 43.113	17.489 ± 8.427	(Erkinaro and Niemelä 1995)
	Parr length	Length	Fork length of parr captured in the autumn (mm)	-	61.0 - 119.0	93.753 ± 10.141	(Achord et al. 2007)
	Relative density	Density	Standardised (by subtracting mean and dividing by SD) total number of salmon caught at each site	-	5 - 1652	564.606 ± 386.737	(Grant and Imre, 2005)
	Year (fixed numeric)	Year	Year that smolts were recaptured – test for trend in $MSGR$	-	2005 – 2017		(Nater et al. 2018)

Table 2.2. Total number of days with missing water temperature data for each overwinter period. The overwinter period was defined as the period between 1 September and 31 May for each period.

Overwinter period	**Months with missing data**	**Total number of days with missing data**
2005-2006	September, October, December	28
2007-2008	September, October	9
2008-2009	December, January, February	10
Total		47

2.4 Results

A total of 3899 smolts that had been tagged as parr were recaptured in the RST between 2005 and 2018. The year with the most tagged smolts captured was 2007, followed by 2009 and 2008. The year with the fewest smolts recaptured was 2018, followed by 2017 and 2015 (Table 2.3). The mean $MSGR$ over the study period was 0.012 mm^{-1} d^{-1} (standard error = 0.060). The overwinter period with the lowest mean $MSGR$ was 2012-2013 (mean = 0.011 mm^{-1} d^{-1}; standard error = 0.057), with 2015-2016 having the highest mean $MSGR$ (mean = 0.014 mm^{-1} d^{-1}; standard error = 0.069) (Fig. 2.3). The mean annual values for each environmental and biological variable are in Fig. 2.2.

The best and most parsimonious model selected via AIC is given by:

$$MSGR = \alpha + \beta_1(DD) + \beta_2(CV\ temp) + \beta_3(CV\ flow) + \beta_4(CV\ flow)^2 + \beta_5(DurHFT2) + \beta_6(Distance) + \beta_7(Length) + \beta_8(Density) + \upsilon_Y + \upsilon_S + \varepsilon$$

This model included both year and site as random effects (Table 2.4; Figure A1.2). The fitted values closely matched the observed values of $MSGR$ (Fig. 2.3). Four of the five environmental variables tested were retained in the best model; only the duration of high flows events in autumn (DurHFT1) was dropped. Of the four retained environmental variables, only the coefficient of variation of flow (CV flow) was included as a quadratic effect; degree days over 6 °C (DD), the coefficient of variation of flow (CV temperature), and the duration of high flows events in winter (DurHFT2) was linear terms in the best model (Fig. 2.3; Table 2.4). The non-environmental variables included in the best model were distance upstream of autumn capture (Distance), length (Length), and relative density (Density), while year as a trend was dropped. (Fig. 2.3; Table 2.3). The difference in AIC (ΔAIC) between the best model and the next best model was 7.91. The conditional R^2 value of the best model was high at $R^2 = 0.98$ due to the inclusion of both spatial and temporal random effects, with the marginal R^2 value also high at $R^2 = 0.48$ (Table 2.4).

The marginal effects of each explanatory variable revealed that DD, CV temp, and DurHFT2 had positive effects on $MSGR$ and CV flow had a negative quadratic effect on $MSGR$ (Fig. 2.5). This means that warmer water (more DD), more variation in water temperatures (higher CV temp), and longer periods of flows ≥ Q10 from January to the end of each overwinter period (higher DurHFT2) led to higher rates of growth among juvenile salmon during the winter. Also, higher variation in flow (CV flow) led to higher overwinter growth rates, until CV flow reached the standardised value of 0.073 (CV flow value prior to standardisation = 0.466), after which increasing flow lead to lower growth rates. Of the non-environmental variables, only distance upstream had a positive effect on $MSGR$, meaning that the further upstream a parr was captured the more it grew during the winter. Both parr length and relative density had negative effects on $MSGR$, although the effect of density on $MSGR$ was small. This means that smaller parr grew more overwinter than one would expect given their initial size, and that parr in denser sites grew more slowly than parr in less dense sites (Table 2.5; Fig. 2.4; Fig. 2.5).

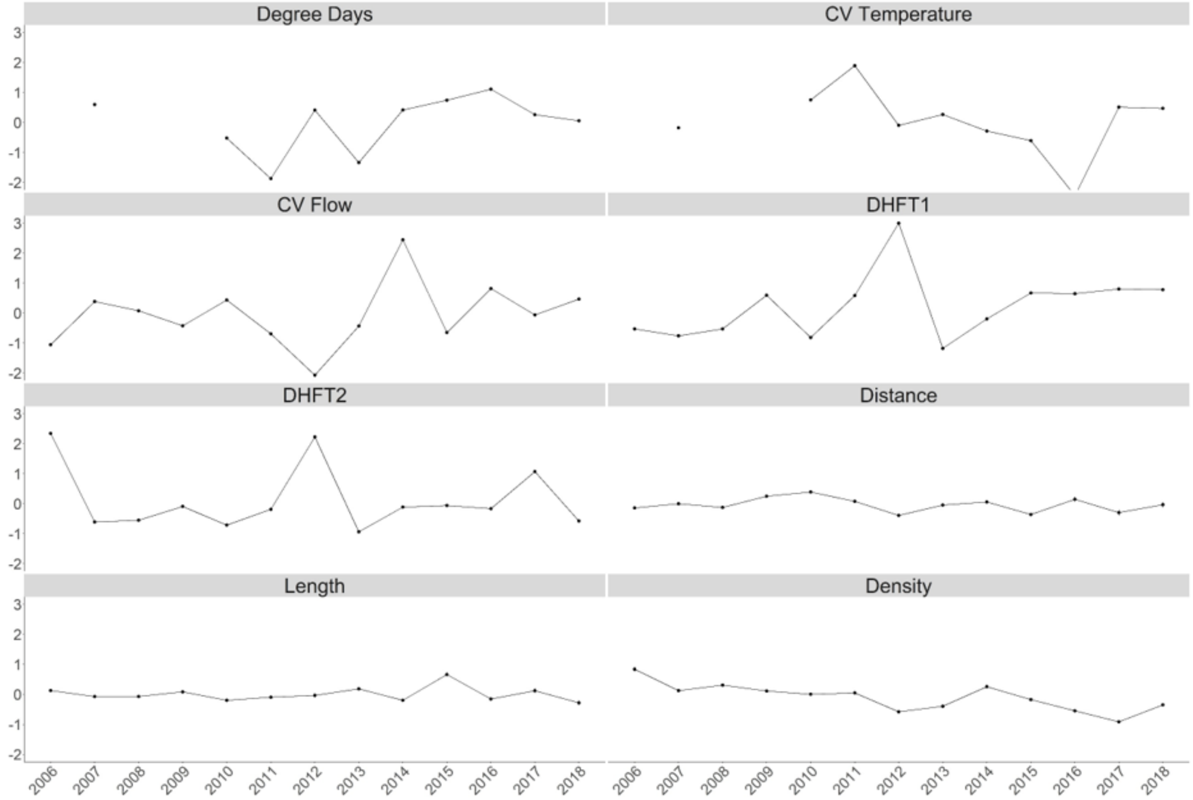

Figure 2.2 Annual mean standardised value for degree days (A), coefficient of variation of temperature (B), coefficient of variation of flow (C), duration of high flow events in the autumn (D), duration of high flow events in the winter (E), distance upstream (F), parr length (G), and relative density (H). Standard errors are shown as the vertical lines surrounding each point.

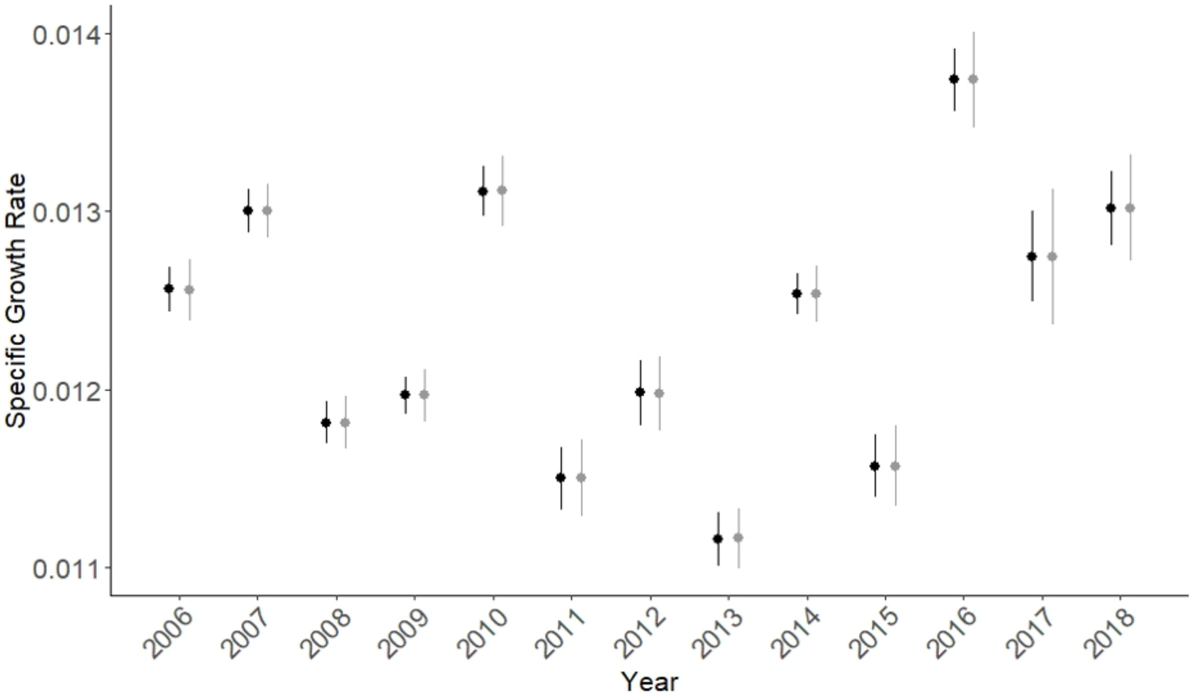

Figure 2.3. Fitted and observed values of MSGR by year from the best model. The black circles are the fitted value from the best model and the grey circles are the observed values. The vertical lines show the standard errors.

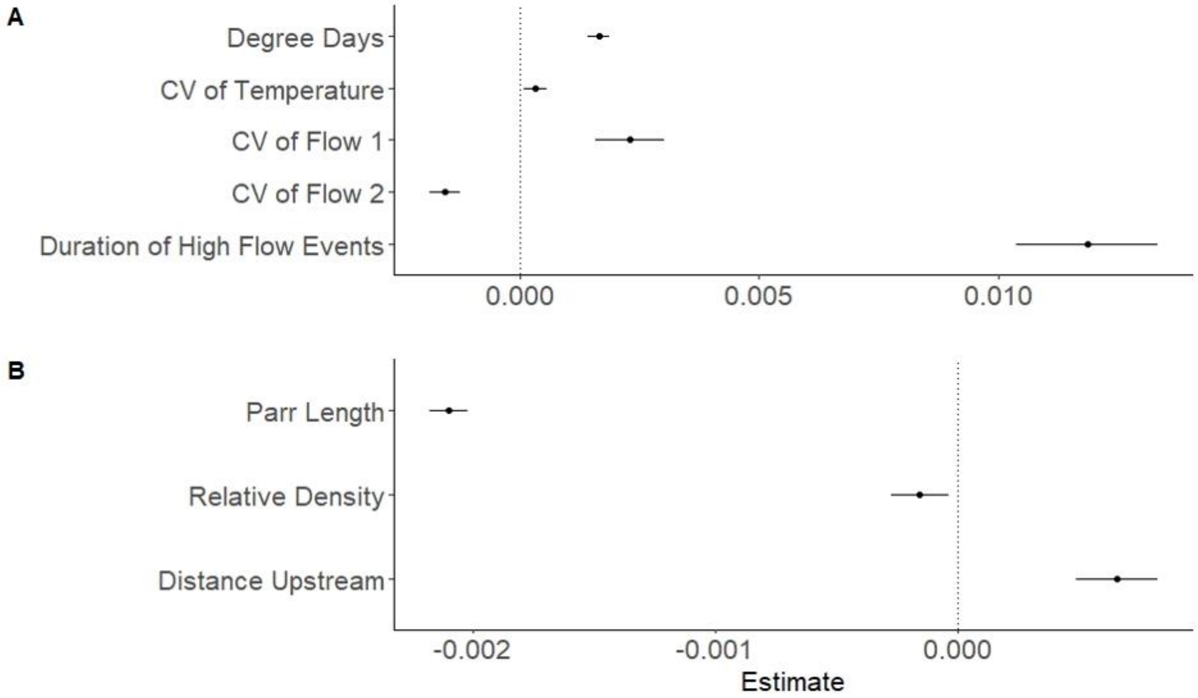

Figure 2.4. Maximum likelihood estimates of fixed effects of environmental variables (A) and biological variables (B). The points are the estimated values and the lines show the 95% confidence intervals for each value.

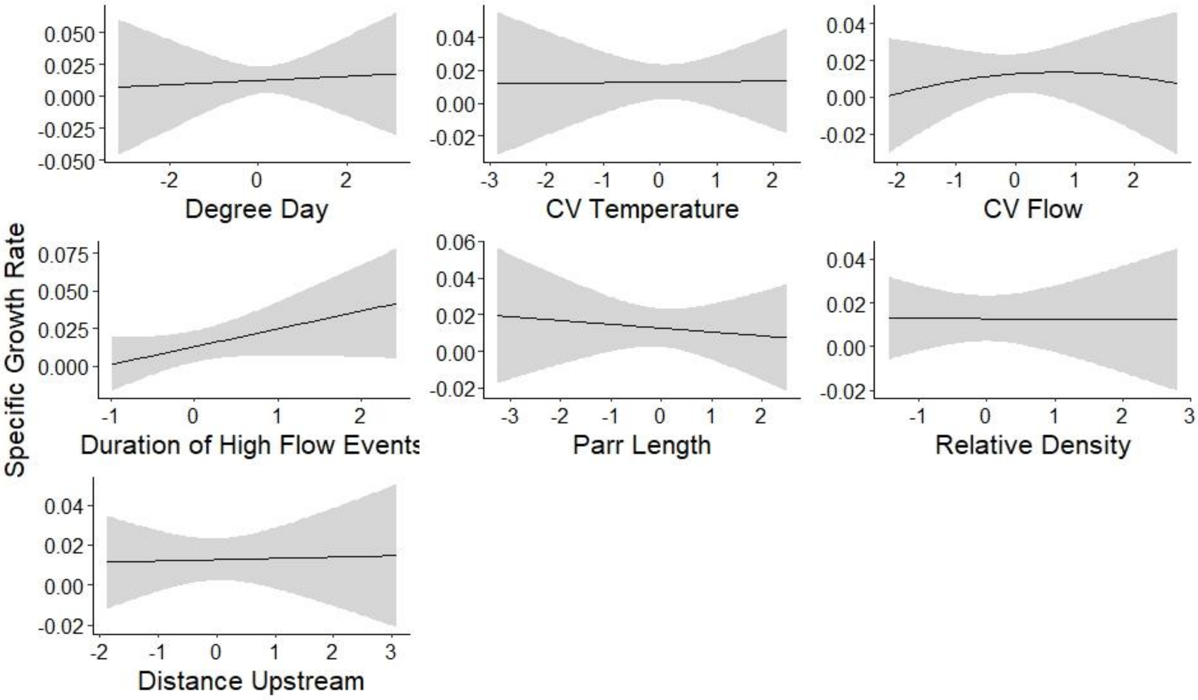

Figure 2.5. Marginal effects plots of each standardized explanatory variable. The shaded areas represent the 95% confidence interval.

Table 2.3. Total number of PIT-tagged smolts caught in the RST each spring.

Year	**Number of Smolts caught in RST**
2006	316
2007	609
2008	389
2009	419
2010	356
2011	224
2012	223
2013	330
2014	303
2015	220
2016	233
2017	141
2018	136

Table 2.4. The top five candidate models explored together with the hypothesis each model was designed to test. The median AIC, marginal R^2, and conditional R^2 across the models fitted to the multiple MICE imputed datasets are also displayed.

	Model Description		**Comparisons**		**R^2**	
	Parameters	**Hypothesis tested**	**AIC**	**ΔAIC**	**Marginal**	**Conditional**
1	Fixed: CV temp, CV flow^2, Distance, Length, DD, Density, DurHFT2 Random: Tag site, Year	Excluded year as a fixed effect to test whether there was a trend across years in the data	-36419.00	0	0.471	0.980
2	Fixed: CV temp, CV flow^2, Distance, Length, DD, Density, DurHFT2, Year Random: Tag site, Year	Included year as a fixed effect to test whether there was a trend across years in the data	-36404.87	14.13	0.450	0.980
3	Fixed: CV temp, CV flow^2, Length, DD, Density, DurHFT2 Random: Tag site, Year	Excluded distance as a fixed effect to test whether distance upstream affected growth	-36402.81	2.06	0.472	0.980
4	Fixed: CV temp, CV flow^2, Length, DD, Relative density, DurHFT2, Year Random: Tag site, Year	Included year, but excluded distance	-36388.70	14.11	0.452	0.981
5	Fixed: CV temp^2, CV flow^2, Length, DD, Density, DurHFT2 Random: Tag site, Year	Included year as a quadratic term to test shape of effect	-36386.65	2.05	0.473	0.980

Table 2.5. Coefficient estimates for variables included in the best model.

Fixed Effects	Estimate	Standard error	Lower Confidence Interval	Upper Confidence Interval
Intercept	0.0017	0.0001	0.0089	0.0160
DD	0.0003	0.0002	-0.0019	0.0052
CV temp	0.0023	0.0004	-0.0036	0.0039
CV flow 1	-0.0016	0.0002	-0.0013	0.0059
CV flow 2	0.0119	0.0007	-0.0051	0.0020
DurHFT2	-0.0021	0.0000	0.0083	0.0154
Length	-0.0002	0.0001	-0.0057	0.0015
Density	0.0007	0.0001	-0.0037	0.0034
Distance	0.0017	0.0001	-0.0029	0.0042

2.5 Discussion

The results reveal that several factors influenced the juvenile *S. salar* overwinter growth rates, which might then be expected to influence their length at smoltification and, by implication, their subsequent survival at sea (Gregory et al. 2019). Higher water temperatures and the distance upstream of the parr sampling site had positive effects on overwinter growth rate, while population density had a negative effect on growth. Year as a fixed effect was excluded from the best model, indicating that, over the study period, overwinter $MSGR$ did not change overall. Across the variables in the best model, there were two findings contrary to the hypotheses: the positive effect of CV temperature and the duration of high flow events on overwinter growth, which were hypothesised to be negative.

Of the biological variables tested, parr length and relative density had negative effects on the overwinter growth rate of juvenile *S. salar*. Parr that were larger in autumn grew more slowly over winter compared to smaller parr, a result that has been found in other salmonid species, such as *Oncorhynchus tshawytscha* in Snake River, Idaho (Achord et al. 2007). The smaller parr in this study not only grew faster than the larger parr, as previously recorded in salmon growth studies (e.g. Achord et al. 2007; Bacon et al. 2005), but they actually grew faster than expected for their body size. The higher growth rate of smaller parr may be at least partially related to there being a threshold size for juvenile salmonids to reach before they undergo smoltification (Metcalfe 1998). The physiological 'decision' to smoltify occurs several months before the event (Metcalfe et al. 1988), influenced by factors such as whether the fish has adequate resources (Metcalfe 1998), with the majority (> 95%) of *S. salar* in the Frome smolting at age one year (Ibbotson et al. 2013). With the 'decision' to smoltify the following spring already made, smaller parr may have to grow faster than larger parr to reach this threshold size (Triebenbach et al. 2009). Whilst relative density was retained in the best model, with fish at higher densities growing more slowly than fish at lower densities, this effect was relatively minor over the range (5 – 1652 parr per site) of population densities encountered. This contrasts with other studies that have revealed overwinter growth in juvenile salmonids as being strongly density dependent (Kaspersson and Höjesjö 2009; Teichert et al. 2010; Tattam et al. 2017). Some studies have suggested that growth is density dependent when a salmonid population experiences exploitative competition, which occurs when resources are limited (e.g. Imre et al. 2005; 2010). That population density had only a small effect on overwinter growth here could be because the River Frome remains relatively warm and ice-free during the winter period, thus providing a productive habitat throughout the season (Berrie 1992). Resource competition during the overwinter period might therefore be lower in this river compared to more northerly rivers where density dependent overwinter growth is more evident (Kaspersson and Höjesjö 2009; Teichert et al. 2010). In future studies, it is suggested that the role of variation in parr densities and resource availability (food, habitat) are investigated on juvenile overwinter growth rate, which could then be combined with analyses to also test the influence of the distance upstream on growth.

