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Medium-term environmental changes influence age-specific survival estimates in a salmonid population

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Abstract

1. Human-induced environmental change is a major stressor on freshwater habitats that has resulted in the population declines of many freshwater species. Ontogenetic shifts in habitat use and associated (st)age-specific requirements mean that impacts of environmental stressors can influence (st)ages in a population differently, and yet relatively few studies of freshwater fish populations account for their detail.
2. We aimed to identify environmental and biotic factors affecting survival estimated for six age-classes of a European grayling population in the River Wylye, UK over a 17-year period. We used a Bayesian age-structured state space model to estimate survival of grayling cohorts between subsequent life stages (eggs to age 5 adults) for 16 annual transitions (2003–2004 to 2018–2019), whilst accounting for imperfect sampling of the population. We quantified the effects of seasonal water flow and temperature, in-stream habitat and prey resource, and potential competitors and predators on survival between subsequent life stages. We used Bayesian variable selection to gauge their relative importance on survival.
3. Grayling abundances declined during the study period (>75% in all age-classes), predominately driven by a loss of mature adults. Changes to seasonal flows negatively influenced their survival: increased days of summer low flow related to decreased survival of subadults and mature adults, and lower winter flows related to reduced recruitment of juveniles from eggs. Higher summer macrophyte cover negatively influenced juvenile and subadult survival and increasing days of high temperature in summer appeared detrimental to juvenile survival. Abundance of brown trout (a potential competitor and predator) did not negatively influence grayling survival.
4. Our results reveal the implications of environmental change on a salmonid population, where recent low summer flows and high temperatures, and below average winter flows, have negatively influenced grayling survival. These conditions appear to be becoming more frequent and persistent in our study river, which is towards the species' southern range limit, which could render the population vulnerable to climate change. Our study demonstrates how careful analysis of long-term

population monitoring and environmental datasets can identify factors affecting (st)age-specific fish population dynamics, and when combined with local expertise, results in realistic mitigation proposals to promote wildlife population persistence.

KEYWORDS
age-structured, European grayling, In-stream habitat, Seasonal flows, state space model

1 | INTRODUCTION

Wildlife populations are increasingly threatened by the negative impacts of human-induced environmental changes on their abundances and vital rates, such as survival (Reid et al., 2018; Tilman et al., 2017). For example, populations of many commercially valuable fish species are on the verge of collapse due to long-term, intense fishing pressure and habitat degradation (Worm et al., 2006). Populations are, however, rarely threatened by a single environmental change; rather, they tend to be affected by multiple environmental changes (stressors) that often act additively or synergistically (Brook et al., 2008).

Decoupling the effects of these multiple stressors on animal populations remains challenging but is important if the population is to persist, especially in freshwater habitats, as these are among the most threatened of habitats globally (Reid et al., 2018). As populations are complex entities comprising of different life stages and ages, then single stressors can act on different components of the population in contrasting ways and, therefore, their effects can vary according to the population demographic structure (Coulson et al., 2001). Intrinsic mechanisms, such as density-dependent processes, can be important regulators of the impacts of environmental stressors on juvenile survival in salmonid fishes, as they can lead to elevated growth rates among surviving individuals with fewer conspecific competitors (Bassar et al., 2016; Nislow & Armstrong, 2012). Conversely, the regulation of older and sexually mature life stages tends to be due to density-independent processes, such as acute and chronic environmental stress, thereby influencing current and future population size with little scope for demographic compensation (Nislow & Armstrong, 2012). Despite this ubiquitous complexity, relatively few studies address (st)age-specific effects of environmental variables, especially among freshwater fish populations (but see Letcher et al., 2015).

River habitat degradation due to anthropogenic activities has been highly apparent in recent decades (Dias et al., 2017). Issues including sediment and pollutant inputs from agricultural practices, disrupted water flow and temperature regimes, and channel modification are recognised as substantial problems in many rivers (Cole et al., 2020; Pankhurst & Munday, 2011; Reid et al., 2018; Xu et al., 2010). These pressures are predicted to increase as human populations grow and the effects from climate change intensify (Dudgeon, 2019). Combinations of these impacts are thought to have contributed to recent declines in European grayling (*Thymallus thymallus*; grayling hereafter) populations throughout their native northern Europe range (Dawnay et al., 2011; Ibbotson et al., 2001; Mueller et al., 2018). Like most cold-water stream fish, habitat use by grayling is relatively dynamic, and varies depending on the season, presence of predators and competitors, and life stage (Mallet et al., 2000; Nykänen et al., 2001; Rabeni & Sowa, 1996; Riley et al., 2009). Different age-classes of grayling exhibit strong and narrow habitat preferences (Mallet et al., 2000; Nykänen & Huusko, 2002), and so a viable population will require a broad range of habitats to support a complete life cycle (Mallet et al., 2000).

As a typically rheophilic species, all life-stages of grayling are likely to be sensitive to changes in seasonal flow regimes (Mallet et al., 2000), especially when they act additively or synergistically with other stressors. For example, low summer flows often coincide with warm summers leading to warming of water temperatures beyond critical thresholds, as well as reducing the downstream drift of macroinvertebrate prey resources (Dewson et al., 2007; Nuhfer et al., 2017). Reduced winter flows can restrict the scouring of deposited sediment from gravels prior to spawning, leading to reduced egg survival (Batalla & Vericat, 2009; Chapman, 1988). Grayling are predominately potamodromous and exhibit high site fidelity (Ovidio et al., 2004), therefore there is potential to assess concomitantly the impacts of freshwater environmental change on all life-stages. As grayling are more sensitive to high water temperatures and changes in water quality than other salmonids (Ibbotson et al., 2001; Jonsson & Jonsson, 2009), grayling can be considered as an indicator species for the effects of environmental change on these other salmonids (Huml et al., 2020). Consequently, understanding the factors affecting grayling survival could inform knowledge gaps on the survival of other salmonid species.

In this study, we aimed to quantify the relative importance of a range of environmental variables that were hypothesised to influence (st)age-specific grayling population dynamics. Specifically, we quantified the effect of seasonal water flow and temperature, in-stream habitat and prey resource, and potential competitors and predators on estimated survival between subsequent life stages. These explanatory variables, and their hypothesised effects on grayling survival, were drawn from previously published studies on grayling and related studies (Table 1). Using long-term data from a chalk stream population located towards the southern edge of their natural range, we developed a Bayesian age-structured state space model to test the influence of these explanatory variables on estimated grayling survival, a latent or unobserved parameter. This approach allowed us to test these hypotheses while accounting for issues such as imperfect sampling (e.g. low catch probabilities for

TABLE 1 Hypothesised relationships between selected explanatory abiotic and biotic variables and the survival of juvenile, subadult and mature adult grayling

Variable	Description	Influences	Reference	Hypothesis
Trout abundance	Older, large brown trout (fork length >150 mm) abundance (site-specific)	Predation on grayling eggs and juveniles, and interspecific competition reduce abundance of all age-classes	Greenberg (1999)	High large trout abundance reduces survival of juvenile/adult grayling.
Invertebrate biomass	Estimate of invertebrate biomass in autumn and in total (sum of spring and autumn samples)	Greater prey resource will support greater numbers of fish.	Haugen and Rygg (1996)	Greater autumn/total invertebrate biomass will increase survival of juvenile and adult grayling, respectively
Pre-spawning winter flow	Mean discharge between 1 December and 28/29 February	High winter flows clean out silted gravel, creating suitable spawning substrate, resulting in higher juvenile recruitment.	Acornley and Sear (1999)	High winter discharge increases egg to juvenile survival
Spawning temperature	Mean air temperature between 1 March and 30 April	Higher spawning temperature increases survival rates of eggs and growth potential of fry.	Bašić et al. (2018)	Elevated water temperature increases egg to juvenile survival
		Higher spawning temperature increases mortality rates of post-spawned fish.	Pankhurst and Munday (2011)	Elevated water temperature reduces survival of mature adults
Low summer flow	Number of days between 1 April and 31 August with discharge ≤Q90	Low flows result in a greater probability of local water temperatures exceeding survival thresholds and/or issues of drying/low dissolved oxygen, reduced available habitat etc.	Bašić et al. (2018)	Low summer discharge reduces survival of juvenile/adult grayling
High summer temperature	Number of days between 1 April and 31 August with air temperature >20°C (at >20°C air temps, mean water temperature in Wylye = 17.5°C)	Water temperatures >18°C exceed optimal thresholds for Wylye grayling, so high number of days above this increases mortality risk/movement downstream out of study area	Crisp (1996)	Elevated air/water temperatures reduce survival of juvenile/adult grayling
Macrophyte cover	Mean summer macrophyte cover	High cover of in-river vegetation reduces access to gravel areas for benthic foraging	Ibbotson (1993)	Higher summer macrophyte cover reduces survival of juvenile/adult grayling

juvenile grayling). We discuss the model results with respect to their implications for the management of grayling and other salmonid populations in areas towards the southern edge of their range.

