


# Environmental conditions modify density-dependent salmonid recruitment: Insights into the 2016 recruitment crash in Wales

Stephen D. Gregory<sup>1</sup>  | Victoria E. Bewes<sup>2</sup> | Andrew J.H. Davey<sup>2,3</sup> | Dylan E. Roberts<sup>1</sup> | Peter Gough<sup>4</sup> | Ian C. Davidson<sup>5</sup>

<sup>1</sup>Salmon & Trout Research Centre, Game & Wildlife Conservation Trust, East Stoke, UK

<sup>2</sup>WRc plc, Blagrove, Swindon, UK

<sup>3</sup>APEM Limited, Abingdon, UK

<sup>4</sup>Natural Resources Wales, Cardiff, UK

<sup>5</sup>Natural Resources Wales, Buckley, UK

## Correspondence

Stephen D. Gregory, Salmon & Trout Research Centre, Game & Wildlife Conservation Trust, East Stoke, Dorset BH20 6BB, UK.

Emails: sgregory@gwct.org.uk; stephendavidgregory@gmail.com

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## Abstract

1. Understanding the effects of density-dependent and density-independent factors on recruitment is often inhibited by difficulties quantifying their relative contributions in highly variable recruitment data. Use of data-driven statistical methods with data that include one or more extreme recruitment events could help overcome these difficulties.
2. Juvenile Atlantic salmon and trout abundances in Wales have declined over the last 2 decades, and 2016 was a notably poor recruitment year in rivers around southern Europe, including England and Wales. The 2016 recruitment crash coincided with extreme winter weather conditions, leading to speculation that unusually warm temperatures and high flows adversely affect salmonid recruitment and caused the 2016 crash, although this remains untested.
3. We developed data-driven statistical models to: (1) describe juvenile salmonid recruitment from density-dependent and density-independent factors; and (2) assess whether the density-independent factors probably contributed to the 2016 salmon recruitment crash. We compiled salmon and trout young-of-year juvenile abundances from electrofishing surveys, egg deposition estimates and river flow and air temperature data from 2001–2017 for seven Welsh rivers, broadly representative of rivers around Wales. We used river flow and air temperature data to derive ecologically and behaviourally meaningful density-independent explanatory variables.
4. Salmonid recruitment in Wales was best described using density-dependent and density-independent factors, especially for salmon: after accounting for a concave relationship with egg deposition, salmon juvenile abundance was reduced under (1) warmer spawning temperatures that might inhibit spawning, and (2) higher flood frequencies during pre-emergence and emergence that might washout eggs or alevins. Results were less clear for trout, perhaps because they are behaviourally more plastic.
5. Our findings provide empirical support for general and predictable effects of temperature and flow during spawning and emergence on salmonid—especially salmon—recruitment in Wales. Furthermore, we suggest that the 2016 salmon recruitment crash was caused—in part—by particularly inclement spawning and

emergence conditions, which could be more common under future climate change. Our findings suggest that future salmonid stock assessment models could include the effects of density-independent variables on recruitment to improve their predictive power.

#### KEYWORDS

climate change, egg survival, river flow, spawning, water temperature

## 1 | INTRODUCTION

Changes in fish populations are driven primarily by variation in recruitment (Rothschild, 2000), which can be defined as the number of fish surviving to a certain early life history stage. Given its important role in fish population dynamics, there has been considerable effort devoted to understanding variation in recruitment, as embodied in numerous large meta-analyses. For example, Myers (2001) used a meta-analytic approach to identify general patterns in recruitment variation from across over 700 fish populations and found that variation was highest in small populations of high-fecundity species at the edge of their geographical range. Stige et al. (2019) explored patterns of recruitment in six economically important marine fish populations and found that variation was size- and stage-specific, perhaps related to competition for limiting habitat. However, despite these and many similar studies, our understanding of factors affecting recruitment in wild fish populations is still considered poor (Maunder & Thorson, 2019), in part due to the simplifying assumptions we make when statistically analysing recruitment data (Dickey-Collas, Hintzen, Nash, Schön, & Payne, 2015). Our limited understanding of the factors causing variation in recruitment has hindered the development of fish stock assessment models and threatens to render them obsolete in the future (Subbey, Devine, Schaarschmidt, & Nash, 2014).

Atlantic salmon *Salmo salar* and trout *Salmo trutta*, here referred to collectively as *salmonids*, are economically important species throughout their geographical range, and notably across the British Isles (Butler, Radford, Riddington, & Laughton, 2009; Mawle, 2018). Their populations have, however, declined in abundance across large parts of their range in recent decades (Ahlbeck-Bergendahl et al., 2019; Limburg & Waldman, 2009; Mills, Pershing, Sheehan, & Mountain, 2013; Parrish, Behnke, Gephard, McCormick, & Reeves, 1998). Together, these factors have motivated substantial effort to understand the strength and direction of factors thought to drive changes in salmonid population abundances, with a particular focus on recruitment dynamics in freshwater. For example, Clews, Durance, Vaughan, and Ormerod (2010) explored the effects of climatic factors on juvenile salmonid abundances in the River Wye, Wales, between 1985 and 2004 and found that composite variables representing hotter and drier summers best captured observed fluctuations and declines in their relative densities. Similar studies have been undertaken on salmonids in other rivers around the British Isles, including on the River Foyle in north-west of Ireland

(Honkanen, Boylan, Dodd, & Adams, 2018), the Girnock Burn, a tributary of the Scottish Dee (Gurney et al., 2010), and rivers of the Upper Severn in Wales (Cowx & Gould, 1989).

By understanding factors affecting salmonid recruitment, we strive to predict how changes in those factors might affect future population sizes and what we might do to mitigate their negative impacts (Subbey et al., 2014). With this in mind, it is desirable to identify general rules that govern salmonid recruitment during their freshwater life stage. Indeed, several authors have attempted to synthesise empirical evidence for different factors affecting salmonid recruitment (Jonsson & Jonsson, 2009; Jonsson, Jonsson, & Hansen, 1998; Milner et al., 2003). For example, Milner et al. (2003) reviewed the evidence for just such governing rules and concluded that although there was empirical support for some basic tenets of population dynamics, such as a role for density-dependent competition for limiting resources and common density-independent factors affecting later freshwater life stages, there was also plenty of empirical support to the contrary, and general governing rules were still beyond our understanding. Some authors have suggested that inconsistent findings across recruitment studies might be due to differences in their spatial or temporal focus, the life-stages and explanatory variables they considered, and the simplifying assumptions embodied in the statistical methods that they used (Milner et al., 2003).

Even if general governing rules about the factors affecting recruitment were available, disentangling their relative contributions to observed recruitment would be challenging. For example, Rose (2000) listed six reasons that could complicate quantifying the influence of different factors on recruitment, including imperfect measurement and the possibility that effects could be sublethal or cumulative. Several authors have considered whether different statistical approaches could help overcome some of these difficulties, with a focus on disentangling density-dependent factors (e.g. spawning stock biomass) from density-independent factors (e.g. environmental variables, such as sea surface temperature) (e.g. Maunder & Thorson, 2019). For example, Dickey-Collas et al. (2015) explored how methods embodying different forms of density-dependence in recruitment, e.g. deterministic versus random walk, affected inferences drawn from three contrasting recruitment datasets. They suggested that methods with strong assumptions about the form of density-dependence in recruitment, such as the Beverton-Holt model, were appropriate for single data-rich stocks (e.g. Baglinière, Marchand, & Vauclin, 2005; Basic, Britton, Cove, Ibbotson, & Gregory, 2018), but that more data-driven, statistical models were

more appropriate for data-poor single stocks or analyses designed to draw inference from multiple stocks (Dickey-Collas et al., 2015). Such data-driven methods have already been used to investigate the relative influences of density-dependent and density-independent factors on recruitment in many species. For example, Daskalov (1999) used generalised additive models to show that spawning biomass, wind, and atmospheric pressure influence recruitment dynamics of four marine fishes, although in different ways.