It was hypothesised that water temperature (as degree-days) would positively influence the overwinter growth of juvenile salmon and this was supported by the models. This is potentially important, given that climate projections for southern England suggest river temperatures will increase in future winters (Watts et al. 2015). Given the positive effect of temperature on overwinter growth, these elevated temperatures are likely to result in faster winter growth rates (French et al. 2017; Harstad et al. 2018). Whether faster growth would result in smolts leaving the river at a larger size is, however, uncertain given that smolt migrations are anticipated to commence earlier in the season as warming rates increase (Kennedy and Crozier 2010; Otero et al. 2014). The final model also predicted that juvenile salmon grew faster when they experienced higher wintering temperature variations, a finding contrary to the hypothesis and also several other studies that have investigated links between juvenile salmonid growth and thermal stability (e.g Dieterman et al. 2012; French et al. 2014). For example, French et al. (2017) found that in groundwater-fed rivers in North America, stable thermal conditions improved juvenile growth rates, with this stability more important than prey quality and abundance. The reasons for the inconsistencies in the results between these studies and our study are unclear, although they might relate to species-specific factors, given most of the work in this area has been focused on naturalised *S. trutta* in North America, whereas here the focus was on native *S. salar* (Dieterman et al. 2012; French et al. 2014, 2017). This also suggests that care is needed when developing hypotheses for *S. salar* based on literature from other salmonid species (where relevant literature is not otherwise available), as despite their taxonomic similarities, there might be some differences in how their traits are expressed in relation to different environmental variables.

The influence of flow variability on juvenile salmon growth was predicted as important, albeit that the effect was non-linear and the effect size was relatively low. The quadratic effect suggested that juvenile *S. salar* growth rate increased with increasing flow variability, until it reached a threshold beyond which flow variability was detrimental to growth rate. Chalk streams, such as the River Frome, tend not to have a large range of flow rates (Berrie 1992). The range of CV flow in the study river was 0.26 to 0.72, far lower than in more northerly rivers where CV flow can be high. For example, Arnekleiv et al. (2006) revealed that CV flow ranged from approximately 40 to 100 in the River Stjørdalselva, Norway. This suggests that low to moderate variation in winter flow is positive for growth rate in relatively benign rivers such as the Frome, perhaps because occasional higher flows replenish dwindling food supplies (Parrish et al. 2004). It also suggests, however, that if winter flow rates were to become more variable in the Frome, as could occur under some climate change scenarios (Watts et al. 2015), there could potentially be negative consequences for juvenile salmon overwinter growth rates. Aside from CV flow, the model showed a positive effect of the duration of high flow events on overwinter $MSGR$, meaning that more frequent events of flows exceeding Q10 results in increased juvenile salmon overwinter growth rates. This result is contrary to the hypothesis, as we predicted that longer periods of high flows would have a negative effect on the overwinter growth of juvenile *S. salar*. High flood events have been noted to displace juvenile salmonids and their prey downstream, away from their preferred habitats (Tetzlaff et al. 2005). However, large, stochastic flood episodes are relatively infrequent on the Frome, with periods of elevated flow due to high rainfall events rather than snowmelt. While the variable of duration of high flow events was considered an accurate representation of high flow events in the River Frome, it might be that these events were not sufficiently extreme to detrimentally increase the energetic costs of swimming or to displace the parr. For example, the magnitude of the difference between the Q10 and Q95 values in the Frome (x2) is much smaller than those of the Girnock Burn catchment (x20) of Tetzlaff et al. (2005), where negative effects of high flows were apparent. Moreover, studies that test the effects of high and low flow velocities within ranges that do not displace the fish downstream indicate that elevated flows can be beneficial for growth due to the fish increasing their foraging rates in these periods (Parrish et al. 2004).

Finally, the last fixed effect that was tested was the distance upstream, with this having a positive effect on overwinter growth. There is little literature that examines the relationship between distance upstream and growth, and distance upstream might be considered a proxy for other variables, such as gradient and channel width, that influence flow rates. Indeed, flow rates often vary between upstream and downstream reaches of a river, with upstream areas often experiencing higher mean flows (Leopold 1953). However, all variables were tested for correlation, with distance upstream and CV flow, and distance and DurHFT2, not being highly correlated (Pearson's r = 0.08). Alternatively, food abundance may vary with river distance. Data on food abundance was not included in the design for this study and thus was not available for the time series but should be considered in future research. The underlying mechanism for this spatial outcome thus requires further investigation, given it might be a proxy for another variable, or even multiple interacting variables.

A major challenge of this study was working with a long-term dataset containing missing values for water temperature, data that were the basis of two of the environmental variables used in the models. This is a common issue for researchers to contend with when working with large, long-term datasets (Nakagawa and Freckleton 2008). Other studies have used a variety of methods to overcome such deficiencies, such as deleting cases where one or more variables have missing values, or using single imputation methods, maximum likelihood estimation, and/ or multiple imputation (Raghunathan 2004; Horton and Kleinman 2007; Nakagawa and Freckleton 2008; Penone et al. 2014). Specifically, when dealing with missing water temperature data, as was the case with this study, researchers sometimes use regression analysis with air temperature to estimate water temperature (Caissie et al. 2001; Gregory et al. 2017). While this might be acceptable during warm periods, the relationship between water and air temperature often breaks down during cold periods in winter (Letcher et al. 2016). Deleting cases with missing information is the most common method used for dealing with missing data, but it is problematic because it increases estimation bias (Nakagawa and Freckleton 2008). Indeed, Penone et al. (2014) demonstrated that if 30% or more of a variable in a dataset has missing values, very substantial biases can occur when researchers opt to simply cut all individuals with the variable missing from the dataset. In our River Frome dataset, DD and CV temp variables were missing for 28% of the cases, with this overcome by application of multivariate imputations by chained equations that enabled a substantial number of cases to be retained that might otherwise have been thrown out of the data set. This method also helped overcome issues that arise from using air temperature data to estimate water temperature, which can lead to statistically noisy results (Arismendi et al. 2014; Letcher et al. 2016). The use of MICE also allowed uncertainty in the imputation model to propagate into the model results, thereby treating the imputed data points as being uncertain.

This study shows positive effects of many of the tested environmental variables on overwinter growth. These variables are all expected to increase in magnitude, frequency or both in freshwater under climate change (e.g. Garner et al. 2017; Walsh and Kilsby 2007). As *S. salar* do not smolt younger than age one (Jonsson and Jonsson 2009), higher winter growth rates that result from warmer winters could conceivably mean larger smolts in temperate rivers, such as the Frome, although they might also emigrate earlier, weakening this potentially positive effect (Jonsson and Jonsson 2009; Kennedy and Crozier 2010; Otero et al. 2014). In more northernly rivers than the Frome, smoltification occurs only after several years in freshwater (Metcalfe and Thorpe 1990; Jensen et al. 2014). Although smoltification may occur at a younger age following a warmer-than-normal winter (Jonsson and Jonsson 2005; Strothotte et al. 2005), some studies have reported that faster juvenile growth in warmer winters can lead to younger smolts that have smaller body lengths (Økland et al. 1993; Strothotte et al. 2005). An extensive review of the possible implications of climate change on *S. salar* and S. *trutta* life histories suggested that as rivers become warmer during winter, emigrating smolts will have smaller body lengths than in previous years (Jonsson and Jonsson 2009). This is worrying, as increased lengths and condition of emigrating smolts increase their probability of successfully returning from sea as adults to their natal river to spawn (Russell et al. 2012; Armstrong et al. 2018; Gregory et al. 2019). Given that many rivers are already experiencing relatively low return rates of *S. salar* adults (Chaput 2012), then our results, coupled with these predictions of the impacts of climate change, suggest that attempts to increase adult return rates by attempting to increase the size and condition of emigrating smolts could be highly challenging in future. In the future, maximizing the size and/or condition of smolts may be achieved via a variety of measures, including improving nursery habitats, ensuring optimal thermal conditions through increased shading, or other measures to improve environmental conditions experienced during the early life stages of *S. salar*.

Chapter 3: Biological and environmental influences on the migration phenology of Atlantic salmon *Salmo salar* in a chalkstream in southern England.

3.1 Abstract

Migration enables animals to access important resources throughout their lifetime but exists in a trade-off with elevated mortality risk. In spring, juvenile Atlantic salmon ('smolts') migrate from their natal rivers for marine feeding grounds, with the timing of their marine entry a potentially important determinant of their long-term survival. However, there is relatively little known on how the interaction of biological and environmental factors affect smolt migration phenology at the individual level, and how these vary throughout the duration of the smolt seaward migration ('run').Using 15-year tag recapture and detection datasets of individual smolts (marked with passive integrated transponder tags) from a chalk stream in southern England, the influences of a range of biological and environmental variables were tested on the run timing of individual smolts, measured as the timing of their arrival in a lower river reach. The probability of smolts arriving earlier in the lower river reach was elevated following winters that were relatively warm, and when there were larger positive daily changes in water temperature and discharge during the run. Early migrants tended to be larger individuals and from sites lower in the catchment, from where the smolts had to migrate relatively shorter distances. Later migrants were more likely to migrate in schools, but with schooling behaviour also more likely to occur during daylight than at night. The relative influence of some of these variables altered throughout the run. Relative changes in daily water temperature were not important during the middle period of the smolt run but were important at the start and end of the run. Relative changes in daily discharge were most influential towards the end of the run, when even relatively small changes in discharge had a strong influence on migration. These results reveal the importance of a wide range of biological and environmental variables on the phenology of smolt migrations, and how their influence can alter throughout the run. With predictions of annually increasing river temperatures, more frequent and intense discharge events, and associated shifts to earlier migration, these results emphasise that such changes in climate are likely to have substantial consequences on the future success of smolt migrations and thereby future numbers of returning adult spawners.

3.2 Introduction

Migration enables animals to access greater prey resources, leading to faster growth and, ultimately, greater fitness (Otero et al. 2014; Jonsson et al. 2017). However, long-distance migrations exist in a trade-off with increased mortality risk (such as from predation) and higher energetic costs (Milner-Gulland et al. 2011; Jonsson et al. 2017). These risks and costs can be reduced through behavioural adaptations, including in migration timing (‘phenology’) that can reduce predator exposure, minimize energy expenditure and/ or enable the timing of arrival in the new habitat to be coincident with abundant prey resources (Hedenstrom 2008; Otero et al. 2014; Jonsson et al. 2017).

Atlantic salmon (*Salmo salar*) are generally anadromous, whereby juveniles undertake long migrations from freshwater to ocean feeding grounds in the North Atlantic, subsequently returning to their natal rivers to spawn as adults after 1 to 3 years at sea (Thorstad et al. 2011). Their juvenile (‘smolt’) migration downstream from riverine nursery areas to the sea (‘smolt run’) is hazardous, with mortality risks including predation by piscivorous birds, fish, and mammals (Jepsen et al. 2006, 2019), and migration barriers such as weirs and dams can impede their progress (Kärgenberg et al. 2020). Migration between freshwater and marine environments requires physiological and morphological adaptation to both long-distance migration and the new environment (McCormick, Shrimpton, et al. 1998; Stich, Bailey, et al. 2015). Morphological changes in juvenile *S. salar* include body pigmentation becoming increasingly silver and body shape becoming more streamlined, and physiological changes that include increased salinity tolerance and a switch to a higher metabolic rate (Thorstad et al. 2012). These changes are cued by increasing water temperature and photoperiod in the early spring (McCormick and Saunders 1987; McCormick, Shrimpton, et al. 1998). This ‘smoltification’ generally requires the individual fish to have attained a minimum size-dependent developmental stage (Gregory et al. 2017), suggesting that the extent of growth in the preceding months is an important determinant of whether an individual undergoes smoltification in spring (Simmons et al. 2020). However, other evidence suggests the decision to undergo the parr to smolt transformation (‘smoltify’) in the spring might be made as early as the previous autumn (Metcalfe et al. 1988).

Once smoltified, the migration timing of a smolt is then cued by biological and environmental conditions that enhance the likelihood of the smolt being able to move downstream in an efficient manner (McCormick, Shrimpton, et al. 1998; Antonsson and Gudjonsson 2002; Aldvén et al. 2015). These 'releasing factors' predominantly involve water temperature and river discharge, although other factors might also contribute to migratory release (McCormick, Shrimpton, et al. 1998; Antonsson and Gudjonsson 2002; Aldvén et al. 2015). The cumulative water temperature and the relative changes in daily water temperature experienced by smolts have both been found to influence the timing of smolt migration (Zydlewski et al. 2005; Teichert et al. 2020). Increased river discharge has also been reported as an important releasing factor, although whether it is more important than water temperature appears river-specific (Jonsson and Ruud-Hansen 1985; Aldvén et al. 2015). As the smolt run progresses through the springtime, temperature and discharge conditions change; thus, it is possible for their relative effect on migration timing to change as well, though the nuance of this has yet to be examined thoroughly. Moon phase might also act as a migratory releasing factor, with some individuals initiating nocturnal migration on darker nights as a predator avoidance strategy (Lothian et al. 2018).

There has been comparatively less focus on biological releasing factors compared with environmental cues; this is despite body size, schooling behaviour, and the distance that individuals must migrate being potentially important for smolt migration phenology (Bohlin et al. 1996; Riley et al. 2014; Stich, Bailey, et al. 2015). This could be because of a lack of individual-level data to assess the relative effects of biological versus environmental cues on their migration. Nevertheless, studies of related species suggest that body size might act as a releasing factor, such as in anadromous brown trout *Salmo trutta*, where the probability of migration on each day during the smolt run increased as their body size increased, perhaps because later leaving smolts had more time to continue growing (Bohlin et al. 1993). Schooling might also affect the timing of migration of individual smolts, with those migrating at night being more reliant on environmental releasing factors, while those moving in the day more likely to migrate when part of a school (Riley et al. 2014). While there has been little focus on how individual migration distances affect smolt phenology, evidence from released hatchery-reared *S. salar* smolts suggests that those stocked higher up in the catchment initiate their migration earlier than those that were released further downstream (Stich, Bailey, et al. 2015; Stich, Kinnison, et al. 2015).

In general, studies on the smolt run have strived to identify the biological and environmental conditions influencing their migration phenology. Anecdotal observations suggest that the influential conditions vary both between populations, but also within populations during the entirety of the smolt run (Ibbotson et al. 2013; Riley et al. 2014). Despite this, no studies appear to have comprehensively explored how the importance of these conditions varies across the migration period. Understanding which and whether their influence might change with progression through the smolt run is important for two reasons. Firstly, the timing of the smolt run is an important predictor of subsequent survival rates (Antonsson et al. 2010). Secondly, contemporary changes in riverine environments (including elevated temperatures and altered discharge patterns; Teichert et al. 2020) and changes in biological parameters (including decreasing juvenile *S. salar* body sizes; Gregory et al. 2019) could precipitate lasting changes in smolt migration phenology and their subsequent marine survival rates. Here, we use a 15-year dataset of individually tagged *S. salar* smolts migrating from the River Frome in southern England with the aim of investigating the probability of a smolt migrating to the lower part of the river by a given day of the smolt run according to a range of environmental and biological variables. For this, we developed an *a priori* set of hypotheses through literature review (Table 1), tested how these variables influenced their subsequent downstream migration across the entire smolt run, and then tested how their influences altered between different periods of the smolt run.

3.3 Methods

3.3.1 Study site and fish surveys

The River Frome is a lowland chalk stream in Dorset, UK, rising in Evershot ($50.50.24$°N; $02.36.12$°W), and after joining Poole Harbour, reaching the sea after a further minimum distance of 10.5 km ($50.40.04$°N;$56.48.51$°W). It is a low-gradient river, with an elevation of 175 m at its source, and has a rather braided course in its middle reaches. The main discharge is derived directly from Cretaceous aquifers and contains an ample supply of nutrients for plant growth (Berrie, 1992). As is characteristic of chalk streams, it is a highly productive system with most juvenile *S. salar* being fast growing and migrating to sea at age 1+ years (Simmons et al. 2020).

Between 2005 and 2019, approximately 10,000 age 0+ *S. salar* were captured each August and September using electric-fishing (pulsed DC with a square-wave waveform fished at 50 Hertz, ~200 volts and 25%–30% duty cycle). Each individual was anaesthetised (2-phenoxy-ethanol), measured (fork length, nearest mm), marked by removal of their adipose fin, and tagged by implanting 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 (March to May), seaward-emigrating 1+ smolts were sampled to estimate the smolt run size as part of a long-term monitoring program. These emigrating smolts were sampled by diverting them into a small side-channel of the river at East Stoke ($50.40.47°$N; $02.11.2°$W) using a bioacoustic fence, following which they had to pass through one of two PIT-tag readers located in a fluvarium to continue their migration downstream. The autumn tagging sites were between 0.29 and 48.91 km upstream of the PIT-tag readers. A rotary screw trap (RST) was positioned immediately downstream of the fluvarium that captured a sample of the smolts (Ibbotson et al, 2013; Fig 3.1.). From 2006 to 2013, the RST was operated continuously over most of the duration of the smolt run (see Riley et al. 2018 for dates). Since 2014, it has only operated during periods where previous data suggested the *S. salar* smolts were most likely to be migrating. Up to 2019, this meant that it ran for more than 12 hours a day for at least 35 days of each annual smolt run. In 2020, due to Covid-19 pandemic restrictions, this was reduced to 28 days. During operation, the RST was checked for trapped fish every 30 minutes when all captured fish were removed, anaesthetized, checked for the presence of a PIT tag and measured (fork length, nearest mm). They were then placed into a container of fresh river water to recover normal behaviour before being released downstream.

3.3.2 Data preparation

Two datasets were used to test how biological and environmental variables influenced smolt migratory phenology. The ‘detection dataset’ comprised records of individual fish detected on the PIT-tag readers. As these readers operate 24 hours day^{-1} during the smolt run, they were assumed to provide an unbiased sample of smolt migratory behaviour that was independent of sampling effort and relatively unaffected by prevailing environmental conditions. Capture-mark-recapture experiments have suggested that the efficiency of these readers is $\sim 81.5\ \%$, but with some variation due to environmental conditions (see Appendix 2 for calculation). The 'RST dataset' comprised records of individual fish recaptured in the RST. This was not an exact subset of the 'detection dataset', as approximately 8% of smolts included in the RST dataset had not been detected by the PIT-tag readers. The RST dataset was not considered a completely unbiased sample of smolt migratory behaviour as: (i) from 2014, the RST was operated only when it was assumed most smolts were migrating; and (ii) it is possible that larger smolts, which are likely to have better swimming abilities than smaller smolts, could be better at evading capture in the RST (Tattam et al. 2013). However, the RST dataset provided individual smolt body lengths that were unavailable from the detection dataset, enabling their inclusion in models. Length at tagging was available for all individuals in the detection and RST datasets, but it was unclear how well it would represent smolt length at migration because recent work has demonstrated that overwinter growth rates of River Frome parr are highly variable and smaller parr grow more than would be expected given their size at tagging (Simmons et al. 2020).

The duration of the smolt run was defined as starting on the 82nd day of the year (DoY) and ending on the 136th DoY, as these represented the first and last dates of available RST recapture data across all years. These dates encapsulate the main *S. salar* smolt migration period previously reported for the chalk streams of southern England. We calculated the DoY for each PIT-tagged smolt record in both datasets using the `yday` function in the R package `lubridate` (Grolemund and Wickham 2011). Daily mean water temperatures were calculated from measurements at two sets of water temperature loggers (Fig. 1; see Simmons et al. (2020) for details). Using these, we calculated degree-days (DD) as the sum of daily water temperatures ≥ 6°C from 07 January until the date of capture of each smolt, as juvenile salmonids are relatively metabolically inactive at temperatures below this (Elliott and Elliott 2010). We chose 07 January rather than 01 January, as temperature data before this date were absent. Additionally, the water temperature during these dates is usually below 6°C. Using daily mean temperature data, the relative change in water temperature (RCT) was also calculated for each day as the slope of the linear relationship between temperature on a given day and temperature on the previous day (Spence and Dick 2014). River discharge ($\mathrm{m}^3\mathrm{s}^{-1}$) was recorded every 15 minutes at two locations on the River Frome at East Stoke (Fig. 1; UK Centre for Ecology & Hydrology 2021) throughout the 15-year period and was used to calculate a daily mean flow for every day of the smolt run each year. As with temperature, the relative change in discharge (RCD) was calculated for each day as the slope of the linear relationship between discharge on a given day and discharge on the previous day (Otero et al. 2014).