2 | METHODS

2.1 | Study river

The River Wylye, a tributary of the Hampshire Avon located in southern England (Figure 1), is a chalk stream characterised by high permeability chalk bedrock and a mixture of arable agriculture and grassland cover (Table S1, National River Flow Archive [NRFA], 2020). The Hampshire Avon and all its tributaries contain important grayling populations within the native range of grayling (Ibbotson et al., 2001). Grayling are thought to be present throughout the River Wylye (R. Wellard, personal communication). It is primarily groundwater-fed with seasonally consistent flows and thermal regimes when compared to surface-fed rivers (Sear et al., 1999). Following periods of low summer discharge, groundwater aquifers are recharged by precipitation in the autumn and winter months (Sear et al., 1999). Groundwater abstraction by the regional water

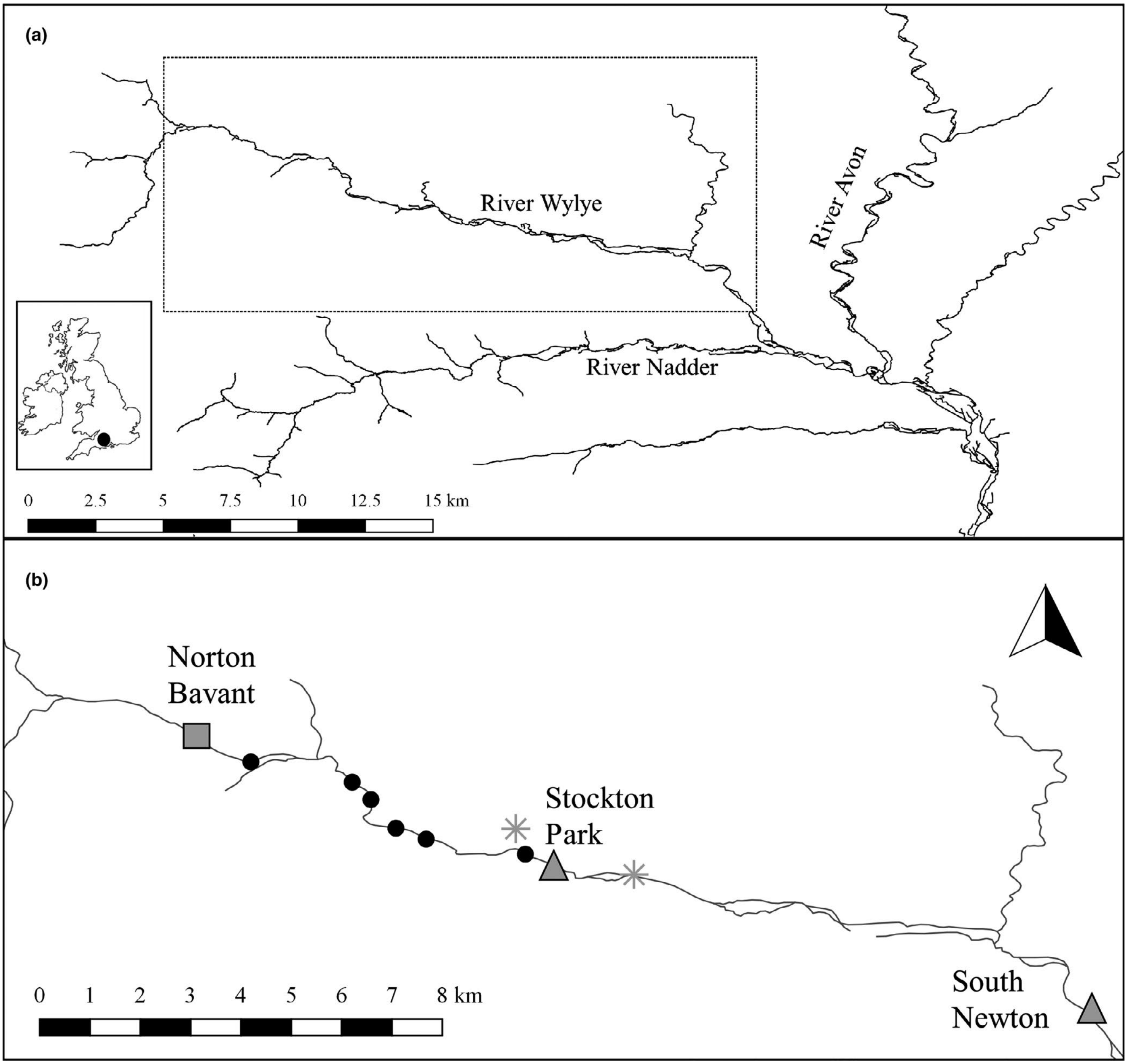

FIGURE 1 Location of (a) the study area (dashed box) in the River Wylye within the River Avon catchment and in the UK (inset map) and (b) long-term fishing sites (black circles) and abiotic and biotic data sampling locations within the study area. Grey symbols show locations of macroinvertebrate sampling at Norton Bavant (square), flow gauging stations at Stockton Park and South Newton (triangles), and the upstream and downstream limits of the macrophyte survey (asterisks)

company (Wessex Water plc.) is the primary water resource management activity, with strategies in place to reduce abstraction rates during periods of low river flow (≤Q95) (Environment Agency, 2020).

2.2 | Fish sampling

Grayling and brown trout (*Salmo trutta*; trout hereafter) populations have been surveyed for 24 years in the River Wylye. In this study, we used 17 years (2003–2019) of these data, covering the period when trout data were most consistently recorded alongside the grayling data. Fish were sampled in late September/early October at six long-term sites (200 m length; Figure 1) using either single pass electrofishing (2003–2008), or multiple (k) pass depletion electrofishing (2009–2019), where typically three fishing passes returned a depletion of >50% fish caught between passes (Beaumont, 2016). During fishing, each site was closed through deployment of stop nets (upstream and downstream) that remained in place until the fishing was completed. Captured grayling and trout were removed after each pass. Biometric data were collected under light anaesthesia (2-phenoxyethanol; 0.2 ml/L), with fish identified to species, and measured for fork length (nearest mm) and mass (to 0.1 g). A scale sample (three to five scales per fish) was taken from each grayling using sterilised instruments, from between the dorsal fin and lateral line, to enable age assessment while accounting for known bias in aging of older fish (Horká et al., 2010). Following their recovery to normal behaviour, all fish were released back alive into the river section where they were captured. Due to relatively high angling interest in this grayling population, no individual fish were removed from the river, thus heuristic data on their reproductive traits and characteristics (e.g. sex ratio, age at first spawning, and spawning frequency) were used in the subsequent model development, with use of published values from similar chalk stream populations in southern England. Grayling age was verified as one of eight age-classes (0–7) through scale ageing on a projecting microscope (×20 to ×30 magnification). Trout were classified as juveniles (fork length ≤ 150 mm) or older, large trout (fork length > 150 mm) based on length-frequency histograms (Figure S1).