Aside from choice of statistical methods, our understanding of how different factors affect recruitment could be improved when data include one or more extreme recruitment events, together with associated ancillary data to inform possible mechanisms (Altwegg, Visser, Bailey, & Erni, 2017). For example, Blum, Kanno, and Letcher (2018) found that extreme seasonal river flows explained a non-negligible amount of the observed high variation in young-of-year (hereafter age 0+) juvenile brook trout *Salvelinus fontinalis* counts collected over 28 years and 115 sites in Virginia, USA. Interestingly, they used the same data-driven generalised additive models as Daskalov (1999). Milner et al. (2003) highlighted the potential importance of observed extreme events in understanding and quantifying the factors affecting salmonid population dynamics. Just such an extreme event was observed in rivers throughout southern Europe that reported all-time low juvenile salmonid abundances in 2016, notably in England and Wales (APEM, 2018; ICES, 2017, 2018). Given the spatial extent of this 2016 recruitment crash, the factors precipitating it were hypothesised to be climatic, and to include: (1) record high rainfall associated with the arrival of storm Desmond in December 2015 that caused high river flows affecting salmonid spawning behaviour and egg to fry survival; (2) record high temperature during the winter of 2015/2016 that affected salmonid egg to fry survival, and (3) local factors, such as fluctuations in river-specific salmon spawning stocks (APEM, 2018; ICES, 2017, 2018). These hypotheses are hitherto untested and there has been no formal, quantitative comparison of

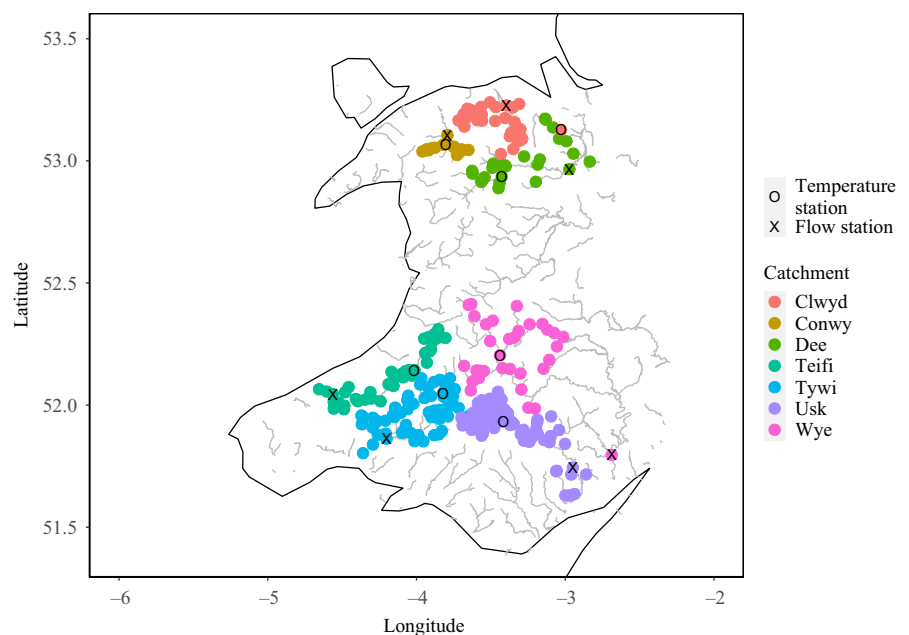
their empirical support compared to alternative explanations, such as river conditions at other times of the year.

The aims of this study were: (1) to describe annual variations in juvenile salmonid recruitment in Wales over the last 2 decades using explanatory variables representing density-dependent factors and a range of ecologically and behaviourally meaningful density-independent factors; and (2) to assess the extent to which these density-independent factors might have contributed to the salmon recruitment crash observed in 2016. We predicted that salmonid recruitment would be density-dependent and lower in years of high overwinter river flows and temperature and high spring river flows. Furthermore, we predicted that these conditions would characterise the spawning conditions preceding the 2016 recruitment crash. We tested our predictions using data collected by Natural Resources Wales/Cyfoeth Naturiol Cymru (and predecessor organisations, hereafter NRW) between 2001 and 2017 on seven Welsh rivers, broadly representative of rivers around Wales. We tested our predictions using data-driven statistical models that limited the number and impact of any simplifying assumptions.

## 2 | METHODS

### 2.1 | Study area and fish sampling

We used abundance data for juvenile salmonids from a subset of the NRW spatial and temporal salmonid monitoring programme data collected between 2001 and 2017 on seven Welsh rivers, namely, Clwyd, Conwy, Dee, Teifi, Tywi, Usk, and Wye (Figure 1). Our analysis focused on annual single-run electrofishing surveys (hereafter survey) undertaken in a standardised way, i.e. always done in July–September, using similar personnel and sampling methods, and equipment and settings (e.g. methodical upstream, bank-to-bank



**FIGURE 1** Locations of electrofishing sites in Wales, coloured by river catchment, sampled by Natural Resources Wales for juvenile salmonid abundance between 2001 and 2017. Stations used for temperature and flow data are also shown [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

