ORIGINAL ARTICLE

WILEY
Ecology of
FRESHWATER FISH

Roles of discharge and temperature in recruitment of a cold-water fish, the European grayling *Thymallus thymallus*, near its southern range limit

Tea Bašić[1,2,3] 🆔 | J. Robert Britton[3] 🆔 | Richard J. Cove[4] | Anton T. Ibbotson[2] |
Stephen D. Gregory[2] 🆔

[1]Salmon and Freshwater Team, Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, UK

[2]Salmon and Trout Research Centre, Game & Wildlife Conservation Trust, FBA River Laboratory, Wareham, UK

[3]Faculty of Science and Technology, Centre for Conservation Ecology and Environmental Sciences, Bournemouth University, Poole, UK

[4]Natural Resources Wales/Cyfoeth Naturiol Cymru, Buckley, UK

Correspondence
Tea Bašić, Salmon and Freshwater Team, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, UK.
Email: tea.basic@cefas.co.uk

Abstract

Recruitment of salmonids is a result of density-dependent factors, specifically egg production in the previous year, and density-independent environmental processes driven by discharge and temperature. With the plethora of knowledge on major drivers of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* recruitment, there is a requirement to explore less known species, such as European grayling *Thymallus thymallus*, whose postemergence time coincides with period of increasing temperature and low discharge. This study assessed drivers of grayling recruitment in a southern English chalk stream, a system vulnerable to discharge and temperature alterations under future climate change predictions. The analyses explored age 0+ grayling survival in relation to conspecific and heterospecific densities and discharge- and temperature-derived factors. The final mixed-effects model revealed a positive relationship between age 0+ grayling survival and incubation temperature anomaly and age 0+ trout abundance. Similarly, postincubation temperature anomaly had a positive effect on 0+ grayling survival, but only up to a threshold temperature of 13.5°C, beyond which it had a negative effect. In contrast, increasing number of days with low discharge postincubation negatively influenced age 0+ grayling survival, with no evidence of an effect of elevated discharges following spawning. Our results emphasise the importance of maintaining natural discharge regimes in salmonid rivers by tackling multiple stressors operating at the catchment scale, including land and water use to mitigate for predicted climate driven changes. In addition, further research on recruitment drivers in less stable, rain-fed systems, is required.

KEYWORDS
chalk streams, climate change, discharge, recruitment, salmonids, temperature

1 | INTRODUCTION

Recruitment in fish is affected by a range of factors impacting on life stages from egg deposition through to sexual maturity (Milner et al., 2003). Density-dependent factors acting on recruitment are usually functions of spawning stock biomass or egg production in the previous year that influence the numbers of con- and heterospecific competitors during the cohort's early life stages (Subbey, Devine, Schaarschmidt, & Nash, 2014). Once these processes have reduced juvenile abundance to where food resources are no longer limiting, the cohort is then more susceptible to density-independent factors that influence their recruitment, such as the effects of variability in river discharge rates and water temperature (Jonsson & Jonsson, 2009).

Discharge can impact salmonid recruitment directly by regulating food supply and thereby mediating density-dependent competition in early life stages (Richard, Cattanéo, & Rubin, 2015); it can also act indirectly, for example by altering temperature conditions, sediment structure, oxygen content and habitat availability (Warren, Dunbar, & Smith, 2015). Temperature can influence salmonid recruitment directly through its effect on egg development and survival rates (Saltveit & Brabrand, 2013) and indirectly via influencing larval emergence timing (Skoglund, Einum, Forseth, & Barlaup, 2012) and juvenile growth (Jonsson & Jonsson, 2009). Discharge and temperature can also interact to influence recruitment as observed for Arctic grayling *Thymallus arcticus*, with recruitment being dependent on both discharge and temperature during their early life. Specifically, recruitment was negatively correlated with mean summer discharge and positively correlated with stream temperature (Deegan, Golden, Harvey, & Peterson, 1999; Luecke & MacKinnon, 2008).

A potentially important issue with episodic spates or floods during the incubation and emergence stages is the "wash out" of eggs and larvae from spawning gravels (Warren et al., 2015). For example, 0+ trout population densities can be reduced in years when discharges were relatively high during the cohort's incubation and/ or emergence (Cattanéo, Lamouroux, Breil, & Capra, 2002). Conversely, high discharges can sometimes have a positive influence on recruitment, with maximum daily discharges in the spawning period being positively related to recruitment, possibly via reductions in fine sediment content within spawning gravels that increases egg survival (Cattanéo et al., 2002). Low discharge conditions can also impact upon juvenile survival and therefore recruitment. A long-term study on brook trout *Salvelinus fontinalis* revealed consistent rates of reduced survival in summers of higher temperatures and lower discharges (Letcher et al., 2015). In areas of low summer rainfall, as Southern England, the issues of low discharges can become exaggerated when there is also high groundwater abstraction, such as in many chalk streams, and thus results in potentially poor recruitment conditions in periods of prolonged low rainfall (Gibbins & Heslop, 1998).

Given the importance of discharge and temperature for salmonid recruitment, climate change has been identified as a major threat to riverine salmonid populations (Ruiz-Navarro, Gillingham, & Britton, 2016). Predicted temperature increases could affect biochemical reactions, hence impacting development, growth, behaviour and survival of salmonids (Jonsson & Jonsson, 2009), with salmonid populations in Southern England likely to be particularly heavily impacted (UKCP09: Murphy et al., 2009). Furthermore, groundwater abstraction is forecast to increase with human population expansion, and so there will be less water for the locally adapted salmonid populations (Crisp, 2000). Regarding precipitation, increased winter and spring flood events could result in local population extinctions if they coincide with the critical periods of salmonid incubation and emergence (Warren et al., 2015).

Most studies on the long-term recruitment drivers of salmonids have focused on salmon and/ or trout, with a paucity of knowledge on other salmonids, such as European grayling, despite these fish often being an important fisheries resource across Europe (Ibbotson et al., 2001), and with apparent declines in many populations in recent years (Dawnay, Dawnay, Hughes, Cove, & Taylor, 2011). Although there have been studies of many aspects of grayling ecology, including their recruitment (reviewed in Ibbotson et al., 2001), these studies have tended to focus on the recruitment process and were of short duration (e.g. Bardonnet & Gaudin, 1990, 1991; Bardonnet, Gaudin, & Thorpe, 1993). Grayling populations have similar ecological requirements to other salmonids, with discharge and temperature tending to be important determinants of recruitment (Charles, Mallet, & Persat, 2006; Ibbotson et al., 2001). Density dependence is thought to affect grayling recruitment, as it does other salmonids, particularly because they are potamodromous, that is migrates within freshwater systems only, and their juveniles do not move far from their place of emergence (Grimardias, Faivre, & Cattaneo, 2012; but see Leeuwen, Dokk, Haugen, Kiffney, & Museth, 2017).

There are, however, important differences between their spawning behaviours with other salmonids. Grayling reproduce later than other salmonids, generally in spring when temperatures are warmer (Charles et al., 2006). They also lay their eggs relatively shallower in gravels (Bardonnet & Gaudin, 1990) than do salmon and trout, and the thermal tolerance of their eggs is narrower, the optimal range being: 4–18°C versus 0–33°C in salmon and 7–22°C in trout (Ibbotson et al., 2001; Jonsson & Jonsson, 2009). Given these characteristics, they can be considered to represent a strong salmonid model species for testing the potential effects of warming and flooding on recruitment processes in salmonids, particularly in relation to density-dependent influences. The aim of this study was to quantify the role of density-dependent and density-independent factors affecting the annual recruitment of grayling over eight years using a population in an English chalk stream near the southern edge of their range. The hypothesis tested was that density-dependent and density-independent factors will significantly affect grayling recruitment rates, but via impacts acting on different stages of their early development.

2 | MATERIALS AND METHODS

2.1 | Study species and locations

The native range of grayling is northern Europe, ranging from Britain and France in the west to the Ural Mountains in Russia in the east (Ibbotson et al., 2001). In Great Britain, their native range is restricted to a relatively small number of rivers, including the Hampshire Avon and its tributaries (Ibbotson et al., 2001). In general, grayling spawn in early spring when water temperatures are 3–11°C. Eggs are spawned in pockets on the gravel surface or buried at up to 5 cm depth, where they remain until hatching after ≈180 degree-days. After hatching, larvae remain in the gravel for another 4–5 days until emergence. Both eggs and larvae are susceptible to various biotic and abiotic pressures, including predation, floods and droughts (Ibbotson et al., 2001).
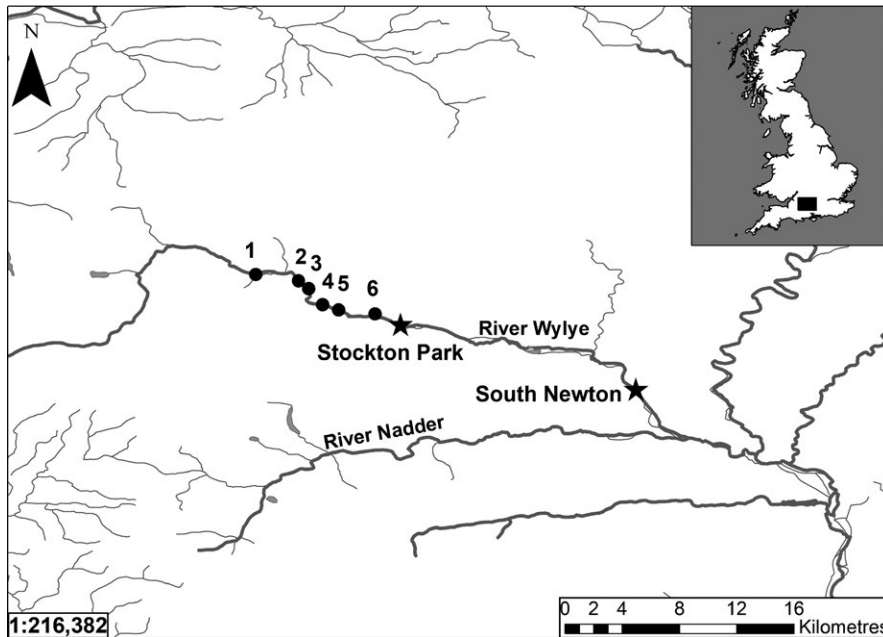
FIGURE 1 A map showing the location of the River Wylye in the UK (inset map) and numbered sites on the Wylye since 2009, starting from the upstream site: (1) Below viaduct (lower Parsonage), (2) Lower Knook, (3) Upton Lovell, (4) Heronry, (5) Below Boyton and (6) Stockton (Ordnance survey, 2005, 2015). Stars indicate locations of discharge (Stockton Park) and temperature (South Newton) stations

This study was undertaken on the River Wylye, a tributary chalk stream of the River Avon in Hampshire (henceforth, Hampshire Avon). The Wyle is a typical chalk stream of ≈45 km length, with sequences of riffles and pools of depth rarely exceeding 1 m, channel widths up to 8 m, and macrophytes are dominated by _Ranunculus_ spp. As a chalk stream, the Wylye has relatively invariable discharge and temperature regimes compared to rain-fed rivers with hard bedrock; mean discharge is 4.05 m³/s, Q95 is 1.11 m³/s, and Q10 is 8.59 m³/s (NERC, 2017), with increases in discharge January–May and stochastic episodes of elevated discharge (5–30 m³/s), driven by local rainfall patterns (NERC, 2017). High discharge events have become more frequent since the early 1990s, occurring in general every two to four years and last for at least six months (NERC, 2017). Similarly, low discharge conditions can occur between these high discharge events, with the recovery time following rainfall often prolonged due to groundwater fed nature of the river.

2.2 | Fish sampling

Fish sampling was completed each October between 2009 and 2016 and covered six sites (Figure 1). Sampling was completed by hand-held, single anode electric fishing, with between three and five passes completed per site until the depletion in captured grayling was ≥ 50% between the final two passes. Sampling at each site involved fishing a 200 m stretch that was delimited with stop nets set at both ends. The Wylye fish community is highly dominated by salmonids and predominantly grayling and trout, but salmon and Eurasian dace _Leuciscus leuciscus_ are rarely captured. Following a UK Home Office licensed procedure (PPL 30/3277), all captured grayling and trout were lightly anaesthetised (2-phenoxyethanol; 0.2 ml/L) and measured for fork length (FL) to 1 mm and mass to 0.1 g. Young of year grayling (age 0+; identified by their FLs <170 mm; Figure S1) were tagged using unique passive integrated transponder (PIT) tags

inserted into the peritoneal cavity, while individuals of age 1 year and over (age 1+) were tagged with a unique visible implant (VI) tag inserted subcutaneously behind the eye. All tagged grayling also had their adipose fin removed, to ensure recaptures could be identified despite potential tag loss, and a scale sample taken for age validation, with a minimum number of three scales taken between the dorsal fin and lateral line. VI tags were used for age 1+ grayling as they would potentially lose a PIT tag during spawning (Summers, Roberts, Giles, & Stubbing, 2006). Following recovery to normal swimming behaviour, all fish were returned alive to the site of their capture.

Recruits were taken to be annual age 0+ grayling _T. thymallus_ estimates from 2009 to 2016 (min–max numbers caught: 19–389). These were estimated using the general weighted _k_-pass estimator proposed by Carle and Strub (1978) implemented in the function _removal_() in R package FSA (Ogle, 2017; Figure S2). This estimator was appropriate for these data because they were collected in a manner consistent with the assumptions of the underlying calculations.