As *S. salar* parr are territorial (Keenleyside and Yamamoto 1962), it was assumed individuals overwintered close to the site where they were captured during the August/September electric fishing survey (Beall et al. 1994; Webb et al. 2001). Thus, the distance that each smolt had to migrate in the spring was calculated as the distance upstream (km) of their tagging site from the tidal limit, determined using the `riverdistance` function in the R package `riverdist` (Tyers 2017). Whilst some *S. salar* parr on the River Frome are known to migrate out of their territories in the autumn and are known as ‘autumn migrants’ (Pinder et al. 2007), it was assumed that the distances they migrated in spring related to their autumn tagging site.

To determine whether a smolt was a daytime migrant, the time of sunrise and sunset each day was determined using the function `getSunlightTimes` in the R package `suncalc` (Thieurmel and Elmarhraoui 2019). Any smolt that was detected between sunrise and sunset was considered a daytime migrant (coded as 1), and those detected between sunset and sunrise was considered a night-time migrant (coded as 0). Moon phase for each day of the smolt run was determined using the `getMoonIllumination` function from the R package `suncalc` (Thieurmel and Elmarhraoui 2019), where it was calculated as a fraction from 0.0 (new moon) to 1.0 (full moon).

Assuming photoperiod is the ultimate cue for initiating smoltification (McCormick et al. 1998), then the urge to migrate might increase with DoY and so is important in describing smolt migratory behaviour / timing. As DoY was our response variable, it could not be used as an explanatory variable, nor could photoperiod be used given its high correlation with DoY. Instead, the smolt run was divided into three equal periods: 'early', 'middle', and 'late', with exploration of how smolts responded differently to environmental variables between the three periods. The 'early' period included any smolts detected and/or caught from DoY 82 to 100, the middle period covered DoY 100 to 118, and the late period covered DoY 118 to 136.

For the RST dataset only, the relative length of each individual was calculated as the difference between their measured body length and their expected body length on the DoY of their capture. Their expected body length was estimated from a linear regression between body length and DoY for each year, using the `lm` function from the R package `stats` (R Core Team 2020) (Table A2.1). The use of relative length rather than measured body length in analyses was to control for increases in the latter with DoY, as smolts continue to feed and grow prior to migrating, thus later-running individuals could be larger than those running earlier. To determine schooling behaviour, we used the detection dataset to identify every smolt that was detected within 10 seconds of another tagged smolt in the fluvarium. The identified smolts were coded as having been part of a school, whereas all other tagged smolts were coded as not identified as part of a school. We chose the threshold of 10 seconds because a previous study in this system showed that multiple tag detections frequently occurred within 10 seconds of each other, particularly during the day (Riley et al, 2014). We chose a minimum number of two tags to identify a school because only 8 to 17% of smolts captured in the RST were tagged, suggesting that 80 to 90% of smolts were untagged and could be travelling with tagged smolts in schools (Table A2.2).

3.3.3 Statistical analyses

The statistical analyses were designed to quantify and compare the relative strength and direction of the effects of the explanatory variables on the probabilities of a given smolt arriving at East Stoke by a given day of the smolt run. The variables were tested for collinearity (Pearson's correlation); only variables that had $r \leq 0.70$ were retained (Dormann et al. 2013). Ordered probit models were developed to describe the response variable day of year (DoY), expressed as an ordered categorical variable using explanatory variables as per the hypotheses developed following the literature review

(Table 3.1). We elected to treat DoY as an ordered categorical variable for two reasons: (i) we considered day as an ordered classification of time, but time is of too high-resolution scale for analysis of these data, and (ii) we preferred to describe migration phenology in terms of cumulative probabilities so that our findings could be related to smolt runs of different durations. Ordered probit models are rarely employed in ecological studies and this approach differs from the statistical methods of many other smolt migration studies that use time proxies (such as the day of the year that 25%, 50%, and 75% of smolt have migrated) to summarise smolt migration dynamics (e.g., Antonsson and Gudjonsson 2002; Kennedy and Crozier 2010; Otero et al. 2014). These models were run separately for the 'detection dataset' and the 'RST dataset'. The models were built for both datasets using the form:

$$\begin{aligned} DoY \sim & \quad \text{Ordered Probit}(\mu, \gamma) \\ \mu = & \quad \alpha + \beta X \end{aligned}$$

where DoY is the day of year a given smolt was detected/captured, μ is the linear predictor of DoY on the scale $-\infty$ to $+\infty$, γ are the cut-points between each category of DoY, α is the regression intercept term, and β is the vector of coefficients relating to the matrix of explanatory variables X to DoY.

The model parameters were estimated using the `clm` function in the R package `ordinal` and specifying equidistant structured thresholds because we assumed that the response scale had equal distances between adjacent categories; essentially, the same amount of time passes between each day (Christensen 2019). Each model was simplified by removing all covariates that had estimated 95% confidence interval ranges overlapping zero, with this repeated iteratively until the 95% confidence intervals of the remaining terms did not overlap zero. This method was analogous to performing stepwise variable selection, but with our criterion based on confidence intervals overlapping zero rather than Information Criteria or *p*-values. Unlike stepwise selection, this method guards against retaining terms that are statistically significant because of a large sample size, but which are ecologically irrelevant. In instances where interactions involving categorical variables had estimates that did not overlap zero for any level of the categorical variable, that variable was retained in the model. We examined model residuals to assess model fit.

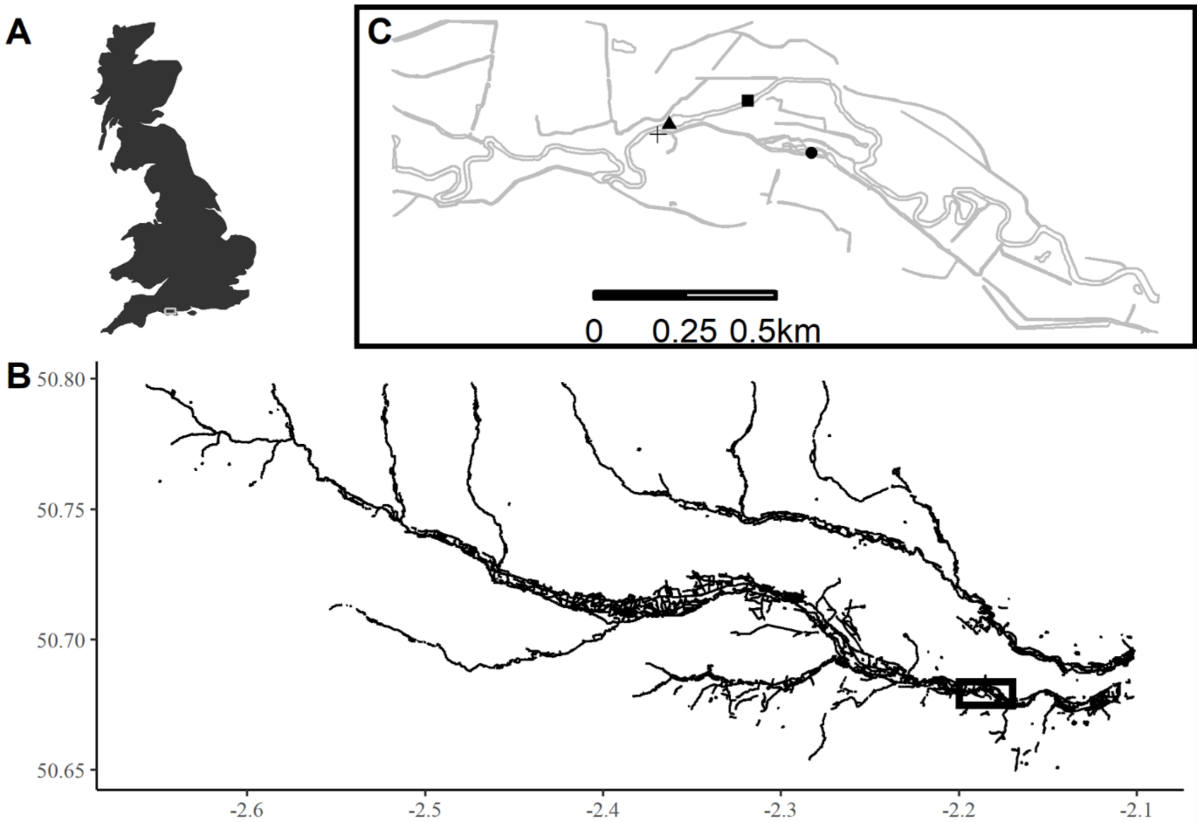

Figure 3.1. Map showing the location in the UK (A) of the River Frome in the grey box (B) with an inset of East Stoke (C) showing the location of the fluvarium and RST (circle), temperature loggers from 2006- 2009 (triangle) and after 2009 (square), and the flow meter (plus sign).

Table 3.1. Hypothesised effects (positive [+] or negative [-]) of each explanatory variable on the probability of any given smolt being detected and/or captured in the RST by a given day of year (DoY) of the smolt run. Variables are presented as 'Main effects' and as 'Interactions'.

Variable	Definition	Name	Hyp. effect	Explanation	Reference
Main effects					
Temperature	Degree days of water temperature from January 7th to *DoY d*	DD	+	Smolts are more likely to arrive in the lower river earlier following a warmer winter	Zydlewski et al. 2005
	Relative change in water temperature between *DoY d* and *d*-1	RCT	+	Smolts are more likely to migrate following a temperature increase from *DoY d*-1 to *d*	Spence and Dick 2014
Discharge	Relative change in discharge between *DoY d* and *d*-1	RCD	+	Smolts are more likely to migrate following a discharge increase from *DoY d*-1 to *d*	Jensen 2012; Otero et al. 2014
Moon phase	Moon phase between 0.0 (new moon) and 1.0 (full moon)	MP	-	Smolts are more likely to migrate when a new moon or only a small fraction of the moon is illuminated	Spence and Dick 2014
Relative length	Difference from expected length on *DoY d*	Len	+	Relatively long smolts are likely to arrive in the lower river earlier than relatively small smolts	Kennedy and Crozier 2010
Distance	Distance upstream	Dist	+	Smolts traveling further will arrive in the lower river later, assuming they travel at approximately the same speed	Stich et al. 2015; Stich et al. 2015a

Schooling	Binary variable indicating when a smolt was detected within 10 seconds of another smolt	Sch	+	Smolts are more likely to move on a particular day if they are part of a school	Riley et al. 2014
Year	Smolt year	Yr	+	Smolts will arrive earlier in the lower river over the course of the 15-year study period	Kennedy and Crozier 2010; Otero et al. 2014
Interactions					
Relative length : Time of day†	Relative length moderated by time of day	Len:Day	+	Diurnal smolts are more likely to be relatively long smolts	Ibbotson et al. 2011; Haraldstad et al. 2017
Schooling : Time of day†	Schooling moderated by time of day	Sch:Day	+	Diurnal smolts are more likely to migrate in schools	Riley et al. 2014
Discharge : Period in run‡	Relative change in discharge moderated by period in run	RCD:Period	-	Smolts will respond more strongly discharge changes late in the run	Based on observations during fieldwork
Temperature : Period in run‡	Relative change in water temperature moderated by period in run	RCT:Period	-	Smolts will respond more strongly to temperature changes late in the run	Ibbotsson et al. 2006
Schooling : Period in run‡	Schooling moderated by period in run	Sch:Period	-	Smolts will migrate in schools more frequently late in the run	

3.4 Results

Across the 15-year study period, a total of 9728 PIT-tagged 1+ *S. salar* smolts were detected on the PIT-tag readers located in the fluvarium, whereas 4312 were captured in the RST (Table 2). Apart from 2013, the number of smolts detected in the fluvarium and captured in the RST have generally decreased year-on-year (Table 3.2; Figure A2.1).

3.4.1 Detection dataset (PIT-tag readers)

The model best describing the variance in DoY of smolt migration in the 'detections dataset' retained all seven main effects and all four interaction effects (Table 3.3). The estimates for the environmental variables were consistent with all hypotheses (Table 3.1). Degree-days ≥ 6°C had a significant and positive effect on smolt migration, with smolts that experienced warmer winters prior to migrating being more likely to arrive in the lower river earlier (Fig. 3.2). Relative change in temperature also had a significant positive effect, but it was less influential during the middle period of the smolt run, suggesting that changes in temperature were most important for initiating and ending smolt migration (Fig. 3.3). Relative change in discharge only influenced smolt migration during the late period, when it had a significant positive effect (Fig. 3.4). Moon phase had a significant negative effect on smolt migration, with individuals more likely to migrate when there is a new moon or only a small fraction of the moon is illuminated than the converse.

The model estimates for the biological variables were also consistent with the hypotheses (Table 3.1). Distance upstream had a significant positive effect, indicating that smolts having further to migrate arrived later at the PIT tag readers than those that had to migrate shorter distances, although this assumes individuals move at the same speed. When moderated by time of day, the effect of schooling was such that individuals were more likely to migrate individually at night and were more likely to migrate in a school during the daytime. Relative to the early period of the smolt run, individuals were more likely to school in the middle and late periods. Finally, year had a significant negative effect on DoY, indicating a trend for smolt migration to take place earlier in later years (Fig. 3.5; see Figure A2.2 for raw data plot).

3.4.2 RST dataset

The model that best described the variance in smolt migration DoY in the RST dataset retained all of the main effects except moon phase, and all four interaction effects except the interaction between relative body length and day (Table 3). As in the detection model, the estimates for the environmental variables were consistent with all hypotheses (Table 3.1), with the effects of degree days $\geq 6^{\circ}$C and with the relative change in temperature being significant and positive (Table 3.3).

The effects of the interactions in the RST model did, however, vary from the detection model (Table 3.3). When the relative change in temperature (RCT) was modified by the smolt run period, it had a significant positive effect during the late period relative to the early period, but a significant negative effect during the middle of the run relative to the early period. This suggested that daily changes in water temperature during the middle of the run increased the probability of a smolt migrating relative to the early period, whereas daily changes in water temperature in the late periods did not affect the probability of smolts migrating relative to the early period. The relative change in discharge had a significant positive effect on DoY (Table 3.3). However, there was a significant negative effect of RCD modified by period in the middle of the smolt run relative to the early period, and a positive, but not significant, effect of RCD modified by period at the end of the smolt run. This suggests that daily changes in discharge were important in the middle of the smolt run, but not at the end, a contrast to the detection model.

The estimates for the biological variables were consistent with the hypotheses (Table 3.1), with relative length having a significant negative effect on smolt migration timing, indicating that larger smolts were more likely to arrive earlier in the lower river (Fig. 3.6). The effects of distance upstream, schooling, and year all had similar effects in the RST models as they did in the detection model, with distance upstream having a positive effect and schooling and year having a negative effect (Table 3.3).

Table 3.2. Number of 1+ smolts detected on the PIT-tag readers or captured in the RST for each year in the River Frome as East Stoke.

Year	Detections	Captures
2006	710	320
2007	1063	610
2008	986	400
2009	896	442
2010	741	356
2011	595	234
2012	387	235
2013	856	341
2014	698	309
2015	545	228
2016	553	238
2017	433	147
2018	434	138
2019	415	130
2020	406	181
Total	9718	4309

Table 3.3. Results from simplified ordered probit detection and RST models, showing the estimated effects of explanatory variable and their 95% confidence intervals. DD = degree days for temperatures ≥6^{o}C; RCT = relative change in temperature; and RCD = relative change in discharge.

	Detection model		RST model	
Effect	Estimate	Confidence Interval	Estimate	Confidence Interval
Relative length			-0.097	(-0.128, -0.065)
DD	0.699	(0.675, 0.722)	0.581	(0.546, 0.616)
RCT	0.219	(0.143, 0.295)	0.167	(0.029, 0.306)
RCD	0.014	(-0.023, 0.051)	0.137	(0.070, 0.203)
Moon phase	-0.031	(-0.052, -0.011)	--	--
Distance upstream	0.058	(0.037, 0.078)	0.091	(0.060, 0.123)
School(Yes)	-1.291	(-1.742, -0.839)	-1.76	(-1.990, -1.531)
Year	-0.255	(-0.277, -0.234)	-0.12	(-0.158, -0.083)
School(No):Day(Yes)	0.284	(0.234, 0.333)	0.496	(0.401, 0.591)
School(Yes):Day(Yes)	-0.167	(-0.330, -0.004)	-0.282	(-0.381, -0.183)
RCD:Period(Middle)	-0.021	(-0.068, 0.026)	-0.137	(-0.215, -0.060)
RCD:Period(Late)	0.101	(0.042, 0.160)	-0.09	(-0.182, 0.002)
RCT:Period(Middle)	-0.28	(-0.361, -0.200)	-0.258	(-0.402, -0.115)
RCT:Period(Late)	-0.036	(-0.118, 0.047)	0.022	(-0.126, 0.170)
School(Yes):Period(Late)	2.402	(1.917, 2.886)	3.309	(3.057, 3.561)
School(Yes):Period(Middle)	1.244	(0.767, 1.721)	1.859	(1.629, 2.090)

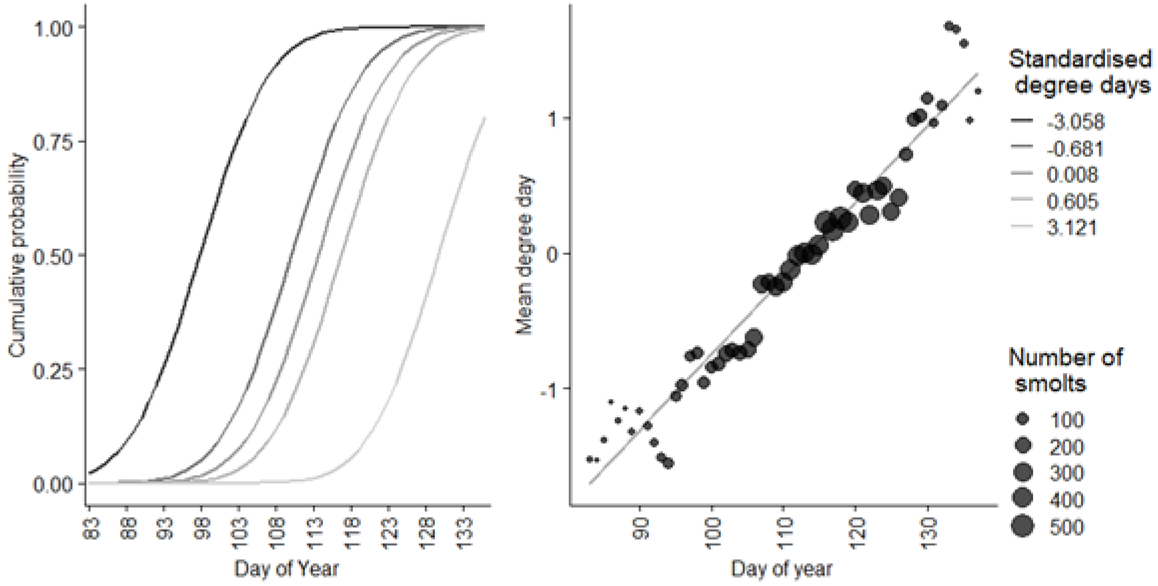

Figure 3.2. The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised degree days (DD) at its 0th, 25th, 50th, 75th, and 100th quantiles from the detection model (A). Raw data plot showing the mean number of degree days at each day of the year, where the point size is proportional to the number of smolts detected on each day, and the grey line is a trend line through the raw data – presented as a visual aid of the direction of the relationship.

