ORIGINAL ARTICLE

Freshwater Biology   WILEY

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

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Funding information
European Regional Development Fund; Bournemouth University; Game and Wildlife Conservation Trust; Department for Environment, Food and Rural Affairs, UK Government

Abstract

1. 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*).

2. 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.

3. 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.

4. 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.

5. 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.

KEYWORDS

juvenile salmonid, migration timing, movement, smolt run, time series

1 | INTRODUCTION

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

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 1–3 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 et al., 1998; Stich 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 et al., 1998; McCormick & Saunders, 1987). 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 that 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 (Aldvén et al., 2015; Antonsson & Gudjonsson, 2002; McCormick et al., 1998). These *releasing factors* predominantly involve water temperature and river discharge, although other factors might also contribute to migratory release (Aldvén et al., 2015; Antonsson & Gudjonsson, 2002; McCormick et al., 1998). 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 (Teichert et al., 2020; Zydlewski et al., 2005). Increased river discharge has also been reported as an important releasing factor, although whether it is more important than water temperature appears river-specific (Aldvén et al., 2015; Jonsson & Ruud-Hansen, 1985). 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, although 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, Zydlewski, 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 et al., 2015; Stich, Zydlewski, 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.

2 | METHODS

2.1 | Study site and fish surveys

The River Frome is a lowland chalk stream in Dorset, U.K., 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 Hz, *c.* 200 V, 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 × 2.12 mm full duplex PIT tag [Wyre Micro Design

Ltd, Lancashire, U.K.]; 2014–2019:12.5 × 2.03 mm full duplex PIT tag [Biomark, USA]). The following spring (March–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; Figure 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 that the *S. salar* smolts were most likely to be migrating. Up to 2019, this meant that it ran for more than 12 hr 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 min when all captured fish were removed, anaesthetised, 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.

2.2 | 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 hr/day 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 *c.* 81.5%, but with some variation due to environmental conditions (see Section S1)). 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: (1) from 2014, the RST was operated only when it was assumed most smolts were migrating; and (2) 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

TABLE 1 Hypothesised effects (positive [+] or negative [−]) of each explanatory variable on the probability of any given smolt being detected and/or captured in the rotary screw trap by a given day of year (DoY) of the smolt run

Variable	Definition	Name	Hyp. effect	Explanation	Reference
Main effects					
Temperature	Degree days of water temperature from 7 January 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, Zydlewski, et al. (2015); Stich, Kinnison, et al. (2015)
Schooling	Binary variable indicating when a smolt was detected within 10 s 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	Ibbotson 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	

Note: Variables are presented as *Main effects* and as *Interactions*.

[†]Time of day (Day) indicated whether migration was diurnal or nocturnal.

[‡]Period in run (Period) indicated whether migration was during the early, middle, or late period of the smolt run as defined in the text. These variables were only included in interaction terms.

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 & Wickham, 2011). Daily mean water temperatures