2.3 | Explanatory variables for recruitment analysis

Environmental variables measured included typical river discharge data (hereafter "discharge"), taken from long-term records, where discharge was recorded every 15 min during the study period (Stockton Park; 51°09′10.62″N, 2°02′13.65″W; National River Discharge Archive; NERC, 2017). For analytical purposes, 15-min records were summarised to daily mean discharges. Data were missing for some days due to equipment failures (Figure S3a). To overcome this, missing daily mean discharges were imputed by minimising the covariance between the daily mean discharges at Stockton Park and the nearby gauge station at South Newton (Figure S3b) using function _impSeqRob_() of R package rrcovNA (Todorov & Filzmoser, 2009). River water temperature was taken from data collected every 15 min during the study period at South

TABLE 1 List of explanatory variables used to describe interannual changes in age 0+ juvenile *Thymallus thymallus* numbers on the River Wylye and their hypothesised influence. This list is a subset of a larger list of explanatory variables that was refined based on their perceived ecological importance and collinearity with other explanatory variables (Table S1)

Names	Symbols	Descriptions	Influences	References
Days with high discharge	Dhf	Number of days between 1st March and 30th April with discharge equal or above Q10 (the 90th percentile discharge in the period 2009–2016)	Egg washout	Clausen and Biggs (2000) Jensen and Johnsen (1999) Warren et al. (2015)
Days with low discharge	Dlf	Number of days between 1st April and 31st of August with discharge equal or below Q90 (the 10th percentile discharge in the period 2009–2016)	Juvenile survival	Mantua, Tohver, and Hamlet (2010) Pyrce (2004) Riley et al. (2009) Warren et al. (2015)
Incubation temperature anomaly	Ianom	Mean temperature between 1st March and 30th April subtracted from mean temperature in that monthly period from 2009–2016	Egg survival/development	Mattern et al. (2017)
Postincubation temperature anomaly	Panom	Mean temperature between 1st April and 31st August subtracted from mean temperature in that monthly period from 2009–2016	Juvenile survival/growth	Mattern et al. (2017)
Conspecific density	SI	Survival index; residuals from a nonlinear stock-recruitment model of 0+ *T. thymallus* (recruits) regressed on estimated numbers of eggs in previous year (spawning stock)	Juvenile survival/growth	de Eyto et al., (2016) Grant and Imre (2005) Gregory et al. (2017)
Heterospecific density	Nt	*S. trutta* 0+ numbers at site and time of capture	Juvenile survival/growth	Degerman et al. (2000)

Newton (51°11′00.4″N, 2°07′58.8″W). Where data were missing (some days in 2014 and 2016, several months in 2015 (Figure S4a), data were again imputed using data from nearby recording stations as for discharge (Figure S4b). Different gauge stations were used for discharge and temperature because the most complete data sets of river discharge and temperature were not available from the same station. These discharge and temperature data were then used to calculate the environmental variables suggested by literature to influence grayling recruitment (Tables 1 and S1; Figure 2).

2.4 | Conspecific and heterospecific densities

Before isolating the influence of environmental variables on grayling recruitment, it was necessary to account for the influence of endogenous regulation (also known as density dependence) on age 0+ grayling densities. This was done using residuals from a "best" stock-recruitment model as a measure of recruitment conditioned for the effects of conspecific density (e.g. de Eyto et al., 2016). Two stock-recruitment models were fitted to the annual grayling survey data: a linear model, representing density independence (Equation 1), and a nonlinear model representing density-dependent recruitment from

eggs to age 0+ (Equation 2; Beverton & Holt, 1957). They were given by:

$$R \sim \text{Normal}(\phi_y, \sigma^2) \tag{1}$$

$$\phi_y = \alpha \times \text{Eggs}_y$$

$$\alpha \geq 0$$

where R is the observed density of recruits in year y (as calculated below), ϕ_y is the expected density of recruits surviving from eggs deposited in year y after suffering a temporally invariant density-independent mortality α, and σ^2 is an independent and identically distributed (i.i.d.) error term; and

$$R \sim \text{Normal}(\phi_y, \sigma^2) \tag{2}$$

$$\phi_y = \frac{\alpha \times \text{Eggs}_y}{1 + (\beta \times \text{Eggs}_y)}$$

$$\alpha \geq 0, \beta \geq 0$$

where the variables and parameters are the same as in Equation 1 with the addition of parameter β representing the negative effect of additional eggs on egg survival when the number of eggs reaches an
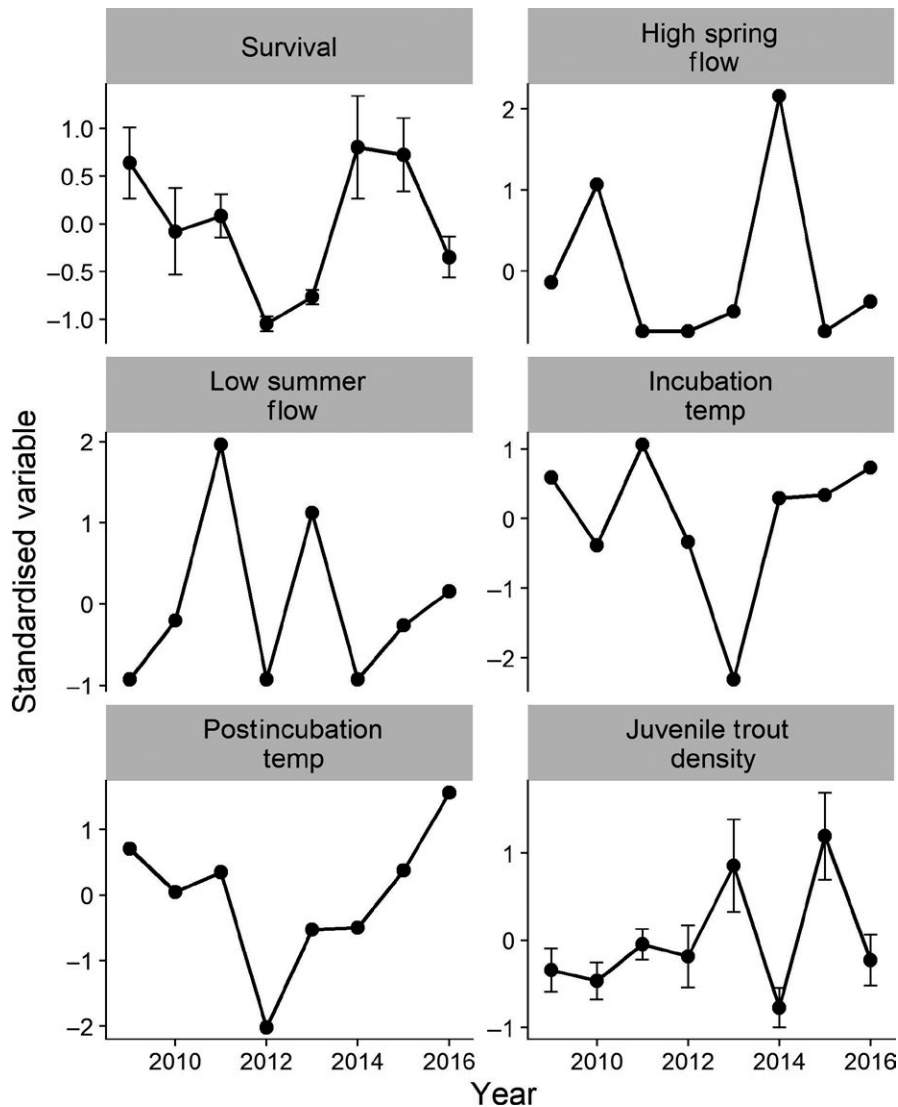
FIGURE 2 Line plots showing the mean and standard error (error bars) of the standardised response variable (SI =survival index) and one of the explanatory variables (Nt = number of 0+ *Salmo trutta*) and standardised environmental variables (Dhf = number of days with high discharge during incubation, Dlf = number of days with low discharge during postincubation, Ianom = incubation temperature anomaly, Panom = postincubation temperature anomaly) plotted across investigated years (2009–2016)

unknown threshold, that is, an estimate of negative density dependence on egg survival.

The estimated numbers of eggs produced in years 2010 to 2016 (see below for details on 2009) were calculated by summing the mean weight of spawning individuals for each age class, site and year combination (i.e. the site- and year-specific spawning stock biomass), and multiplying it by a coefficient relating grayling weight to the numbers of eggs produced. Where individual weight was missing, it was imputed from a linear regression of log length on log weight for 1046 individuals measured throughout the survey ($F_{1,1044}$ = 65643.0, r^2 = .98, p < .01; Figure S5). (Note: individuals were pooled over years, as there was no evidence for a difference in the weight-length slopes between years.). The coefficient relating grayling weight to number of eggs produced was estimated using data from a separate study in which 42 mature grayling were captured on the River Wylye in 2002, euthanised, measured (nearest 1 mm), weighed (nearest 0.1 g) and dissected. For each dissection, the grayling sex was recorded and gonads removed and, in the case of females, the eggs were counted. The

coefficient was estimated from a linear regression of log egg number on log weight for 17 female grayling ($F_{1,15}$ = 123, r^2 = .89, p < .01; Figure S6). It was assumed that 0+ grayling are immature and do not spawn and that only 60% of 1+ adults spawned, as estimated from the fecundity data. As sex ratio was assumed to be 1M:1F, and thus, the number of eggs was divided by two (Ibbotson et al., 2001).

For 2009, the total numbers of grayling eggs could not be estimated as above because only single-pass quantitative surveys were done in 2008. This was resolved using the ratio of site-specific first-pass and multiple-pass spawning stock biomass estimates for years 2009 to 2016 to estimate site-specific empirical Gaussian kernel densities, using the *density*() function in R, from which a random value was drawn and used to calculate a possible site-specific spawning stock biomass for 2008. This was repeated 10,000 times to produce 10,000 data sets. For each data set, the linear and nonlinear stock-recruitment model fits were compared by Akaike information criteria (AIC), and the nonlinear model was selected where its AIC value was a minimum of 2 points lower

than that of the linear model (Burnham & Anderson, 2002). The model used to describe stock-recruitment relationship was then taken to be that which provided the "best" fit to the majority of the 10,000 data sets. Model residuals were then extracted from the 10,000 model fits and averaged to give an index of survival conditioned for any effect of conspecific density and incorporating the uncertainty of the 2008 spawning biomass (hereafter, _survival index_; Table 1).

For heterospecific densities, trout captures were used to estimate the number of 0+ trout per site from 2009 to 2016 (Table 1). Although age estimations from scales were not available for trout, their length frequency distributions suggested that 0+ individuals were < 150 mm (Figure S7). As for grayling, trout density per site and year was estimated using the general weighted _k_-pass estimator (Carle & Strub, 1978).

2.5 | Recruitment models

Survival index of age 0+ grayling (SI) was the response variable in a candidate set of statistical models designed to compare the influence of individual and combinations of environmental explanatory variables on interannual variation in SI. The full set of environmental explanatory variables investigated is presented in Tables 1 and S1. Prior to analysis, explanatory variables were rescaled by subtracting their mean and dividing by their standard deviation using the _scale_() function in R and examined for collinearity (Figure S8). Where explanatory variables were correlated $r \geq |.7|$, the perceived most ecologically important variable was retained for analysis (Figures 2 and S9; Dormann et al., 2013). The statistical models took the form:

$$SI_{s,y} \sim Normal(\mu_{s,y}, \sigma^2) \qquad (3)$$

$$\mu_{s,y} = \alpha + \theta X + \upsilon_s$$

where $\theta = \beta_1, \beta_2,..., \beta_k$ is a vector of K parameters relating explanatory variables $x_1, x_2,..., x_k$ to SI measured at site s in year y, accounting for a Site random effect υ_s with a zero mean and variance τ_s from a Normal distribution. Model parameters were estimated by restricted maximum-likelihood using the function _lmer_() in R package lme4 (Bates, Maechler, Bolker, & Walker, 2015). Prior to fitting multivariate models, it was explored whether each explanatory variable was better represented as a linear or quadratic term in a univariate model (Figure S10).

Candidate models were compared by their goodness of fit using a combination of information theory, for example, Akaike information criteria, and conditional and marginal R^2 values calculated using the method of Nakagawa and Schielzeth (2013) and implemented in function _rsquared_() in R package piecewiseSEM (Lefcheck, 2015).

Parameters representing the influence of each environmental variable on SI were estimated from the "best" model. Parameter p values were calculated using Satterthwaite's approximations (Satterthwaite, 1946) implemented in the function _lmer_() in R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015). There

is no "best practice" method to calculate standard errors for linear mixed-effect models, and so parameter estimates are presented without standard error bands. Plots of the parameter estimates and their partial (or marginal) effects on SI were constructed using the function _ggplot_() in R package ggplot2 (Wickham, 2009). Residuals from the "best" model were tested against the assumptions of normality, homogeneity and independence using standard graphical validations for linear mixed-effect models in R (Figure S11; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

3 | RESULTS

The largest numbers of grayling were caught in the years 2009, 2010, 2014 and 2015, particularly at sites Lower Knook and Below Boyton, with more than 100 individuals counted each year, the majority being age 0+ grayling (Figure S12). Years when high numbers of grayling were captured appeared to coincide with low numbers of trout (except 2015) and with years when the numbers of days of low discharge were few (Figure 2). Lowest numbers of grayling were caught in 2012 and 2013 at all sites, with <25 individuals caught in general, with slightly higher numbers observed at Below Boyton and Stockton (Figure S12). These low captures appeared to be in years when numbers of high discharge days were few (Figure 2). In all cases, numbers of captured grayling were dominated by age 0+ grayling, followed by 1+ and 2+, with >2+ grayling present in lower numbers (Figures S1 and S12).

In terms of conspecific densities, nonlinear stock-recruitment model fits to the site- and year-specific grayling data were better than linear model fits in 98.1% of the cases (Figure 3). Consequently, model residuals were extracted from 10,000 Beverton–Holt stock-recruitment models, and their mean value was taken as an index of age 0+ grayling survival conditioned on conspecific density (SI; Table 1).