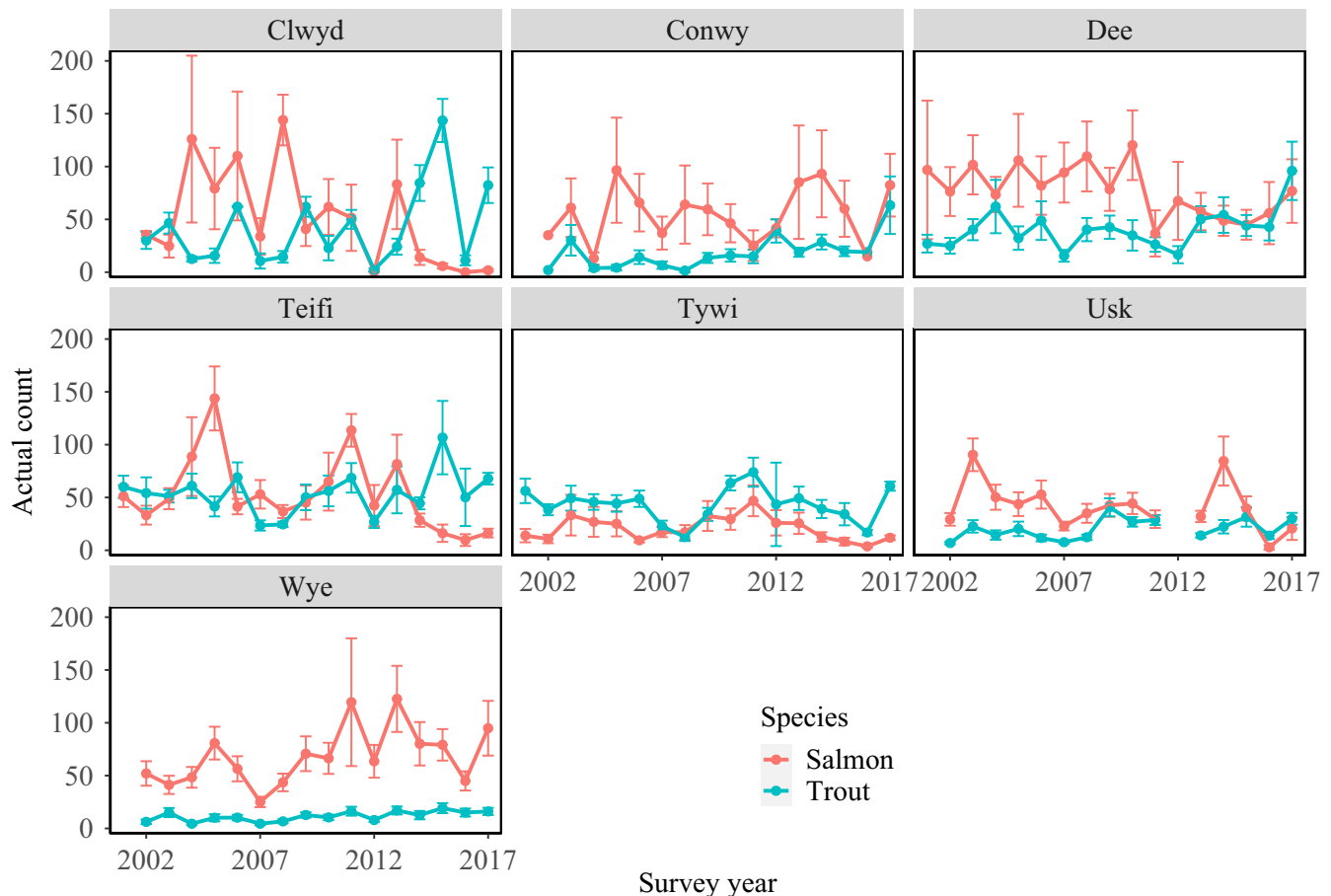
fishing by anode and netsmen using smooth or pulsed direct current to suit conditions of water conductivity); other data from this monitoring programme, such as the second and subsequent electrofishing passes done during multi-pass surveys and timed surveys, were excluded from analysis because they differed in their variability or were limited in time or space. These precautions helped minimise potentially spurious results due to different survey protocols (Millar, Fryer, Millidine, & Malcolm, 2016). We had to further reduce these data to ensure they were unbiased and amenable to our analysis; we removed: (1) sites that local experts deemed to be either inaccessible to adult spawners, to have changed in accessibility during the survey period, or (rarely) where salmon or trout had been stocked; (2) surveys that were outside the normal July-September survey window; (3) surveys where the area electrofished was not recorded; and (4) sites with four or fewer surveys, which would inhibit the estimation of stable random effect variances (Harrison et al., 2018). This left a total of 1,760 surveys undertaken between 2001 and 2017 at a total of 343 sites across 7 catchments for our analyses (Figure 1).

We focused our analyses on age 0+ fish (i.e. young-of-the-year salmonids that hatched from eggs in spring) because: (1) age 0+ fish represent a substantial proportion of juvenile salmonid populations in most of these rivers; (2) the growth and survival of age 0+ fish is expected to be more strongly influenced by prevailing

environmental conditions compared to older juveniles (Nislow & Armstrong, 2012); and (3) part or all of the older cohorts might have migrated downstream as smolts during the previous spring or those that stayed might have adopted unusual life history strategies, such as early maturity (Baglinière & Maise, 1985). We understand that older juvenile salmonids constitute a significant proportion of many Welsh salmonid juvenile stocks, particularly trout (APEM, 2018). Consequently, we note that our findings are limited to understanding the density-dependent and density-independent factors affecting early salmonid recruitment in Wales. Plots of the mean number of age 0+ juveniles caught across all sites per year are shown in for each river in Figure 2 and the numbers of sites surveyed per year for each river is shown in Table 1.

## 2.2 | Spawning level data

To represent the influence of density-dependence in survival from eggs to alevins, which is thought to be a bottleneck in salmonid survival (Jonsson et al., 1998), NRW calculated annual catchment-level estimates of egg deposition for each species based on rod catch and exploitation rate (or count/trap estimate) and the size and sea-age of returning migratory adults. These egg deposition estimates



**FIGURE 2** Line plots showing the mean (with standard error) of age 0+ juvenile salmon and trout counts over sites in seven Welsh river catchments electrofished by Natural Resources Wales between 2001 and 2017 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 1** Numbers of sites surveyed for juvenile Atlantic salmon and trout across seven Welsh river catchments by Natural Resources Wales between 2001 and 2017. Row, column, and overall totals are also given

Year	River catchment							Total
	Clwyd	Conwy	Dee	Teifi	Tywi	Usk	Wye	
2001			5	12	9			26
2002	2	1	9	11	17	52	17	109
2003	20	5	8	35	12	17	26	123
2004	2	7	9	13	12	13	21	77
2005	5	4	12	4	11	20	23	79
2006	2	5	9	13	43	16	22	110
2007	5	5	10	6	7	50	23	106
2008	2	2	9	37	10	25	24	109
2009	23	4	7	6	10	18	27	95
2010	5	6	11	5	53	31	25	136
2011	6	8	19	7	14	15	10	79
2012	4	2	9	8	2	NA	25	50
2013	8	7	23	5	14	57	24	138
2014	5	9	19	32	10	12	30	117
2015	27	9	20	6	11	13	24	110
2016	5	1	11	6	58	15	23	119
2017	17	8	10	38	56	25	23	177
Total	138	83	200	244	349	379	367	1,760

**TABLE 2** Local expert-defined start and end dates for key Atlantic salmon and trout life-history events that could be considered either annually invariant or in the case of pre-emergence, emergence, and post-emergence events, as a function ( $f$ ) of the estimated peak emergence date ( $PE$ ) and temperature ( $T$ )

Period	Salmon		Trout	
	Start	End	Start	End
Pre-spawning	15-Sep	31-Oct	01-Sep	15-Oct
Spawning	01-Nov	31-Dec	16-Oct	30-Nov
Pre-emergence	01-Jan	$f(PE, T) - 15$ d	01-Dec	$f(PE, T) - 15$ d
Emergence	$f(PE, T) - 14$ d	$f(PE, T) + 28$ d	$f(PE, T) - 14$ d	$f(PE, T) + 28$ d
Post-emergence	$f(PE, T) + 29$ d	30-Jun	$f(PE, T) + 29$ d	30-Jun
First summer	01-Jul	31-Aug	01-Jul	31-Aug

were expressed as a percent of the river-specific conservation limits (Centre for the Environment, Fisheries, & Aquatic Science, Environment Agency and Natural Resources Wales, 2019; Natural Resources Wales, 2017).

### 2.3 | Environmental data

Density-independent influences on age 0+ salmon and trout recruitment dynamics were represented using a range of temperature and flow variables (hereafter *environmental variables*). To ensure that these were ecologically and behaviourally meaningful, we defined periods encapsulating key life history events expected to most strongly influence age 0+ recruitment, namely: *pre-spawning*, *spawning*, *pre-emergence*, *emergence*, *post-emergence*, and *first summer*. These periods were defined using a combination of expert opinion

and calculations, summarised in Table 2. First, local fisheries experts, usually NRW staff, were asked to give dates corresponding to the start and end of each key event that could, in the absence of evidence to the contrary, be considered annually invariant. Next, we defined the peak spawning date as 1 December for salmon and 1 November for trout, i.e. the date in the middle of the expert-defined spawning period. Annually variable peak emergence dates were then calculated as a function of peak spawning dates and temperature. The incubation period between spawning and hatching for both species is approximately 100 days at 5°C and 50 days at 10°C, and the period between hatching and emergence is approximately 38 days at 7.5°C (Solomon & Lightfoot, 2008; and verified by J. Taylor). The degree days between peak spawning and peak emergence was therefore calculated as  $100 \times 5 + 38 \times 7.5 = 785$  degree days. With this information, we used year- and location-specific mean daily temperature data to calculate the approximate peak emergence date

in each catchment in each year (Figure 3). Due to the lack of water temperature data for most catchments, we used gridded air temperature data (E-Obs gridded data, version 17.0; <https://www.ecad.eu/download/ensembles/ensembles.php>; Figure 1) and the derived dates were corrected by subtracting 28 days based on a comparison of peak emergence dates calculated using the limited water temperature data available with dates calculated using air temperature data. The start and end dates for the pre-emergence, emergence, and post-emergence periods were then calculated as a fixed number of days before or after the peak emergence date based on expert opinion, as shown in Table 2.