FIGURE 1 Map showing the location in the U.K. (a) of the River Frome in the grey box (b) with an inset of East Stoke (c) showing the location of the fluvarium and rotary screw trap (circle), temperature loggers from 2006–2009 (triangle) and after 2009 (square), and the flow meter (plus sign)
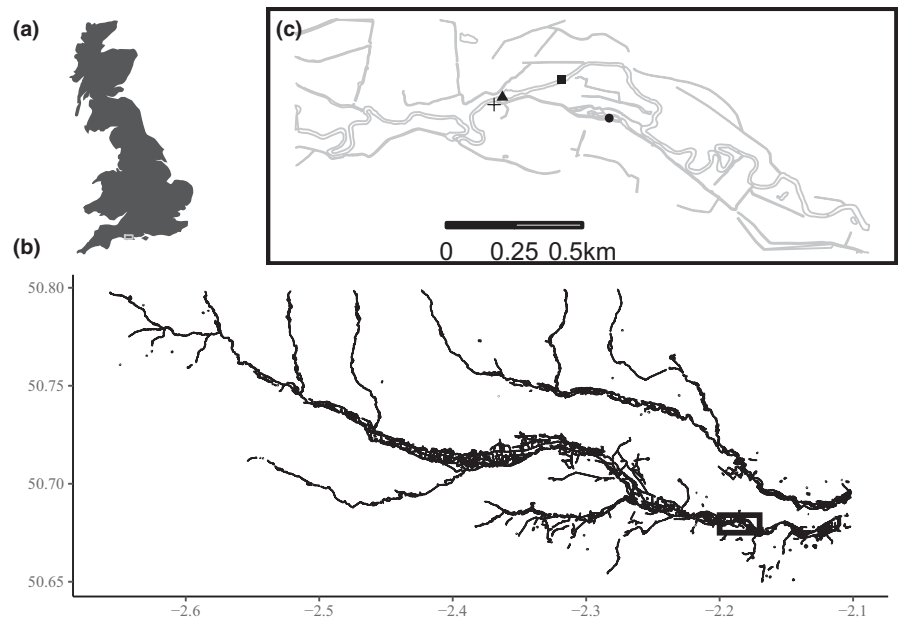
were calculated from measurements at two sets of water temperature loggers (Figure 1; see Simmons et al. (2020) for details). Using these, we calculated degree days as the sum of daily water temperatures ≥6°C from 07 January until the date of capture of each smolt, as juvenile salmonids are relatively metabolically inactive at temperatures below this (Elliott & 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 & Dick, 2014). River discharge (m^3/s) was recorded every 15 min at two locations on the River Frome at East Stoke (Figure 1; National River Flow Archive, 2020) 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 & Yamamoto, 1962), it was assumed that 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 & 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 were considered night-time migrants (coded as 0). Moon phase for each day of the smolt run was determined using the *getMoonIllumination* function from the R package *suncalc* (Thieurmel & Elmarhraoui, 2019), where it was calculated as a fraction from 0.0 (new moon) to 1.0 (full moon).

Assuming that 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 100–118, and the late period covered DoY 118–136.

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) (see Section S2 and Table S1). 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 s 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 s because a previous study in

this system showed that multiple tag detections frequently occurred within 10 s 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%–17% of smolts captured in the RST were tagged, suggesting that 80%–90% of smolts were untagged and could be travelling with tagged smolts in schools (see Section S3 and Table S2).

2.3 | 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 DoY, expressed as an ordered categorical variable using explanatory variables as per the hypotheses developed following the literature review (Table 1). We elected to treat DoY as an ordered categorical variable for two reasons: (1) we considered day as an ordered classification of time, but time is of too high-resolution scale for analysis of these data, and (2) 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 & Gudjonsson, 2002; Kennedy & 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:

$$\text{DoY} \sim \text{Ordered Probit}\,(\mu, \gamma)$$

$$\mu = \alpha + \beta X$$

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.

3 | RESULTS

Across the 15-year study period, a total of 9,728 PIT-tagged 1 + *S. salar* smolts were detected on the PIT-tag readers located in the fluvarium, whereas 4,312 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 2; Figure S1).

3.1 | 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). The estimates for the environmental variables were consistent with all hypotheses (Table 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 (Figure 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 (Figure 3). Relative change in discharge only influenced smolt migration during the late period,

TABLE 2 Number of 1+ smolts detected on the passive integrated transponder tag readers or captured in the rotary screw trap for each year in the River Frome as East Stoke

| Year	Detections	Captures
2006	710	320
2007	1,063	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	9,718	4,309

TABLE 3 Results from simplified ordered probit detection and rotary screw trap (RST) models, showing the estimated effects of explanatory variable and their 95% confidence intervals

Effect	Detection model		RST model	
	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)

Abbreviations: DD, degree days for temperatures ≥6°C; RCD, relative change in discharge; RCT, relative change in temperature.