Among all the explanatory environmental variables, only postincubation temperature anomaly was included as a quadratic term in the multivariate models because of its curvilinear relationship with survival index; all other explanatory variables were included in the multivariate models as linear terms (Figure S10). Six candidate multivariate mixed-effect models were chosen a priori. Among those, the "best" model was Model 2, which omitted a linear effect of days of high discharge compared with the saturated model (Model 1), although the difference in AIC (ΔAIC) was <2. It included a quadratic term for postincubation temperature anomaly and linear terms for incubation temperature anomaly, number of days with low discharge and estimated age 0+ _S. trutta_ numbers (Table 2). The conditional and marginal R^2 values for Model 2 were high, with only Model 1 (the saturated model) explaining more variation in the response variable (Table 2). All explanatory variables in the "best" Model 2 were statistically significant according to the Satterthwaite's approximation and had 95% confidence intervals that did not overlap zero (Figure 4a). The "best" model was validated against the assumptions of linear mixed-effect models and indicated no severe violations of
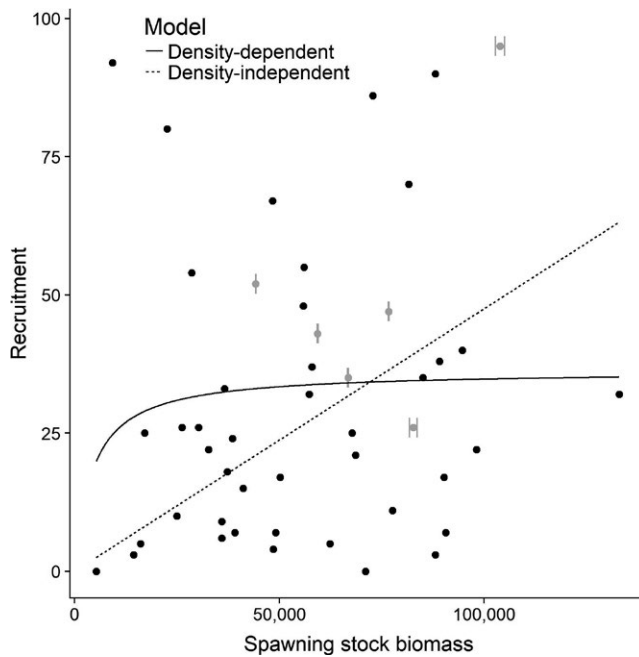
FIGURE 3 Scatter plot of recruitment (estimated 0+ *Thymallus thymallus* numbers) as a function of spawning stock biomass (estimated number of eggs produced). Lines are fitted linear regression (solid line) and nonlinear regression (dashed line) predictions. Black points represent data for years 2009–2016 for all sites combined, and grey points represent predicted data for year 2008 with the range of variability around the estimates presented as standard error

normality, homogeneity or independence in model residuals (Figure S11). In addition, random site effect estimates did not differ from a theoretical Gaussian distribution, confirming the assumption of a Gaussian distribution of random effects (Figure 4b).

Marginal effect plots revealed a concave quadratic relationship between age 0+ grayling survival index and postincubation temperature anomaly, indicating positive effect of postincubation temperature on 0+ grayling survival up to a threshold temperature of 13.5°C beyond which it has a negative effect (Figure 5). In contrast, incubation temperature anomaly had a linear relationship with age 0+ grayling survival, with the increase in incubation temperature suggesting higher survival of age 0+ grayling in the river Wylye for the studied period (Figure 5). Similarly, increasing age 0+ trout numbers had a positive effect on age 0+ grayling survival (Figure 5). However, increasing number of days with low discharge had a negative effect on age 0+ grayling survival in this study (Figure 5).

4 | DISCUSSION

Discharge and temperature affected the annual recruitment success of grayling and, after accounting for the negative density-dependent effect of conspecific density, emphasised the threat posed by climate-driven changes in seasonal conditions on their future population persistence. The threats posed to grayling populations from wet conditions in winter and spring, and low summer rainfall leading to low discharge rates, suggest that specific management measures require implementation to safeguard their populations. Moreover, if grayling is used as an early warning indicator of climate change impacts for salmonid fishes more generally (due to their lower thermal tolerances), these results suggest that protection measures are needed to sustain salmonid populations in the immediate future (Ruiz-Navarro et al., 2016). These measures should include the restoration of natural discharges (Warren et al., 2015), such as via abstraction control (Riley, Maxwell, Pawson, & Ives, 2009),

TABLE 2 Maximum-likelihood statistics comparing fits for the 0+ *Thymallus thymallus* survival models with different combinations of explanatory variables as fixed effects and site as a random effect on the intercept, where Nt = number of 0+ *Salmo trutta*, Dhf = number of days with high discharge during incubation, Dlf = number of days with low discharge during postincubation, Ianom = incubation temperature anomaly, Panom = postincubation temperature anomaly. The table is ordered by difference in Akaike information criteria (ΔAIC) from the "top-ranked" model (model with the lowest AIC). Marginal and conditional R^2 were calculated according to the method of Nakagawa and Schielzeth (2013)

| Models	Model terms	Model fit			Comparisons		R^2	
		Sigma	LogLik	Deviance	AIC	ΔAIC	Marginal	Conditional
2	Panom, Panom^2, Ianom, Dlf, Nt	0.70	−51.7	103.3	119.3	0.0	.48	.50
1	Panom, Panom^2, Ianom, Dlf, Dhf, Nt	0.70	−51.3	102.6	120.6	1.3	.49	.51
3	Panom, Panom^2, Ianom, Dlf	0.71	−54.2	108.4	122.4	3.1	.41	.48
4	Panom, Panom^2, Ianom, Dhf, Nt	0.73	−53.3	106.6	122.6	3.3	.45	.46
5	Ianom, Dlf, Dhf, Nt	0.78	−55.9	111.9	125.9	6.6	.39	.39
6	Panom, Panom^2, Dlf, Dhf, Nt	0.78	−56.5	113.0	129.0	9.7	.37	.38
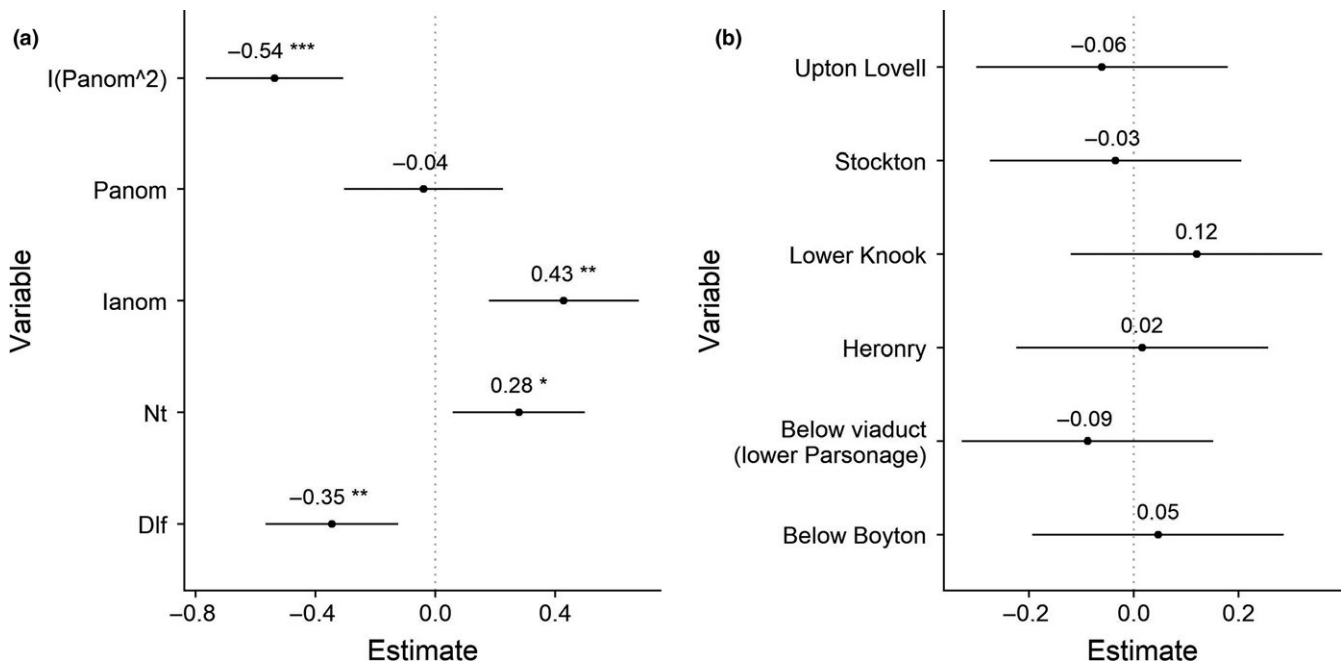
FIGURE 4 Caterpillar plots showing maximum-likelihood estimates of (a) the fixed effects and (b) the random effect for the "best" model. Points are the estimates; lines are the estimate standard errors; labels are the estimate values followed by an indication of their statistical significance, whereby: ***$p < .001$, **$p < .01$ and *$p < .05$. Explanatory variable definitions are as follows: Panom = postincubation temperature anomaly (°C); Ianom = incubation temperature anomaly (°C); Nt = age 0+ *Salmo trutta* abundance; Dlf = number of days with low discharge during postincubation

and increased riparian shading to reduce in-stream temperatures (Thomas, Griffiths, & Ormerod, 2016).

The positive effect of trout population density on grayling recruitment was considered counter-intuitive. Rather, a negative impact of interspecific competition was expected, particularly in years of higher trout abundance. However, the result suggests that years of higher trout abundance were coincident with higher grayling recruitment, and thus, the underlying processes regulating both populations might be similar, especially given that trout recruitment can also be affected by river discharges in spring (Lobón-Cerviá & Rincón, 2004). Indeed, a number of studies have revealed that whilst sympatric age 0+ trout and grayling occupy meso-habitats with similar discharges (Degerman, Näslund, & Sers, 2000; Riley, Ives, Pawson, & Maxwell, 2006), they have limited microhabitat overlap and few competitive interactions due to their utilisation of different depths (Ibbotson et al., 2001) and substratum types (Riley et al., 2006).

The number of days with low discharge was tested against grayling recruitment to capture the effect of low summer discharge rates as an important stressor of the 0+ fish, given that several studies have demonstrated that juvenile salmonid growth and even survival are depressed when summer discharge rates are reduced and vice versa (Davidson, Letcher, & Nislow, 2010; Gregory et al., 2017; Xu, Letcher, & Nislow, 2010). Both Charles et al. (2006) and Letcher et al. (2015) revealed that survival of 0+ grayling and brook trout survival was reduced during years of low summer discharges and higher water temperatures. Moreover, Letcher et al. (2015) revealed these results were consistent spatially and affected different age-classes similarly. Thus, the significant relationship between reduced summer

discharges and low grayling recruitment detected here provides further evidence that low summer discharges have substantial impacts on salmonid population persistence and thus there is an urgent requirement for natural discharge regimes to be promoted in salmonid rivers wherever possible (Enders, Scruton, & Clarke, 2009).

There were two temperature-related variables that significantly influenced grayling recruitment, incubation temperature anomaly and postincubation temperature anomaly. The former had a positive influence on grayling recruitment, with similar findings reported in other salmonid fishes. For example, Skoglund, Einum, and Robertsen (2011) revealed salmon eggs incubated at a higher temperature produced larger eggs with higher survival rates versus those incubated at lower temperatures. The general pattern is warmer winters can result in the production of larger juveniles, perhaps due to a more prolonged growth season (Gregory et al., 2017), with these larger individuals then potentially having higher survival rates via greater access to better feeding areas than smaller conspecifics that might be more easily displaced by other foraging salmonids (Huntingford, Metcalfe, Thorpe, Graham, & Adams, 1990). The postincubation temperature anomaly was parameterised as a quadratic effect and had significant and positive effect on postincubation survival up to a threshold of 13.5°C; at higher temperatures, the effect became negative. The Wylye's mean water temperature was found to be already close to 13.5°C, suggesting that the population might be locally adapted to these conditions (Haugen & Vollestad, 2000), but also highlights its vulnerability to future temperature increases via warming processes (Ruiz-Navarro et al., 2016). Similar patterns of the effect of temperature on postincubation survival have been
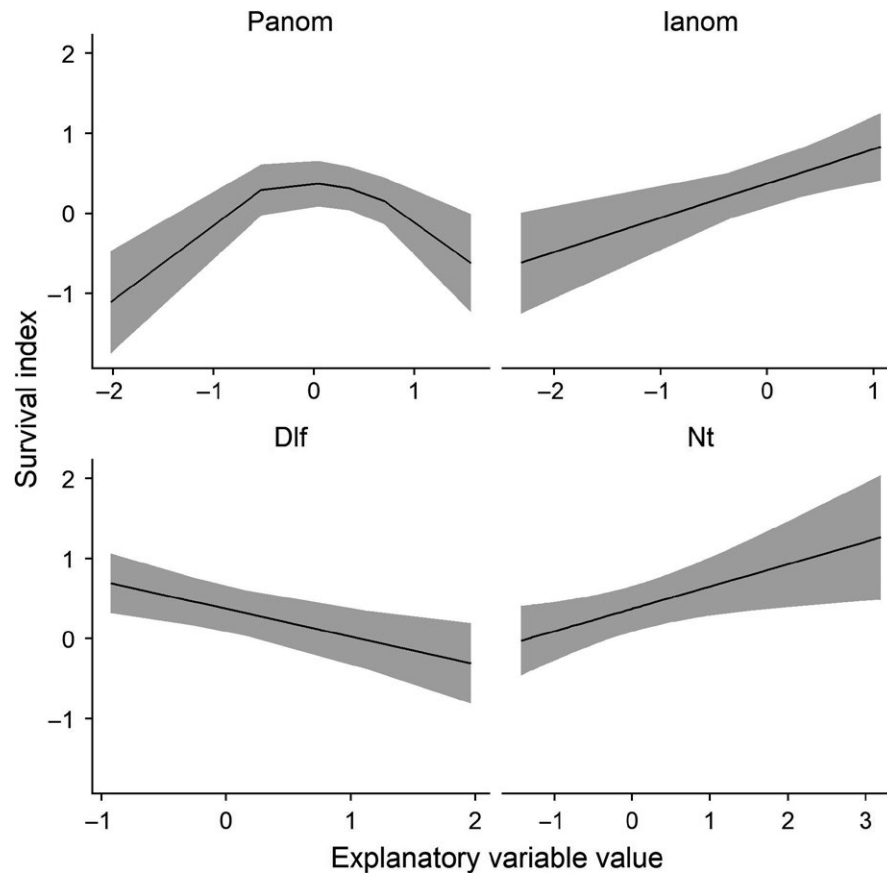
FIGURE 5 Line plots showing the marginal effects of each of the standardised explanatory variables, where Panom = postincubation temperature anomaly, Ianom = incubation temperature anomaly, Nt = age 0+ *Salmo trutta* abundance; Dlf = number of days with low discharge during postincubation, *X*-axis is the explanatory variable value, and *Y*-axis is the response variable. The shaded grey area is the standard error of the estimated effect

detected in other salmonid fishes. For example, Letcher et al. (2015) revealed that brook trout survival in a network of streams in western Massachusetts, USA, was related to summer temperatures, with survival generally reduced at both high and low summer temperatures. Equally, age 0+ grayling survival increased with temperature up to a threshold limit, above which survival rates then reduce once more (Charles et al., 2006).