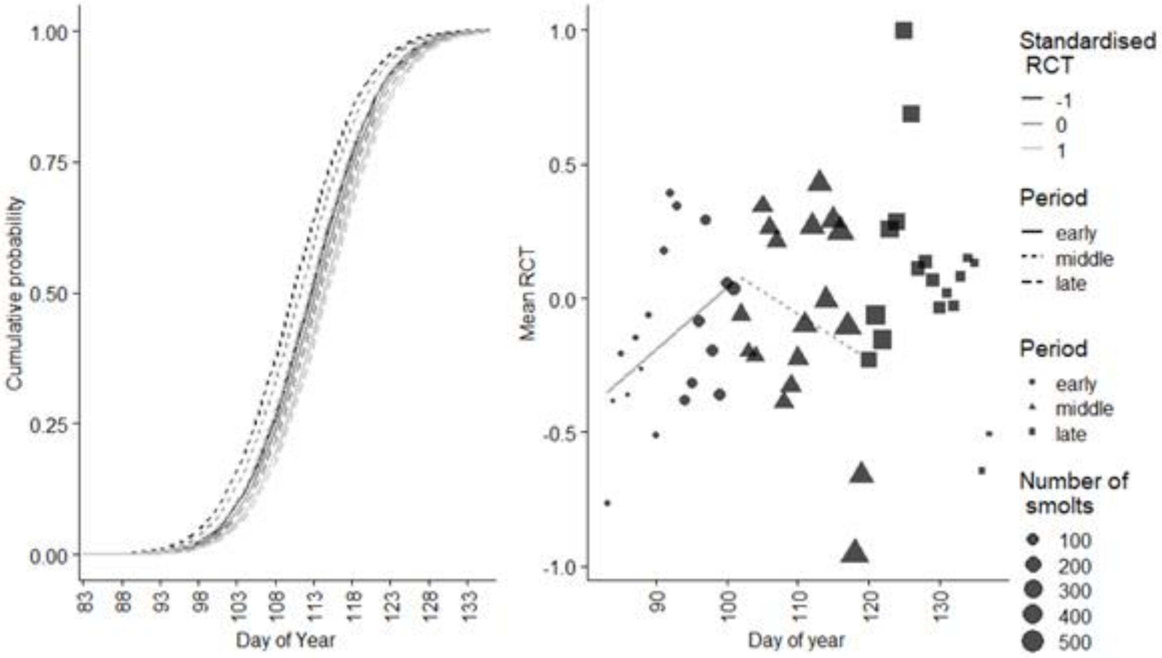

Figure 3.3. The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised relative change in temperature (RCT) as its

25th, 50th, and 75th quartile in each Period from the detection model (A). The mean RST experienced by smolts detected on each day of the year, where the point size is proportional to the number of smolts captured on each day, the point shape represents the Period, and the grey lines a trend line through the raw data for each Period presented as a visual aid of the relationship and absent where no relationship was supported by statistical model (B).

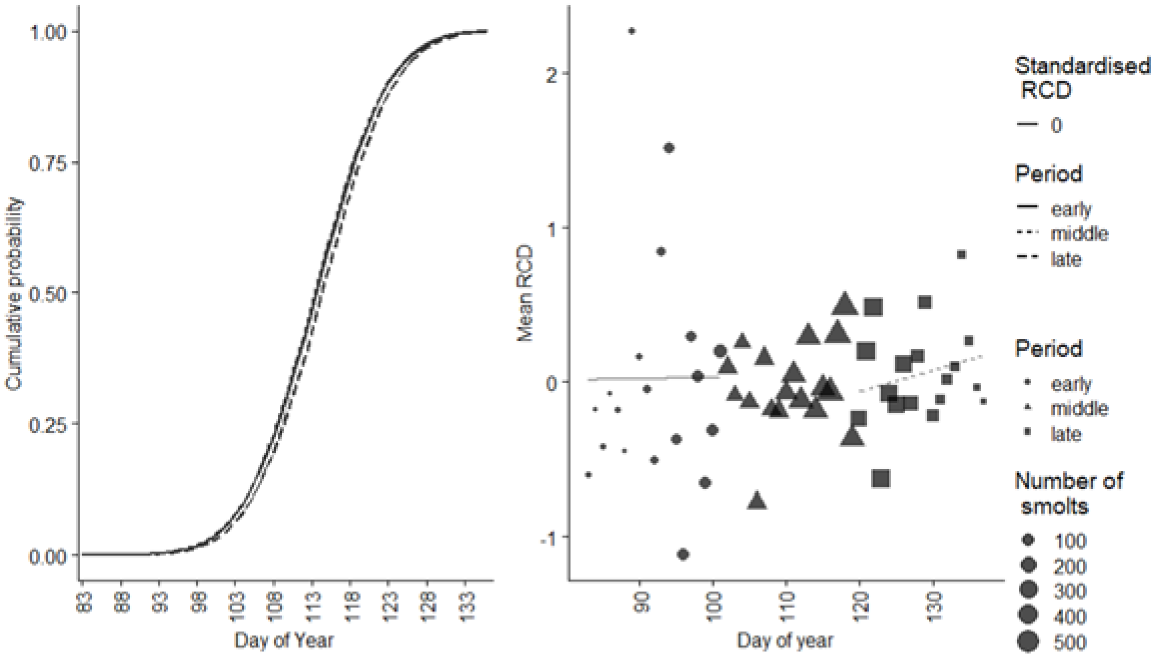

Figure 3.4. The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised relative change in discharge (RCD) at its 50th quartile in each Period from the detection model (A). The mean RCD experienced by smolts detected on each day of the year, where the point size is proportional to the number of smolts captured on each day, the point shape represents the Period, and the grey line is a trendline through the raw data for each Period presented as a visual aid of the direction of the relationship and absent where no relationship was supported by the statistical model (B).

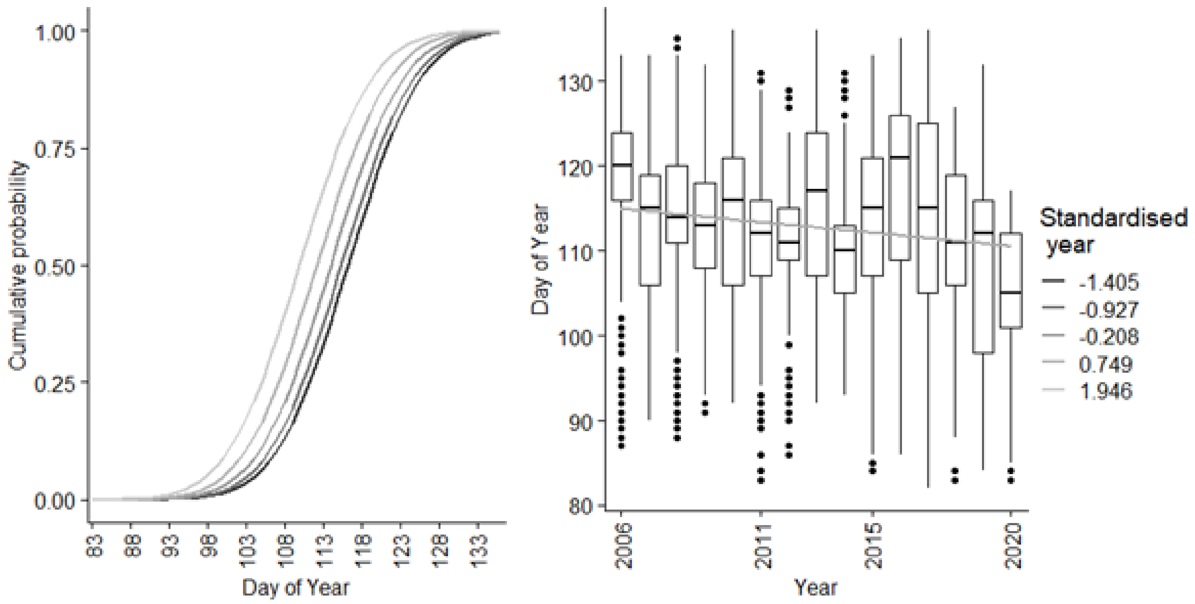

Figure 3.5. The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised year at its 0th, 25th, 50th, 75th, and 100th quantiles from the detection model (A). Boxplots show the day of year smolts were detected for each year (horizontal black line is the median, boxes delimit the 25-75% interquantile range (IQR), whiskers delimit the 1.5 x IQR, and circles represent extreme values > 1.5 x IQR), and the grey line is a trend line through the raw data presented as a visual aid of the direction of the relationship (B).

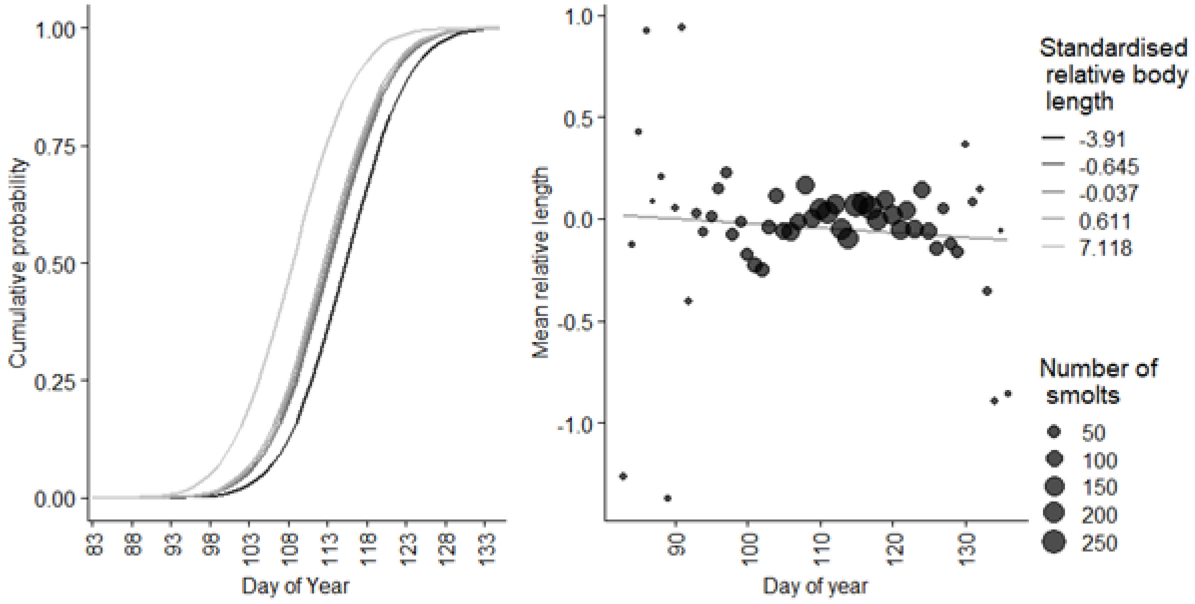

Figure 3.6. The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised relative length at its 0th, 25th, 50th, 75th, and 100th quantiles from the RST model (A). The mean relative length of smolts

captured in the RST on each day, and the grey line is a trend line through the raw data presented as a visual aid of the direction of the relationship (B).

3.5 Discussion

Several environmental and biological factors were found to have influenced the probability of *S. salar* smolt migration to the lower reach of River Frome by a given day of the smolt run, and the influence of these variables changed during the smolt emigration period. Warmer winters, followed by larger positive changes between daily water temperature and discharge rates during the smolt run, resulted in earlier migrations. Similarly, how far upstream a smolt was tagged the previous autumn had a positive effect on the timing of an individual's arrival in the lower river, where smolts from further upstream arrived later at the PIT tag readers and RST. Smolt body length, migrating in a school, and year all had negative effects on smolt migration timing, meaning that they were associated with earlier migrations. Notably, the effect of temperature and discharge varied throughout the smolt run, whereas the effect of schooling varied by time of day. The way all of the explanatory variables acted on the smolts was likely to vary, with the interaction of some biological and environmental variables acting mainly on fish length and physiology to ensure individuals are ready to migrate, with environmental 'releasing' variables then mainly acting on migration initiation (McCormick, Shrimpton, et al. 1998). Generally, the number of smolts captured each year declined throughout the study period, with a notable exception in 2013. The increased number of smolts detected/captured in 2013 was most likely due to the side channel having been dredged following the 2012 smolt run, enabling a greater volume of water to pass through and a higher proportion of smolts to use the channel, rather than increased smolt production.

The environmental variables of water temperature and photoperiod have been identified as important to smoltification once individuals have attained an appropriate body size (McCormick, Shrimpton, et al. 1998; Byrne et al. 2003; Zydlewski et al. 2014). In many populations, including those in colder regions where over-winter growth is minimal, a proportion of *S. salar* parr make the 'decision' to smoltify in the autumn prior to their spring migration (Metcalfe et al. 1988), with this likely to relate to their realized body length at that time. Correspondingly, warmer winters are then mainly important for their physiological development prior to migration (McCormick et al. 2002). However, in the southern range of *S. salar*, such as the River Frome, individuals continue to grow throughout the winter period (Simmons et al. 2020). Thus, an individual that might have been too small in the previous autumn to consider migrating could become large enough by the following spring. Correspondingly, the positive influence of warmer winter temperatures in the models were likely to relate to warmer winters resulting in individuals developing their migratory ‘readiness’ (in both body length, morphological and physiological terms). Moreover, the RST model indicated that larger smolts were more likely to arrive earlier in the lower river during the smolt run than smaller smolts, suggesting the importance of faster growth rates in preceding months that can be at least partially related to temperature (Simmons et al. 2020).

Once smolts have achieved their migratory readiness, both water temperature and discharge are important environmental releasing factors to initiate migration (McCormick, Shrimpton, et al. 1998; Aldvén et al. 2015; Jokikokko et al. 2016). Some studies suggest a specific temperature ‘threshold’ must be attained before the initiation of migration, but others suggest it is controlled by a combination of temperature attained and temperature changes (e.g., Jonsson and Ruud-Hansen 1985). There have been several different methods to quantify how cumulative temperature affects the initiation of migration, including accumulated thermal units and photo-thermal units (e.g., Zydlewski et al. 2005; Teichert et al. 2020). Here, the models used degree-days ≥ 6 °C until smolt detection/capture, with an earlier arrival of smolts in the lower river following warmer winters likely to be the result of a combination of achieving physiological readiness sooner (as discussed earlier), but also of attaining the appropriate water temperature for triggering the initiation of their migration (McCormick et al. 1998). It is, however, acknowledged that decoupling these temperature effects between migratory readiness and migration initiation was not possible here due to the models being based only on detection or capture near to the end of the downstream migration, rather than knowing their date of departure from the nursery grounds.

The effect of the environmental variables that were most likely to be influencing the initiation of migration varied across the smolt run period. The effect of relative changes in temperature (RCT) was positive but less influential during the middle run period (relative to the early run period) when most fish are detected/captured. These results suggest that early in the smolt run when water temperatures are still relatively cool, a larger increase in water temperature increases the probability that physiologically ready smolts will commence their migration. However, during the middle of the smolt run, smaller changes in water temperature can initiate migration, which could be because the ‘threshold’ temperature for migration has already been reached, so the relative change in daily temperatures does not need to be as large to initiate migration as during the early period when water temperatures are cooler. That RCT did not have a significant effect at the end of the smolt run was perhaps unsurprising, as by then any smolts that were physiologically ready to migrate will need to migrate regardless of water temperature if they are to leave before the ‘smolt migration window’ closes (McCormick et al. 1998).

The effect of the relative change in river discharge (RCD) also varied across the smolt run. In the detection model, using RCD as an additive effect resulted in it having a non-significant effect on the probability of a smolt being detected. As chalk streams tend to have stable discharge regimes (Berrie 1992; Sear et al. 1999), then large RCDs in the River Frome might be relatively small compared to those in other rivers, such as upland spate rivers (Berrie 1992). Thus, its effect might be weak in the River Frome as a result. However, when moderated by the smolt run period, RCD had a significant positive effect during the late run period (relative to the early run period), but no effect during the middle run period (relative to the early run period). This suggests that changes in discharge were only important towards the end of the run when they might act as a final impetus to push out the remaining smolts that have yet to migrate (McCormick, Shrimpton, et al. 1998; Aldvén et al. 2015). Interestingly, when we considered RCD in our RST model, with relative smolt length as a covariate, RCD had a significant negative effect during the middle of the smolt run, but a non-significant effect at the end. Although these results appear contradictory to those from the detection model, this could be more of a reflection of how the efficiency of the RST varies with river discharge. Additionally, smolt swimming abilities might affect the likelihood of being captured in the RST, with larger smolts better able to avoid trapping, so this might also be reflected in the results of the RST model (Remen et al. 2016; Cai et al. 2020).

The final environmental variable tested was moon phase. This variable was only retained in the detection model and had a relatively small effect size. Thus, although the moon phase appears to influence migration timing, the other environmental variables appeared to be stronger migration cues. Even though the importance of moon phase was not as strong as other environmental factors, smolts show a preference for migrating on darker nights, with no moon or only a small fraction of the moon, likely as a visual predator avoidance strategy (Spence and Dick 2014; Lothian et al. 2018). As the tidal cycle is controlled by moon phase, the effect of moon phase on migration timing could also reflect the effect of tide on migration through the estuary and Poole Harbour when the smolts exit the river, where smolts have been shown to have preferences for entering the estuary at particular times of the tidal cycle (Davidsen et al. 2009). That moon phase only had a weak effect in the detection model and not at all in RST model is arguably unsurprising, given the effect of moon phase on salmonid migration timing has been mixed, with some studies suggesting a significant effect (e.g., Hvidsten et al. 1995; Roper and Scarnecchia 1999), and others a non-significant effect (e.g., Byrne et al. 2003). Some studies even suggest that the effect of moon phase varies between salmonid populations that are spread over wide geographical regions (Spence and Dick 2014).

Although some studies have investigated the effects of various biological variables on salmonid smolt run phenology (Bohlin et al. 1996; Persson et al. 2019), there have been few studies based on individual-level biological data to test the effects of body length, time of day, and schooling behaviour on migratory behaviours. The RST model revealed that while the effect of body length was relatively small, it did have a significant effect on migration timing, with larger smolts more likely to arrive at the lower river earlier in the smolt run and smaller smolts more likely to arrive later. The interaction between day and body length was not retained in the final RST model, although observations during field data collection over the study period suggested that larger smolts were more likely to migrate in daytime and smaller smolts were more likely to move at night, possibly as a predator avoidance tactic (Ibbotson et al. 2006, 2011). That this interaction between body length and day of the smolt run was not retained in the final model could be due to larger smolts being less likely to be captured in the RST, perhaps because of greater swimming ability (Tattam et al. 2013; Cai et al. 2020). Tattam et al. (2013) found that RST trapping efficiency of rainbow trout smolts (*Oncorhynchus mykiss*) was lower for large smolts relative to small smolts, and that smolts generally were more likely to be caught in the RST during the night than at twilight. Thus, during the day, the *S. salar* smolts in this study might also be more likely to see the trap and attempt to avoid it (Tattam et al. 2013).

The effect of schooling on the migration behaviour of individual smolts, and the effects of schooling when moderated by period, were relatively high. Smolts were more likely to migrate in schools when they were moving during the daytime than at night, with this likely to be again related to predator avoidance, as darkness offers some protection from visual predators at night and schooling in the daytime provides a group-based strategy to avoid predation (Ibbotson et al. 2011; Riley et al. 2014). The significant interactions suggested that schooling was more common in the middle and late periods of the run, relative to the early run period. Early in the smolt run, there are likely to be fewer smolts that are physiologically ready to migrate, and those that are ready most likely use environmental cues to release migration. These individuals are also more likely to migrate at night, perhaps as a predator avoidance strategy (Ibbotson et al. 2006, 2011). During the middle and late periods of the smolt run, smolts are likely to migrate both day and night, to ensure migration is completed during the 'smolt migration window'. Thus, schooling might be more common during these periods as daytime movement increases, though it could also be an artefact of many smolts migrating coincidentally at the same time (Riley et al. 2014). Furthermore, the RST model indicated that smaller smolts are more likely to migrate later in the smolt run, so perhaps schooling is more common later, as smaller individuals group together for protection against predators (Riley et al. 2014).

Smolts that had further to migrate were detected by the PIT detectors and/ or captured in the RST later than those with shorter distances to migrate. While once it was thought smolts moved passively downstream during the migration period, it has now been demonstrated that smolts undertake active migrations, swimming faster than the river discharge (e.g., Davidsen et al. 2005; Svendsen et al. 2007). Observations during the River Frome smolt run suggest that smolts often migrate actively during the day, but that these movements are interspersed with periods of no net downstream progress. However, whether they migrate actively or passively at night has not been explored. As such, considering distance in relation to passive/active movements during the day/night in relation to swimming speed could have important implications for the effect of in-river migration distance. Considering speed in future studies is also important, as it was demonstrated that smolts arrived at the lower river earlier after a mild winter, but it was not possible to determine whether this is due to earlier readiness / release or whether this is due to a greater migration speed following release.

Finally, it was apparent in both sets of models that there was a pattern of the start of the smolt runs being earlier over the course of the study, as concluded from the earlier arrival of smolts at the lower river over time, with this consistent with several other studies (e.g., Kennedy and Crozier 2010; Otero et al. 2014). Annual variability in the timing of the start and end of the smolt run are partly due to differences in water temperature between years (Dolotov 2006; Jonsson and Jonsson 2014; Otero et al. 2014), with climate change widely assumed to be driving this pattern (e.g., Kennedy and Crozier 2010; Hedger et al. 2013; Otero et al. 2014). We tested for correlation between the year and the mean water temperature during March to May for each year, with these not significant ($r = 0.20$, $p = 0.44$), suggesting no significant change in mean water temperature during the spring over the 15-year study period. However, our water temperature measurements were taken at a single site in the lower river, where perhaps water temperature is more stable than in upper reaches (Berrie 1992). Unfortunately, water temperature data were unavailable for sites upstream, which would be more representative of the areas the smolts migrated from. So, while our models show a tendency towards earlier arrival in the lower river during smolt runs in later years, it is not possible to attribute this to a concurrent rise in mean water temperatures. Temperature data from other parts of the catchment could thus enhance future studies.