FIGURE 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 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 (b)
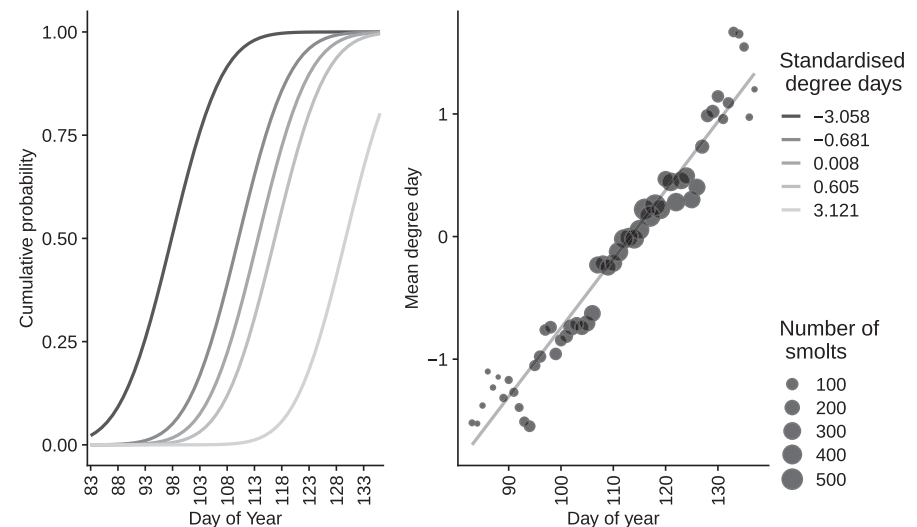

when it had a significant positive effect (Figure 4). Moon phase had a significant negative effect on smolt migration, with individuals more likely to migrate when there is a new moon or only a small fraction of the moon is illuminated than the converse.

The model estimates for the biological variables were also consistent with the hypotheses (Table 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 (Figure 5; see Figure S2 for raw data plot).

3.2 | 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,
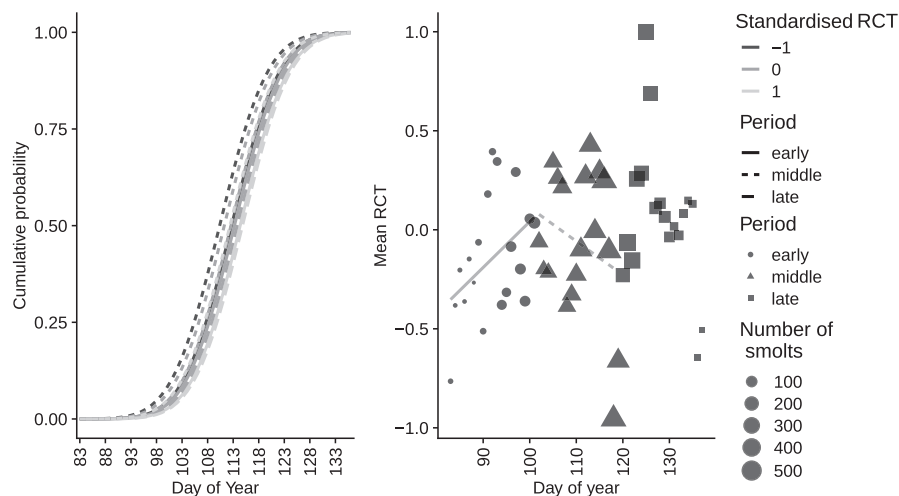
FIGURE 3 The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised relative change in temperature (RCT) at its 25th, 50th, and 75th quartile in each Period from the detection model (a). The mean RCT experienced by smolts detected on each 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 direction of the relationship and absent where no relationship was supported by the statistical model (b)
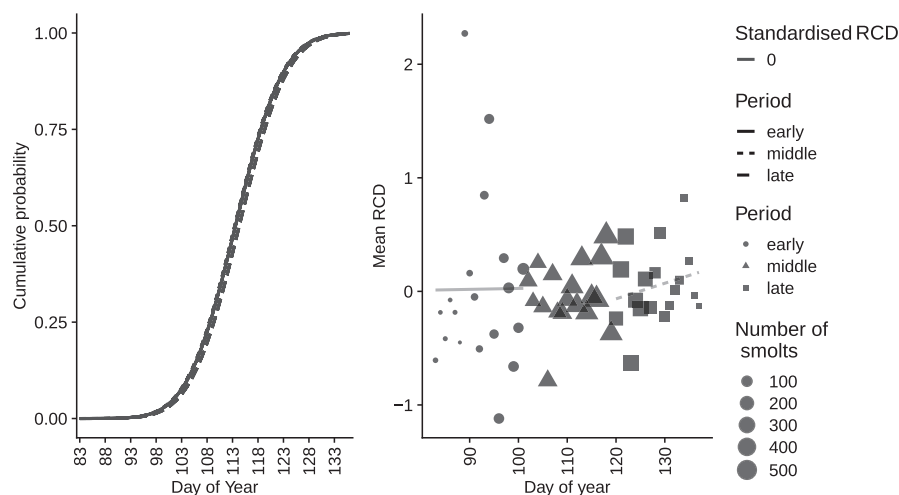
FIGURE 4 The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised relative change in discharge (RCD) at its 50th quartile in each Period from the detection model (a). The mean RCD experienced by smolts detected on each day of the year, where the point size is proportional to the number of smolts captured on each day, the point shape represents the Period, and the grey lines a trend line 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)

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 1), with the effects of degree days ≥6°C and with the relative change in temperature being significant and positive (Table 3).