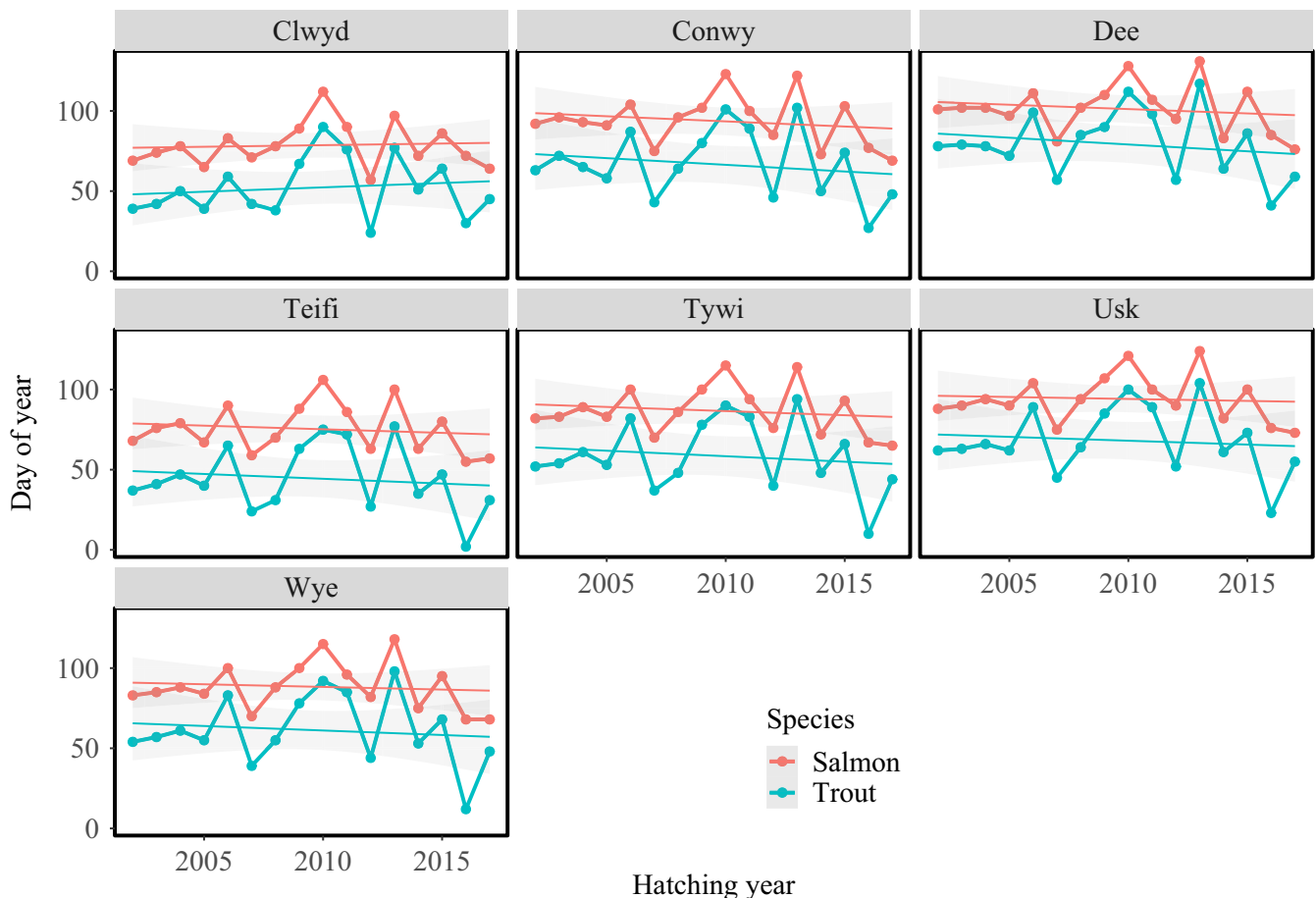
We used the species- and year-specific key life history event dates to define ecologically meaningful environmental variables. Broadly, these were classified as temperature and flow variables. Because temperature variables were necessarily calculated from air temperatures, we restricted variables to period-specific means. A flood was defined as a high pulse when river-specific flow was between 3 and 5 times above the 50% flow (Q50) river level. A drought was defined as a day when river-specific flow was below the Q90 river level. The flow data were obtained for the most complete and downstream gauging station in each river from the National River Flow Archive (<https://nrfa.ceh.ac.uk>; Figure 1) and the Q50 and Q90 values are based on hydrological definitions from the UK Centre for

Ecology and Hydrology (<https://nrfa.ceh.ac.uk/derived-flow-statistics>). We compiled a large number of potential environmental variables (Table S1) and then used opinions gleaned from discussions with local experts, usually NRW staff, and pairwise Pearson's correlations to reduce it to a set of statistically independent environmental variables that were hypothesised to most strongly influence age 0+ salmonid recruitment dynamics (Table 3).

Before analysis, all spawning level and environmental variables were z-standardised by subtracting their mean and dividing by their standard deviation.

## 2.4 | Data analysis

We used generalised additive mixed models (GAMM; Pedersen, Miller, Simpson, & Ross, 2019) to describe juvenile salmonid recruitment using a range of density-dependent and density-independent environmental explanatory variables and generalised linear mixed models (GLMM; Venables & Ripley, 2002) to assess whether 2016 was an unusual salmonid recruitment year compared to other survey years. We included a site nested within catchment random effect in each model that allowed us to generalise our findings beyond the specific sites and catchments considered, while still accounting



**FIGURE 3** Line plots showing the peak emergence date calculated for salmon and trout alevins in each year between 2001 and 2017 for each of seven Welsh river catchments used in this study [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 3** Expert-agreed and statistically independent (pairwise correlations were all  $r < 0.6$ ) ecologically meaningful variables used in models to describe annual variation in age 0+ salmon and trout abundances collected across seven Welsh river catchments by Natural Resources Wales between 2001 and 2017