In summary, the models developed from the two datasets revealed that both biological and environmental variables had important influences on the migration phenology of *S. salar* smolts in the study river, and that the relative effects of these factors varied during smolt emigration period. It was considered that the positive effect of degree-days $\geq 6\,^{\circ}\mathrm{C}$ was acting on the smolts in relation to their migratory readiness, where relative changes in temperature acted on the timing of the initiation of migration. This initiation was also influenced by relative changes in discharge, and to a lesser extent moon phase. The model results also highlighted behavioural differences between fish moving by day and night, where schooling was only apparent in daytime. Most populations of *S. salar* are anadromous; thus, understanding the factors that affect migratory timing of individual *S. salar* can be applicable throughout the range of migratory populations. While the initiation of the smolt run of populations in non-calcareous streams are well known to be related to temperature and river flow (Otero et al. 2014), we demonstrated here using a long-term and individual dataset and careful analysis that their influences can be quite nuanced and change during the run. With annually increasing river temperatures, more frequent and intense discharge events, and earlier migration through the years across the natural range of *S. salar* (Walsh and Kilsby 2007; Jonsson and Jonsson 2009; Kennedy and Crozier 2010; Garner et al. 2017), these novel insights thus highlight that these environmental changes are likely to have consequences, such as environmental mismatches between riverine conditions for migratory cues and marine conditions that favour high survival (McCormick et al. 1998), on future smolt migratory success both in the River Frome and in rivers further afield.

Chapter 4: Predicting how environmental conditions and smolt body length when entering the marine environment impact individual Atlantic salmon *Salmo salar* adult return rates

4.1 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.

4.2 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 and Waldman 2009; Tamario et al. 2019; Merg et al. 2020). Disentangling the factors responsible for this decline is challenging, leading to uncertainty over optimal conservation management strategies (O’Connor and 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 (Renkawitz et al. 2012; Thorstad et al. 2012; Flávio et al. 2021).

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 (Thorstad et al. 2012; Jonsson and Jonsson 2014; McLennan et al. 2018). 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, Shrimpton, et al. 1998; Thorstad et al. 2012; Simmons, Gregory, et al. 2021). Smolt body size is also related to the timing of smolt migration, with larger smolts migrating earlier than smaller smolts (Simmons, Gregory, 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. 2019), and water temperatures, where warmer river conditions and smaller temperature gradients between freshwater and the marine environment result in higher survival rates (Jutila et al. 2005; Stich, Bailey, et al. 2015). Evidence also suggests smolts tend to migrate through estuaries on an ebbing tide (Moore et al. 1995, 1998; Lefèvre et al. 2013). 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; Riley et al. 2011; Mantyniemi et al. 2012).

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 (Gimenez et al. 2007; Auger-Methe et al. 2021). 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 4.1) 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 4.1; 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.

4.3 Methods

4.3.1 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 ($50.40.47^{\circ}$N; $02.11.2^{\circ}$W) using a bioacoustic fence. A rotary screw trap (RST), positioned within the side channel, then captures a sample of the smolts (Figure 4.1; 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.

4.3.2 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 and White 2011).

4.3.3 State process

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

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

The parameters above were set uninformative priors:

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

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.

4.3.4 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.

4.3.5 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 4.1). 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 4.1; Figure 4.1).

Several explanatory variables measured in the river were hypothesised to influence smolt MRR (Table 4.1). 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 4.1) 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 ($\mathrm{m}^3\mathrm{sec}^{-1}$) was recorded by the Environmental Agency every 15 minutes at two locations on the River Frome (Figure 4.1) throughout the 13-year period and used to calculate a daily mean discharge for each DoY of the smolt run each year (UK Centre for Ecology & Hydrology 2021).

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 ($\mathrm{mg\ l}^{-1}$) data from sporadic recordings taken in Poole Harbour (Figure 4.1), 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 (Moore et al. 1995, 1998; Lefèvre et al. 2013), 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 2021). 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 nearshore area, as a smaller gradient might result in higher survival rates (Jutila 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 4.1). 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 A3.1). 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.

4.3.6 MCMC simulations

The JAGS sampler (http://mcmc-jags.sourceforge.net/), run using R package rjags (Plummer 2003), 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 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 effective sample size for each parameter was determined using the `effectiveSize` function from the R package `coda`.

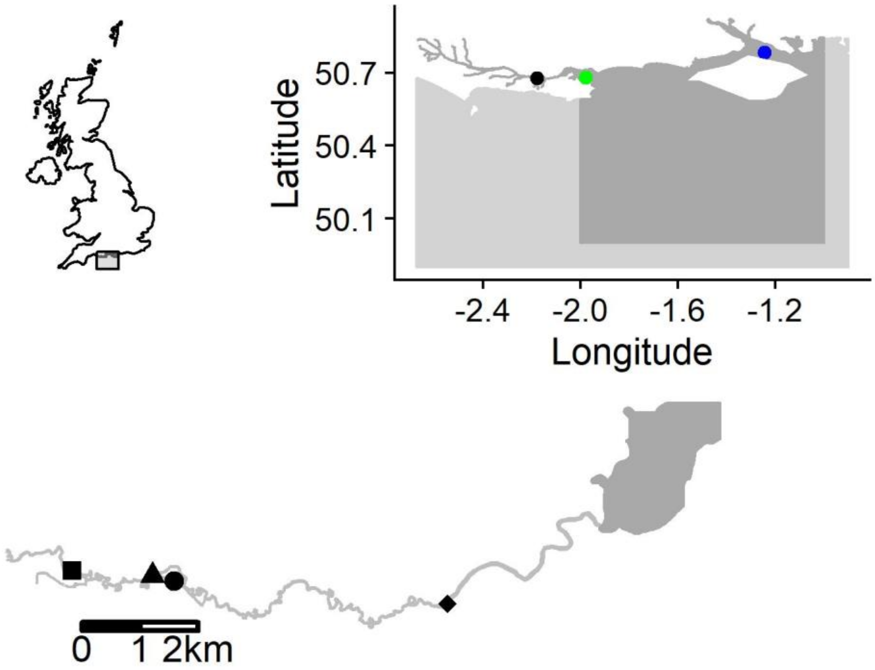

Figure 4.1. A map showing the UK in the top left panel with the study area in a grey box. The study area is shown in the top right panel, with the area that the SST data covers shown in dark gray, the location from which the bass data were collected as a blue dot, the location of the DO logger in Poole 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 antenna is the square.

Table 4.1. 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 and Jonsson 2014; Antonsson et al. 2010
River discharge	River discharge (m3/s-1)	Disc.	Smolts emigrating under higher river discharge will be able to migrate (swim) faster in more turbid water, and thus better avoid predators in the lower river, and are more likely to return as adults	Lothian et al. 2018; Persson et al. 2018
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	Jutila et al. 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	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 predation and so smolts are less likely to return as adults	Riley et al. 2011

Sea surface temperature	Degrees Celsius	SST	Warmer SST outside Poole Harbour will lead to increased survival and so smolts are more likely to return as adults	Jutila et al. 2005

4.4 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 4.2).

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 A3.2 and A3.3). 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 A3.4). The 1SW survival rate parameter was almost twice that of the MSW survival rate parameter (Figure 4.3). 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 4.3) 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 4.3), and its effect on both 1SW and MSW return rate was positive, while accounting for the effects of all other hypothesised variables (Figure 4.4). 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 4.3). 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 A3.5).

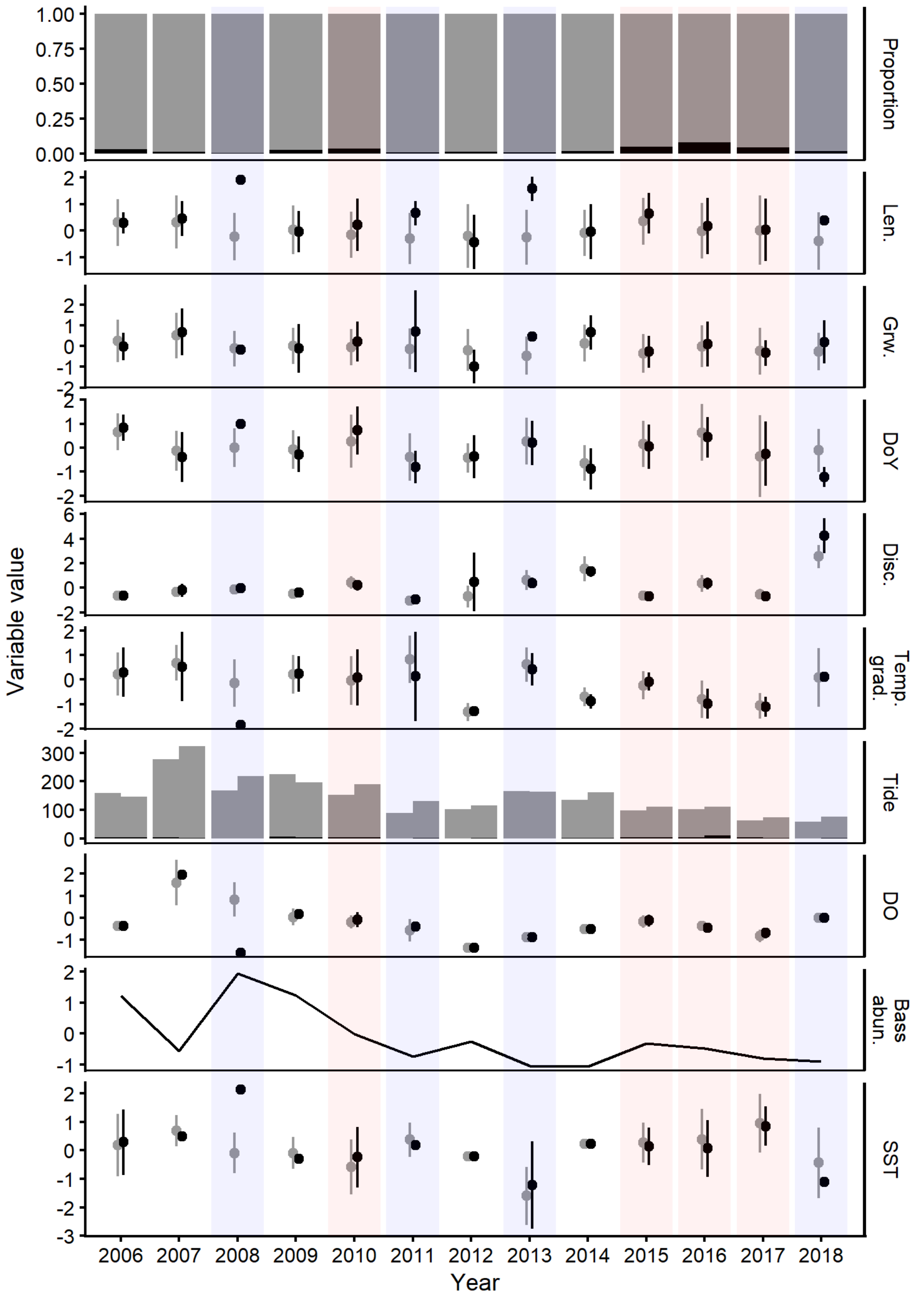

Figure 4.2. Plots of empirical data used in the River Frome Salmo salar survival model, where grey points and bars represent smolts that were not detected returning as an adult and black points and bars represent smolts that were detected returning as an adult. 'Year' on the x- axis refers to the smolt 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 values of various explanatory variables experienced by emigrating smolts each year, with vertical lines indication 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 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.

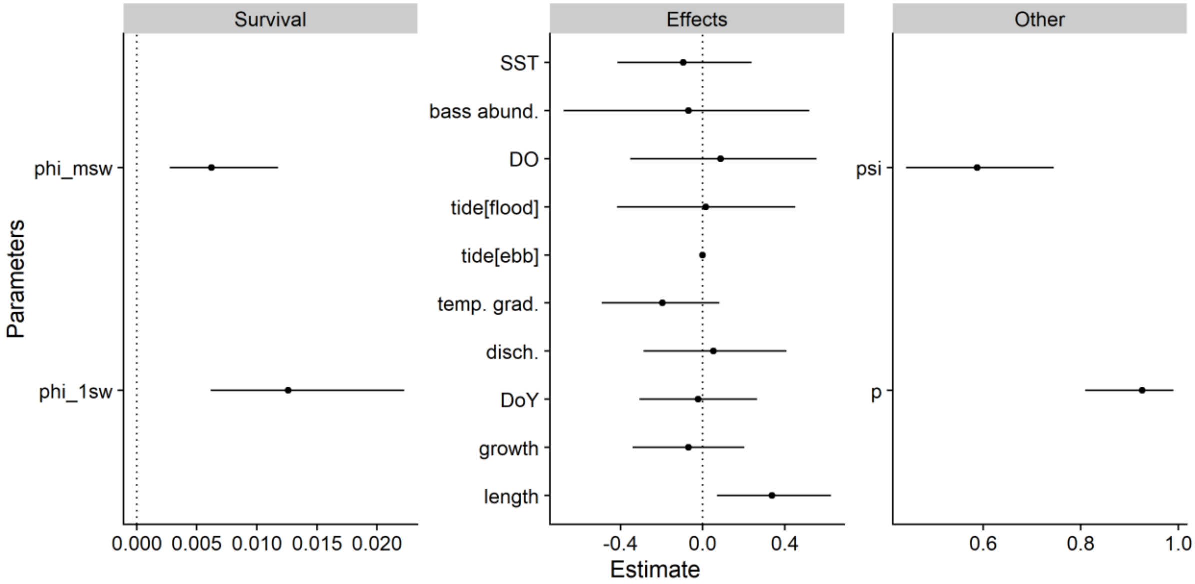

Figure 4.3. MCMC parameter estimates for 1SW and MSW survival ("Survival"), explanatory variable effects on 1SW survival ("Effects") and the remaining parameters ("Other") from the state-space model of River Frome Salmo salar survival. The dashed line indicates zero on the x axis. The points represent the mean estimate and the horizontal bars represent the 95% credible intervals.

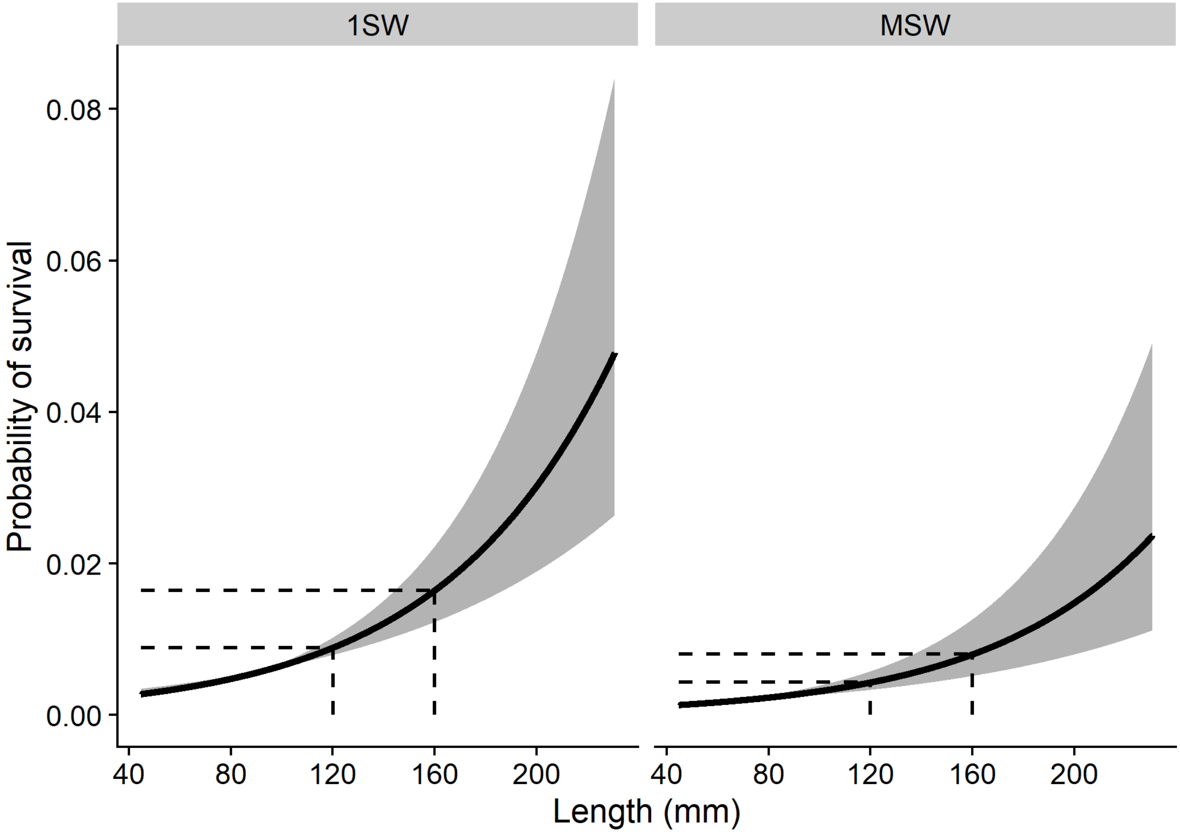

Figure 4.4. The predicted probability of survival for Salmo salar on the River Frome after spending 1 year at sea (1SW) and after spending multiple years at sea (MSW) as a function of its body length as a smolt. The dashed lines show the marine return rate for a 12 cm and 16n cm smolt, respectively. 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 represents the 95% credible interval.

Table 4.2. 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

4.5 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 (Thorstad et al. 2012; Andrews et al. 2019). 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 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, Gregory, 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 (Jutila et al. 2005). Another extrinsic 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 predating 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 note 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 and 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.

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

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See https://eprints.bournemouth.ac.uk/36821/

Chapter 6: Discussion

6.1 Summary of results

The main aim of this thesis was to test the hypothesis that for Atlantic salmon, *Salmo salar*, juvenile body length is an important predictor of subsequent life events, with a focus on growth rates, migration phenology, and survival. Parr body length was revealed to be a driver of overwinter growth rates in the River Frome, with smaller parr exhibiting higher growth rates than expected during this season (Chapter 2). This is likely an example of compensatory growth, where smaller parr must grow more than larger parr to achieve the critical size required to smoltify in the spring. Once the juveniles have smoltified, body size then becomes an important driver of smolt emigration timing, with larger smolts more likely to migrate earlier in the migration period than smaller conspecifics (Chapter 3). The impact of smolt body length appears to then be important when the smolts reach the marine environment. Within the main study site at the River Frome, larger smolts are more likely to survive at sea and return as adults than smaller smolts, and this effect overshadowed all environmental effects (Chapter 4). Additionally, smolt body size was an important predictor of marine return rates in populations of Atlantic salmon spanning 13 degrees of latitude in western Europe, suggesting that this finding can be generalised to salmon populations more broadly (Chapter 5).

The effect of smolt body size is robust even when environmental conditions experienced by the salmon during the early part of their marine migration - a critical period often considered a survival bottleneck for the species - is considered (Chapter 4). In addition to the ways juvenile body length can affect subsequent life history, three of the four studies show how environmental conditions, with a particular emphasis on water temperature and discharge, can affect growth, migration timing, and survival. Firstly, winters of higher and more variable water temperatures, with longer periods of high flows, lead to increased overwinter growth rates for parr (Chapter 2). Secondly, warmer winters and higher daily relative changes in water temperatures and discharge rates lead to earlier smolt migration timing (Chapter 3). Thirdly, the effect of discharge, river-to-estuary temperature gradient, and sea surface temperature in the nearshore had a much larger magnitude of effect than the other environmental explanatory variables, although none except body length were statistically significant in the marine return rate model (Chapter 4).

6.2 Body length as a driver of life history events

6.2.1 Body length in freshwater

To smoltify, parr must reach a critical body size by the spring of the year they will migrate. Often the 'decision' to smoltify is made much earlier in the year, and so smaller conspecifics might have to exhibit compensatory growth to achieve the appropriate size. The mechanism underlying this increased growth rate was not explored in this work, but other studies point towards a possible mechanism: perhaps smaller parr grow more than expected because of their relatively high metabolic rates. For example, in other salmonid species, such as maso salmon *Oncorhynchus masou*, smaller parr have been found to have higher metabolic rates than larger parr (Yamamoto et al. 1998). Higher metabolic rates in these parr are linked to dominance status, with smaller, more metabolically active individuals more likely to engage in aggressive, risk-taking behaviours (Yamamoto et al. 1998). Higher metabolic status is independent of daily energy expenditure, suggesting higher metabolic rate is a potential cause, but not a consequence of, risky behaviours (Houston 2010). Thus, to achieve the extra growth required to reach a suitable size in the spring, smaller parr may be facilitated by their high metabolic rates to take more risks whilst foraging.

