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

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Running title: **Over-winter growth rate of juvenile Atlantic salmon *Salmo salar***

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.

Key words:

Smolt, marine survival, water temperature, river flow, thermal stability, body length

Introduction

Populations of anadromous fishes have declined drastically over the past several decades, as a result of pressures including climate change, overexploitation, and habitat loss (Limburg & Waldman, 2009). This is the case for anadromous Atlantic salmon *Salmo salar* which have experienced such declines since the 1970s (Limburg & Waldman, 2009; Mills, et al., 2013; Parrish et al., 1998). There is increasing evidence that intrinsic factors from their freshwater stages, such as smolt body size, could be important in determining *S. salar* marine mortality rates (Armstrong et al., 2018; Gregory et al., 2019; Russell et al., 2012). 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 severity of the abiotic conditions and increased competition for resources (Cunjak & Therrien, 1998). For example, juvenile salmon survival in a Canadian stream is lower prior to ice formation compared to after, due to highly variable water temperatures and flows during the early winter acclimatization period (Linnansaari & Cunjak, 2010). Harwood, et al. (2001) used an experiment to demonstrate that overwintering juvenile salmon prefer areas of deep water, but they will use areas of shallow water or switch to show higher diurnal activity to avoid the negative effects of competition with brown trout *Salmo trutta* on their growth and survival. Whilst these studies suggest the importance of variability in temperature, flow, and competitor density for overwinter growth and survival, a range of other factors have also been suggested as important, including habitat characteristics and juvenile body length

(Achord et al., 2007; Elliott & Elliott, 2010; Hurst, 2007; Jonsson & Jonsson, 2009; Nunn et al., 2012; Warren et al., 2015).

Some of the consequences of differences in individual over-wintering performance of salmonids are increasingly understood, including influences on the phenology of their spring migration, with colder winters sometimes delaying migration (Cunjak et al.,1998; Cunjak & Therrien, 1998; Huusko et al., 2007; Munsch et al., 2019). Nevertheless, there is limited understanding on how growth during winter contributes to their overall body length at smoltification, despite smolt length being recognised as an important determinant of marine survival (Armstrong et al., 2018; Chaput et al., 2019; Gregory et al., 2019; Kallio-Nyberg et al., 2004). This could be because most studies of over-winter performance have focused on populations that experience overwintering conditions sufficiently harsh 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 & Elliott, 2010; Kemp et al., 2017). In recent years, winters have been getting warmer, with minimum winter temperatures in particular increasing (Davy et al., 2017), so studying populations in temperate rivers could help understand other systems which 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 across the study period (Nakagawa & Freckleton, 2008). How these periods of missing data are handled within analyses is important to consider, such as whether biological data for these periods are also removed from analyses or whether the missing environmental data is inferred from surrogate data or via statistical methods (Nakagawa & Freckleton, 2008). For the latter, multivariate imputation by chained equations (MICE) enable the data to be imputed using a method that accounts for the uncertainty in the estimated values (Buuren & Groothuis-Oudshoorn, 2011; Penone et al., 2014). Unlike single imputation methods, it imputes several estimates for the missing values, and then pools the parameter estimates for subsequent analyses of the multiply-imputed datasets. While it provides a robust method for handling missing data (Buuren & 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 explaining the annual variability in *S. salar* overwinter growth. Models were designed to test the hypotheses that variation in temperature, flow and population abundance affect juvenile salmon overwinter growth rates in accordance with expectations (Table 1). In the River Frome, the majority of smolts leave the river at age one year, unlike northernly rivers where smolts grow more slowly and leave at two or more years. Consequently, their overwinter growth rate could have a strong effect on their smolt length. As with most long-term datasets, there were missing data in the environmental explanatory variables; therefore, MICE was used to inform the modelling process of the possible effects of environmental variables on overwinter growth rates for the periods when environmental data were missing.

Methods

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. 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. 1). 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).