The effects of the interactions in the RST model did, however, vary from the detection model (Table 3). When the 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). 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 1), with relative length having a significant negative effect on smolt migration timing, indicating that larger

FIGURE 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% interquartile range (IQR), whiskers delimit the 1.5 × IQR, and circles represent extreme values >1.5 × 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)
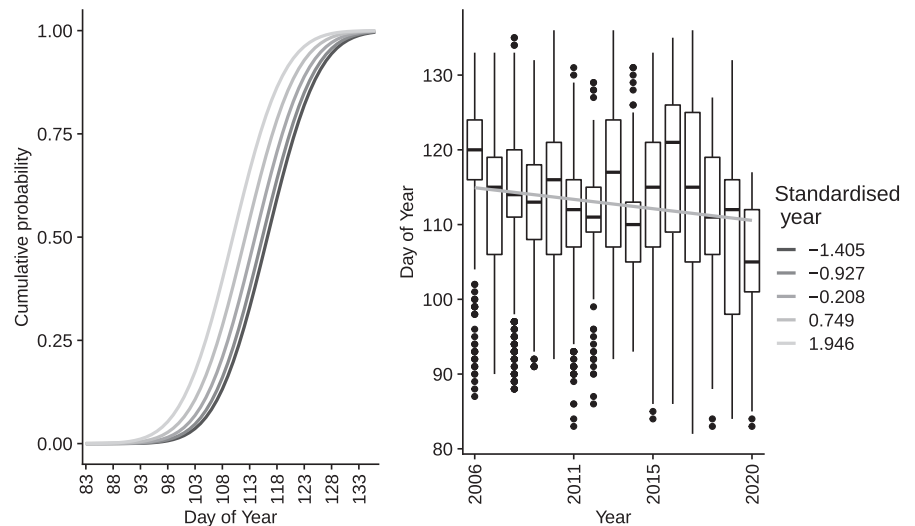
FIGURE 6 The cumulative probability of a smolt migrating by each day of the year as a function of the partial effect of standardised relative length at its 0th, 25th, 50th, 75th, and 100th quantiles from the rotary screw trap (RST) model (a). The mean relative length of smolts captured in the RST on each day of the year, where the point size is proportional to the number of smolts captured 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)
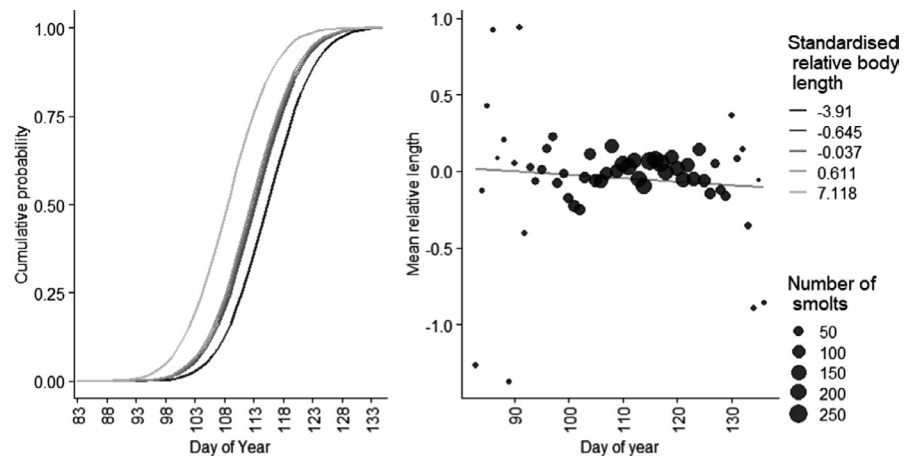
smolts were more likely to arrive earlier in the lower river (Figure 6). The effects of distance upstream, schooling, and year all had similar effects in the RST models as they did in the detection model, with distance upstream having a positive effect and schooling and year having a negative effect (Table 3).