For individuals that reach their critical size and have smoltified, there is a 'smolt migration window' that encapsulates the optimal time to migrate from freshwater to the marine environment (McCormick, Hansen, et al. 1998). This window encompasses the period when the prey resources and environmental conditions (particularly temperature) promote post-smolt survival. Larger individuals achieve the critical size earlier in the spring than smaller individuals; thus, they head out to sea during the beginning of the smolt migration window. As predation can be intense in the lower river and estuary (Dieperink et al. 2001, 2002; Flávio et al. 2019), then larger smolts rely on their large body size to avoid being depredated, but also travel predominantly at night. To compensate for their smaller body size, which can make them more susceptible to gape-limited predation, later migrants are more likely to migrate in schools (Riley et al. 2014; Simmons, Gregory, et al. 2021).

6.2.2 Body length at sea

At sea, the advantages of large body size are likely to be manifold and interacting. As such, body size may be considered a proxy for more complex underlying mechanisms. The advantage of large body size might be direct, with larger post-smolts likely to be better swimmers than smaller smolts (Remen et al. 2016), which might allow them to traverse higher risk regions more quickly. They will also avoid gape-limited predators by merit of their better swimming ability or simply by merit of their larger size (Thorstad et al. 2012; Andrews et al. 2019). Predation is a major contributor to early estuarine and marine mortality, so the advantage of being a better swimmer is considered as likely to be relatively important during this phase of their migration.

There are also likely to be indirect effects of body size linked to physiology. In many salmonid species, such as Chum salmon *O. keta* and steelhead trout *O. mykiss*, energy allocation is allometric, meaning larger fish are more likely to have higher relative lipid stores (Post and Parkinson 2001; Kaga et al. 2013). In sockeye salmon *O. nerka,* higher lipid stores mean individuals are better equipped to stave off starvation risks (Farley et al. 2011). Thus, individuals with higher lipid content may be less likely to engage in risky behaviours whilst foraging, which has been seen in juvenile masu salmon *O. masou* (Yamamoto et al. 1998). Therefore, in Atlantic salmon, body length may be a proxy for lipid content, with larger individuals having relatively higher lipid stores that confers a survival advantage in periods of prey scarcity, enabling individuals to avoid engaging in risky foraging behaviours. Another physiological effect could be the difference in metabolic rate between large and small individuals, as larger juvenile Atlantic salmon tend to have lower metabolic rates (Seppänen et al. 2009). Lower metabolic rates might reduce the susceptibility of larger individuals to adverse environmental conditions, such as hypoxia (Oldham et al. 2019). Again, in juvenile *O. masou*, higher metabolism is linked to aggressive and risk-taking behaviours (Yamamoto et al. 1998). Therefore, smaller individuals may be more likely to take risks due to lower energy stores but also through mechanisms related to their high metabolic rates.

Body size also plays a role in marine foraging behaviours and parasite susceptibility. Post-smolts must attain a critical body size at sea to enable their ontogenetic dietary shift to piscivory (Salminen et al. 2001; Rikardsen et al. 2004). An early shift to piscivory may provide larger individuals with a survival advantage, as feeding at a higher trophic position should confers substantial nutritional benefits and growth opportunities. Individuals with faster marine growth rates and larger length increments tend to be more likely to survive at sea (Peyronnet et al. 2007). With marine parasites, the negative effects of sea lice *L. salmonis* and *Caligus spp.* increases with decreasing smolt and post-smolt size (Vollset 2019). When controlling for smolt body surface area, smaller individuals have higher louse settlement rates, meaning they are more likely to be infested, and settled lice are more likely to survive on smaller smolts than larger individuals (Tucker et al. 2002). There is some evidence in coho salmon *O. kisutch* that smolts already infested with sea lice are more likely to contract fatal diseases, such as infectious salmon anaemia virus (Ferguson et al. 2012). Thus, at sea, larger individuals are likely to shift to higher trophic levels more quickly and be less susceptible to the negative effects of parasites and infection than smaller conspecifics, which together might increase their probability of returning to their natal rivers to spawn.

6.3 Water temperature, discharge, and possible climate implications

Water temperature and discharge have been shown here to impact growth, migration phenology and survival of Atlantic salmon in the River Frome. Although not part of this thesis, another study on this system - to which I contributed to - also showed that juvenile salmon recruitment from eggs was lower in years of higher overwinter water temperatures, especially when they were followed by cool and wet springs (Marsh, Lauridsen, Riley, et al. 2021). Warmer winters lead to higher growth rates and earlier smolt migrations. Higher variation in water temperatures led to faster growth rates, with variation in water temperature being important to cue movement at the beginning and end of the smolt migration period. Though not as important as smolt body length, the sea surface temperature of the nearshore marine environment and the temperature gradient between the lower river and nearshore marine environment had negative effects on MRR, indicating that smaller differences between the marine temperature and the river temperature might increase early marine survival. Variation in discharge was important as well, having a quadratic effect on overwinter growth and was an important migration cue at the end of the smolt migration window.

Under climate change projections, river water temperature and discharge are predicted to alter in future, with warmer, wetter winters generally predicted (Watts et al. 2015). These could produce faster-growing parr (Jonsson and Jonsson 2009), resulting in salmon parr reaching the threshold smoltification size earlier in the year. While faster growth rates might imply larger smolts, it could also lead to earlier migration timing, as warmer winters were demonstrated in Chapter 2 to cue earlier migration for smolts. Thus, such environmental change might ultimately lead to a temporal mismatch in environmental conditions, where smolts enter the marine environment before the marine conditions are optimal. Chapter 3 suggested that warmer marine conditions may contribute to increased probability of surviving at sea. However, if parr are reaching their threshold body size and migrating to sea earlier in the year, oceanic conditions may be relatively cool compared to river conditions, which could negatively impact early marine survival.

6.4 Body size and migration phenology in a changing environment

The effects of climate change and increasing freshwater and marine temperatures will affect other migratory animals as well. As in Atlantic salmon, the ‘bigger-is-better’ theory that larger body size is associated with increased fitness is found widely across the animal kingdom (Sogard 1997; Sokolovska et al. 2000; Wikelski 2003; Kingsolver and Huey 2008). Amongst ectothermic animals, including migratory fishes, the ‘temperature-size rule’, widely recognised as applicable across taxa, indicates that such animals mature at smaller body sizes when exposed to higher temperatures (Atkinson 1994). This is recognised as a general rule in biology, and has been observed across taxa including insects, reptiles, plants, protists, fishes and molluscs (Atkinson et al. 2003; Angilletta 2004; Kingsolver and Huey 2008; Irie and Fischer 2009; Forster et al. 2012). In particular, the temperature-size rule appears to have a stronger effect on aquatic species, where high water temperatures are linked to smaller body sizes at maturity (Forster et al. 2012). With body size seemingly linked to ambient temperature for such organisms, increasing global temperatures might to lead to reduced body size at maturity across taxa (Sheridan and Bickford 2011), a phenomenon already recorded in amphibians, beetles, and marine fishes (Genner et al. 2010; Caruso et al. 2014; Tseng et al. 2018). With body size an indicator of fitness across taxa, and body sizes declining with warming temperatures, the fitness consequences of climate change might be smaller individuals of reduced fitness, the ultimate consequences of which will likely vary by species.

Furthermore, climate change is expected to alter migration phenology broadly across the animal kingdom, not just for salmon. For migratory species, the timing of migration is important for ensuring the conditions of the habitat to which they are emigrating meet their requirements. Some species undergo migrations to feeding grounds, like salmon, whilst other migrate for myriad other reasons, including reproduction. Across the animal kingdom, migration timing is often cued by environmental factors, such as temperature. With increasing global air and water temperatures, as well as changes to wind patterns in terrestrial environments and discharge regimes in aquatic environments, changes in migration timing have already been observed in many species of birds, bats, fishes, and cetaceans (Van Buskirk et al. 2009; Kennedy and Crozier 2010; Ramp et al. 2015; Hauser et al. 2017; Stepanian and Wainwright 2018). The impact of these changes will vary by species, but one of the main risks are trophic mismatches, where the timing of food availability and when the animal requires that food no longer occur simultaneously, a phenomenon already observed across taxa (Edwards and Richardson 2004; Post and Forchhammer 2008; Renner and Zohner 2018; Asch et al. 2019).

6.5 Management implications

Atlantic salmon populations have declined dramatically since the 1970s (Chaput 2012; ICES 2021). To attempt to halt and reverse such declines, managers may turn to restoration projects for salmon-bearing rivers (Lennox et al. 2021). Though sometimes such restoration projects are successful, projects involving the stocking of juvenile salmon in a salmon river, a common restoration approach, often fail (Lennox et al. 2021). The results of Chapter 3 and Chapter 4 suggest that instead of focusing only on increasing the abundance of juvenile salmon, such as via a stocking program, it could also be important to facilitate the natural production of larger juveniles that will be more likely to survive their marine migration. Moreover, in juvenile salmon, intraspecific competition due to intense density dependent pressures can suppress reduce growth rates (Imre et al. 2005; Simmons, Gregory, et al. 2021), and ultimately limit smolt body length (Imre et al. 2005). Thus, intensive augmentation of parr and smolt abundance by stocking could be highly detrimental. Additionally, augmenting stock with hatchery fish can lead to unwanted genetic consequences from domesticated salmon breeding with wild salmon (Perrier et al. 2013; Hagen et al. 2019). Salmonids have genetically distinct populations due to their homing behaviours, that ensure they usually reproduce in the same rivers in which they were born (Garcia de Leaniz et al. 2007; Fraser et al. 2011). Introgression from individuals reared in hatcheries can thus threaten the genetic integrity of these populations (Perrier et al. 2013; Almodóvar, Leal, et al. 2020). Therefore, to bolster Atlantic salmon populations, alternative physical enhancement schemes are preferable, including increasing resilience of the river to environmental change and enhancing foraging opportunities, while also minimising the negative effects of density dependence. Protecting and enhancing spawning grounds, e.g., by removing barriers to up- and downstream migration, such as dams, might also be useful (Belletti et al. 2020).

To promote the natural production of larger smolts in a given population, managers could manipulate river conditions to favour better growth conditions. For example, temperature is an important influence on growth rates, and as water temperatures increase due to climate change, measures can be taken to maintain river temperatures within the optimal range for growth. In particular, fencing that prevents farm animals from accessing river banks to allow riparian vegetation to grow and planting trees along the riparian zone can increase shade in the river and substantially reduce in-river temperatures (Broadmeadow et al. 2011). Discharge is another important factor for growth rates, as it is related to foraging success, where the discharge preferences of parr altering as they grow, with younger parr preferring habitats with slower discharge regimes and older parr preferring faster discharge regimes (Nislow et al. 1999). This might be linked with swimming ability, as larger parr are better able to hold station and swim in higher discharge rates, which increase foraging opportunities as it increases invertebrate drift (Huntingford et al. 1988). Thus, managers should consider the importance of ensuring a variety of microhabitats in the river that provide a range of flow regimes. Aquatic vegetation is also important as it provides both refugia and foraging habitat for parr (Marsh et al. 2021). Improving parr habitats by increasing macrophyte cover, particularly plants from the genus *Ranunculus*, has been demonstrated to improve feeding conditions and increase growth for parr in the River Frome (Marsh et al. 2021).

Aside from the factors that influence growth directly, there are also factors that could affect growth indirectly. For example, spawning habitat availability could be an important consideration. Maximising the amount of suitable spawning habitat throughout the catchment can help redd density in specific areas and so reduce post-emergence density dependent effects. To do so, depth, water velocity, and gravel type need to be considered, with relatively deep habitats with swift velocities preferred (Louhi et al. 2008). Clean gravels are very important for maintaining appropriate oxygen levels for egg incubation, and manually cleaning gravels by removing them, filtering detritus and fine sediments out, and replacing the 'cleaned' gravel has been shown to significantly improve spawning habitats (Meyer et al. 2008), although the effects can be short-lived (Bašić et al. 2017). Another important consideration is the access to spawning habitats available to adult salmon. More than one million barriers (including weirs, dams and culverts), fragment Europe's rivers (Belletti et al. 2020). Such barriers can prevent adult salmon from reaching suitable spawning habitats. Removal of old and unnecessary barriers from rivers is very important for addressing this issue and enabling easier smolt emigration and adult immigration (Pess et al. 2014; Koed et al. 2020).

Beyond considering how freshwater habitats should be managed to promote large smolts, demonstrating that the 'bigger-is-better' theory is generalisable beyond the Frome to other European populations should also be of interest to scientists involved in Atlantic salmon stock assessments. While traditionally a stock assessment functions to simply count the number of fish in a given fish stock to provide managers with information on how to regulate the stock, the work emphasises that marine survival is not just about parr and smolt quantity. Thus, consideration on needed more on smolt quality (using larger body sizes as a proxy of higher 'quality') if the number of returning adult spawners are to return to sustainable levels. Adding biometric data, such as smolt length, to the fisheries data currently used for Atlantic salmon stock assessments should allow fisheries regulators to make more nuanced decisions about regulating salmon stocks (ICES 2020).

6.6 Study limitations and avenues for future research

This work was carried out using a long-term CMR dataset; as such, it benefitted greatly from large sample sizes and a long time series. However, there were still some limitations to the work. Firstly, there are no PIT-tag antenna downstream of East Stoke on the River Frome. Some ‘unusual’ parr, known as ‘autumn migrants’, migrate in the autumn prior to smoltifying and move past the last PIT-tag antenna to overwinter near the tidal limit, i.e., below the detection system (Ibbotson et al. 2013). These individuals were thus excluded from all analyses, as there is no record of whether they smoltified (unless they were detected returning to the river as an adult), nor are there smolt length records for these individuals. As autumn migrants are believed to make up 20% of the River Frome parr population (Pinder et al. 2007), being able to include these individuals in overwinter growth rate analyses (like Chapter 1) and migration timing studies (like Chapter 2) would be illuminating. Further work could aim to understand the drivers of autumn migration, such as whether the ‘decision’ to migrate early is related to environmental variables or to biological factors, like intraspecific density, competition, and even individual characteristics like body size. Perhaps in high density sites with intense density dependent pressures, smaller individuals are more likely to be displaced by larger individuals, and thus initiate an autumn migration. Previous work has shown that at least some autumn migrants smoltify and complete a successful marine migration (Riley et al. 2009); however, the proportion that does so is not yet fully known. To address the marine return rates for individuals that undertake this interesting life history strategy, the work of Chapter 3 could be extended to a state-space model that encapsulates the parr and autumn migrant life stages, in addition to smolt, 1SW, and MSW states. Thus, survival probabilities could be estimated between smolts and adults, like in Chapter 3 and Chapter 4, but also between ‘regular’ parr and smolts, and between autumn migrants and adults.

Additionally, it was not considered whether the parr analyses in Chapter 2 and Chapter 3 had undertaken a precocious life strategy. ‘Precocious’ parr are male juveniles that develop mature gonads and are able to reproduce while still parr (Thorstad et al. 2011). It is thought that at least 60% of recruits can be sired by precocious males (Martinez et al. 2000; Saura et al. 2008). The development of full gonads as parr may mean some energy is allocated away from somatic growth and used for gonad development, which could have implications for overwinter growth rates and the body length attained by the parr at the time of smoltification (Whalen and Parrish 1999). Future work could consider trying to quantify the number of precocious parr, the level of interannual variation in the proportion of parr that mature precociously and whether that might change under climate change, investigate how being precociousness affects growth rates and migratory phenology, and quantify the MRR of recruits sired by precocious males versus ≥1 SW males.

In Chapter 4 and Chapter 5, the manner in which the MRR of MSW was calculated could be improved in future work. Currently, the MRR of MSW fish is calculated by adding a fixed term representing the additional mortality of an individual that stays at sea for an additional winter. With additional data and / or a different parameterisation, the model could be used to estimate the effect of the covariates on the additional mortality experienced by MSW directly.

Some recent work has suggested that male and female salmon exhibit different growth rates at sea (Tréhin et al. 2021). As marine growth is often considered influential in terms of whether salmon survive (Peyronnet et al. 2007), future marine return rate work could consider sex as an important covariate. This data can be derived from genetic analysis of fin clips or scale tissue (King and Stevens 2020). Likewise, smolt age could be used as an additional covariate, as some evidence suggests smaller smolts are more likely to become MSW fish (Salminen 1997; Jonsson and Jonsson 2007), who experience additional mortality risks from delaying returning to their river to spawn (Gregory et al. 2019). If smolt size was related to smolt age, smolt age might also be useful for predicting MRR.

There is still much unknown about the migratory route and pressures faced by salmon at sea. Future studies could combine CMR data with genetic data from salmon caught at sea and stable isotope data from salmon that have successfully returned to their rivers to try and deduce the various migratory routes that different populations take, to better determine the potential risk factors causing marine mortality (Trueman et al. 2012; Almodóvar, Nicola, et al. 2020; Bradbury et al. 2021; Gilbey et al. 2021). Pop-up satellite tags could also be employed to validate these migratory routes (Lacroix 2013). Improved knowledge of the migratory passage could allow survival models to include environmental and prey parameters from different parts of the route.

6.7 Conclusions

In conclusion, this work has unequivocally demonstrated the importance of juvenile body size, as well as environmental variables, on Atlantic salmon growth, migration phenology, and marine survival. The future avenues of research discussed above, including its extension and improvement, should broaden its application for conservationists and managers. As a species of high conservation, economic, and cultural importance, it is crucial to continue to monitor and study this species to be better able to protect it as the climate continues to change.

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Appendix 1: Influence of environmental and biological factors on the over-winter growth rate of Atlantic salmon *Salmo salar* parr in a UK chalk stream

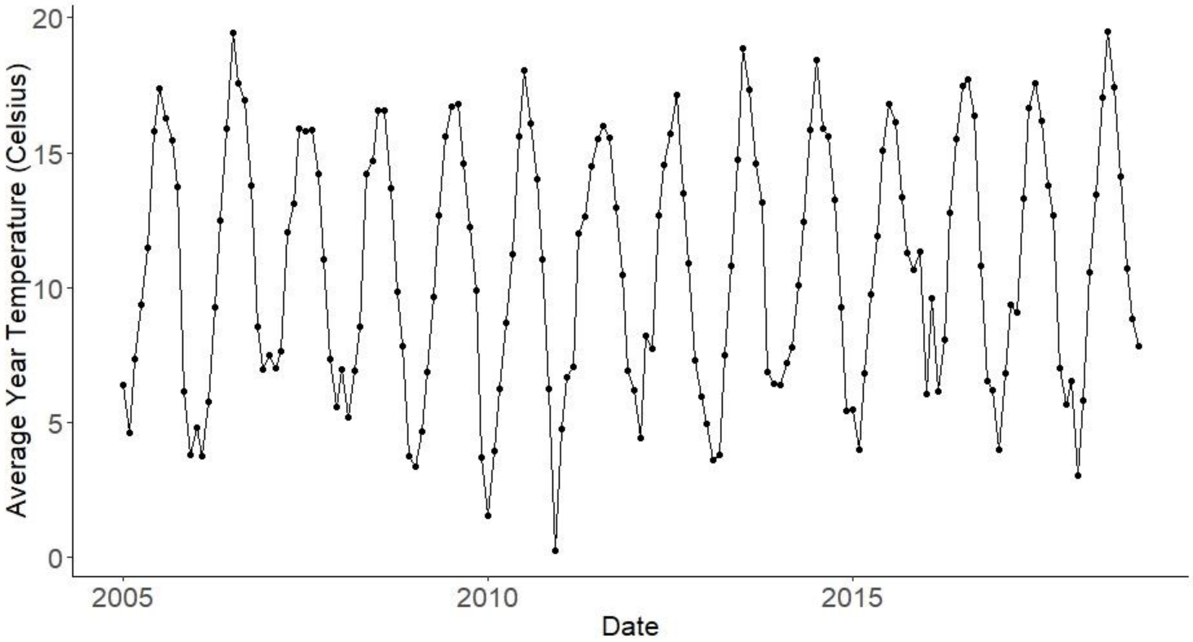

Figure A1.1. Line plot of monthly mean air temperatures.