Type	Period	Life stage	Variable name	Variable description	Hypothesised direction of effect	References
Egg deposition		Fry	Egg deposition	Estimated egg deposition as a percent of river conservation limit	+/-	1
Flow	Pre-spawning	Spawning adult	Pre-spawning flow	Mean flow during pre-spawning	+/-	2,3
Flow	Pre-spawning	Spawning adult	Pre-spawning floods	Number of high flow pulses between 3 and 5 times long-term Q50 during pre-spawning	+/-	2,3
Flow	Spawning	Spawning adult	Spawning flow	Mean flow during spawning	+/-	2,3
Flow	Pre-emergence	Egg & embryo	Pre-emergence flow	Mean flow during pre-emergence	+	2,4
Flow	Pre-emergence	Egg & embryo	Pre-emergence floods	Number of high flow pulses between 3 and 5 times long-term Q50 during pre-emergence	-	5,4
Flow	Emergence	Fry	Emergence flow	Mean flow during emergence	+	2,4
Flow	Emergence	Fry	Emergence floods	Number of high flow pulses between 3 and 5 times long-term Q50 during emergence	-	5,4
Flow	Post-emergence	Fry	Post-emergence flow	Mean flow during post-emergence	+/-	6,4
Flow	Post-emergence	Fry	Post-emergence droughts	Number of days below long-term Q90 flow during post-emergence	-	7,4
Flow	Post-emergence	Fry	Post-emergence floods	Number of high flow pulses between 3 and 5 times long-term Q50 during post-emergence	-	6,4
Flow	First summer	Fry	First summer droughts	Number of days below long-term Q90 during first summer	-	8,4
Temperature	Pre-spawning	Spawning adult	Pre-spawning temp.	Mean temperature during pre-spawning	+/-	9
Temperature	Spawning	Spawning adult	Spawning temp.	Mean temperature during spawning	+/-	9
Temperature	Pre-emergence	Egg & embryo	Pre-emergence temp.	Mean temperature during pre-emergence	+/-	10,11
Temperature	Emergence	Fry	Emergence temp.	Mean temperature during emergence	+/-	12
Temperature	Post-emergence	Fry	Post-emergence temp.	Mean temperature during post-emergence	+/-	13,10
Temperature	First summer	Fry	First summer temp.	Mean temperature during first summer	+/-	12,13
Day of year		Fry	Day of year	Day of year of the survey	-	

References: 1, Milner et al. (2003); 2, Malcolm et al. (2012); 3, Parry, Gregory, Lauridsen, and Griffiths (2018); 4, Warren et al. (2015); 5, Crisp and Carling (1989); 6, Jonsson, Hansen, and Jonsson (1991); 7, Riley, Maxwell, Pawson, and Ives (2009); 8, Nislow, Sepulveda, and Folt (2004); 9, Taranger and Hansen (1993); 10, Basic et al. (2018); 11, Jonsson and Jonsson (2009); 12, Elliott (1994); 13, Elliott and Elliott (2010).

for the variation in abundance observed at the lowest level of spatial organisation, i.e. the site. Separate models were fitted for salmon and trout.

For both GAMM and GLMM, we used site-level survey counts as our response variable. Site-level counts were highly variable in space and time. Furthermore, the surveys often recorded an absence of age 0+ salmon or trout. Consequently, we assumed a zero-inflated negative binomial error structure with a log-link, which estimates an overall probability of a given count mixed with the probability of drawing a zero given an expected count. Such a model is designed to quantify the effects of explanatory variables on observed counts while accounting for high variability due to spatio-temporal differences in counts, zero counts and the high variation in the recruitment process or our observations of it. The models took the general form (omitting year notation for simplicity):

$$p(n_{s,c}|\omega, \mu_{s,c}, \theta) = \begin{cases} \omega + (1-\omega) \times \text{negbin}(0|\mu_{s,c}, \theta) & \text{if } n_{s,c} = 0, \text{ and} \\ (1-\omega) \times \text{negbin}(n_{s,c}|\mu_{s,c}, \theta) & \text{if } n_{s,c} > 0 \end{cases}$$

$$\mu_{s,c} = \exp\left(\alpha + \sum_{m=1}^M f_m(x_m, k_m) + v_s + v_c + \ln(\text{Area})\right)$$

$$v_s \sim \text{Student-t}(0, \sigma_s, 3)$$

$$v_c \sim \text{Student-t}(0, \sigma_c, 3)$$

where  $n_{s,c}$  is the number of age 0+ fish captured in site  $s$  in catchment  $c$ , which is estimated as a mixture of the following probabilities: the probability  $1 - \omega$  of  $n_{s,c}$  being zero and drawing a zero value from a negative binomial distribution with mean expected count  $\mu_{s,c}$  given dispersion parameter  $\theta$ , and the probability of drawing the true value from the same negative binomial distribution when  $n_{s,c}$  is greater than zero. The expected count  $\mu_{s,c}$  is a function of constant  $\alpha$ , smooth terms  $f_m$  with  $k_m$  degrees of freedom representing the effects of  $M$  annual explanatory variables  $x_m$  on  $\mu_{s,c}$ , nested random effects of site  $v_s$  within catchment  $v_c$ , and their respective variances  $\sigma_s$  and  $\sigma_c$  assumed to take a Student- $t$  distribution that is better suited to data with possible outliers (Burkner, 2017). A  $\ln(\text{Area})$  offset was included to correct for differences in counts due to area fished, which is analogous to describing densities, but allowing for a more natural treatment of over-dispersion with or without abundant zeros.

To explore the factors affecting salmon and trout recruitment, we modelled combinations of environmental explanatory variables as semi-parametric smooth and parametric polynomial terms. To facilitate model inference, we simplified semi-parametric smooth terms to parametric polynomials: if the variance (effective degrees of freedom) of the smooth term was estimated  $\leq 1$ , then it was simplified to a first-order polynomial, i.e. a linear term, else if the variance of the smooth term was  $> 1$  and  $\leq 2$ , then it was simplified to a second-order polynomial, i.e. a quadratic term, else the smooth term was retained, unless it was judged visually that the smooth term could be simplified to a first- or second-order polynomial without loss of ecological meaning. Where the credible intervals of the second-order polynomial term overlapped zero, the complexity was

considered ecologically meaningless and the term was simplified to a first-order polynomial.

After simplifying semi-parametric smooths to parametric polynomial terms, we further simplified the models by removing terms whose estimated effect size was considered to be ambiguous. We removed terms iteratively, removing all terms whose estimated 95% credible interval range overlapped zero, until the 95% credible intervals of the remaining terms did not overlap zero. We used this final model for inference. This approach was similar to a frequentist backwards step-wise model selection procedure, only we removed terms based on their 95% probable effect size to reduce the possibility of retaining ecologically meaningless but statistically significant terms.

To assess whether 2016 was an unusual recruitment year compared to other survey years, we included only a fixed year effect ( $\beta_{\text{year}}$ ) as an explanatory variable in the GLMM, i.e.  $f_m$  was reduced to a linear term with  $k_m = 1$  relating a matrix of dummy variables representing different years to  $\mu_{s,c}$ . We set 2016 as the contrast level so that the effect of all other years would be contrasted against recruitment year 2016, and then extracted and plotted the effect (and their uncertainties) of each year on the expected age 0+ count.

The posterior distributions of GLMM and GAMM parameters were estimated from 4,000 Markov chain Monte Carlo iterations (four parallel chains run for 20,000 iterations with a 10,000 iteration warmup and thinning rate of 10) using NUTS sampling implemented in Stan (<https://mc-stan.org/>) and specified using R (<http://www.r-project.org/>) package brms (Burkner, 2017). Convergence was assessed by visual examination of Markov chain Monte Carlo trace plots and the Gelman–Rubin statistic (Brooks & Gelman, 1998), and were considered stable if the chains were mixing and non-convergent, i.e.  $r$  ratio of the Gelman–Rubin test  $< 1.05$  for all parameters. We used weakly informative priors: Normal ( $\mu = 0, \sigma = 1$ ) for the coefficients representing explanatory variable effects on juvenile salmonid abundances; Student- $t$  ( $\mu = 0, \sigma = 10, \nu = 3$ ) for the random effect variances, which included the smooth term variances; and Gamma ( $\mu = 0.01, \alpha = 0.01$ ) and Beta ( $\mu = 1, \phi = 1$ ) for the negative binomial shape parameter  $\theta$  and the zero-inflated probability parameter  $\omega$ , respectively.