2.3 | Abiotic and biotic variables

We used records of abiotic and biotic data collected during the study period (2003–2019) to calculate explanatory variables hypothesised to influence grayling survival (Figure 2). River discharge (as daily means, m^3/s) were available from the Stockton Park gauging station (Figure 1; NRFA, 2020). To account for missing data ($n = 36$), we used the *impSeqRob*() function in R package rrcovNA (Todorov, 2020) to impute daily mean discharges by minimising the covariance between daily mean discharges at Stockton Park and the nearby gauging station at South Newton (Figure S2). We used data collected at Stockton Park because it was closer to fish sampling sites and was upstream of a confluence northwest of South Newton (Figure 1). As water temperature data were only available for some of the study period, local air temperature estimates from the Europe-wide E-OBS gridded dataset (E-OBS v20.0e, Cornes et al., 2018) were used as daily mean air temperature to calculate spring and summer temperature variables. This was considered a reasonable approach as: (1) there was a strong relationship between daily mean air and water temperatures in years of available data (Figure S3); (2) we used temperatures recorded during spring and summer, when the relationship between daily air and water temperatures were considered to be synchronised (Letcher et al., 2016; Figures S4–S5); and (3) the majority (97%) of daily air temperatures fell in the range of 0–20°C where stream temperatures are considered to change linearly with air temperatures (Mohseni & Stefan, 1999).

Biotic data included macroinvertebrate abundance sampled annually in spring and autumn, upstream of the fishing sites at Norton Bavant, as part of a separate monitoring programme (Figure 1; Environment Agency/Wessex Water). Following a standardised 3-minute kick-sample (Brua et al., 2011), individuals were identified to family (to species from 2014) and counted. It is widely recognised that there are considerable inter- and intra- taxa differences in macroinvertebrate sizes that distort the relationship between abundance and biomass (e.g. Saint-Germain et al., 2007), the latter which we considered a better measure of prey resource. To account for this, we estimated macroinvertebrate biomass from these data. We used the species-level data to identify families with one genus/species identified (66/73 families) and considered these taxa to represent all individuals sampled. We calculated a weighted average maximum body-size of these taxa from a trait database that used fuzzy-coding to assign each individual taxon probable maximum body-size categories (Tachet et al., 2010). We used published length-mass relationships to estimate biomass for each taxon, multiplied the individual biomass by the family-level abundance and summed across all taxa to produce a measure of biomass in spring and autumn. The seven families with multiple genus/species entries were excluded from biomass calculations but occurred rarely ($n = 1$–3) during the study period and were considered unlikely to influence temporal changes in macroinvertebrate biomass. Percentage cover of macrophytes, predominately *Ranunculus* spp., was estimated from 100 m long bankside surveys done each summer (late July/early August) at 20 locations at the downstream end of the fishing sites, as part of a separate monitoring programme (Figure 1; Environment Agency/Wessex Water). The final biotic variable included was the abundance of the older, large trout at each fishing site, estimated from the depletion electrofishing surveys (Figure 2).

2.4 | Grayling survival model

We estimated apparent survival of grayling cohorts using a Bayesian age-structured state space model. We used this approach to allow us to estimate annual survival transitions from the available fish survey data, but also to describe and test whether they were influenced by a suite of hypothesised explanatory variables, while still

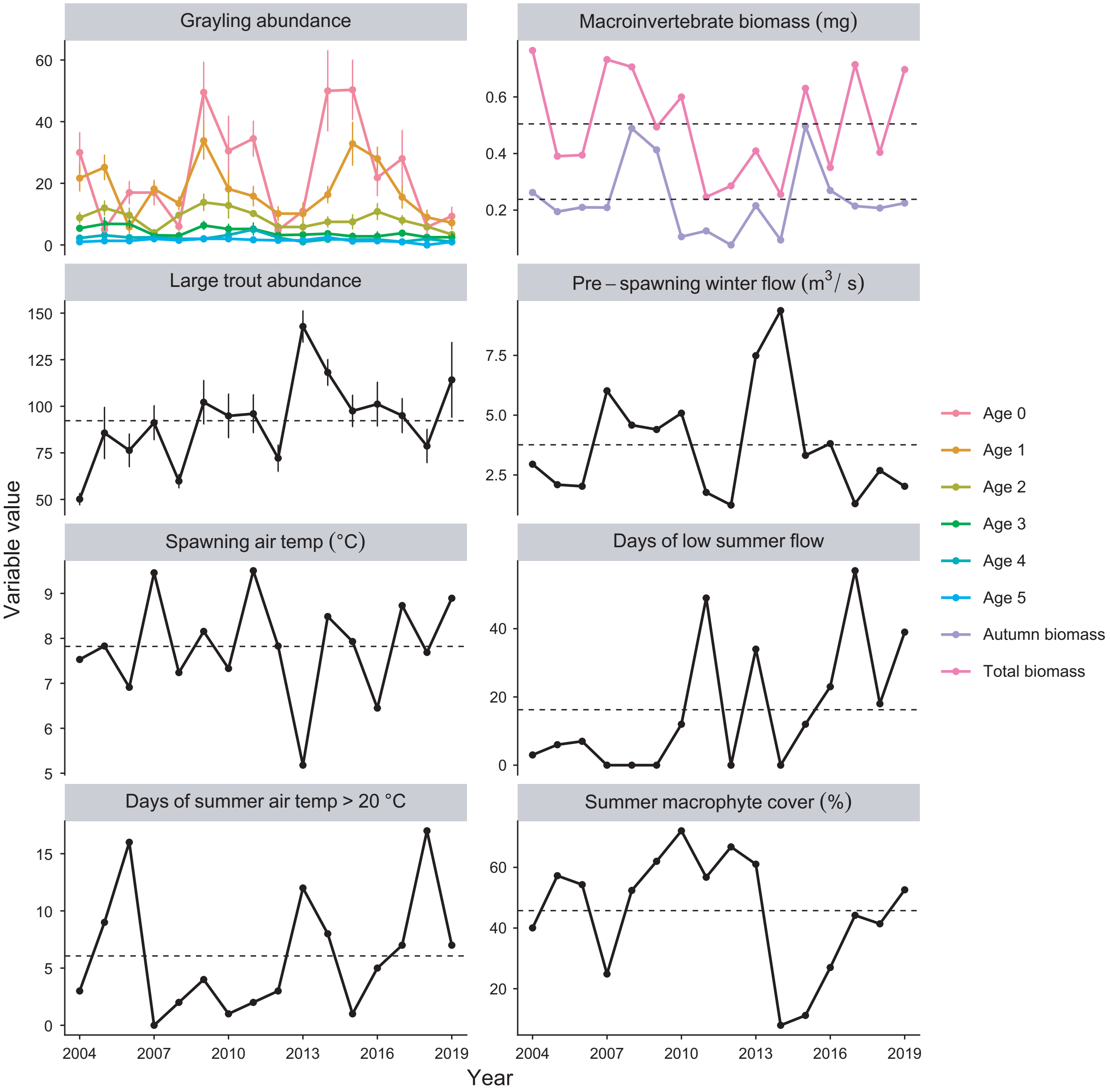

FIGURE 2 Abiotic and biotic variables considered in the grayling survival model, including the response variable (grayling abundance), calculated for each year (and age, in the instance of grayling abundance) of the study period. Grayling and trout abundance are averaged across sites. The dashed line shows the 16-year mean for each explanatory variable

accounting for imperfect sampling efficiency; such multifaceted models are most easily specified and estimated in a Bayesian framework (Gregory et al., 2018). The model was designed to estimate 16 annual survival transitions (from the 2003–2004 to the 2018–2019 transition) between subsequent age-classes while separating the unknown ecological process (i.e. survival between age-classes) from the observation process (i.e. imperfect sampling of total population size). Explicitly, survival was estimated and thus was a latent or unobserved parameter (although we refer to estimated survival in this study as *survival* for brevity), and annual survival was estimated for the following transitions: eggs to age 0, age 0 to age 1, ..., and age 4 to age 5 (Figure 3). We use the term *apparent survival* because we assumed that the populations were closed, and immigration and emigration were negligible, an assumption supported by studies demonstrating high site fidelity in grayling. For example, Ovidio et al. (2004) found grayling made small-scale movements (mean ± *SE* distance from home range of 258 ± 65 m) during pre- and post-spawning periods, and rapidly homed back to established residences after their spawning migration (mean ± *SE* migration distances of 1,234 ± 328 m). Production (eggs) and survival (juveniles and adults) estimates were produced for each site and year of the study period, with 2003 representing the initial state of each stage/age-class. The