Days with high discharge was expected to negatively affect recruitment patterns because elevated spring discharges could displace eggs from gravels ("egg washout"), particularly due to the propensity of grayling to lay their eggs relatively shallow or even on the gravel surface (Warren et al., 2015). The nonsignificant relationship detected here suggests that the spring discharges were never sufficient to have a detectable impact, perhaps due to the underlying chalk geology and groundwater influence of the study river resulting in relatively stable discharge and temperature regimes compared with other salmonid rivers. For example, the spring discharges detected during the study period (1.38–4.73 m³/s) might have lacked the energy to displace eggs and/ or recently emerged larvae versus other studies where such impacts have been recorded, such as Jensen and Johnsen (1999) where impacts occurred at discharges of 75–232 m³/s and Mundahl (2017) who recorded impacts

at 100–200 m³/s. Indeed, the stable discharge conditions afforded by chalk stream rivers have resulted in the recruitment of other fishes being more dependent on environmental factors other than periods of elevated discharge rates, even in nonsalmonid fishes, such as roach *Rutilus rutilus* (Beardsley & Britton, 2012). Consequently, the deleterious impacts of high discharge events on age 0+ salmonids might be limited to less stable rivers that are prone to high discharge events (Warren et al., 2015), especially during critical life-stage periods such as emergence, given that even extreme floods in late summer can result in minimal impacts on salmonid populations (George, Baldigo, Smith, & Robinson, 2015).

The present study uncovered evidence to support a negative impact of intraspecific density dependence on grayling recruitment, which is supported by a number of studies demonstrating that salmonid growth and survival can be related to conspecific density. For example, de Eyto et al. (2016) found that a Beverton–Holt model was a better fit to trout stock-recruitment data than a density-independent model in the River Burrishoole, Ireland, although the opposite was true for salmon. This result was anticipated for grayling because, as previously mentioned, grayling is potamodromous, and juveniles remain close to their place of emergence (Grimardias et al., 2012). Although the Beverton–Holt fit to the grayling data was not strong,

it was a better fit than the density-independent model. However, the high variance in the number of recruits was not sufficiently captured in the model, suggesting that the population was not closed, perhaps because juvenile (Leeuwen et al., 2017) and adult grayling (Ovidio, Parkinson, Sonny, & Philippart, 2004) can undertake considerable in-river migrations. If these movements were apparent in the study river, then this would undermine the relationship between spawning stock size and the number of recruits at a site level and thus have impacted the model fit. In addition, low temporal resolution could have impacted the observed fit, and if more data were available the importance of conspecific density could have diminished.

In the present study, and as with all such correlative studies completed using field data, there were potential issues around the choice of explanatory variables that were explored within analyses. Environmental variables explored here were all derived from water discharge and temperature data, and, although these are all generally considered as important determinants of fish population dynamics, they are also the most commonly available parameters of in-river environmental conditions. The impact of grayling removal (culling) on grayling recruitment was excluded from the analysis, because it has not been applied in Southern English chalk streams since the early 1990s (Ibbotson et al., 2001), so it was not considered to affect population dynamics in the River Wylye. Although it was beyond the scope of the present study, other variables could have been considered for measurement and testing, including in-river vegetation cover (Riley & Pawson, 2010), water quality (Whitehead, Wilby, Battarbee, Kernan, & Wade, 2009) and substratum composition (Kemp, Sear, Collins, Naden, & Jones, 2011). These issues, combined with the generalities of some of the results reported here (i.e. several significant correlates of environmental variables with recruitment), suggest that the relationships between recruitment and biotic and abiotic variables might be context-dependent at the site level. Any such context dependency could be important because it would inhibit the results being readily transferable to other sites and rivers (Warren et al., 2015). Nevertheless, the general pattern of the results presented here was that the early life stages of grayling were susceptible to several aspects of discharge and water temperature, and this was manifested in their annually variable recruitment success. These outcomes thus do retain high management utility, especially in this era of declines in salmonid populations (Northcote, 1995), and so emphasise the importance of management interventions that seek to increase population resilience via restoring natural discharge regimes (Vehanen, Huusko, Yrjänä, Lahti, & Mäki-Petäys, 2003) and limiting future temperature increases (Ruiz-Navarro et al., 2016).

ACKNOWLEDGEMENTS

ORCID

Tea Bašić [ID] http://orcid.org/0000-0001-8761-5750

J. Robert Britton [ID] http://orcid.org/0000-0003-1853-3086

Stephen D. Gregory [ID] http://orcid.org/0000-0002-8230-0191

REFERENCES

Bardonnet, A., & Gaudin, P. (1990). Diel pattern of emergence in grayling (*Thymallus thymallus* Linnaeus, 1758). *Canadian Journal of Zoology*, *68*, 465–469. https://doi.org/10.1139/z90-068

Bardonnet, A., & Gaudin, P. (1991). Influence of daily variations of light and temperature on the emergence rhythm of grayling fry (*Thymallus thymallus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 1176–1180. https://doi.org/10.1139/f91-141

Bardonnet, A., Gaudin, P., & Thorpe, J. E. (1993). Diel rhythm of emergence and first displacement downstream in trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and grayling (*Thymallus thymallus*). *Journal of Fish Biology*, *43*, 755–762. https://doi.org/1095-8649, 1993.tb01152.x

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beardsley, H., & Britton, J. R. (2012). Recruitment success in a roach *Rutilus rutilus* population of a hydrologically stable chalk river: Relative influences of temperature and discharge. *Ecology of Freshwater Fish*, *21*, 168–171. https://doi.org/10.1111/j.1600-0633.2011.00549.x

Beverton, R. J. H., & Holt, S. J. (1957). *On the dynamics of exploited fish populations. Fisheries investigations series II, volume XIX*. London, UK: Her Majesty's Stationery Office.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd edn. New York, NY: Springer-Verlag.

Carle, F. L., & Strub, M. R. (1978). A new method for estimating population size from removal data. *Biometrics*, *34*, 621–630. https://doi.org/10.2307/2530381

Cattanéo, F., Lamouroux, N., Breil, P., & Capra, H. (2002). The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 12–22. https://doi.org/10.1139/f01-186

Charles, S., Mallet, J. P., & Persat, H. (2006). Population dynamics of grayling: Modelling temperature and discharge effects. *Mathematical Modelling of Natural Phenomena*, *1*, 31–48. https://doi.org/10.1051/mmnp:2006002

Clausen, B., & Biggs, B. J. F. (2000). Discharge variables for ecological studies in temperate streams: groupings based on covariance. *Journal of Hydrology*, *237*, 184–197. https://doi.org/10.1016/S0022-1694(00)00306-1

Crisp, D. T. (2000). *Trout and Salmon: Ecology, conservation and rehabilitation*. Oxford, UK: Wiley Blackwell. https://doi.org/10.1002/9780470999776

Davidson, R. S., Letcher, B. H., & Nislow, K. H. (2010). Drivers of growth variation in juvenile Atlantic salmon (*Salmo salar*): an elasticity analysis approach. *Journal of Animal Ecology*, *79*, 1113–1121. https://doi.org/10.1111/j.1365-2656.2010.01708.x

Dawnay, N., Dawnay, L., Hughes, R. N., Cove, R., & Taylor, M. I. (2011). Substantial genetic structure among stocked and native populations of the European grayling (*Thymallus thymallus*, *Salmonidae*) in the United Kingdom. *Conservation Genetics*, *12*, 731–744. https://doi.org/10.1007/s10592-010-0179-4

Deegan, L. A., Golden, H. E., Harvey, C. J., & Peterson, B. J. (1999). Influence of environmental variability on the growth of age-0 and adult Arctic grayling. *Transactions of the American Fisheries Society*, *128*, 1163–1175. https://doi.org/10.1577/1548-8659(1999) 128<1163:IOEVOT>2.0.CO;2

Degerman, E., Näslund, I., & Sers, B. (2000). Stream habitat use and diet of juvenile (0+) brown trout and grayling in sympatry. *Ecology of Freshwater Fish*, 9, 191–201. https://doi.org/10.1111/j.1600-0633.2000.eff090401.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Münkemüller, T., … Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Enders, E. C., Scruton, D. A., & Clarke, K. D. (2009). The "natural discharge paradigm" and Atlantic salmon - moving from concept to practice. *River Research and Applications*, 25, 2–15. https://doi.org/10.1002/rra.1214

de Eyto, E., Dalton, C., Dillane, M., Jennings, E., McGinnity, P., O'Dwyer, B., … Taylor, D. (2016). The response of North Atlantic diadromous fish to multiple stressors, including land use change: A multidecadal study. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1759–1769. https://doi.org/10.1139/cjfas-2015-0450

George, S. D., Baldigo, B. P., Smith, A. J., & Robinson, G. R. (2015). Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. *Freshwater Biology*, 60, 2511–2522. https://doi.org/10.1111/fwb.12577

Gibbins, C. N., & Heslop, J. (1998). An evaluation of inter-basin water transfers as a mechanism for augmenting salmonid and grayling habitat in the River Wear, North-East England. *Regulated Rivers: Research and Management*, 14, 357–382. https://doi.org/10.1002/(SICI)1099-1646(199807/08)14:4<357:AID-RRR508>3.0.CO;2-8

Grant, J. W. A., & Imre, I. (2005). Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *Journal of Fish Biology*, 67, 100–110. https://doi.org/10.1111/j.0022-1112.2005.00916.x

Gregory, S. D., Nevoux, M., Riley, W. D., Beaumont, W. R., Jeannot, N., Lauridsen, R. B., … Roussel, J. M. (2017). Patterns on a parr: Drivers of long-term salmon parr length in UK and French rivers depend on geographical scale. *Freshwater Biology*, 62, 1117–1129. https://doi.org/10.1111/fwb.12929

Grimardias, D., Faivre, L., & Cattaneo, F. (2012). Postemergence downstream movement of European grayling (*Thymallus thymallus* L.) alevins and the effect of discharge. *Ecology of Freshwater Fish*, 21, 495–498. https://doi.org/10.1111/j.1600-0633.2012.00572.x

Haugen, T. O., & Vollestad, L. A. (2000). Population differences in early life-history traits in grayling. *Journal of Evolutionary Biology*, 13, 897–905. https://doi.org/10.1046/j.1420-9101.2000.00242.x

Huntingford, F. A., Metcalfe, N. B., Thorpe, J. E., Graham, W. D., & Adams, C. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, 36, 877–881. https://doi.org/10.1111/j.1095-8649.1990.tb05635.x

Ibbotson, A. T., Cove, R. J., Ingraham, A., Gallagher, M., Hornby, D. D., Furse, M., & Williams, C. (2001). A review of grayling ecology, status and management practice: recommendations for future management in England and Wales. R & D Technical Report W245. Bristol, UK: Environment Agency.

Jensen, A. J., & Johnsen, B. O. (1999). The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology*, 13, 778–785. https://doi.org/10.1046/j.1365-2435.1999.00358.x

Jonsson, B., & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and discharge. *Journal of Fish Biology*, 75, 2381–2447. https://doi.org/10.1111/j.1095-8649.2009.02380.x

Kemp, P., Sear, D., Collins, A., Naden, P., & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, 25, 1800–1821. https://doi.org/10.1002/hyp.7940

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). Package 'lmerTest'. R package version, 2(0).