4 | 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 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 probably 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 (Byrne et al., 2003; McCormick et al., 1998; 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 realised 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 was likely to relate to warmer winters resulting in individuals developing their migratory *readiness* (in both body length and 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 (Aldvén et al., 2015; Jokikokko et al., 2016; McCormick et al., 1998). Some studies suggest a specific temperature *threshold* must be attained before the initiation of migration, but others suggest that it is controlled by a combination of temperature attained and temperature changes (e.g. Jonsson & 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. Teichert et al., 2020; Zydlewski et al., 2005). 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 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 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 (Aldvén et al., 2015; McCormick et al., 1998). 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 (Cai et al., 2020; Remen et al., 2016).

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, probably as a visual predator avoidance strategy (Lothian et al., 2018; Spence & Dick, 2014). 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 & 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 & Dick, 2014).

Although some studies have investigated the effects of various biological variables on salmonid smolt run phenology (e.g. Bohlin et al., 1996; Persson et al., 2018), 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 (Cai et al., 2020; Tattam et al., 2013). 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 are most likely to 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 that migration is completed during the smolt migration window. Thus, schooling might be more common during these periods as daytime movement increases, although 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 it was once thought that 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 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 & Crozier, 2010; Otero et al., 2014). Annual variability in the timing of the start and end of the smolt run is partly due to differences in water temperature between years (Dolotov, 2006; Jonsson & Jonsson, 2014; Otero et al., 2014), with climate change widely assumed to be driving this pattern (e.g. Hedger et al., 2013; Kennedy & Crozier, 2010; 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 being 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 once ≥6°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* (Garner et al., 2017; Jonsson & Jonsson, 2009; Kennedy & Crozier, 2010; Walsh & Kilsby, 2007), 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.

CONFLICT OF INTEREST

There are no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Supplementary Material

S1. PIT 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.

S2. Results of linear regression for smolt body length

Table S1. 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

S3. Percent of smolts captured in RST that had PIT-tags

Table S2. 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	17.400530
2007	5765	622	10.789245
2008	3998	432	10.805403
2009	4066	461	11.337924
2010	4568	363	7.946585
2011	3060	247	8.071895
2012	2700	247	9.148148
2013	4251	345	8.115737
2014	2466	310	12.570965
2015	1810	229	12.651934
2016	2856	238	8.333333
2017	1104	156	14.130435
2018	1615	140	8.668731
2019	1663	133	7.997595
2020	1664	182	10.937500
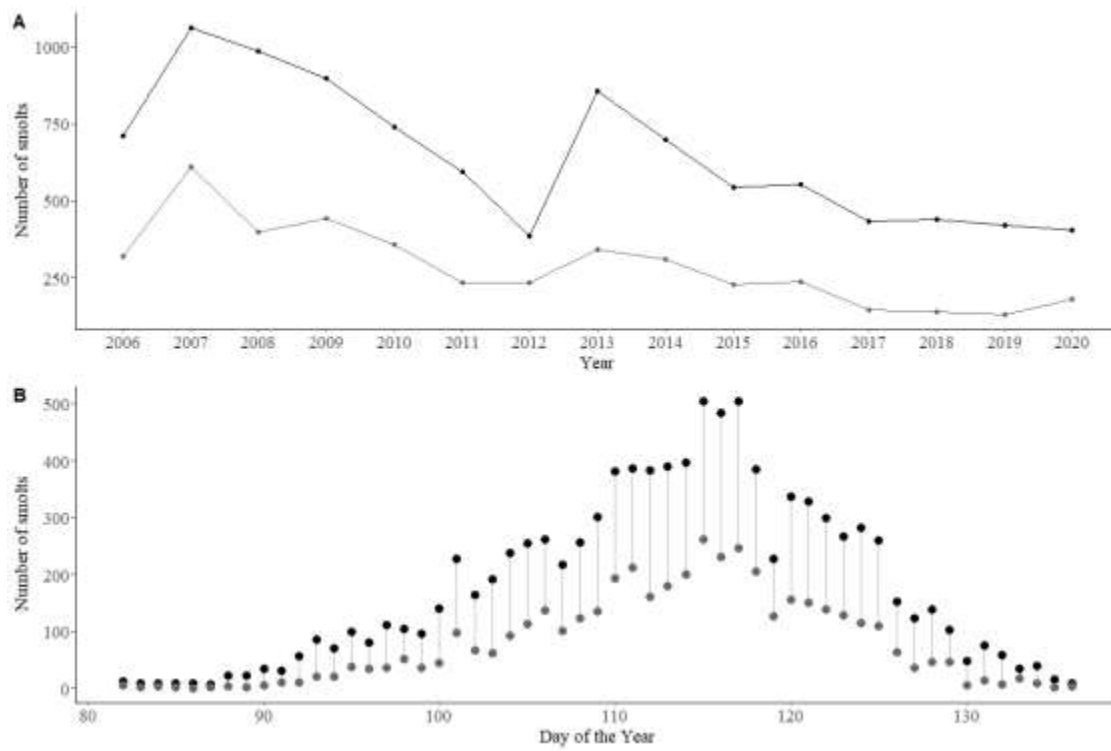
Figure S1. Numbers of smolts detected (black) and captured in the RST (grey) for each year (A) and DoY (B).