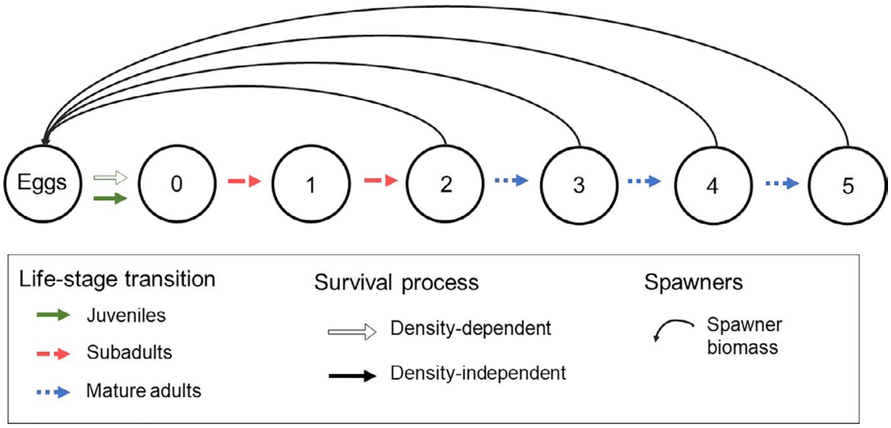

FIGURE 3 A summary of the age-structured grayling population life cycle and ecological survival processes. Circles represent ages, including eggs; coloured arrows represent survival transitions for the different life stages; the survival transition from eggs to age 0 juveniles includes both density- dependent and independent processes; and black arrows represent the contribution of spawners to numbers of eggs deposited. Time and space have been omitted from the schematic for simplicity

probability of cohorts surviving from each age-class to the next was followed through time from eggs to age 5 adult grayling; we did not consider survival to age 6 and 7 grayling because there were too few abundance data for reliable estimation (<0.5% of the total catch; Figure S6).

2.4.1 | Ecological process equations

The ecological process was represented by an age-structured grayling population life cycle (Figure 3). The total number of eggs $Egg_{s,y}$ produced in each site s and each year y was estimated as a deterministic function:

$$Egg_{s,y} = \left(W_{s,y-1} \times f\right) \times r.$$

where $W_{s,y-1}$ is the spawner biomass (g) in site s in year y–1, f is a fecundity constant taken to be 8.1 (the coefficient relating spawner mass to the number of eggs produced; see Figure S7 for details of this calculation), and r is a sex ratio taken to be 0.5 (i.e. 1M:1F; Ibbotson, unpublished data). We considered fish aged 2 and older to represent mature spawners (Ibbotson et al., 2001). $W_{s,y-1}$ was taken to be the total mass of spawners in site s in year y–1. This could not be calculated directly because some spawners were not observed (i.e. $p_g < 1$, see *Observational process equations*). Instead, it was estimated for year y–1 as the sum of age 2, ..., 5 individual spawner mass in site s and the product of the mean mass of age a spawners across sites in year y–1 and the estimated number of unobserved age a spawners in site s. The few captured aged 6 and 7 individuals were included in the calculation of $W_{s,y-1}$. Individual mass measurements were missing for years 2003 to 2009 and 2015 and were imputed using the strong linear relationship between log mass and log length ($F_{1,2,391} = 733{,}600.0$, $r^2 = 1$, $p < 0.001$; Figures S8–S9). For simplicity, we assumed that all eggs produced by the females were viable and could produce a recruit (Rivot et al., 2004).

Recruitment from eggs to age 0 juveniles was estimated as a density-dependent function modified by explanatory variables, as there is evidence for a negative effect of conspecific densities on annual grayling recruitment in the River Wylye (Bašić et al., 2018). We assumed the commonly used Ricker recruitment function with correlates given by:

$$N_{s,1,y} \mid Egg_{s,y}, \alpha_0, \beta_0, \theta_0 X_0, \in \sim \text{logNormal}\left(\alpha_0 \times Egg_{y,s} \times e^{\left(-\beta_0 \times Egg_{y,s} + \theta_0 X_0\right)} + \in\right),$$

where α_0 and β_0 are parameters of the Ricker function that is modified by J additive density-independent explanatory variables $X_0 = x_1, x_2, \ldots, x_J$ whose effects on the juvenile numbers are represented by a vector of coefficients $\theta_0 = \beta_1, \beta_2, \ldots, \beta_J$. We assumed that the variability in the number of juvenile recruits was proportional to the total number of eggs by including a multiplicative error term ϵ (additive on the log scale).

Survival transitions between subsequent grayling ages were estimated as functions of explanatory variables. Grayling exhibit ontogenetic shifts in habitat use as they develop from juveniles to subadults and mature adults (Mallet et al., 2000). Moreover, we expected that size-dependent influences on survival, such as thermal tolerance or ability to evade gape-limited predators, would affect older-aged grayling similarly given the overlap in their length distributions (Figure S10). To reflect this and to maximise the data available to estimate these transitions, we defined $L = 2$ subsequent survival transitions: subadults ($0 \rightarrow 1$ and $1 \rightarrow 2$) and mature adults ($2 \rightarrow 3$, $3 \rightarrow 4$ and $4 \rightarrow 5$), which assumed that explanatory variables would influence these stages in a similar direction and magnitude. Annual survival transitions were estimated for each year y from a binomial process given by:

$$N_{s,a,y} \mid N_{s,a-1,y-1}, \phi_{s,y,l} \sim \text{Binomial}\left(N_{s,a-1,y-1}, \phi_{s,y,l}\right)$$
$$\text{logit}\left(\phi_{s,y,l}\right) = \alpha_l + \theta_l X_l,$$

where $a = 2, \ldots, 6$ represent ages $1, \ldots, 5$ respectively, α_l is the intercept of the lth survival transition linear predictor and $\theta_l = \beta_{l,1}, \beta_{l,2}, \ldots, \beta_{l,M}$ is a vector of coefficients relating the influences of M explanatory variables $X_l = x_{l,1}, x_{l,2}, \ldots, x_{i,M}$ on the survival transitions.

2.4.2 | Observational process equations

The observation process was based on the electrofishing depletion method that uses successive electrofishing passes to estimate and adjust estimated age-specific abundances for their capture probability. We estimated the abundance of each site-specific grayling age class from their catch in each of 3 electrofishing passes. However, we estimated the capture probability p separately for a reduced number of age groups g: age 0 juvenile fish and age 1–5 adult fish. This was done for two reasons: (1) literature reports lower capture probabilities for juvenile fish relative to larger fish, probably due to size-dependent responses of the fish to the electrofishing method of capture, i.e. smaller sized fish are less susceptible (e.g. Dauphin et al., 2019); and (2) there were fewer data in older age classes with which to estimate age-specific capture probabilities. For each year y (year notation omitted for simplicity), the depletion sampling was represented by a sequential series of binomial equations emulating the removal of the site- and age-specific catch in each of $K = 3$ passes ($c_{s,a,1}, \ldots, c_{s,a,K}$) from the total site- and age-specific population ($N_{s,a}$):

$$c_{s,a,1} \mid p_g, N_{s,a} \sim \text{Binomial}\left(N_{s,a}, p_g\right)$$

$$c_{s,a,2} \mid p_g, N_{s,a}, c_{s,a,1} \sim \text{Binomial}\left(N_{s,a} - c_{s,a,1}, p_g\right)$$

$$c_{s,a,3} \mid p_g, N_{s,a}, c_{s,a,1}, c_{s,a,2} \sim \text{Binomial}\left(N_{s,a} - \left(c_{s,a,1} + c_{s,a,2}\right), p_g\right)$$

where a = 1, ..., 6 representing ages 0, ..., 5 respectively and p_g is the group-specific capture probability which was 1 for age 0 juvenile fish and 2 for age 1–5 adults. Note that p was treated as annually and spatially invariant because the fish surveying was done by the same team over the same few days every year for the study duration.