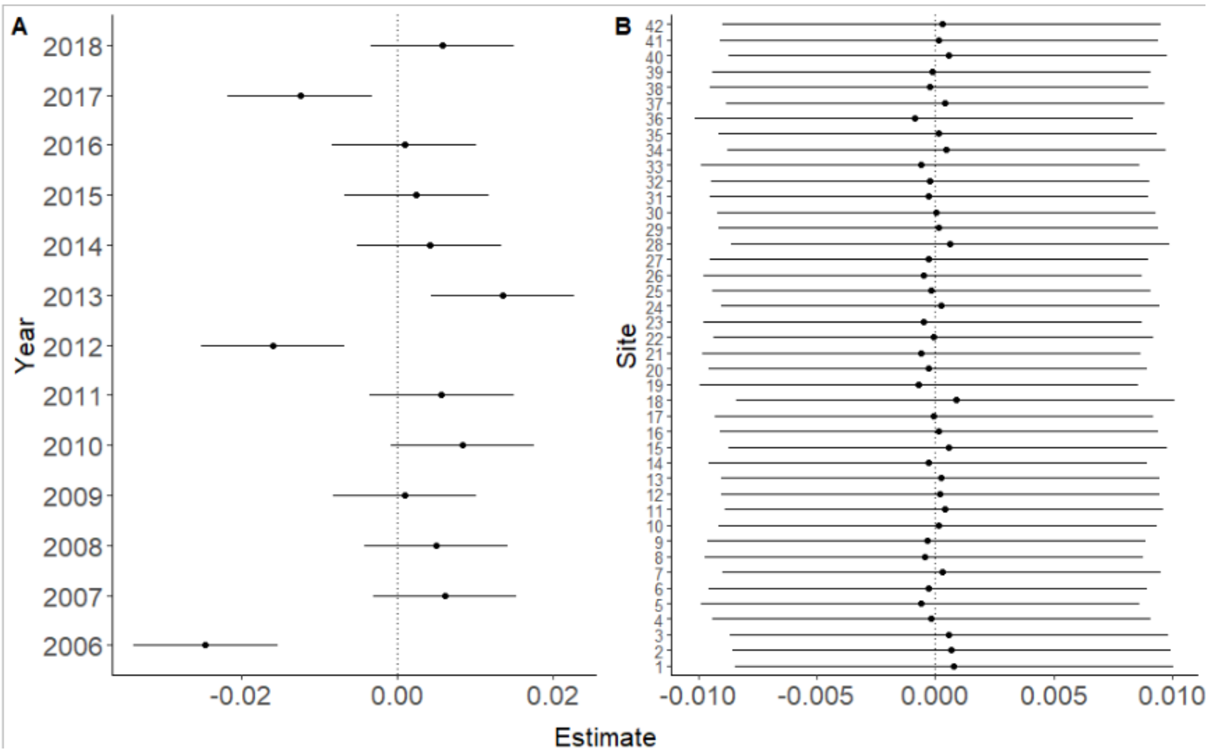

Figure A1.2. Caterpillar plot of maximum likelihood estimates of random effects year (A) and site (B). The points are the estimated values and the lines show the 95% confidence intervals for each point.

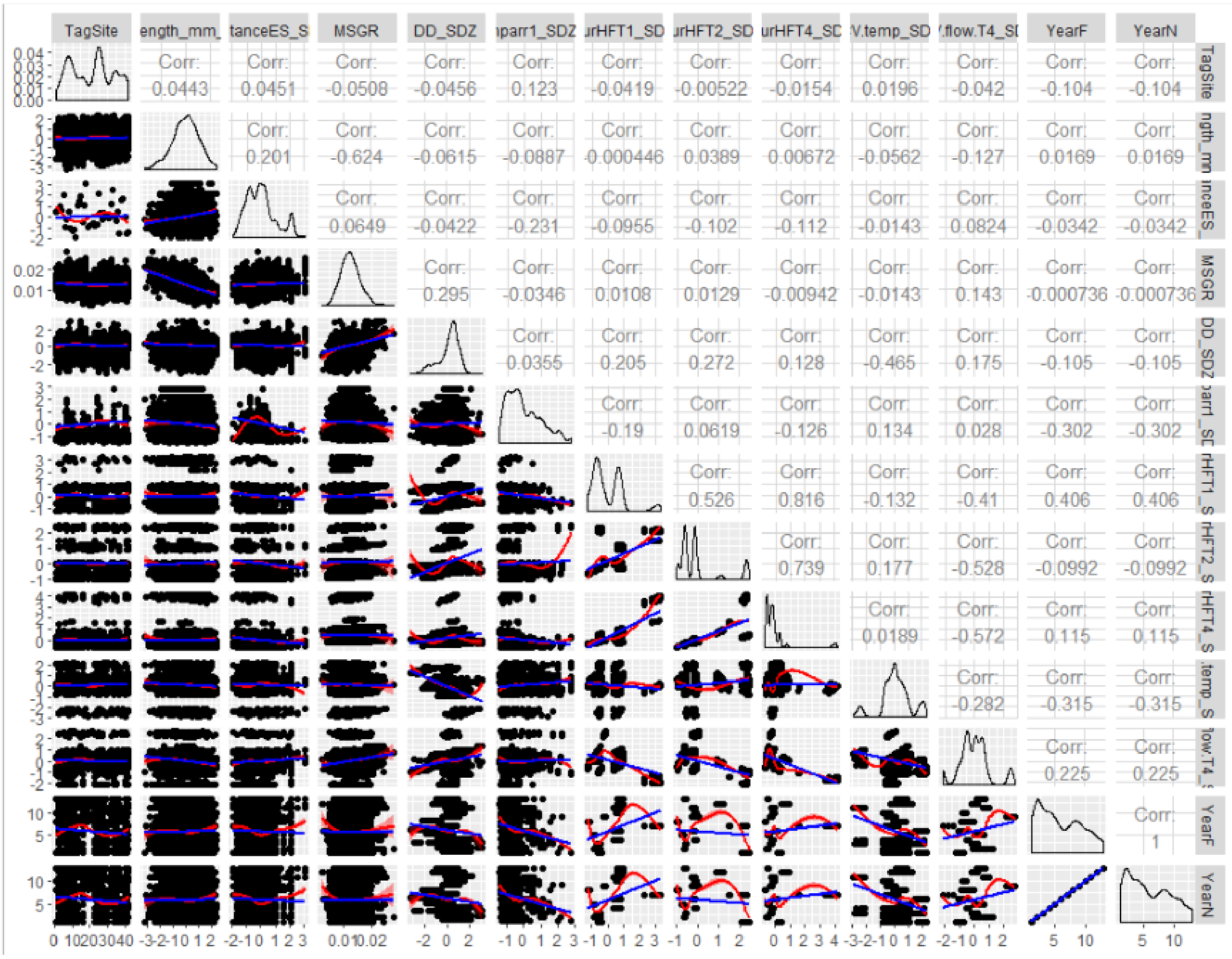

Figure A1.3. Correlation plot of response variable, fixed effects, and random effects.

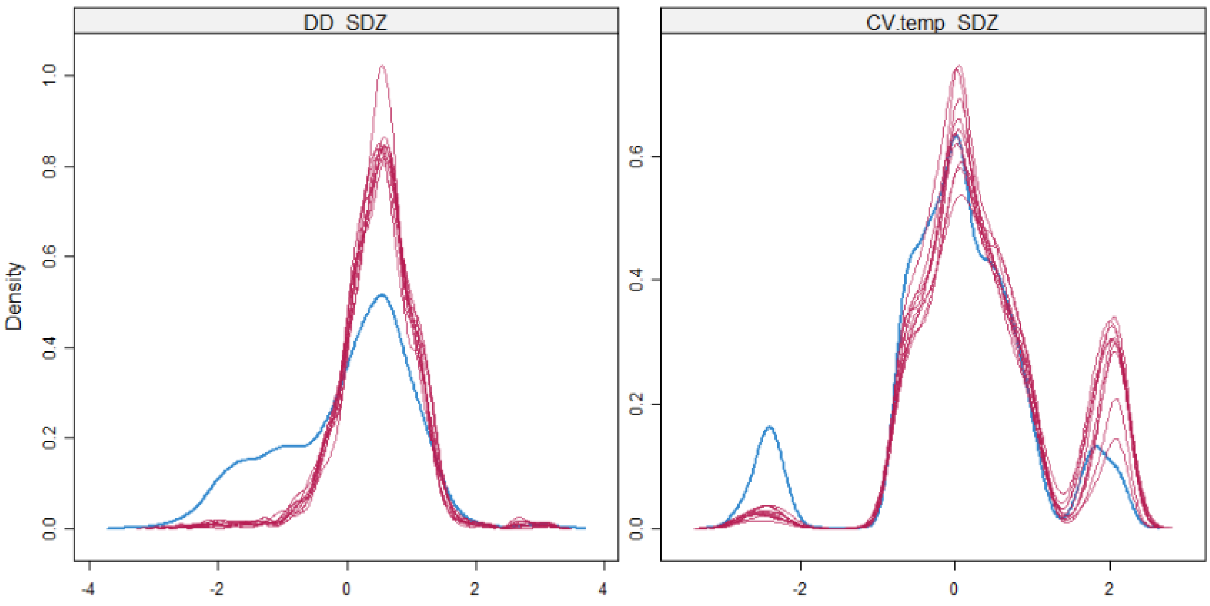

Figure A1.4. Density plot showing distribution of observed data (blue) and each imputed dataset (red) for degree days and CV temperature.

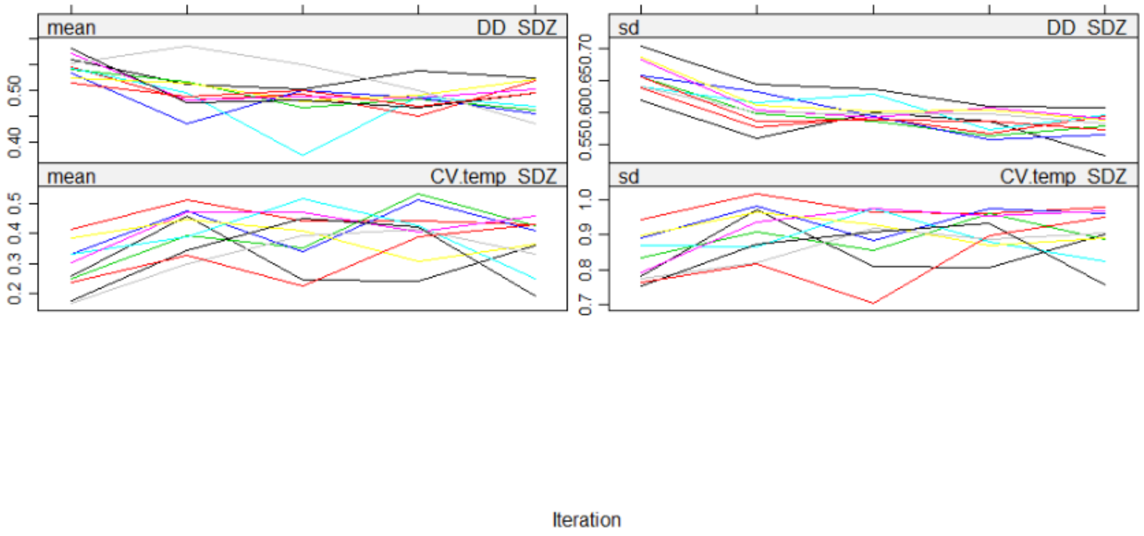

Figure A1.5. Trace plots showing convergence of each iteration during MICE procedure for degree days and CV temperature.

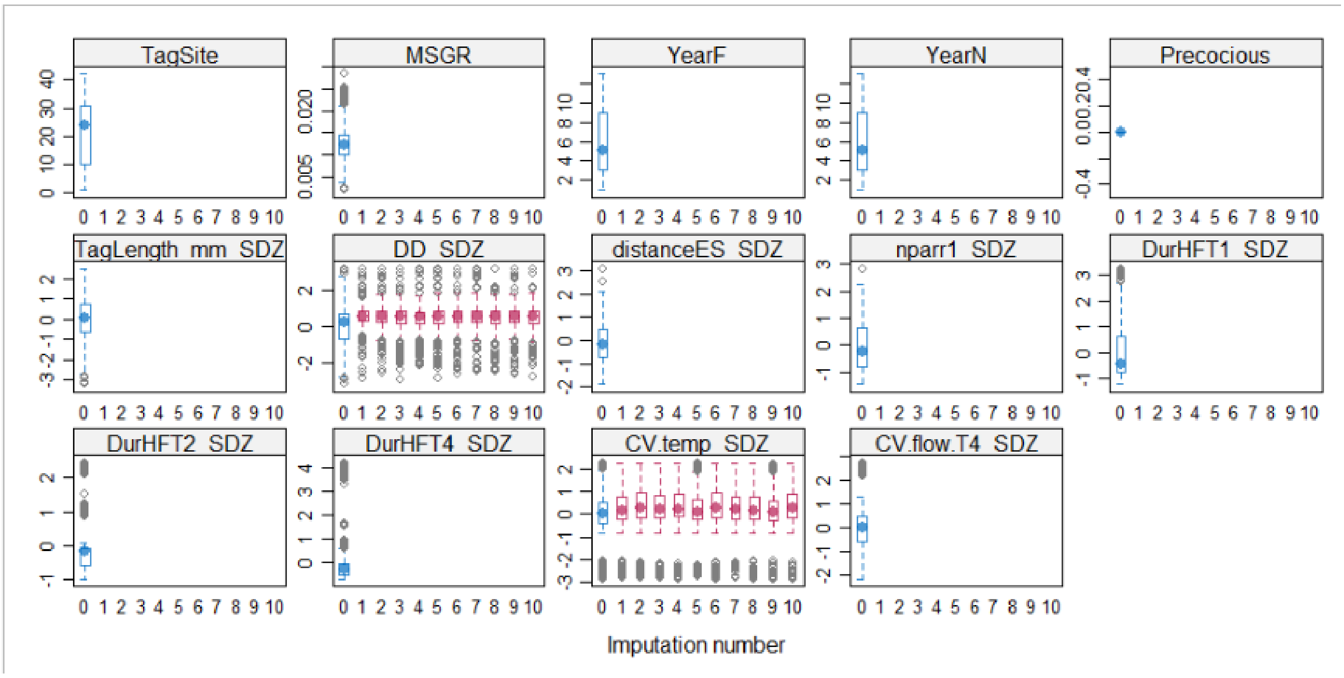

Figure A1.6. Boxplots of each variable used in the MICE procedure. Blue boxplots represent observed values, red boxplots represent imputed values for each of ten imputations.

Appendix 2: Biological and environmental influences on the migration phenology of Atlantic salmon *Salmo salar* smolts in a chalk stream in southern England

PIT-tag reader efficiency

We found the PIT readers in the fluvarium to have an efficiency of 81.5%. This was calculated using the number of smolts detected in the fluvarium as described in the methods section above, as well as the number of individuals detected on a PIT-reader located just downstream of the fluvarium, as:

$$\text{Detection efficiency} = \frac{N^*}{N} * 100\%$$

where $N^* = 1564$ is the number of smolts detected in the fluvarium and in the Mill Stream PIT-reader, and $N = 1918$ is the total number of individuals detected at the Mill Stream.

Table A2.1. Results of the linear regression used to calculate relative body length. To calculate the relative length for smolts captured in the RST, we used the residuals from a linear regression with DoY and year included as fixed effects. The results of the lm showed a positive effect of DoY on body length and a negative effect of year. This indicates that being captured later in the smolt run allowed smolts to gain a larger body length and that smolt body length decreased over the years.

Variable	Estimate	Lower CI	Upper CI
Intercept	324.681	158.263	491.099
DoY	0.222	0.183	0.262
Year	-0.104	-0.187	-0.022

Table A2.2. Calculation of percentage of smolts captured in the RST that were PIT-tagged. We used the 'detection' dataset to identify schooling behaviour. We calculated the percentage of PIT-tagged smolts captured in the RST each year, by dividing the number of PIT-tagged individuals by the total number of smolts captured. This varied between 8 and 17%. Thus, most fish captured in the RST (and thus, most fish swimming through the fluvarium) are untagged, and we cannot know exactly the number of fish that are in a school. We assumed that if two PIT-tagged fish are detected within a ten second window, they are a part of a school of unknown size containing untagged individuals as well as tagged individuals. We assumed the probability of more than one individual passing by the PIT reader within ten seconds of each other and not being a part of a school was negligible.

Year	Total number of smolts in RST	Number of tagged smolts in RST	Percent of smolts with tags (%)
2006	1885	328	17.4
2007	5765	622	10.8
2008	3998	432	10.8
2009	4066	461	11.3
2010	4568	363	7.9
2011	3060	247	8.1
2012	2700	247	9.1
2013	4251	345	8.1
2014	2466	310	12.6
2015	1810	229	12.7
2016	2856	238	8.3
2017	1104	156	14.1
2018	1615	140	8.7
2019	1663	133	8.0
2020	1664	182	11.0

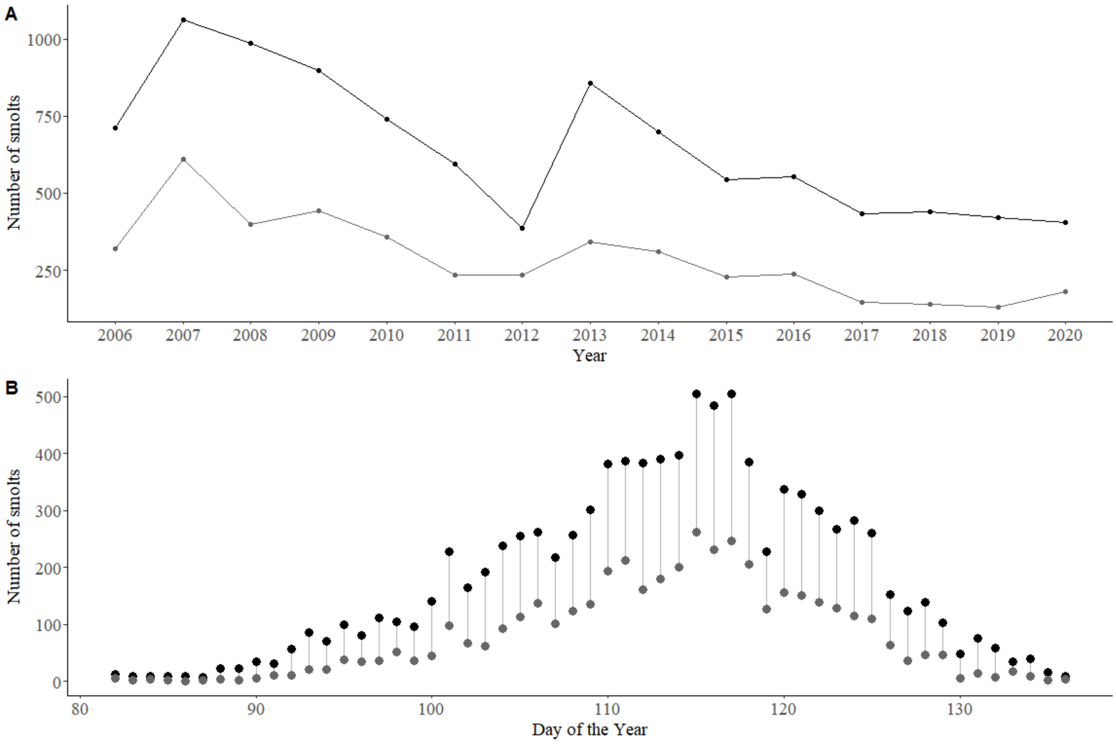

Figure A2.1. Numbers of smolts detected (black) and captured in the RST (grey) for each year (A) and DoY (B).