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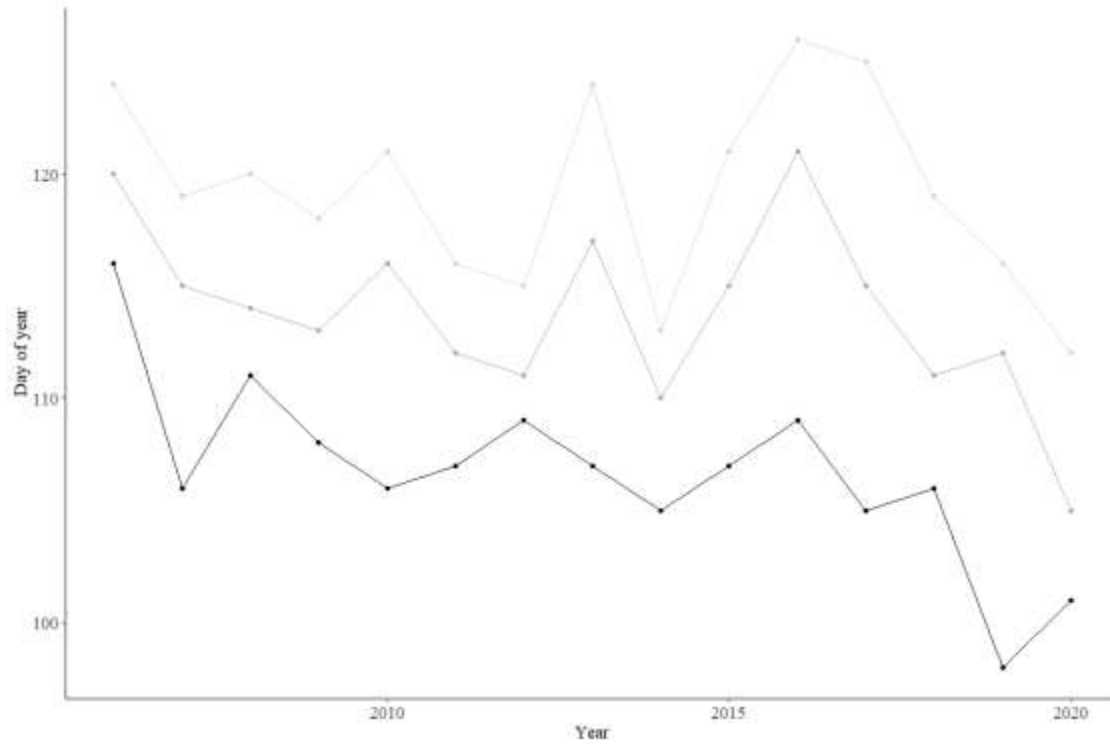
Figure S2. Day of year that 25% of PIT-tagged smolts (black), 50% of PIT-tagged smolts (medium gray), and 75% of PIT-tagged smolts (light gray) were detected in the fluvarium. Several studies have used the DoY of 25% smolt detections as a proxy for the onset of the smolt migration, to compare the onset of migration between years (i.e. Antonsson and Gudjonsson, 2002; Otero et al., 2014)