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. 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. 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 °C for each overwinter period (as *S. salar* parr are considered not to grow at water temperatures below this in Britain (Elliot and Elliot, 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. 1) and used to calculate a daily mean flow (National River Flow Archive). 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 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 1). We hypothesised the effect of each explanatory variable on the response variable $MSGR$ from evidence in the literature (Table 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 ($n \leq 7$).

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). 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 (MetOffice, 2019). None of the three overwinter periods with missing temperature data (Table 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 (Supporting Information).

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 & 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 (Supporting Information). Trace plots of the five iterations showed that the algorithm converged for both variables (Supporting Information). 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’.

Statistical analysis

Prior to analysis, all explanatory variables (Table 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); 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 1).

The statistical models took the form:

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

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

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., 2015). 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 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).

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 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. 3). The mean annual values for each environmental and biological variable are in Fig. 2.

The best and most parsimonious model selected via AIC is given in Equation 1:

Equation 1. $MSGR = \alpha + \beta_1(DD) + \beta_2(CV\ temp) + \beta_3(CV\ flow) + \beta_4(CV\ flow)^2 +$

$\beta_5(DurHFT2) + \beta_6(Distance) + \beta_7(Length) + \beta_8(Density) + \upsilon_\gamma + \upsilon_S + \varepsilon$

This model included both year and site as random effects (Table 4). The fitted values closely matched the observed values of $MSGR$ (Fig. 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 ºC (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. 3; Table 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. 3; Table 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 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. 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 5; Fig. 4; Fig. 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 & Höjesjö, 2009; Tattam et al., 2017; Teichert et al., 2010). 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 river 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 & 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 & 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 & 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 (Horton & Kleinman, 2007; Nakagawa & Freckleton, 2008; Penone et al., 2014; Raghunathan, 2004). 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, El-Jabi, & Satich, 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 (Nakagaw & 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 & Kilsby, 2007). As *S. salar* do not smolt younger than age one (Jonsson & 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 & Jonsson, 2009; Kennedy & Crozier, 2010; Otero et al., 2014). In more northernly rivers than the Frome, smoltification occurs only after several years in freshwater (Jensen et al., 2014; Metcalfe & Thorpe, 1990). Although smoltification may occur at a younger age following a warmer-than-normal winter (Jonsson et al., 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 & 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 (Armstrong et al., 2018; Gregory et al., 2019; Russell et al., 2012). 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.

Acknowledgements

Special thanks to the staff and volunteers at the Game and Wildlife Conservation Trust and CEFAS for the collection of this data, and John Davy-Bowker for access to the River Lab Long Term Monitoring project temperature data. The study was part funded by the European Regional Development Fund through the Interreg Channel VA Programme and by a studentship from Bournemouth University. We thank the anonymous reviewers of this manuscript for their helpful comments.

Data availability statement

Data available upon reasonable request from the authors.

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Authors' Contribution Statement

Conceived and designed the investigation: OS, RB, PG, SG. Performed field and/or laboratory work: OS, SG. Analysed the data: OS, SG. Wrote the paper: OS. Revised the paper: OS, RB, PG, RB.

Table 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 $\boldsymbol{MSGR}$	Range of observed values	Mean ± Standard Deviation	References
Environmental Variables	Degree days over 6 ºC	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; Nina Jonsson, Jonsson, & Hansen, 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, Vondracek, Ferrington, Finlay, & Dieterman, 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, Finstad, & Rønning, 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, Cunjak, & Benfey, 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 & 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 & Imre, 2005)
	Year (fixed numeric)	Year	Year that smolts were recaptured – test for trend in $MSGR$	-	2005 – 2017		(Nater et al., 2018)

Table 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**

Table 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 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 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

Figure Captions

Figure 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 2005-2009, and the triangle shows the location of the temperature loggers from 2009-2018, as well as the location of the RST each spring.

Figure 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 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 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 5 Marginal effects plots of each standardized explanatory variable. The shaded areas represent the 95% confidence interval.