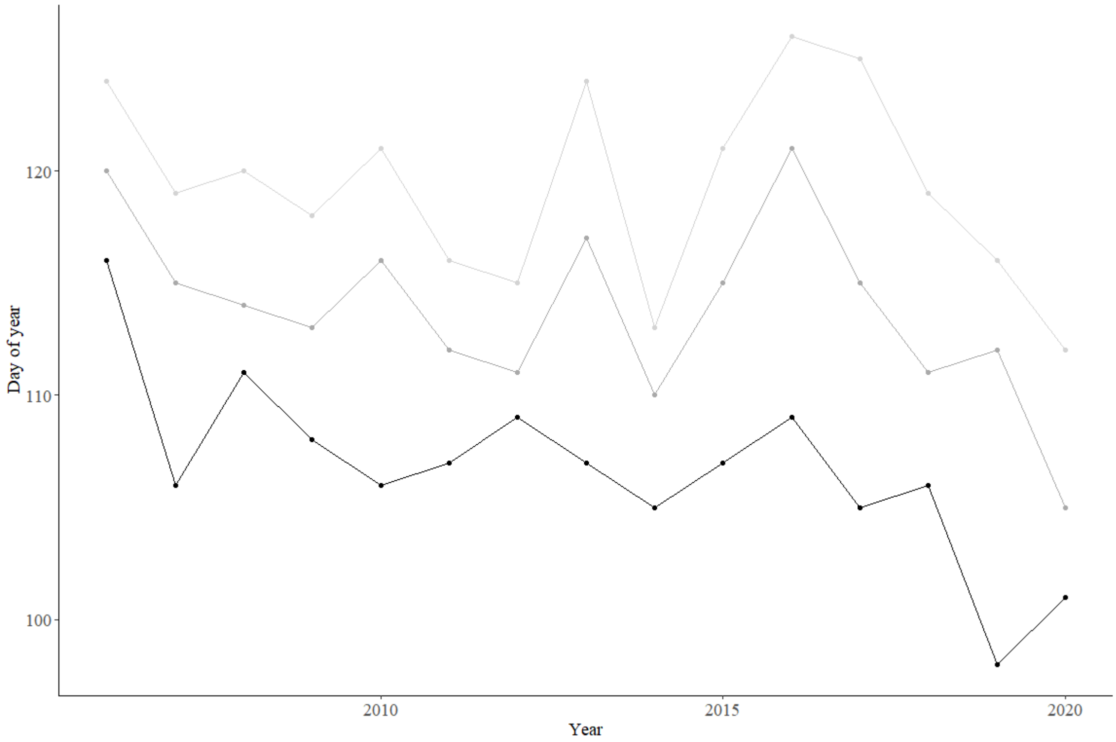

Figure A2.2. Day of year that 25% of PIT-tagged smolts (black), 50% of PIT-tagged smolts (medium gray), and 75% of PIT-tagged smolts (light gray) were detected in the *fluvarium. Several studies have used the DoY of 25% smolt detections as a proxy for the onset of the smolt migration, to compare the onset of migration between years (i.e. Antonsson and Gudjonsson, 2002; Otero et al. 2014).*

Appendix 3: Predicting how environmental conditions and smolt body length when entering the marine environment impact individual Atlantic salmon *Salmo salar* adult return rates

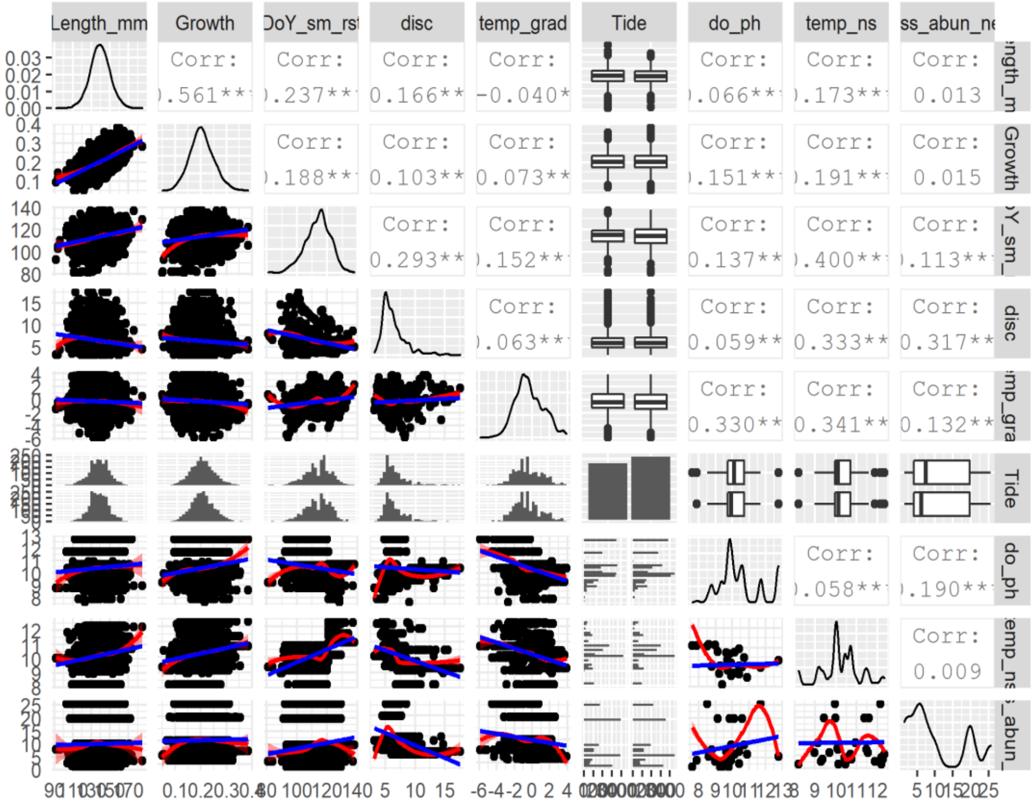

Figure A3.1. Pearson's correlation coefficient for each pair of explanatory variables.

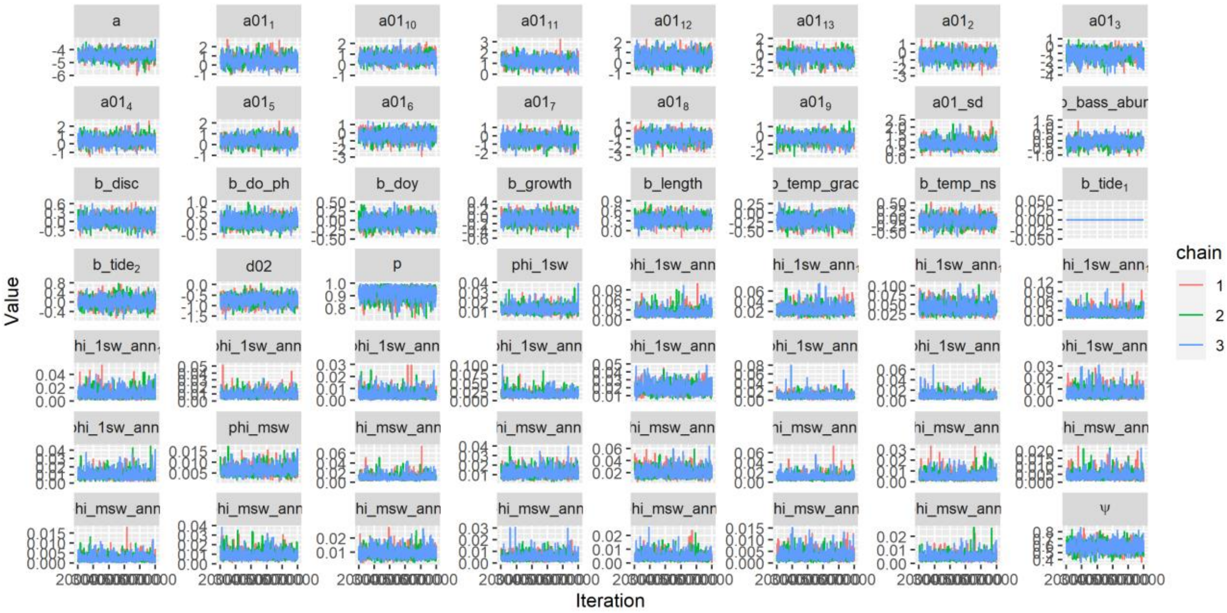

Figure A3.2. Trace plots for model.

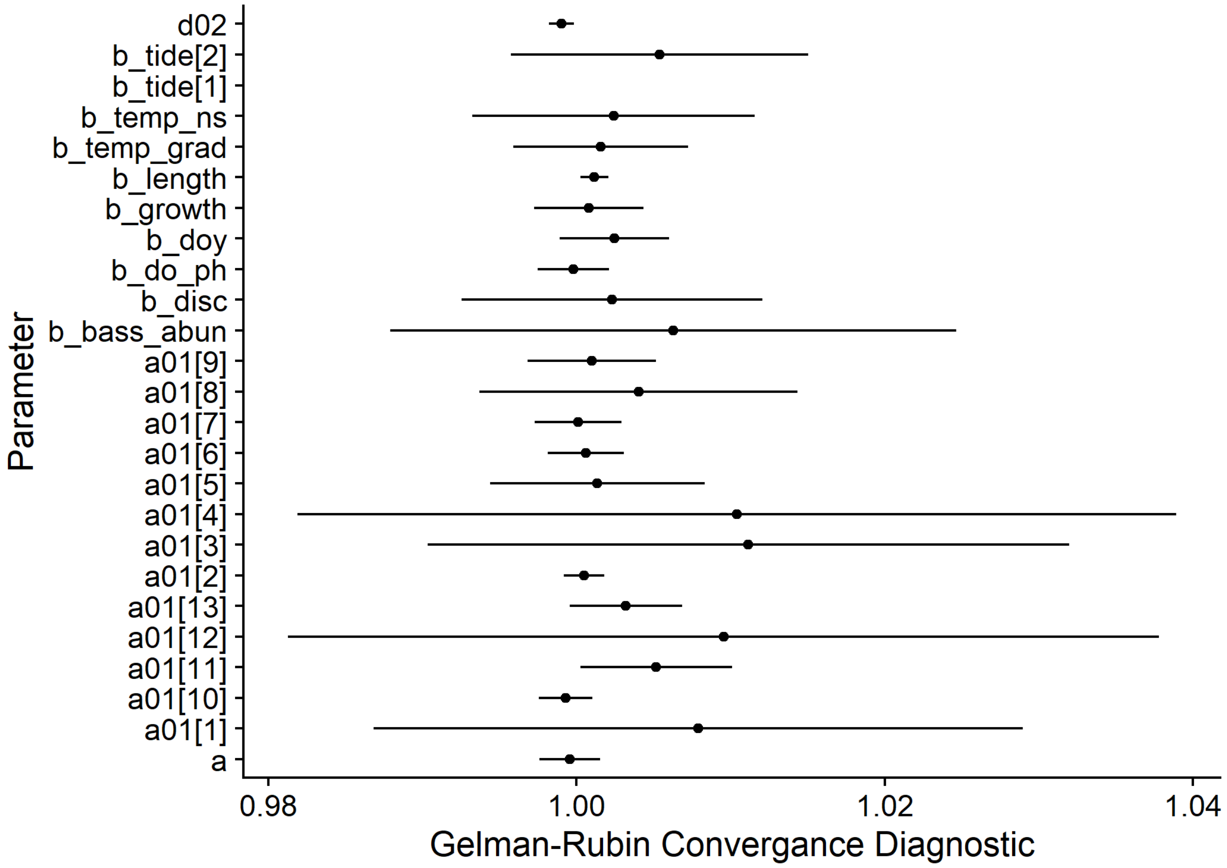

Figure A3.3. Gelman-Rubin convergence statistics for the model. The point is the statistic and the lines represent the 95% credible interval.

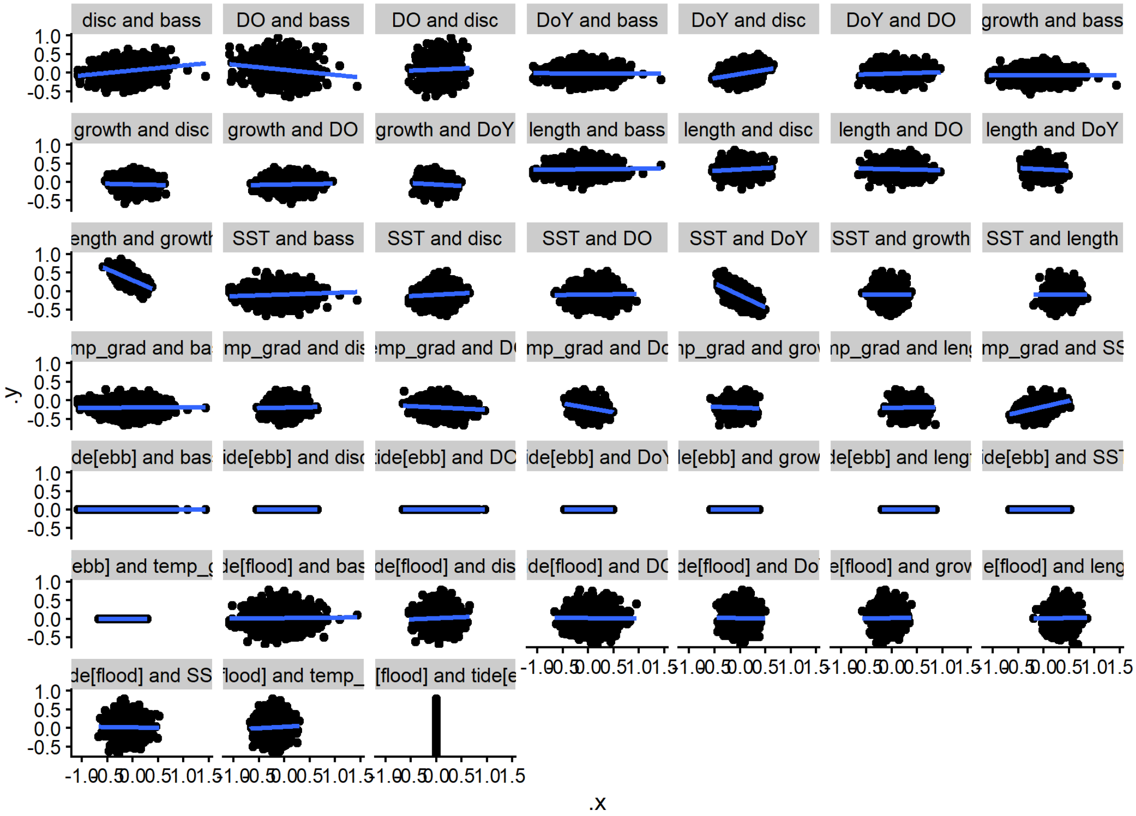

Figure A3.4. Pairwise scatterplots of the posterior distributions of the fixed effects.

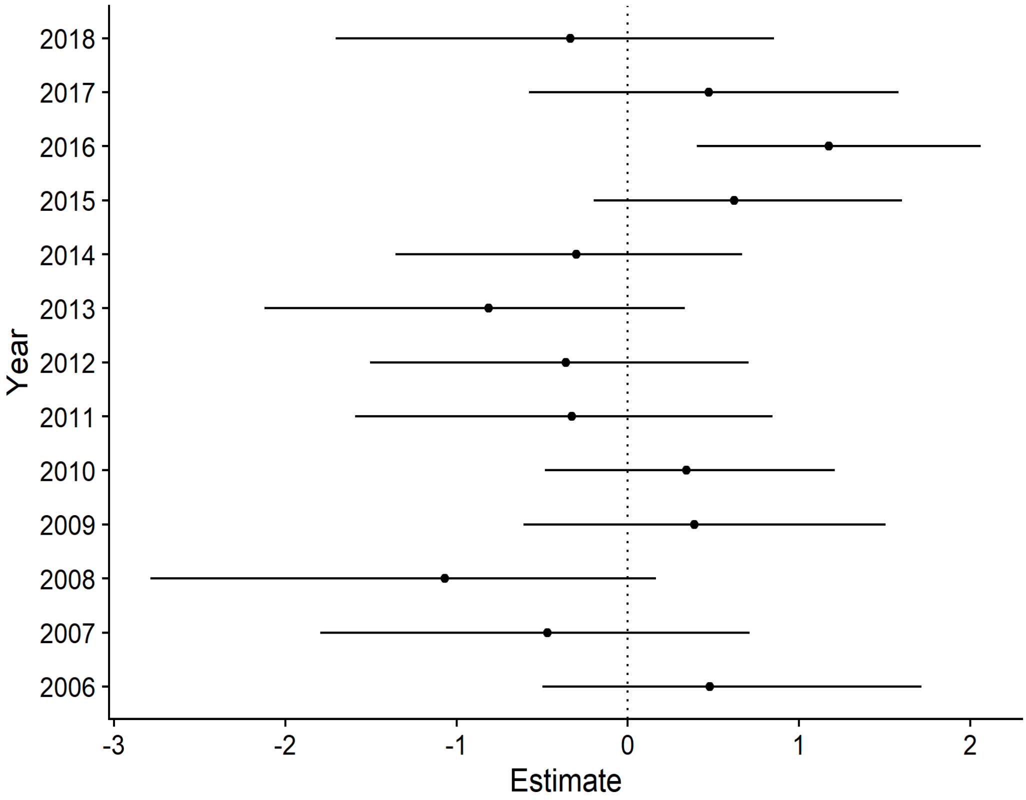

Figure A3.5. Year random effect estimates.

Appendix 4: Adult return rates of the anadromous Atlantic salmon: influences of smolt length across a latitudinal gradient

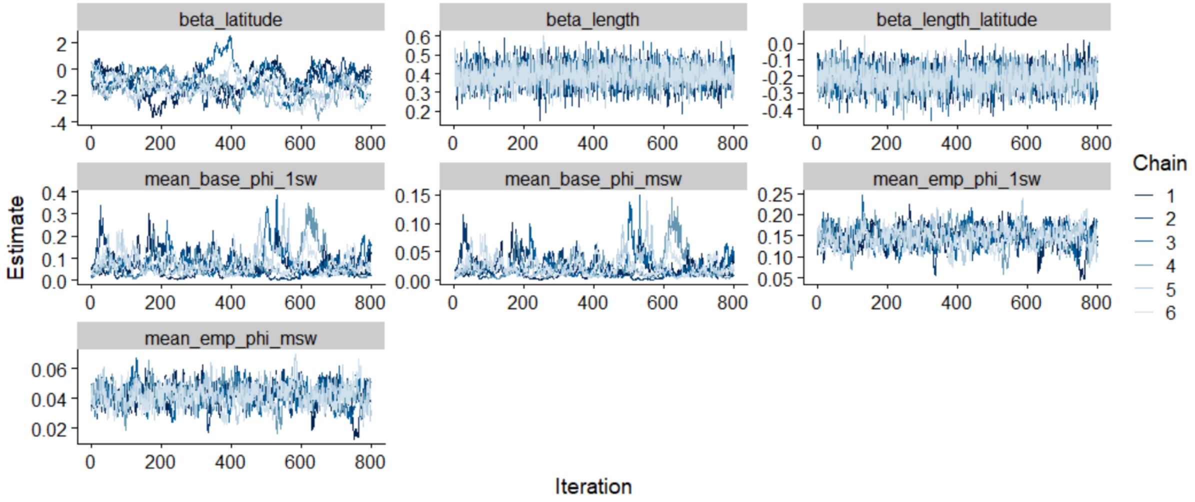

Figure A4.1. Trace plots of MCMC chains.

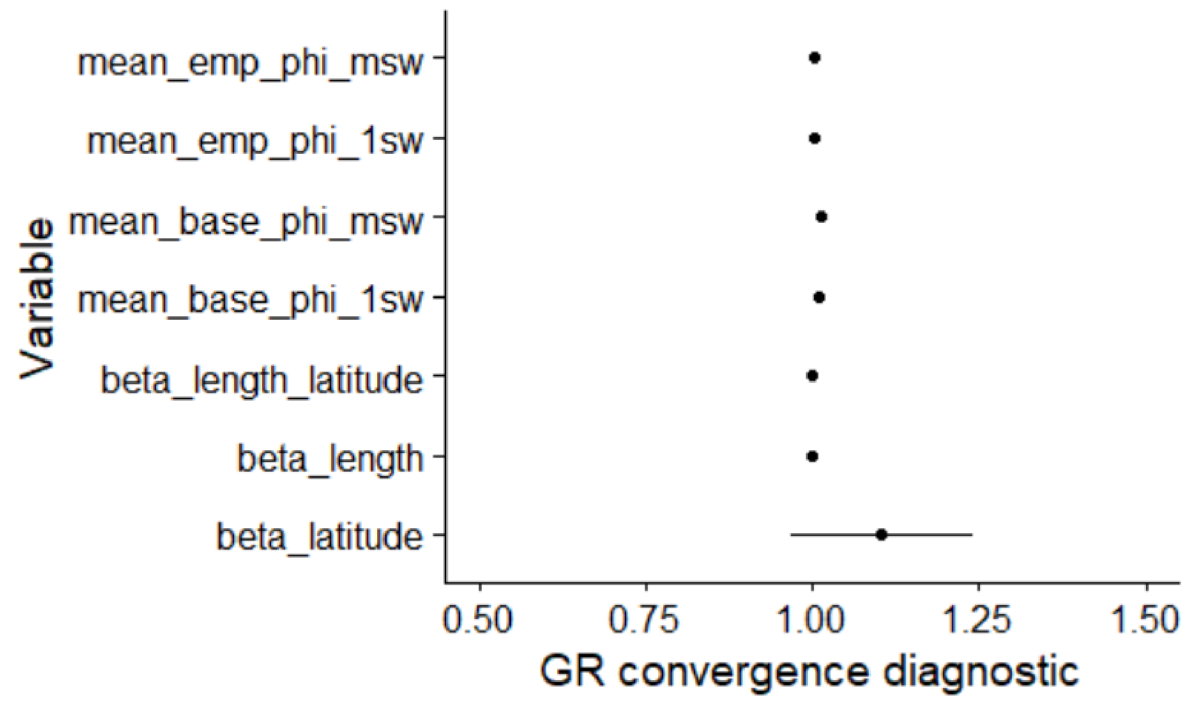

Figure A4.2. Gelman-Rubin convergence statistic.