Leeuwen, C. H. A. V., Dokk, T., Haugen, T. O., Kiffney, P. M., & Museth, J. (2017). Small larvae in large rivers: observations on downstream movement of European grayling *Thymallus thymallus* during early life stages. *Journal of Fish Biology*, 90, 2412–2424. https://doi.org/10.1111/jfb.13326

Lefcheck, J. S. (2015). piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579. https://doi.org/10.1111/2041-210X.12512

Letcher, B. H., Schueller, P., Bassar, R. D., Nislow, K. H., Coombs, J. A., Sakrejda, K., … Dubreuil, T. L. (2015). Robust estimates of environmental effects on population vital rates: An integrated capture-recapture model of seasonal brook trout growth, survival and movement in a stream network. *Journal of Animal Ecology*, 84, 337–352. https://doi.org/10.1111/1365-2656.12308

Lobón-Cerviá, J., & Rincón, P. A. (2004). Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. *Oikos*, 105, 641–646. https://doi.org/10.1111/j.0030-1299.2004.12989.x

Luecke, C., & MacKinnon, P. (2008). Landscape effects on growth of age-0 Arctic grayling in tundra streams. *Transactions of the American Fisheries Society*, 137, 236–243. https://doi.org/10.1577/T05-039.1

Mantua, N., Tohver, I., & Hamlet, A. (2010). Climate change impacts on stream discharge extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change*, 102, 187–223. https://doi.org/10.1007/s10584-010-9845-2

Mattern, T., Meyer, S., Ellenberg, U., Houston, D. M., Darby, J. T., … Seddon, P. J. (2017). Quantifying climate change impacts emphasises the importance of managing regional threats in the endangered Yellow-eyed penguin. *PeerJ*, 5, e3272. https://doi.org/10.7717/peerj.3272

Milner, N., Elliott, J., Armstrong, J., Gardiner, R., Welton, J., & Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research*, 62, 111–125. https://doi.org/10.1016/S0165-7836(02)00157-1

Mundahl, N. D. (2017). Population dynamics of brown trout in a Minnesota (USA) stream: A 25-year study. *River Research and Applications*, 33, 1235–1245. https://doi.org/10.1002/rra.3170

Murphy, J. M., Sexton, D. M. H., Jenkins, G. J., Boorman, P. M., Booth, B. B. B., Brown, C. C., … Betts, R. A. (2009). UK climate projections science report: UKCP09. Exeter, UK: Met Office Hadley Centre: Exeter, UK.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

NERC (Natural Environment Research Council) (2017). National River Discharge Archive. Wallingford, UK: Centre for Ecology & Hydrology (CEH). Retrieved from http://nrfa.ceh.ac.uk/data/station/meandischarge/43008

Northcote, T. G. (1995). Comparative biology and management of Arctic and European grayling (Salmonidae, *Thymallus*). *Reviews in Fish Biology and Fisheries*, 5, 141–194. https://doi.org/10.1007/BF00179755

Ogle, D. H. (2017). FSA: Fisheries Stock Analysis. R package version 0.8.14. Retrieved from http://derekogle.com/fishR.

Ordnance Survey (2005). GB National Outlines, Scale 1:250000. Retrieved from http://digimap.edina.ac.uk

Ordnance Survey (2015). Strategi® Map, River Wylye, GB, Scale 1:250000. Retrieved from http://digimap.edina.ac.uk

Ovidio, M., Parkinson, D., Sonny, D., & Philippart, J.-C. (2004). Spawning movements of European grayling *Thymallus thymallus* in the River Aisne (Belgium). *Folia Zoologica*, 53, 87–98.

Pyrce, R. (2004). Hydrological low discharge indices and their uses. Report (04-2004). Peterborough, Ontario: Watershed Science Centre, (WSC), Trent University.

Richard, A., Cattanéo, F., & Rubin, J. F. (2015). Biotic and abiotic regulation of a low-density stream-dwelling brown trout (*Salmo trutta* L.) population: effects on juvenile survival and growth. *Ecology of Freshwater Fish*, *24*, 1–14. https://doi.org/10.1111/eff.12116

Riley, W. D., Ives, M. J., Pawson, M. G., & Maxwell, D. L. (2006). Seasonal variation in habitat use by salmon, *Salmo salar*, trout, *Salmo trutta* and grayling, *Thymallus thymallus*, in a chalk stream. *Fisheries Management and Ecology*, *13*, 221–236. https://doi.org/10.1111/j.1365-2400.2006.00496.x

Riley, W. D., Maxwell, D. L., Pawson, M. G., & Ives, M. J. (2009). The effects of low summer discharge on wild salmon (*Salmo salar*), trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in a small stream. *Freshwater Biology*, *54*, 2581–2599. https://doi.org/10.1111/j.1365-2427.2009.02268.x

Riley, W. D., & Pawson, M. G. (2010). Habitat use by *Thymallus thymallus* in a chalk stream and implications for habitat management. *Fisheries Management and Ecology*, *17*, 544–553. https://doi.org/10.1111/j.1365-2400.2010.00756.x

Ruiz-Navarro, A., Gillingham, P. K., & Britton, J. R. (2016). Predicting shifts in the climate space of freshwater fishes in Great Britain due to climate change. *Biological Conservation*, *203*, 33–42. https://doi.org/10.1111/gcb.13230

Saltveit, S. J., & Brabrand, Å. (2013). Incubation, hatching and survival of eggs of Atlantic salmon (*Salmo salar*) in spawning redds influenced by groundwater. *Limnologica*, *43*, 325–331. https://doi.org/10.1016/j.limno.2013.05.009

Satterthwaite, F. E. (1946). An approximate distribution of estimates of variance components. *Biometrics Bulletin*, *2*, 110–114. https://doi.org/10.2307/3002019

Skoglund, H., Einum, S., Forseth, T., & Barlaup, B. T. (2012). The penalty for arriving late in emerging salmonid juveniles: Differences between species correspond to their interspecific competitive ability. *Functional Ecology*, *26*, 104–111. https://doi.org/10.1111/j.1365-2435.2011.01901.x

Skoglund, H., Einum, S., & Robertsen, G. (2011). Competitive interactions shape offspring performance in relation to seasonal timing of emergence in Atlantic salmon. *Journal of Animal Ecology*, *80*, 365–374. https://doi.org/10.1111/j.1365-2656.2010.01783.x

Subbey, S., Devine, J. A., Schaarschmidt, U., & Nash, R. D. M. (2014). Modelling and forecasting stock-recruitment: current and future perspectives. *ICES Journal of Marine Science*, *71*, 2307–2322. https://doi.org/10.1093/icesjms/fsu148

Summers, D. W., Roberts, D. E., Giles, N., & Stubbing, D. N. (2006). Retention of visible implant and visible implant elastomer tags in brown trout in an English chalk stream. *Journal of Fish Biology*, *68*, 622–627. https://doi.org/10.1111/j.0022-1112.2006.00924.x

Thomas, S. M., Griffiths, S. W., & Ormerod, S. J. (2016). Beyond cool: adapting upland streams for climate change using riparian woodlands. *Global Change Biology*, *22*, 310–324. https://doi.org/10.1111/gcb.13103

Todorov, V., & Filzmoser, P. (2009). An object-oriented framework for robust multivariate analysis. *Journal of Statistical Software*, *32*, 1–47. https://doi.org/10.18637/jss.v032.i03

Vehanen, T., Huusko, A., Yrjänä, T., Lahti, M., & Mäki-Petäys, A. (2003). Habitat preference by grayling (*Thymallus thymallus*) in an artificially modified, hydropeaking riverbed: a contribution to understand the effectiveness of habitat enhancement measures. *Journal of Applied Ichthyology*, *19*, 15–20. https://doi.org/10.1046/j.1439-0426.2003.00354.x

Warren, M., Dunbar, M. J., & Smith, C. (2015). River discharge as a determinant of salmonid distribution and abundance: a review. *Environmental Biology of Fishes*, *98*, 1695–1717. https://doi.org/10.1007/s10641-015-0376-6

Whitehead, P. G., Wilby, R. L., Battarbee, R. W., Kernan, M., & Wade, A. J. (2009). A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal*, *54*, 101–123. https://doi.org/10.1623/hysj.54.1.101

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer. https://doi.org/10.1007/978-0-387-98141-3

Xu, C. L., Letcher, B. H., & Nislow, K. H. (2010). Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream discharge. *Journal of Fish Biology*, *76*, 2342–2369. https://doi.org/10.1111/j.1095-8649.2010.02619.x

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Spring Science and Business Media. https://doi.org/10.1007/978-0-387-87458-6

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Supplementary material

Table S1 List of explanatory variables excluded from further analysis due to high correlation with several other variables (see Figure S7), their hypothesised influence and the sources of those information.