Model goodness-of-fit was measured by Bayesian  $r^2$ , which can be interpreted as the proportion of variance explained by the model. In the case where there is a random structure, i.e. the site nested within catchment random effect structures used in these models, the  $r^2$  value can be broken down into conditional  $r^2$  that is an overall  $r^2$  value and a marginal  $r^2$  that measures the variance explained by the fixed effect structure, i.e. the annual density-dependent and density-independent factors in these models.

## 3 | RESULTS

### 3.1 | Long-term trends

Annual mean age 0+ salmon and trout counts were variable for these rivers, as would be expected given that they represent both



**TABLE 4** Model estimated coefficients values (and their 95% credible intervals) for density-dependent and density-independent factors affecting age 0+ salmon abundances collected across seven Welsh river catchments by Natural Resources Wales between 2001 and 2017. Models started with the Saturated model including all variables and was simplified by variable deletion over two steps (Simplified 1 and 2) and a final simplification step to produce the final model. Conditional  $r^2$  is the variance explained by the model; marginal  $r^2$  is the amount of that explained by the fixed terms, i.e. the variables of interest

Variable name	Term order	Model			
		Saturated	Simplified 1	Simplified 2	Final
Intercept		-3.22 (-3.95 to -2.42)	-3.26 (-3.96 to -2.48)	-3.18 (-3.86 to -2.48)	-3.18 (-3.88 to -2.38)
Egg deposition	1	10.53 (6.07 to 14.83)	9.91 (5.6 to 14.34)	9.73 (5.63 to 13.74)	9.65 (5.32 to 13.89)
	2	-10.29 (-13.58 to -7.14)	-9.78 (-12.93 to -6.56)	-9.82 (-12.79 to -6.77)	-9.76 (-12.76 to -6.75)
Pre-spawning flow	1	0.07 (-0.06 to 0.2)	0.06 (-0.07 to 0.19)		
Pre-spawning floods	1	-0.09 (-0.23 to 0.05)	-0.07 (-0.2 to 0.06)		
Pre-spawning temp.	1	-0.11 (-0.22 to 0)	-0.09 (-0.19 to 0.01)		
Spawning flow	1	6.98 (-0.51 to 14.36)	0.1 (-0.05 to 0.25)		
	2	-3.04 (-6.29 to 0.08)			
Spawning temp.	1	-2.25 (-8.29 to 3.95)	-1.01 (-7.05 to 4.9)	0.07 (-4.4 to 4.42)	-0.45 (-4.81 to 3.87)
	2	-12.36 (-16.07 to -8.45)	-11.47 (-15.22 to -7.71)	-8.54 (-11.26 to -5.77)	-8.15 (-10.79 to -5.43)
Pre-emergence flow	1	-0.08 (-0.24 to 0.1)	-0.03 (-0.18 to 0.12)		
Pre-emergence floods	1	-0.09 (-0.2 to 0.01)	-0.11 (-0.21 to -0.01)	-0.09 (-0.16 to -0.03)	-0.09 (-0.16 to -0.03)
Pre-emergence temp.	1	0.25 (0.11 to 0.39)	0.21 (0.08 to 0.35)	0.03 (-0.05 to 0.11)	
Emergence flow	1	-6.55 (-14.61 to 1.75)	-0.15 (-0.28 to 0)		
	2	0.44 (-3.96 to 4.73)			
Emergence floods	1	-0.1 (-0.3 to 0.1)	-0.14 (-0.28 to -0.01)	-0.17 (-0.26 to -0.08)	-0.17 (-0.26 to -0.09)
Emergence temp.	1	0.36 (0.2 to 0.51)	0.34 (0.2 to 0.48)	0.3 (0.18 to 0.43)	0.27 (0.17 to 0.37)
Post-emergence flow	1	-0.05 (-0.18 to 0.08)	-0.02 (-0.15 to 0.11)		
Post-emergence floods	1	-0.01 (-0.28 to 0.26)	-0.06 (-0.32 to 0.2)		
Post-emergence droughts	1	-0.16 (-0.37 to 0.04)	-0.15 (-0.35 to 0.06)		
Post-emergence temp.	1	-0.03 (-0.13 to 0.07)	0 (-0.09 to 0.09)		
First summer droughts	1	0.13 (-0.05 to 0.31)	0.13 (-0.05 to 0.31)		
First summer temp.	1	0.06 (-0.04 to 0.16)	0.05 (-0.05 to 0.15)		
Day of year	1	-0.07 (-0.15 to 0)	-0.07 (-0.15 to 0)		
Conditional $r^2$		0.599	0.599	0.585	0.585
Marginal $r^2$		0.016	0.017	0.013	0.013

variation in recruitment in these populations and the single pass survey method that is used to measure them (Figure 2). Based on these data, the mean age 0+ salmon counts on the rivers Clwyd, Dee, Teifi, Tywi, and Usk have decreased over the duration of these surveys, in some cases to extremely low levels; counts on the Conwy and Wye show less evidence for a decrease over the duration of these surveys (Figure 2). In contrast, the mean age 0+ trout counts show little evidence of a trend for any of these rivers (Figure 2).

### 3.2 | Density-dependent and independent recruitment factors

Results from our models suggest that age 0+ salmon recruitment is influenced by both density-dependent and density-independent variables, and that the effects of these factors on recruitment were

consistent with our hypotheses and effects observed in other stocks throughout their range.

Egg deposition was retained in the most parsimonious model for the age 0+ salmon counts (Final in Table 4), together with only four of the 19 possible environmental variables (Figure S1). Three of these terms—egg deposition, spawning temperature, and emergence temperature—were included as polynomial terms; the others were linear terms. This model explained over 58% of the total variance in the data, although the fixed terms accounted for only 1.3% (Table 4). Age 0+ salmon counts were negatively influenced by low and high egg deposition (i.e. egg to age 0+ salmon survival was maximised at intermediate egg deposition), negatively influenced by low and high temperatures during spawning (i.e. age 0+ salmon recruitment was maximised at intermediate spawning temperatures), positively influenced by higher temperatures at emergence, and negatively influenced by floods during pre-emergence and emergence (Figure 4).

Results from our models suggest that age 0+ trout recruitment is influenced by both density-dependent and density-independent variables, but that the effects of these factors on recruitment were not always consistent with our hypotheses. Notably, the effect of density-dependence was unexpectedly monotonically positive suggesting that there was no negative effect of high egg deposition on recruitment in these data and the effects of some environmental variables were unexpected, such as the positive effect of summer droughts.