2.4.3 | Hypotheses testing

To decide which explanatory variables to consider and to develop hypotheses about the survival transitions they might affect and how, we reviewed the literature and supplemented this with authors' knowledge and opinion. Our final set of explanatory variables and their associated hypotheses are in Table 1. We explored the influence of these explanatory variables using Bayesian variable selection (reviewed in Hooten & Hobbs, 2015); this estimates the degree of support for the inclusion of each explanatory variable in the estimation of survival of each life-stage. Specifically, we used the 'slab' and 'spike' approach (George & McCulloch, 1993), where the coefficient of the ith explanatory variable β_i was given a normally distributed prior with a mean of 0 and a 'slab' (wide) or 'spike' (narrow) variance depending on a Bernoulli indicator variable that evaluates to 0 or 1 with probability $pind_i$ (Table 2). Explanatory variables with estimated indicator variable values ≥0.5 were considered as influential in estimating survival at each life-stage (Hooten & Hobbs, 2015), and were used in inference.

2.4.4 | Simulation testing

Prior to using the observed data for inference, we evaluated the performance of the model by simulations. We used the same model to simulate grayling abundance data with the same indexing as the model (i.e. 17 years, six sites, five adult age-classes, three electrofishing passes), including the effect of an explanatory variable on each survival transition and compared the simulated data with the abundance and parameters estimated by the model. We repeated this with multiple randomly simulated datasets. Overall, the model returned reasonable estimates of grayling abundance, parameter values, and convergence of the Markov chain Monte

TABLE 2 Prior distributions for initial state variables and unknown parameters estimated in the grayling survival model

Model component	Parameter	Prior
Ecological process		
Initial state variables	$N_{s,a\,[1],y\,[1]}$	~Uniform (0, 5,000)
	$N_{s\,,a\,[2\ldots6],y\,[1]}$	~Uniform (0, 2,000)
Juvenile survival	$\log(\alpha_0)$	~Uniform (−10, 0)
	β_0	~Normal (0, 0.01)
	$log(\sigma^2)$	~Uniform (−13.8, 13.8)
	β_j	~Normal (0, τ_in)
Adult survival	α_l	~Normal (0, τ_in_l)
	$\beta_{l,m}$	~Normal (0, τ_in_l)
Observation process		
Probability of capture	p_g	~Beta (1,1)
Model selection process		
Stochastic indicator variable	τ_in/τ_in_l	$\begin{cases}\text{Gamma}(0.001, 0.001), & ind_{j/l,i} = 1 \\ 1,000, & ind_{j/l,i} = 0\end{cases}$
	$pind_j/pind_{l,m}$	~Beta (5,5)
	$ind_j/ind_{l,m}$	~Bernoulli ($pind_j/pind_{l,m}$)

Carlo (MCMC) chains for all simulated data sets (see Figures S11–S15 for output for an example simulated data set). Note that we did not implement Bayesian variable selection in the simulation testing.

2.4.5 | Model fitting

We fitted a single saturated model with Bayesian variable selection to estimate River Wylye grayling annual survival transitions and the effects of the explanatory variables. We used Pearson's correlation to show that no pairs of explanatory variables were highly correlated prior to their inclusion in the model ($r \geq |0.6|$; Dormann et al., 2013, Figure S16). To compare the effects of variables measured at different scales, all explanatory variables were standardised prior to analyses by subtracting their mean and dividing by their standard deviation.

To allow us to estimate the 2003–2004 survival transition, we had to specify probability distributions for $N_{s,a,y}$ for y = 2003. We assigned weakly informative priors for these and all other estimated parameters of the model (Table 2). We fitted the age-structured state-space models with the R package rjags (Plummer, 2016) using Just Another Gibbs Sampler (JAGS; Plummer, 2003) and R (R Core Team, 2020). Parameter values were estimated by MCMC simulation using three parallel chains. We ran 100,000 iterations in an adaption phase followed by 100,000 iterations of burn-in, before running 100,000 iterations to sample posterior parameter distributions with a thinning rate of 100 to reduce autocorrelation between iteration estimates. We visually inspected MCMC trace plots and calculated the Gelman–Rubin convergence statistic to determine convergence and mixing of the chains.

3 | RESULTS

Of the explanatory variables tested, three variables appeared to show a temporal trend: days of low summer flow and days of high summer temperature have been above the 16-year average in the last 4 and 3 years, respectively, and mean winter flow has been below the 16-year average in the last 5 years (Figure 2).

Estimated abundance of each Wylye grayling age-class decreased during the study period, with this trend particularly pronounced in the older age-classes (Figure 4). The estimated number of eggs per year also declined temporally (Figure S17). Whilst the

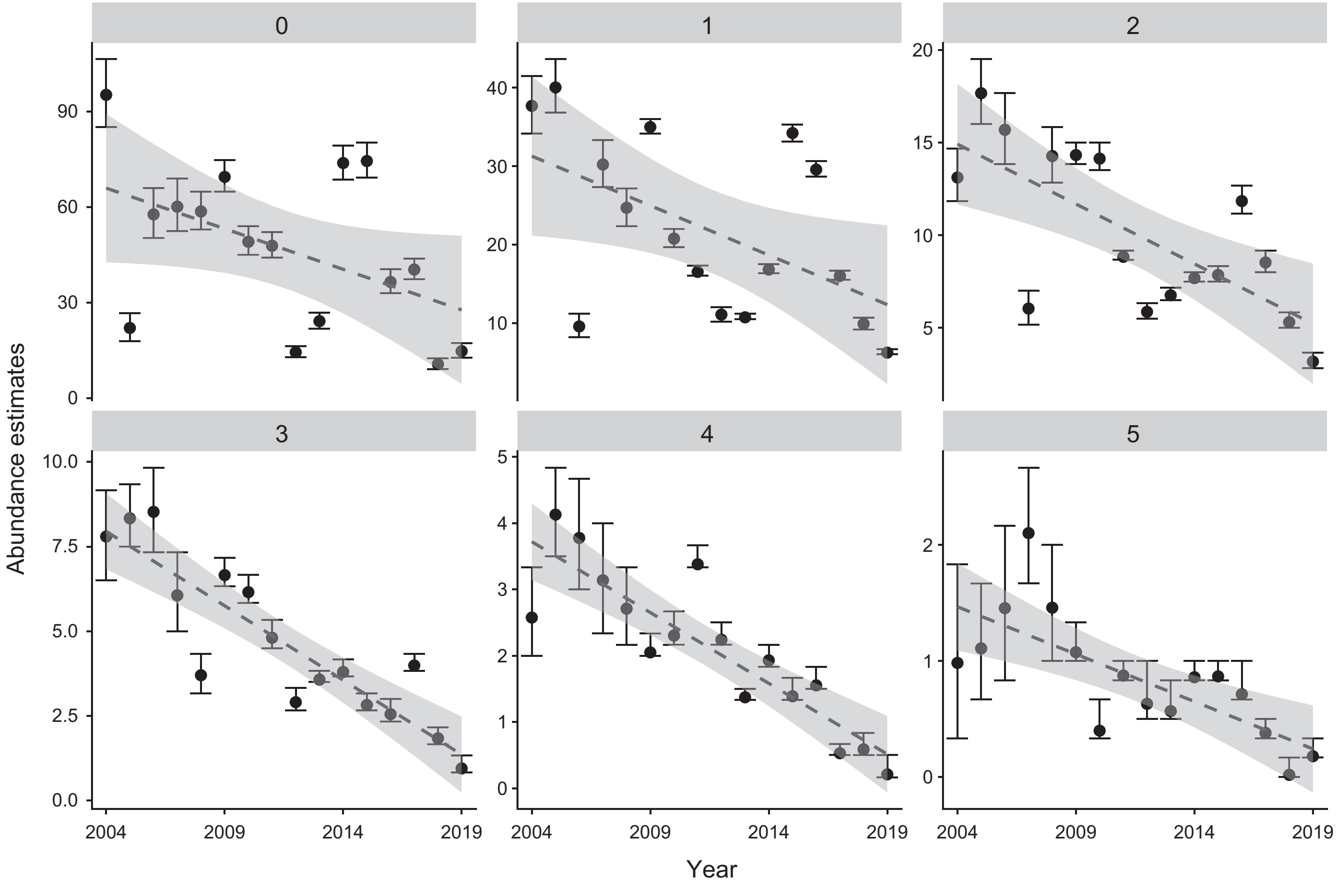

FIGURE 4 Estimated abundance of each age-class of grayling (0–5) during the study period, averaged across six long-term sites. Black circles are the point estimate and error bars denote the 95% Bayesian credible intervals. The grey dashed line (and grey shaded area) were added post hoc (i.e. after the modelling process) and are used only to indicate any linear trend (and associated uncertainty) through the mean annual abundances