Name	Symbol	Description	Influence	Reference
High flow	Qmax	Maximum discharge in spring (1st March and 30th April)	Egg washout	Charles et al., 2006 Grimardias et al., 2012 Mantua et al., 2010
Post-incubation minimum discharge	Fmin	Minimum discharge during 7 consecutive days from 1st April till 31st of August	Juvenile survival	Mantua et al., 2010 Riley et al., 2009 Warren et al., 2015
Incubation temperature	Ti	Mean temperature between 1st March and 30th April	Egg survival / development	Jonsson & Jonsson, 2009 Wedekind & Küng, 2010
Post-incubation temperature	Tp	Mean temperature between 1st April and 31st August	Juvenile survival/growth	Wedekind & Küng, 2010
Incubation degree days	DTi	Sum of the daily differences between mean daily temperatures and threshold (5 °C; Chezik, Lester, & Venturelli, 2013; Mallet, Charles, Persat, & Auger, 1999; Webb and Walsh 2004) between 1st March and 30th April	Egg survival / development	Gregory et al., 2017
Post-incubation degree days	DTp	Sum of the daily differences between mean daily temperatures and threshold (5 °C) between 1st April and 31st August	Juvenile survival / growth	Gregory et al., 2017
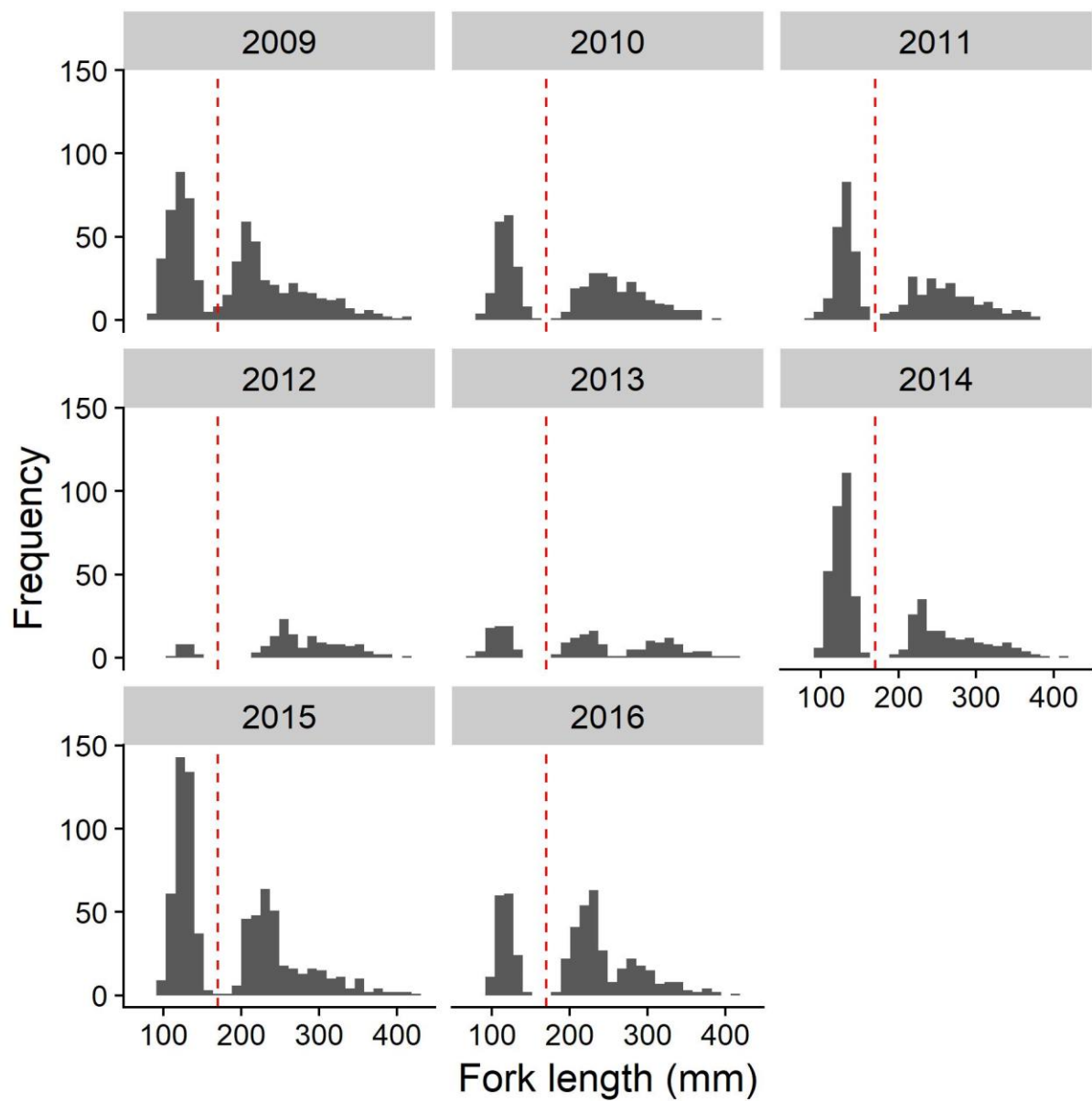
Figure S1 *Histograms of grayling fork lengths for each investigated year in the river Wylye.*
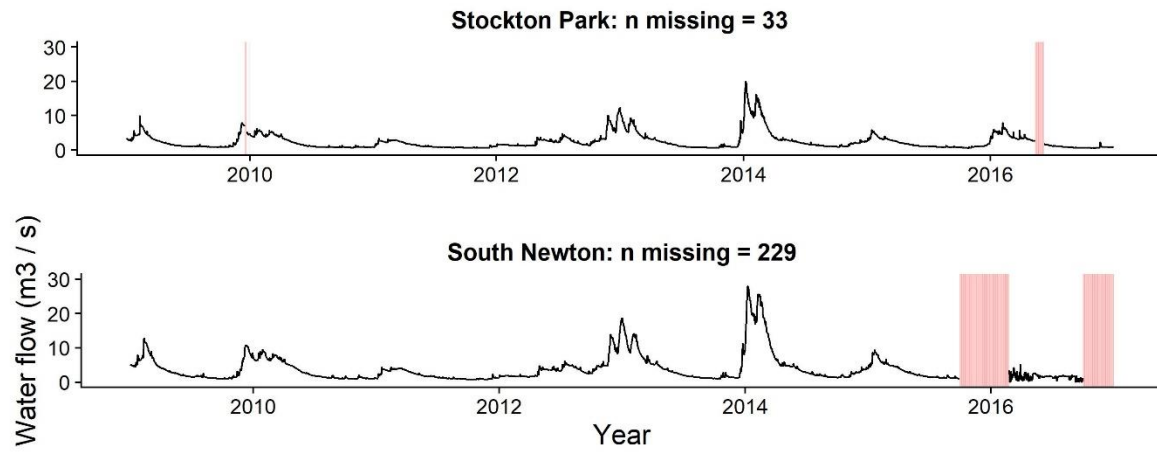*Vertical dashed red lines represent cut-off length (170 mm) for age 0+ grayling.*
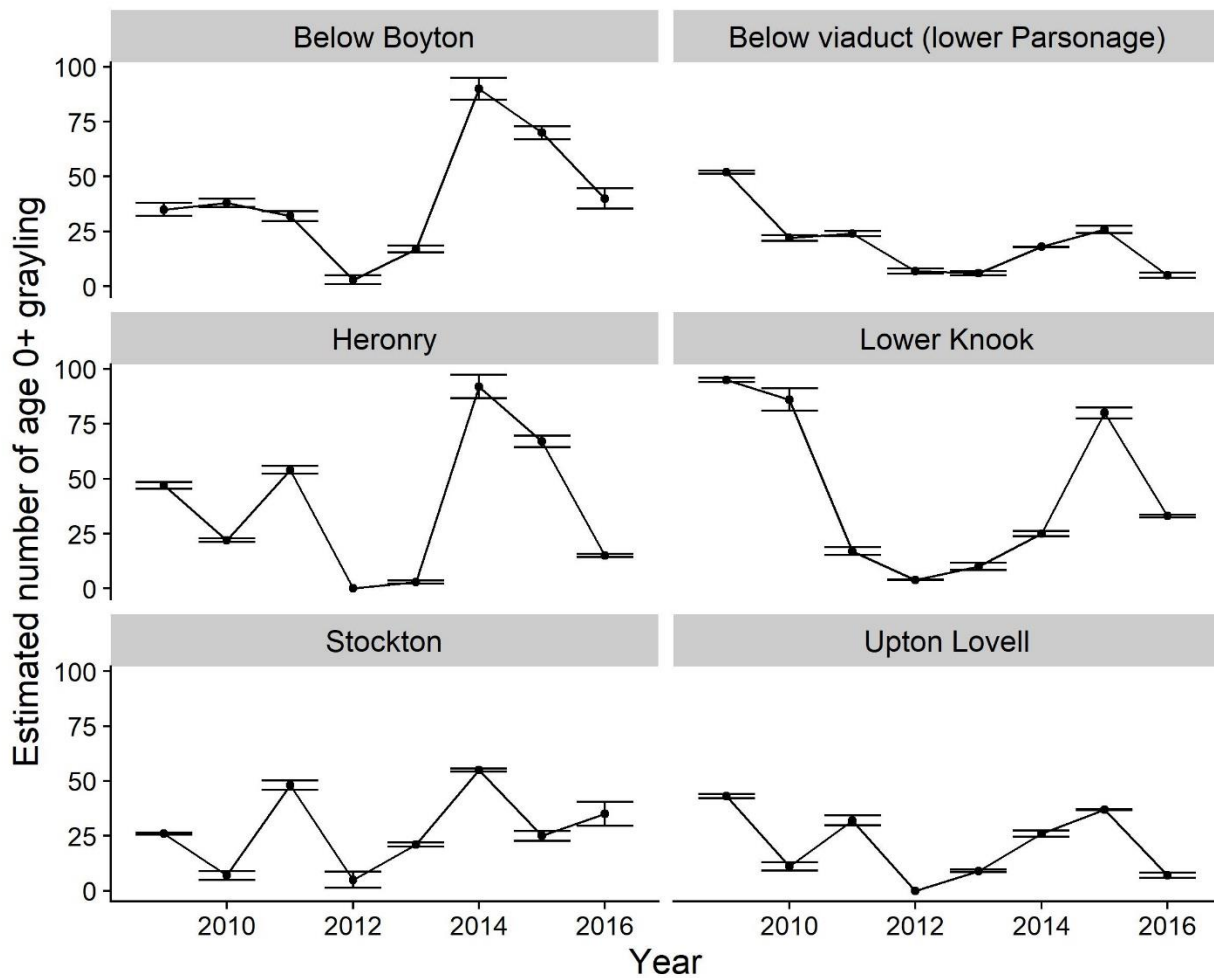
Figure S2 *Point and line plots with standard error (error bars) showing the estimated number of 0+ grayling at 6 sites on the river Wylye between 2009 and 2016.*
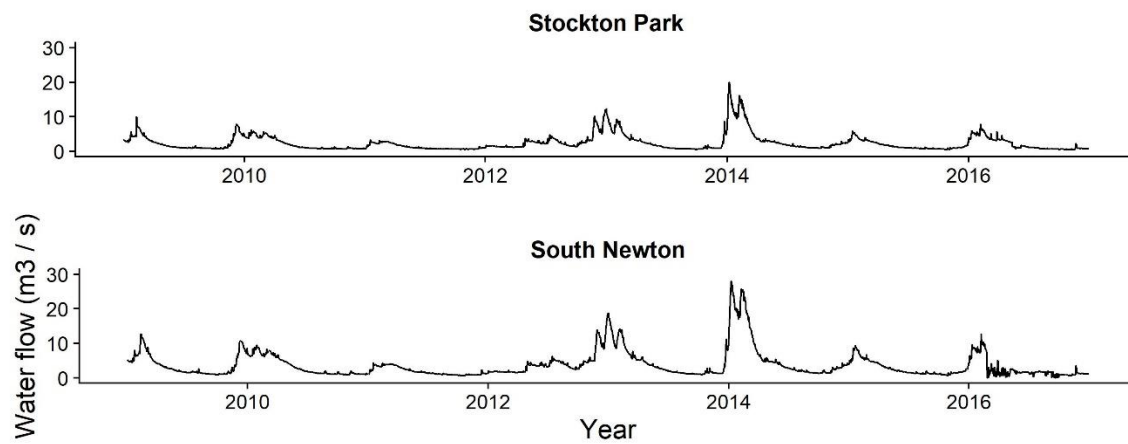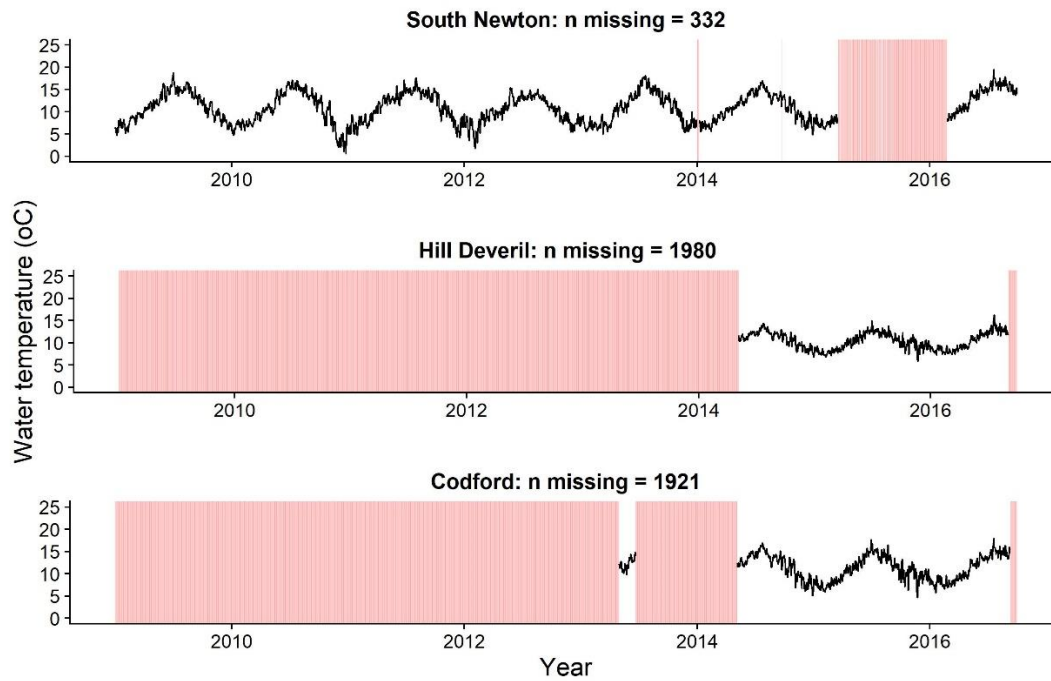
a)

b)

Figure S3 *Lineplots showing the mean daily flow measured (a) and estimated (b) at Stockton Park and South Newton from 2009 to 2016. Missing data are represented with red rectangles.*

a)