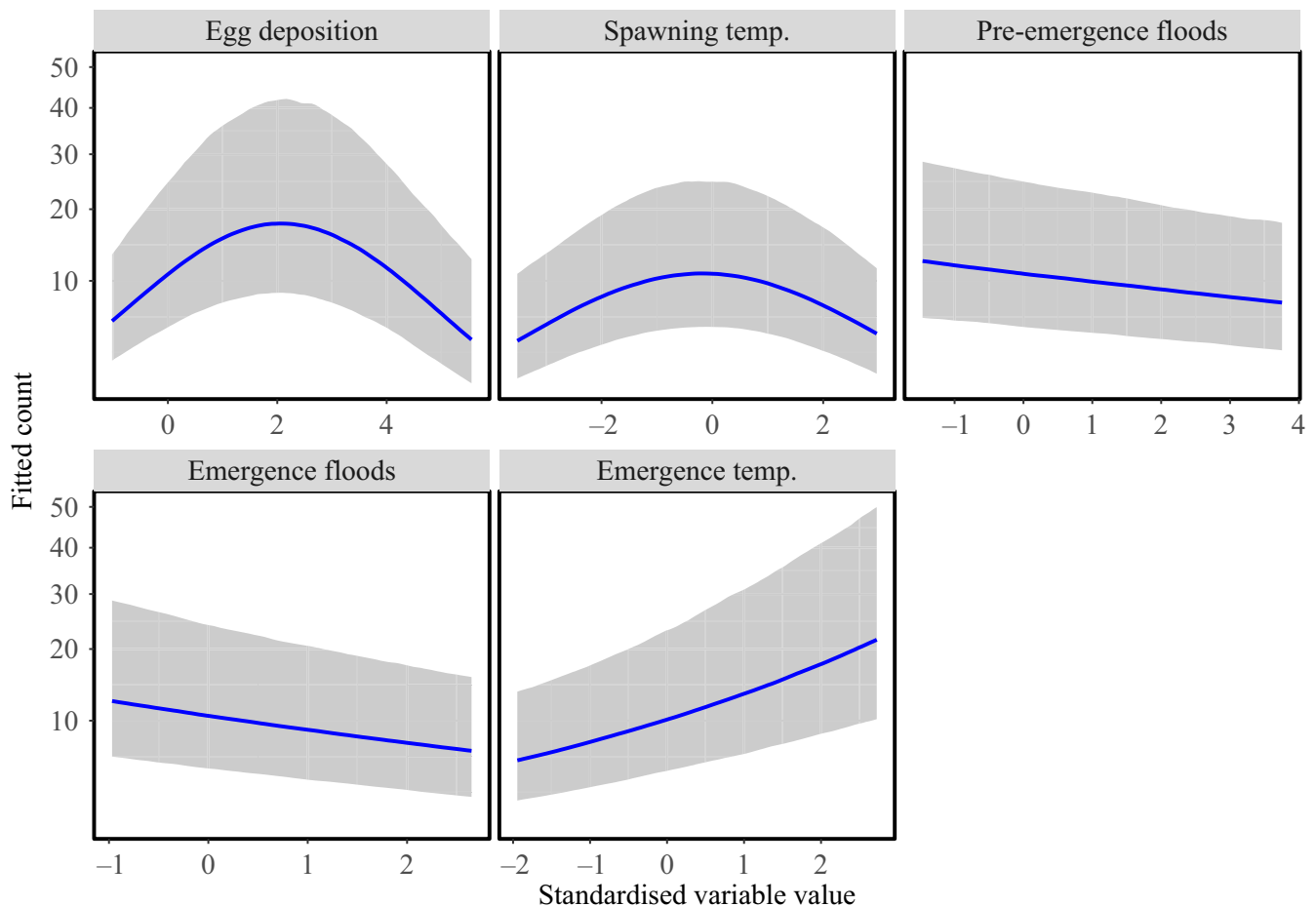
Only eight of the 19 possible environmental variables (Figure S2) were retained in the most parsimonious model for the age 0+ trout counts (Final in Table 5). Only one of these terms—post-emergence temperature—was included as a polynomial term; the others were included as linear terms. This model explained over 57% of the variance in the data, and the fixed terms accounted for 21.7% of this (Table 5). Age 0+ trout counts were positively influenced by egg deposition rates, negatively influenced by high pre-spawning and first summer temperatures, pre-spawning floods, high pre-emergence flow, and low and high post-emergence temperatures. In contrast, age 0+ trout counts

were positively influenced by high emergence temperature and first summer droughts (Figure 5).

### 3.3 | Was 2016 a recruitment crash?

Setting 2016 as a contrast level and plotting the estimated year effects suggested that 2016 was indeed an unusual recruitment year, especially for salmon: mean age 0+ salmon counts in 2016 were the lowest recorded during the study period, and significantly lower than every other year in these data (Figure 6, Table S2). We note also that 2016 was one in a series of declining mean counts since 2009. The effect for trout was less pronounced than for salmon, although 2016 was among the lowest counts for age 0+ trout; only 2 years had a lower mean count (2007 and 2008), although three others were similarly low (Figure 6, Table S2).

Our decision to assume a zero-inflated negative binomial error structure was supported by the data. For all species-age groups, the credible intervals (CrI) for the error family parameters



**FIGURE 4** Line plots showing the polynomial representations of environmental variable effects estimated from a model describing age 0+ juvenile salmon counts over sites in seven Welsh river catchments electrofished by Natural Resources Wales between 2001 and 2017. The blue line is the fitted effect of the ( $z$ -standardised) variable on the expected abundance  $\mu_{s,c}$ , labelled here as Fitted count. The grey band is the 95% credible interval band. Note: the order of each polynomial term was assigned based on a smooth shown in Figure S1 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 5** Model estimated coefficients values (and their 95% credible intervals) for density-dependent and density-independent factors affecting age 0+ trout abundances collected across seven Welsh river catchments by Natural Resources Wales between 2001 and 2017. Models started with the Saturated model including all variables and was simplified by variable deletion over two steps (Simplified 1 and 2) and a final simplification step to produce the final model. Conditional  $r^2$  is the variance explained by the model; marginal  $r^2$  is the amount of that explained by the fixed terms, i.e. the variables of interest