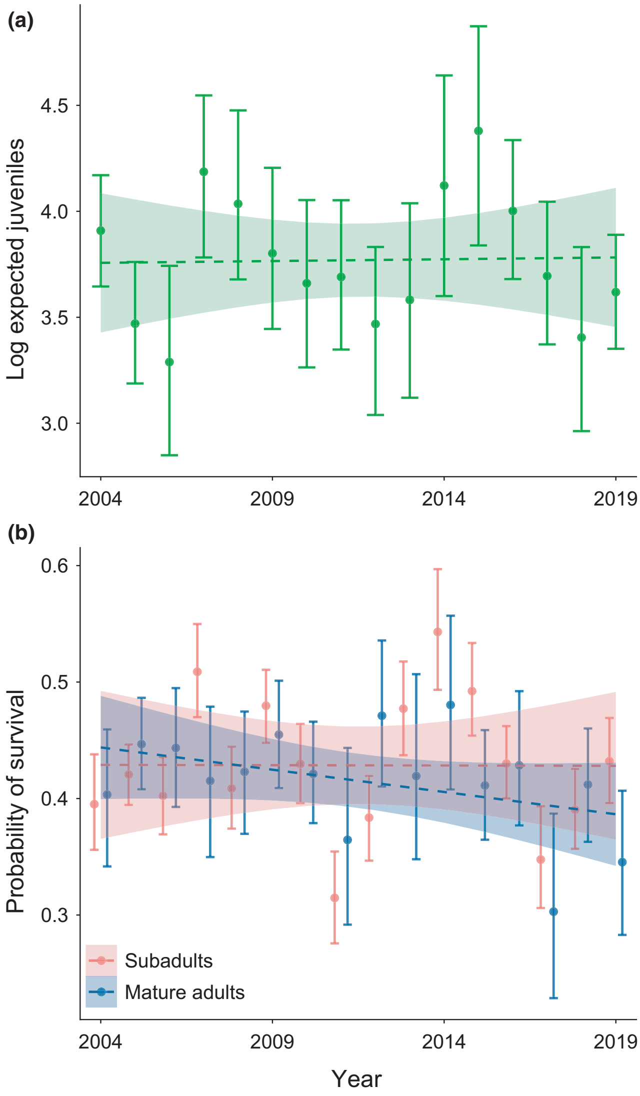

FIGURE 5 Annual estimates of (a) expected numbers of juveniles surviving from the mean number of eggs estimated, as a function of the net effect of tested explanatory variables, and (b) subadult and mature adult survival between each annual transition as a function of the net effect of tested explanatory variables. Estimates are averaged across the six long-term sites, circles are the mean estimate and error bars denote the 95% Bayesian credible intervals. The dashed lines (and shaded areas) were added post hoc (i.e. after the modelling process) and are used only to indicate any linear trend (and associated uncertainty) through the mean annual survival

estimated abundance of ages 0–2 were more variable, abundances of all age-classes in 2019 had decreased by over 75% compared to the start of the study.

There was evidence for density-dependent regulation of juvenile recruitment (Figure S18). Figure 5 shows the estimated juvenile recruitment, when holding the effect of eggs constant, and the estimated survival probability of subadults and mature adults as a function of the net effect of tested explanatory variables. The estimated juvenile recruitment (Figure 5a), and the estimated survival probability of subadults (Figure 5b) did not reveal a consistent temporal pattern. In contrast, the estimated probability of survival for mature adults declined through time, albeit not steeply (Figure 5b). Mean survival estimates ranged from 0.31 to 0.54 for subadults and 0.30 to 0.48 for mature adults. The lowest survival estimates for both life-stages were in 2011 and 2017. Juvenile probability of capture was estimated as 0.30 (95% Bayesian credible intervals: 0.28–0.32) and higher for adults (0.63; 0.61–0.65).

Four variables influenced juvenile and subadult grayling survival, and two variables were retained to estimate mature adult survival (Table 3, Table S2). Low summer flow, summer macrophyte cover, and macroinvertebrate biomass were important explanatory variables, being retained in the survival models of at least two of the three grayling life-stages (Figure 6). High summer temperatures had a negative influence on juvenile survival (Figure 7a) and low summer flow had a negative influence on subadult and mature adult survival (Figure 7b). Summer macrophyte cover had a negative influence on juvenile and subadult survival (Figure 7c–d). Macroinvertebrate biomass had a positive influence on juvenile and subadult survival (albeit a weak relationship with the former), but a weak, negative influence on mature adult survival (Figure 7e–f). Juvenile survival was weakly, positively influenced by mean winter flow (Figure 7g), and trout abundance was positively associated with subadult survival (Figure 7h). Visual assessment of the MCMC chains and Gelman's diagnostic statistics suggested that the MCMC chains were stationary and well-mixed (Table S3, Figure S19).

4 | DISCUSSION

Our results indicated a temporal decline in grayling population abundance, which was driven predominately by a loss of mature adults in the population. Changes to seasonal flows negatively influenced grayling survival, with increasing days of summer low flow related to decreasing adult survival, and lower winter flows related to reduced juvenile recruitment. Disruption to these flow regimes might also indirectly influence grayling survival due to the relationships between reduced summer and winter flows on higher summer temperatures and macrophyte cover respectively, both of which negatively influenced grayling survival. Our study highlights how the use of an age-structured state space model effectively identified factors influencing grayling survival that were common or specific to different life stages and thereby help prioritise actions to mitigate for these negative impacts.

The importance of seasonal flow patterns to grayling survival was expected, given that they are a typical rheophilic species (Mallet et al., 2000). Here, we found a negative influence of increasing days of summer low flow on the survival of both subadult and mature adults, but not juveniles. This contrasts with studies suggesting juvenile grayling survival is reduced in low flow conditions (Bašić et al., 2018; Riley et al., 2009), but is consistent with a study on brook trout (*Salvelinus fontinalis*), which demonstrated that extreme low summer flows reduced large trout survival in small streams, but had no significant effect on smaller-sized trout (Xu et al., 2010). This could reflect the reduced availability of refugia suitable for larger salmonids to avoid predators and harsh environmental

TABLE 3 Mean model parameter estimates (and 95% Bayesian credible intervals) of explanatory variables included in the survival model for each grayling life-stage

Model parameter	Grayling life-stage Juvenile	 Subadult	 Mature adult
Intercept	0.003 (0.002, 0.004)	−0.290 (−0.376, −0.202)	−0.361 (−0.475, −0.251)
Winter flow	**0.094 (−0.034, 0.315)**	–	–
Spawning temp	−0.002 (−0.140, 0.117)	–	−0.010 (−0.104, 0.061)
Low summer flow	0.025 (−0.070, 0.189)	**−0.214 (−0.285, −0.146)**	**−0.169 (−0.303, −0.022)**
High summer temp	**−0.178 (−0.376, 0.005)**	0.012 (−0.040, 0.070)	−0.030 (−0.157, 0.046)
Macrophyte cover	**−0.164 (−0.349, 0.004)**	**−0.069 (−0.143, −0.009)**	0.006 (−0.062, 0.091)
Invertebrate biomass	**0.098 (−0.037, 0.305)**	**0.093 (0.004, 0.195)**	**−0.100 (−0.278, 0.024)**
Trout abundance	−0.016 (−0.154, 0.070)	**0.312 (0.239, 0.389)**	0.050 (−0.039, 0.199)

Note: Bold values represent the mean model parameter estimate (with 95% Bayesian credible intervals in brackets) for variables that were retained by stochastic variable selection for inference. Winter flow = pre-spawning winter flow, invertebrate biomass = autumn biomass for juveniles and total biomass for subadults and mature adults.