b)
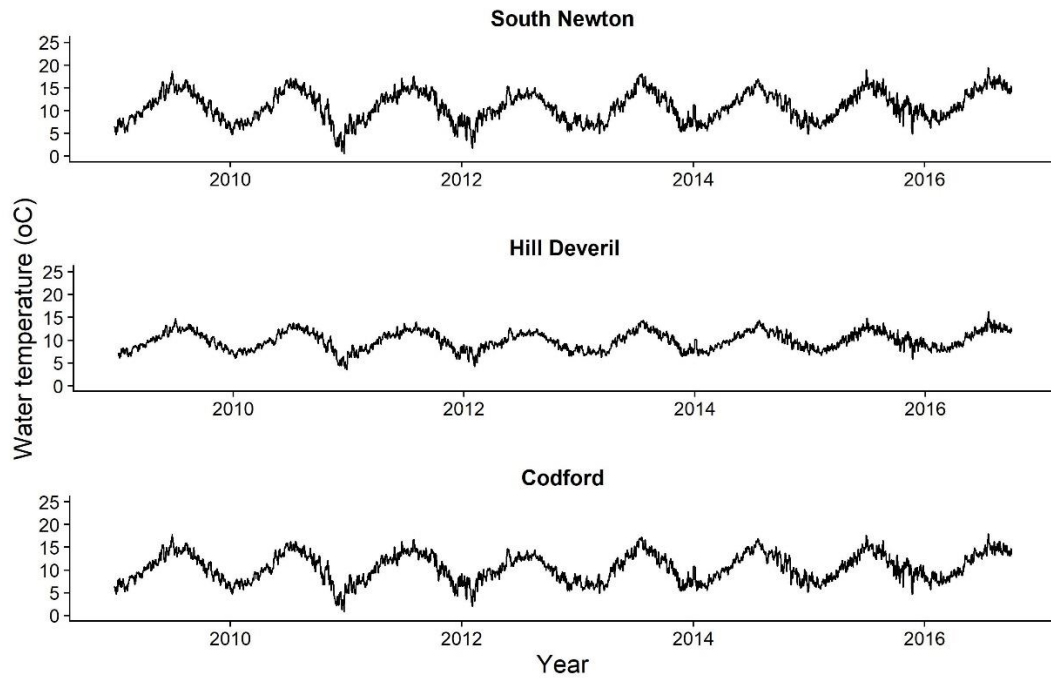
Figure S4 *Lineplots showing the mean daily water temperature measured (a) and estimated (b) at South Newton, Hill Deveril and Codfod from 2009 to 2016. Missing data are represented with red rectangles.*
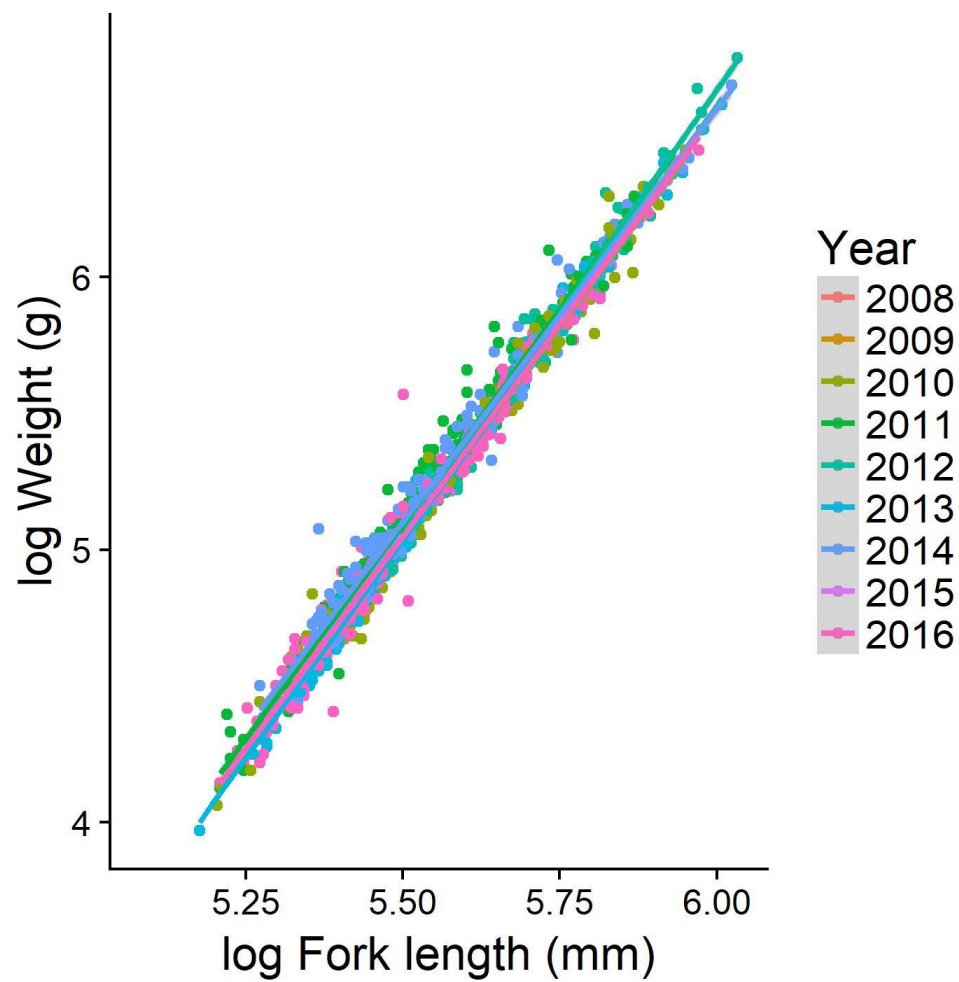
***Figure** S5 Scatter plot of fish weight as a function of fish fork length in logarithmic scale. Lines are fitted linear regression predictions for each year.*
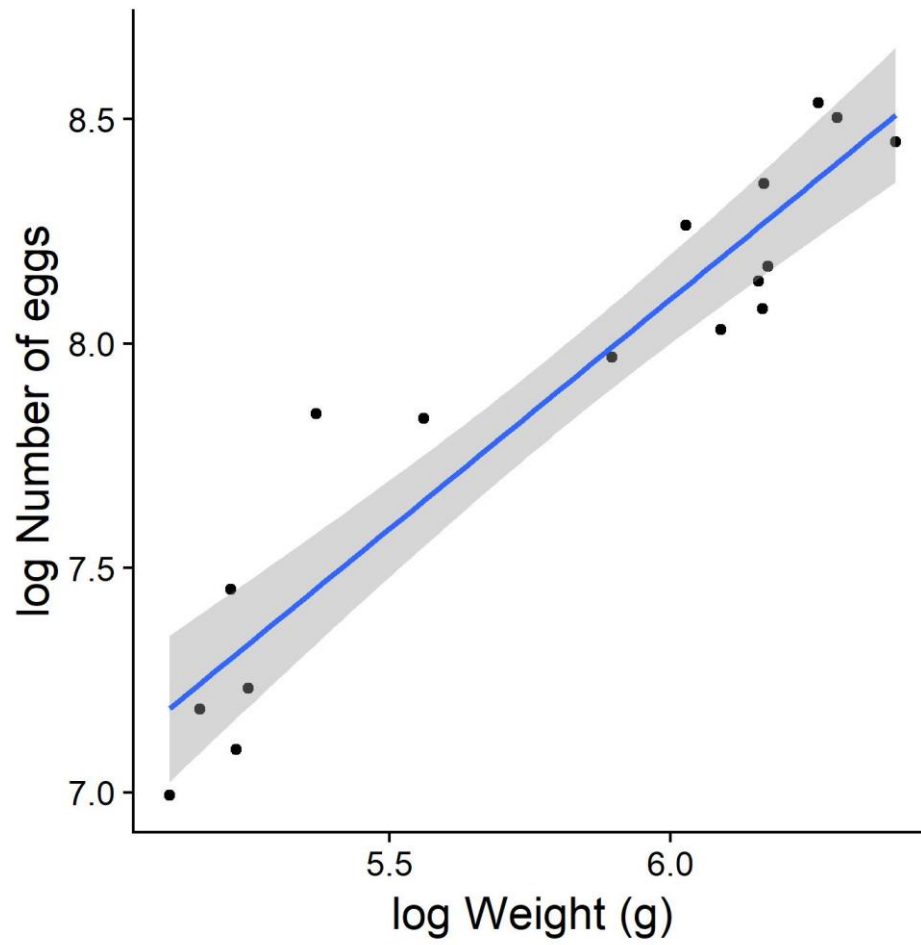
Figure S6 *Scatter plot of number of eggs produced as a function of female fish weight in logarithmic scale. Blue line is fitted linear regression prediction.*
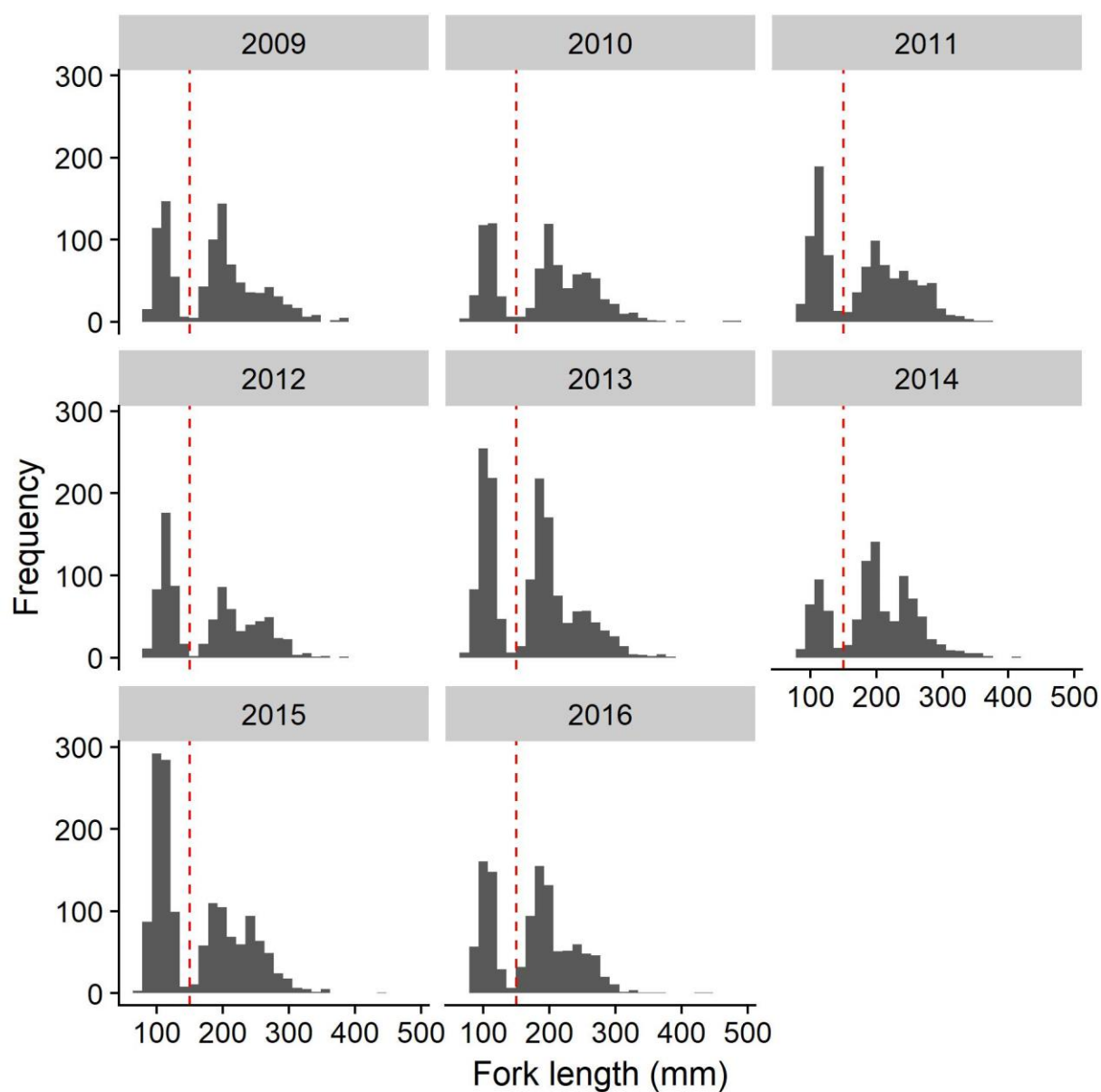
***Figure* S7** *Histograms of trout fork lengths for each investigated year in the river Wylye. Vertical dashed red lines represent cut-off length (150 mm) for 0+ trout.*
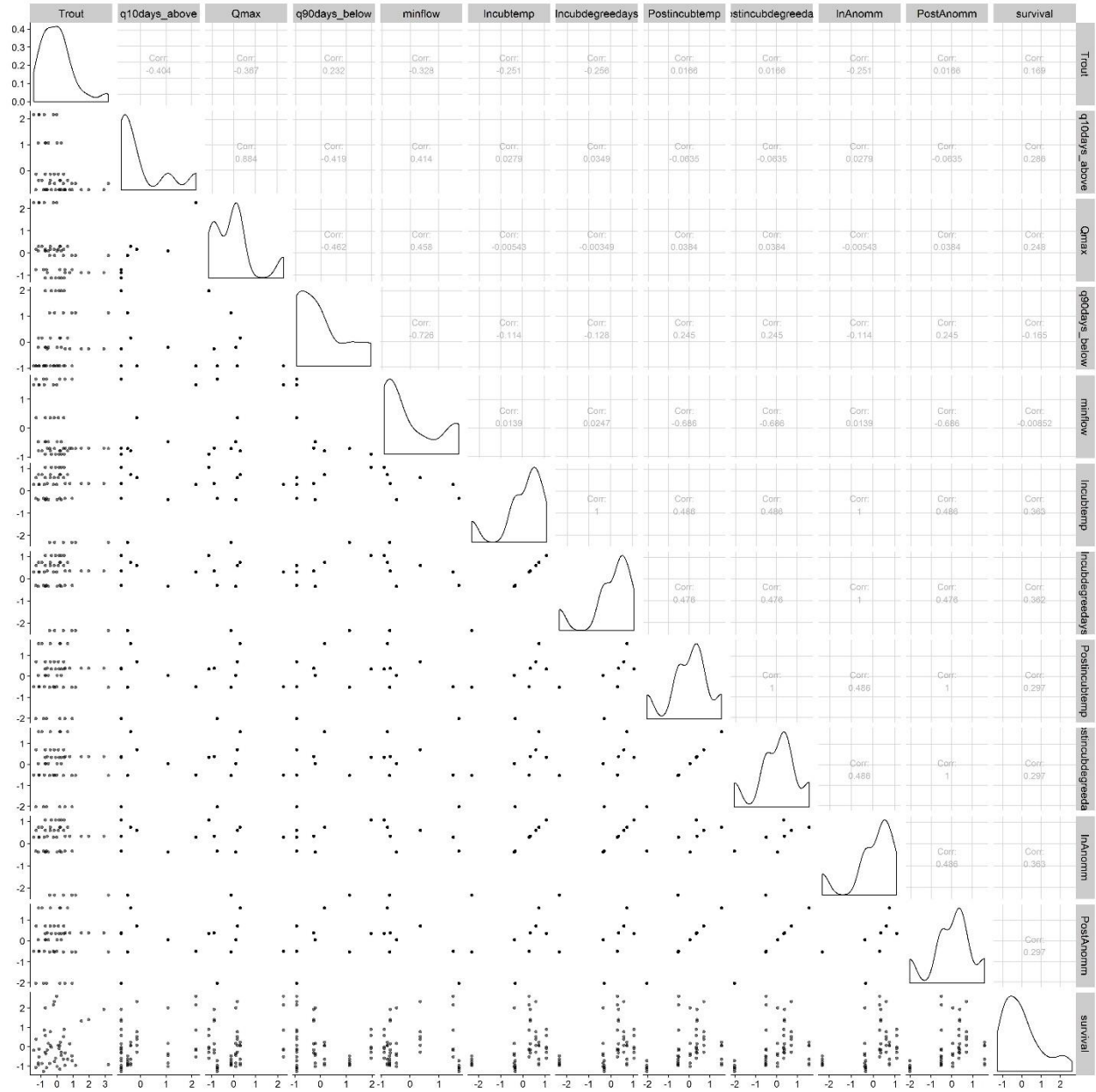
Figure S8 *Pairs plots showing correlation between all explanatory variables, where Nt = number of 0+ trout, Dhf = number of days with high flow during incubation, Qmax = maximum discharge during incubation, Dlf = number of days with low flow during post-incubation, Fmin = minimum flow in 7 consecutive days during post-incubation, Ti = mean incubation temperature, Dti = incubation degree days, Tp = mean post-incubation temperature, Dtp = post-incubation degree days, Ianom = incubation temperature anomaly, Panom = post-incubation temperature anomaly, SI = survival index.*