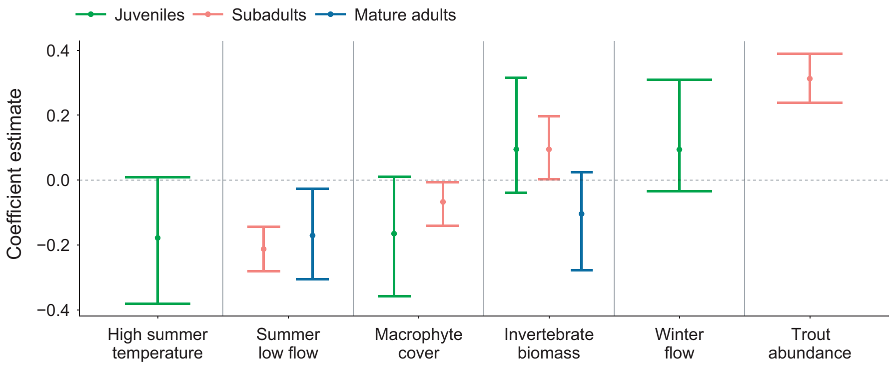

FIGURE 6 Coefficient estimates of the explanatory variables retained in the survival model for each grayling life-stage. Circles show the mean estimate and error bars denote the 95% Bayesian credible intervals. Winter flow = pre-spawning winter flow, invertebrate biomass = autumn biomass for juveniles and total biomass for subadults and mature adults

conditions, such as deep pools and river margins (Riley et al., 2009; Xu et al., 2010). Additionally, in reduced flows, invertebrate prey resources might become depleted as some taxa actively drift out of stressful environments (Dewson et al., 2007), and prey encounter rates and/or capture success of larger prey items could decrease (Nislow et al., 2004; O'Brien & Showalter, 1993). Separating the precise mechanism underpinning our observed effect of low summer flow on all grayling was not possible without further information, such as data on microhabitat use to inform habitat availability or changes to water quality, for which we do not have data, and so is beyond the scope of this work. While juvenile survival was not directly affected by low flows, survival decreased as days of high summer temperatures increased. Similarly, juvenile brook trout densities did not respond acutely to experimentally reduced summer flows, but rapidly warming water temperatures caused by the reduced flows was suggested to reduce suitable thermal habitat by 80% (Nuhfer et al., 2017). The use of air temperature data as a surrogate of water temperatures revealed conditions were close to the optimal threshold for grayling and corresponds with findings that juvenile recruitment declined in the Wylye as water temperatures exceeded 13.5°C (Bašić et al., 2018).

Higher pre-spawning winter flows were related to increased juvenile survival, perhaps because riverbed mobilising flows clear out fine interstitial material that otherwise reduce oxygen availability and so, decrease egg development and survival rates (Chapman, 1988). Although the effect of winter flows on juvenile survival was relatively weak (perhaps because it did not capture variance in flows, discussed below), this finding suggests a need to reconcile habitat management strategies for salmonids with different life histories. As other salmonid species spawn earlier than grayling, high winter flow events can be detrimental to early life-stages by causing egg wash-out (Warren et al., 2015) and have been shown to contribute to reduced survival of juvenile Atlantic salmon *Salmo salar* (Gregory et al., 2020). Consequently, it has been suggested that flow management, i.e. water abstraction, during winter could ameliorate river conditions during incubation/emergence periods for salmonids (Nislow & Armstrong, 2012), which our result suggests could be detrimental for juvenile grayling. Furthermore, a loss of high flow

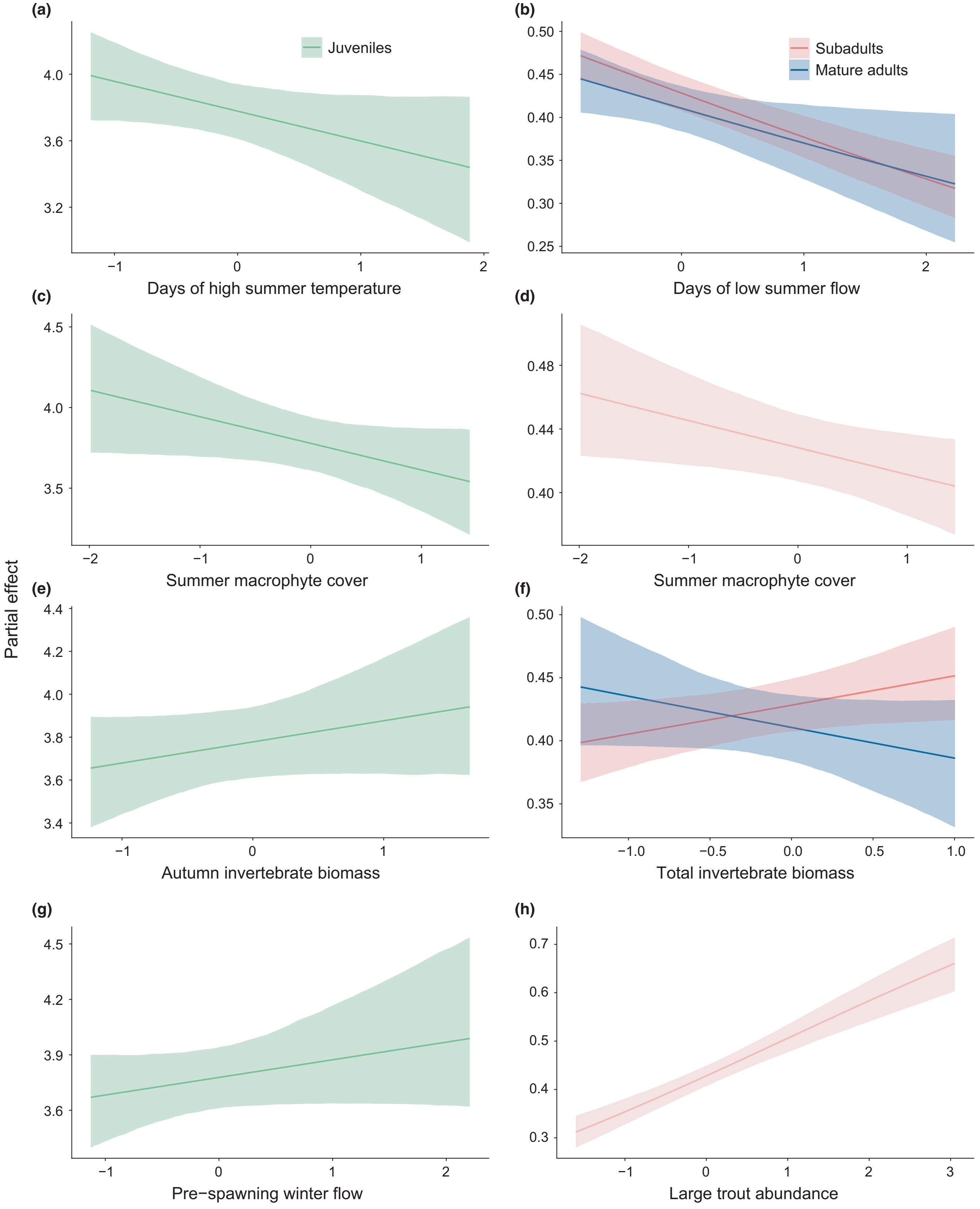

FIGURE 7 Partial effects of the standardised explanatory variables retained in the juvenile and adult grayling survival models. Panels (a), (c), (e), (g) show the partial effects of variables on the log expected number of juveniles after accounting for the effect of density dependence at the overall mean number of eggs, and panels (b), (d), (f), (h) show the partial effects of variables on subadult and mature adult survival. In all panels, the solid line is the mean estimate and the shaded area is the 95% Bayesian credible intervals

events during winter could favour accumulation of macrophyte biomass (Franklin et al., 2008), resulting in dense plant stands that trap fine sediments and reduce access to available spawning and rearing habitats (Batalla & Vericat, 2009).