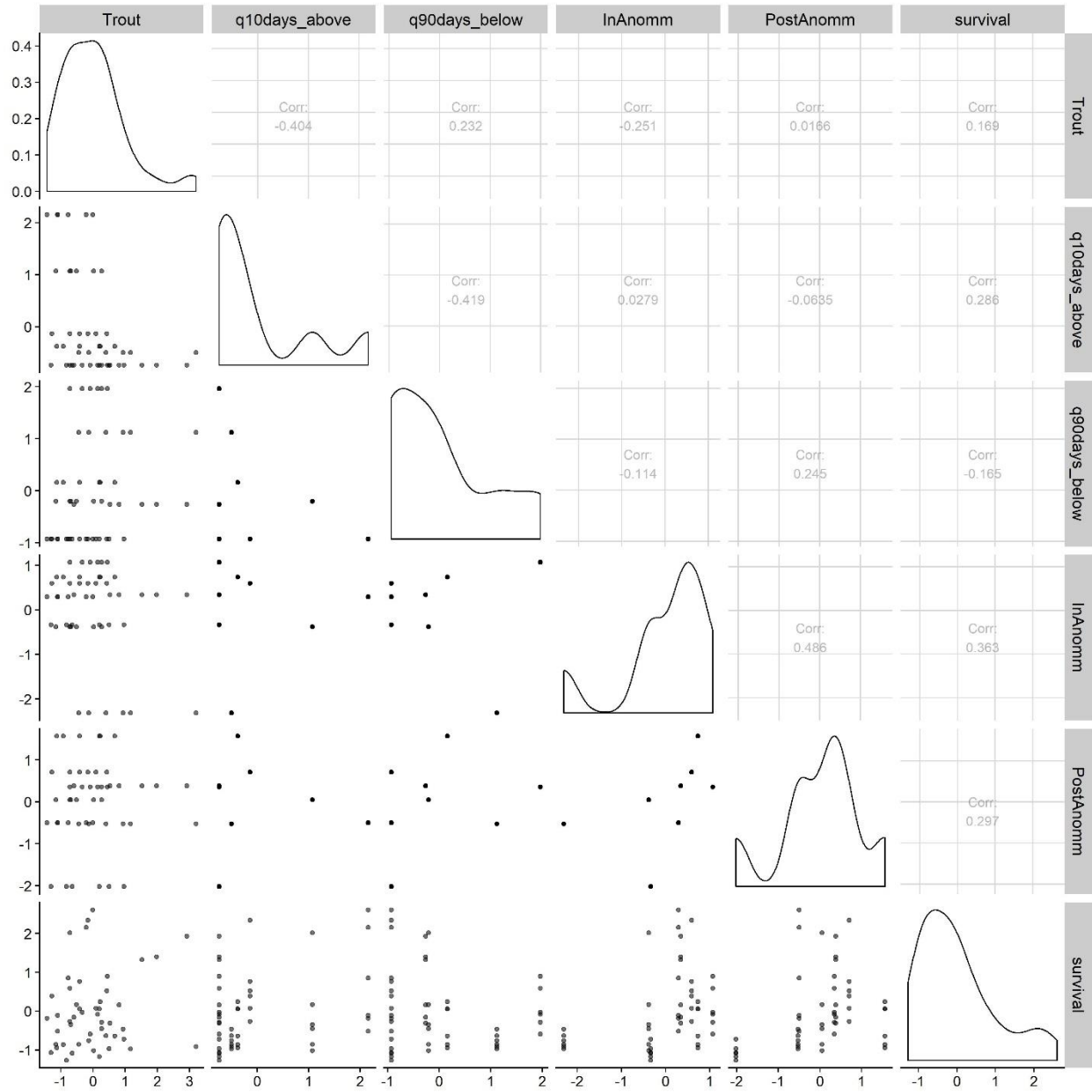**Figure S9** *Pairs plots showing correlation between final explanatory variables, where Nt = number of 0+ trout, Dhf = number of days with high flow during incubation, Dlf = number of days with low flow during post-incubation, Ianom = incubation temperature anomaly, Panom = post-incubation temperature anomaly, SI = survival index.*
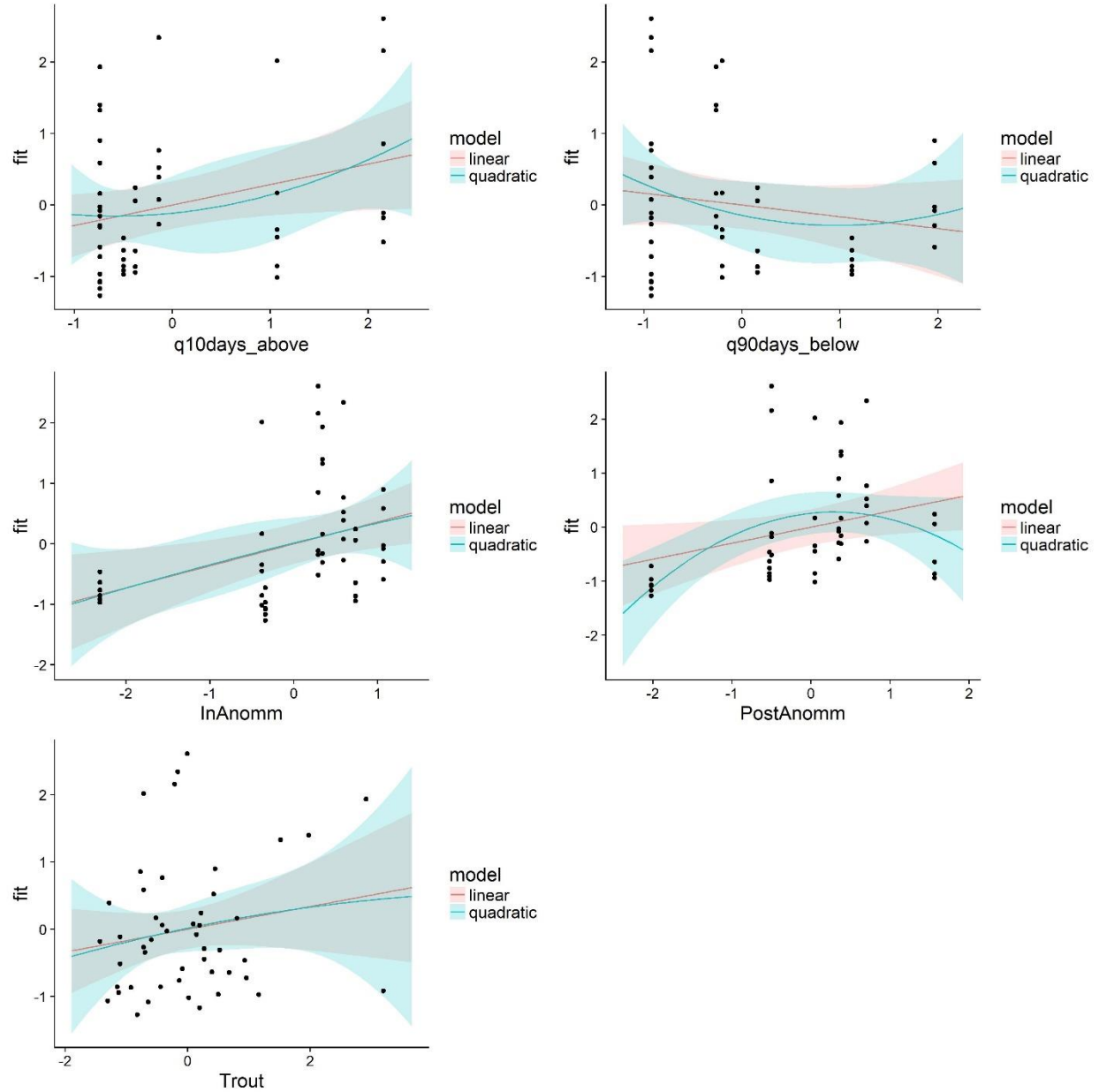
Figure S10 *Scatter plot of standardized survival index as a function of standardized explanatory variables, where Dhf = days of high flow during incubation, Dlf = days of low flow during post-incubation, Ianom = incubation temperature anomaly, Panom = post-incubation temperature anomaly, Nt = number of 0+ trout. Lines are fitted linear regression (red line) and quadratic regression (blue line) predictions.*
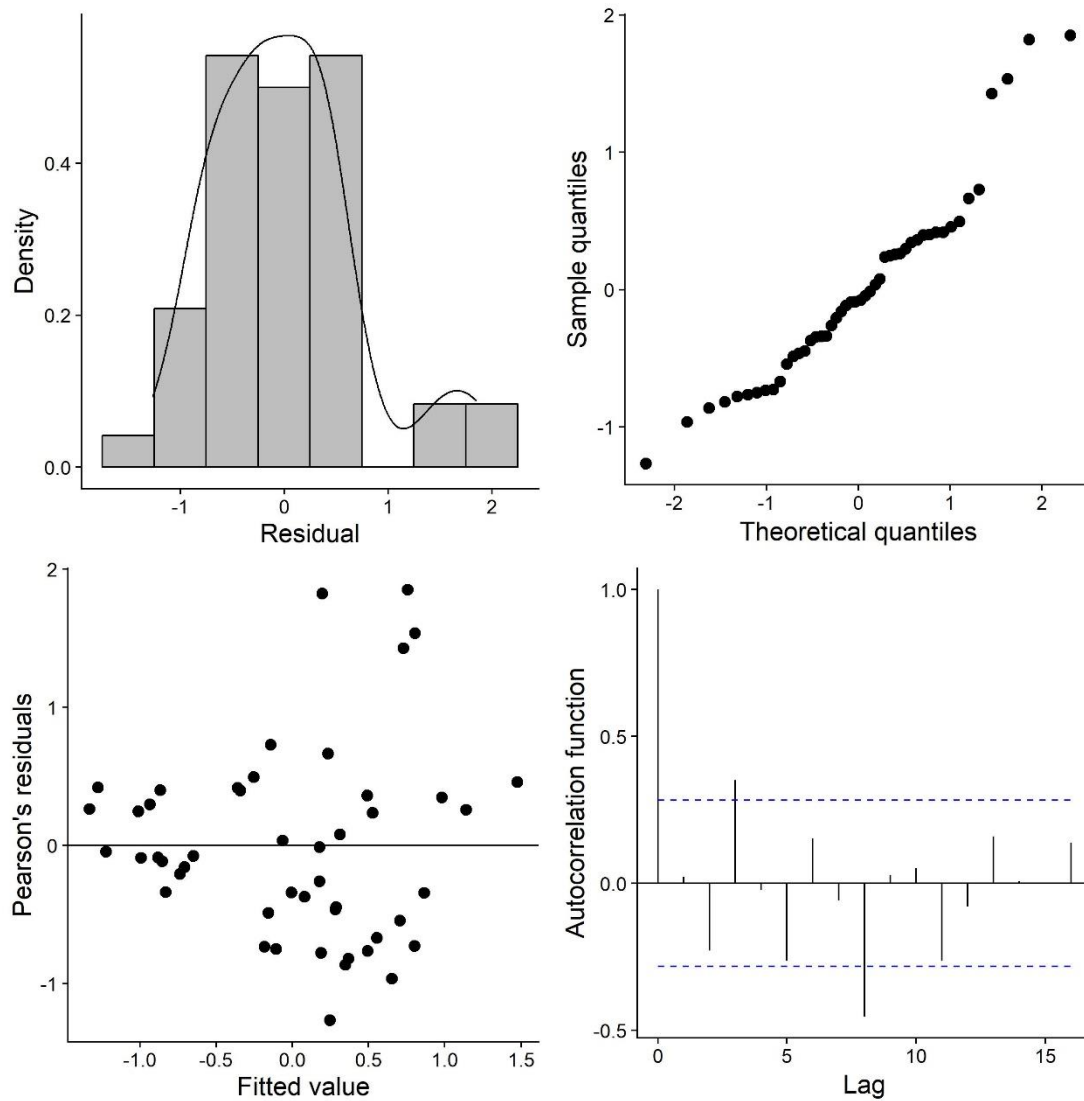
Figure S11 *Plots suggesting that the assumptions of normally distributed, homoscedastic and independent residuals of the "top-ranked" model were not severely violated.*
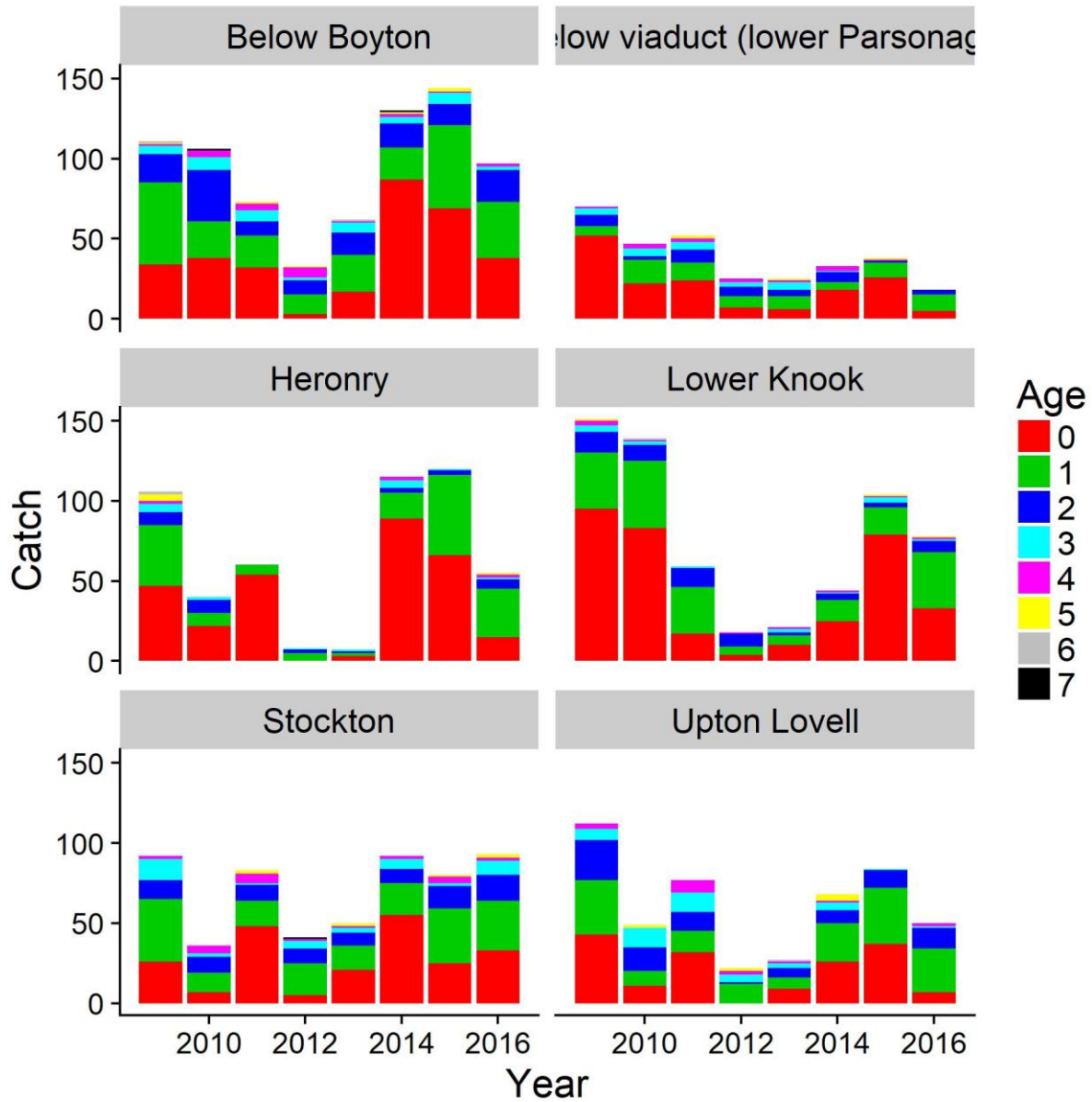
Figure S12 *A barplot showing the number of grayling captured of each age in each year at each site during the investigated period.*