Survival of juveniles and subadults was negatively related to increasing summer macrophyte cover, which consisted predominately of *Ranunculus*. When *Ranunculus* dies back in late summer, beds of retained organic material are exposed and subsequently utilised by macrophytes such as *Apium nodiflorum* and *Rorippa nasturtium-aquaticum* (Dawson, 1988). High summer *Ranunculus* cover might therefore lead to high macrophyte cover during autumn, reducing access to the benthos for feeding. Indeed, juvenile and subadult survival was positively related to higher macroinvertebrate biomass, suggesting that young grayling were sensitive to changes in prey availability. Reduced resources can slow summer growth, which is crucial for salmonids if they are to gain sufficient size and therefore swimming performance to avoid predators, particularly those that are gape-limited (Zabel & Achord, 2004). Indeed, the size attained as a juvenile salmonid has the potential to impact survival processes throughout its lifetime (Zabel & Achord, 2004). Environmental conditions, such as low flows, can reduce juvenile salmonid growth but not survival (Nislow et al., 2004; Nuhfer et al., 2017), which could reduce their size as spawning adults, lowering their reproductive potential (Barneche et al., 2018). Understanding how environmental factors influence grayling growth rates, and the extent to which growth impacts survival, was beyond the scope of this study, but is a logical next step for these data.

Our results suggested that adult trout were not negatively impacting grayling survival through interspecific competition or predation. Rather, we found a positive association between adults of the two species, perhaps representing a preference for similar habitats, such as deep pools and faster velocities (Riley et al., 2009). We might therefore expect adult trout to be similarly sensitive to environmental changes as grayling, although the higher abundance of adult trout relative to adult grayling in our study river suggests that trout might be more resilient, perhaps by merit of their plasticity and less restrictive habitat requirements (Klemetsen et al., 2003).

We highlight several benefits of our modelling approach for understanding the factors affecting population dynamics. Our approach estimated actual population sizes despite imperfect sampling of the population, a common scenario when studying freshwater fish populations (Radinger et al., 2019). Incorporating a group-specific probability of capture was justified, as juvenile capture efficiency was estimated to be low compared to older, larger life stages (Dauphin et al., 2019). Developing a single model to simultaneously estimate survival of different life stages as a function of environmental effects allowed for propagation of uncertainty among linked model components and thus improved the robustness of estimated environmental effects (Letcher et al., 2015; Rivot et al., 2004). We note, however, that our analysis was limited by the data available for analysis; other variables such as fine deposited sediment, dissolved oxygen, angling pressure, and predators other than trout might also impact grayling population dynamics, but we lacked data to test them. Moreover, where these variables have been tested on grayling populations, their effects have been context specific. For example, predation by cormorants (*Phalacrocorax* spp.) was estimated to have caused mortality of >70% of grayling tagged in Danish rivers across a 10-year period (Jepsen et al., 2018), whilst Suter (1995) found no evidence to suggest a negative impact of cormorant predation on grayling population dynamics in a Swiss river.

The River Wylye grayling surveying programme was designed to monitor grayling at fixed long-term sites rather than random locations each year, which enabled measurement of changes to the resident population and their relationships to annually varying explanatory variables while holding constant (at least relatively) differences in other variables, including upstream location, proximity to pollution source, major habitat differences and adjoining land use. However, this also potentially exposed individual fish to repeated capture by electrofishing, albeit with capture events only occurring once per year. While electrofishing can cause fish mortality, it is generally acknowledged that this method causes negligible impact to population abundances (e.g. McMichael et al., 1998). Moreover, a previous study on grayling age analysis using Wylye survey data revealed individual recapture rates by electrofishing were sufficiently high to enable an age-validation exercise (Horká et al., 2010), thus at least some individuals were surviving capture by electrofishing.

Chalk streams provide relatively stable temperature and flow regimes (Sear et al., 1999), and so the flow conditions of the study river might not represent those encountered by non-chalk stream populations. Correspondingly, we suggest that other extreme discharge events than those tested here could be relevant to grayling survival. For example, mean winter discharge was used to test the hypothesis that higher winter flow would promote greater juvenile survival (through cleaning of spawning gravels). Although we detected a positive influence of mean winter flow on juvenile survival, the effect was weak and variable, which could suggest that winter flow is not an important influence on juveniles or that this variable did not capture extreme discharge events well. While we did initially explore the number of high flow events during winter, there was insufficient variation to enable testing for an influence of high winter flow on grayling survival. However, we would recommend consideration of this variable in grayling studies in non-chalk stream environments. Indeed, it might be beneficial to have comparative grayling studies established on higher latitude, rain-fed rivers in order to test whether factors affecting survival are context-specific or can be generalised across the species range and river types. Nonetheless, that we detected effects of temperature and flow on grayling survival in a river with some buffering against extremes suggests that these variables might have even stronger effects on populations that inhabit more dynamic river systems.

Our findings raise some important management issues and suggest tangible pathways to improve the outlook for this and other salmonid populations. Limiting abstraction of water for public supply during sensitive periods of the year could mitigate impacts, and water trading between neighbouring water companies could be a viable option to minimise impacts whilst still supplying consumer demand.

Measures have been in place on the River Wylye since 2018 to ensure that natural Q95 is not reduced by more than 10% during summer/autumn and 15% in winter, beyond which the reduced flow is likely to negatively impact freshwater species (UKTAG, 2008). While these limits were devised using long-term hydrological records, these data are not current, and the explanatory variables here suggest that flow conditions are changing (e.g. above average days of low summer flow on the Wylye in the last 5 years). We suggest an adaptive management approach that regularly reassesses these regulations to account better for current trends and any shifts in natural Q95 levels. Identifying habitats used predominately by grayling would help direct targeted restoration or maintenance, such as removing macrophytes from known spawning areas during low flow winters. Similarly, reaches with 'naturally' limited macrophyte growth (due to deep water or shading) could be improved to act as 'grayling recruitment zones'. A mosaic of riparian canopy cover achieved from tree planting or management could reduce macrophyte cover with limited in-river disturbance, whilst also providing shade to alleviate high summer temperatures (Cole et al., 2020). This might also promote macrophyte cover in unshaded areas during the summer months to support other salmonid species that benefit from macrophyte cover (Marsh et al., 2020), and ensure abundant macroinvertebrate prey to improve survival of both juvenile and adult grayling. Although not directly tested in our model, we considered the negative impact of reduced winter flows on juvenile recruitment was likely to be linked to increased sediment within spawning gravels (Chapman, 1988). A medium-term aim might be to reduce sediment (and nutrient) input into rivers, such as the River Wylye, through measures such as phosphate stripping at water treatment works, where the introduction of sand filters to meet a tighter phosphorus consent will further reduce suspended solids in the effluent (A. House, personal communication, July 2020). Ultimately, however, longer-term strategies to reduce sediment input from intense agricultural practices, such as riparian buffers to trap sediment and nutrients and the adoption of less intensive agricultural practices should be targeted (Cole et al., 2020).

In summary, our results reveal the implications of environmental change on a salmonid population, where recent low summer flows and high temperatures, and below average winter flows, have negatively influenced grayling survival. These conditions appear to be becoming more frequent and persistent in our study river, at the species' southern range limit, which together suggests that this population might be highly vulnerable to future climate change (Huml et al., 2020). Our study emphasises how combining: (1) long-term and detailed population monitoring datasets; (2) expertise in the analysis of these data together with data of environmental change; and (3) expertise in local issues, such as habitat management and water industries, can identify the influences of environmental change on fish population dynamics and propose realistic mitigation measures to promote their future persistence.

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DATA AVAILABILITY STATEMENT

The data and code for a replicable simulated example are available upon reasonable request from the authors.

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SUPPORTING INFORMATION

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

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