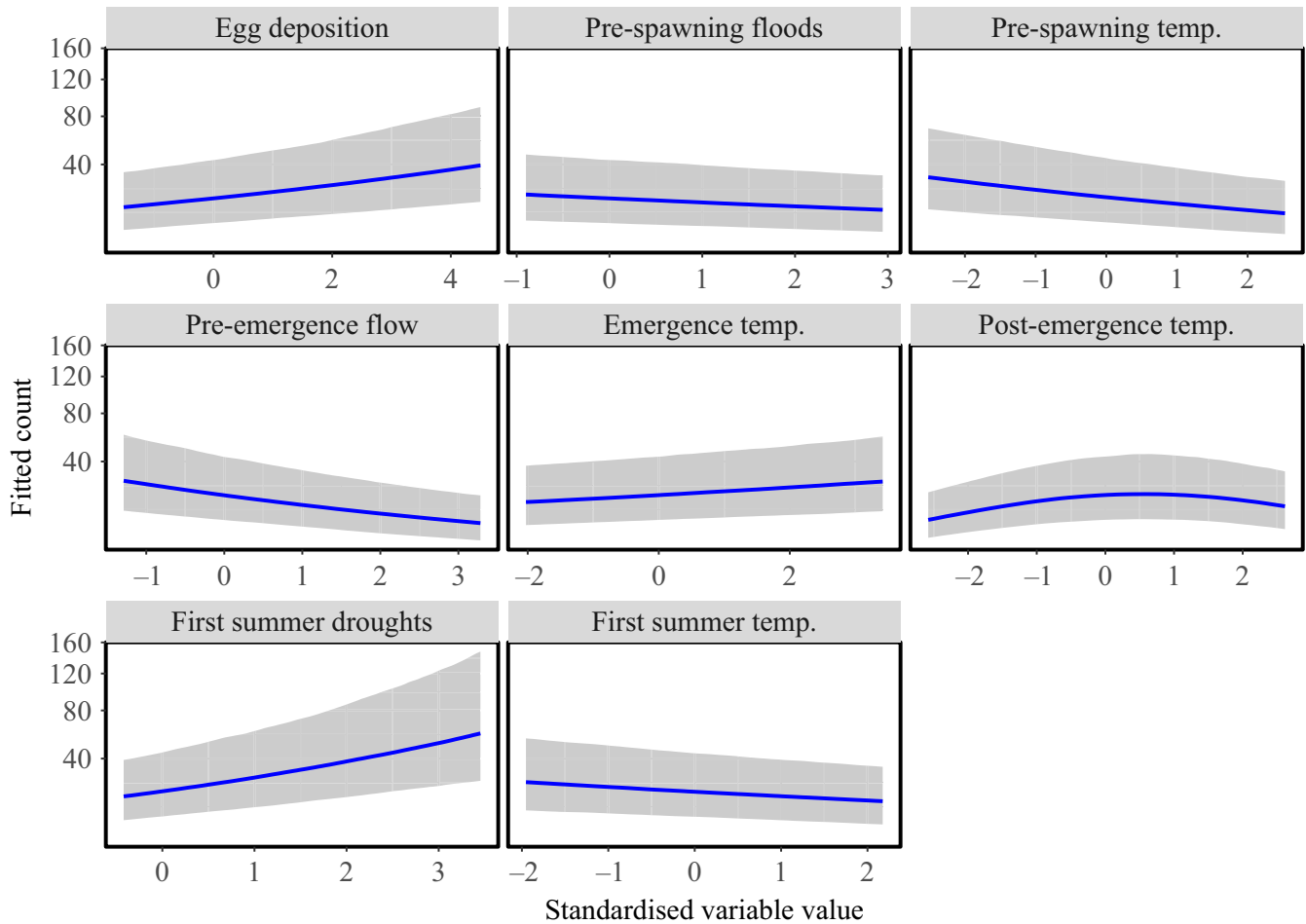
Variable name	Term order	Model			
		Saturated	Simplified 1	Simplified 2	Final
Intercept		-2.37 (-3.11 to -1.57)	-2.35 (-3.04 to -1.56)	-2.37 (-3.09 to -1.63)	-2.41 (-3.12 to -1.64)
Egg deposition	1	6.4 (3.3 to 9.45)	0.14 (0.07 to 0.21)	0.15 (0.09 to 0.22)	0.15 (0.09 to 0.22)
	2	-0.94 (-3.47 to 1.59)			
Pre-spawning flow	1	0.08 (-0.03 to 0.18)	0.08 (-0.03 to 0.18)		
Pre-spawning floods	1	-0.19 (-0.31 to -0.08)	-0.19 (-0.31 to -0.08)	-0.1 (-0.17 to -0.04)	-0.1 (-0.16 to -0.04)
Pre-spawning temp.	1	-0.29 (-0.39 to -0.18)	-0.31 (-0.4 to -0.2)	-0.16 (-0.23 to -0.1)	-0.17 (-0.24 to -0.1)
Spawning flow	1	0.16 (0.04 to 0.28)	0.15 (0.02 to 0.27)	0.05 (-0.03 to 0.12)	
Spawning temp.	1	0.03 (-0.07 to 0.14)	0.04 (-0.07 to 0.14)		
Pre-emergence flow	1	-0.49 (-0.64 to -0.33)	-0.49 (-0.64 to -0.34)	-0.27 (-0.36 to -0.18)	-0.25 (-0.34 to -0.16)
Pre-emergence floods	1	-0.55 (-4.15 to 3.18)	-0.01 (-0.09 to 0.07)		
	2	0.46 (-2.23 to 3.32)			
Pre-emergence temp.	1	0.1 (-0.04 to 0.23)	0.11 (-0.03 to 0.24)		
Emergence flow	1	0.07 (-0.07 to 0.19)	0.07 (-0.06 to 0.2)		
Emergence floods	1	0.01 (-0.06 to 0.08)	0.01 (-0.05 to 0.08)		
Emergence temp.	1	0.09 (0.01 to 0.17)	0.09 (0.02 to 0.16)	0.09 (0.04 to 0.15)	0.09 (0.03 to 0.14)
Post-emergence flow	1	0.12 (-0.04 to 0.29)	0.12 (-0.03 to 0.28)		
Post-emergence floods	1	0.07 (-0.07 to 0.21)	0.09 (-0.04 to 0.23)		
Post-emergence droughts	1	-0.04 (-0.21 to 0.13)	-0.04 (-0.21 to 0.12)		
Post-emergence temp.	1	7 (2.09 to 11.96)	7.63 (2.67 to 12.47)	4.22 (1.06 to 7.4)	5.13 (2.27 to 8.03)
	2	-8.03 (-11.38 to -4.72)	-8.07 (-11.25 to -4.71)	-5.25 (-7.43 to -3.05)	-5.1 (-7.32 to -2.89)
First summer droughts	1	0.32 (0.18 to 0.47)	0.32 (0.18 to 0.47)	0.3 (0.16 to 0.44)	0.31 (0.17 to 0.45)
First summer temp.	1	-7.5 (-11.11 to -3.97)	-0.2 (-0.29 to -0.11)	-0.11 (-0.18 to -0.05)	-0.11 (-0.18 to -0.04)
	2	-1.7 (-3.88 to 0.59)			
Day of year	1	-0.05 (-0.11 to 0.01)	-0.05 (-0.11 to 0.01)		
Conditional $r^2$		0.588	0.585	0.573	0.572
Marginal $r^2$		0.194	0.191	0.213	0.217

supported their inclusion. The negative binomial dispersion parameter ( $\theta$  in Table 6) CrIs did not include 1, albeit that the age 0+ salmon lower CrI was close to 1. Similarly, the zero-inflated parameter ( $\omega$  in Table 6) CrIs did not include 0. Moreover, the Gelman–Rubin  $r$  values for these parameters, as well as for all other parameters in the models, were  $<1.05$  indicating well-behaved estimates.

Conditional  $r^2$  values were above 55% for both models, which is considered a good explanatory performance. Most of the explained variance was, however, explained by the spatial random effects; the marginal  $r^2$  values were less than 1 and 15% for the salmon and trout models, respectively. These low marginal  $r^2$  values are entirely in line with expectations because we used only a single variable—year—as a fixed categorical effect (with 16 parameters) to explain variance in the survey counts across all seven rivers.

### 3.4 | How was 2016 unusual?

Boxplots of the environmental variables retained in the age 0+ salmon final model are shown in Figure 7. These revealed that 2016 was notable for exceptionally high spawning temperatures and exceptionally low emergence temperatures, which were found to negatively and positively influence age 0+ juvenile salmon counts, respectively (Figure 7). In contrast to 2016, spawning and emergence temperatures in 2011 were exceptionally low and high, respectively (Figure 7). Pre-emergence and emergence floods were also retained in the final model and negatively influenced age 0+ juvenile salmon counts, but they were not considered exceptional in 2016 (Figure 7): pre-emergence floods were high in 2016, but were consistently higher in 2007 and 2014, and emergence floods were high in 2016, but consistently higher in 2001 and 2017 and generally higher but more variable in 2007, 2008, and 2014.



**FIGURE 5** Line plots showing the polynomial representations of environmental variable effects estimated from a model describing age 0+ juvenile trout counts over sites in seven Welsh river catchments electrofished by Natural Resources Wales between 2001 and 2017. The blue line is the fitted effect of the (z-standardised) variable on the expected abundance  $\mu_{s,e}$ , labelled here as Fitted count. The grey band is the 95% credible interval band. Note: the order of each polynomial term was assigned based on a smooth shown in Figure S2 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 4 | DISCUSSION

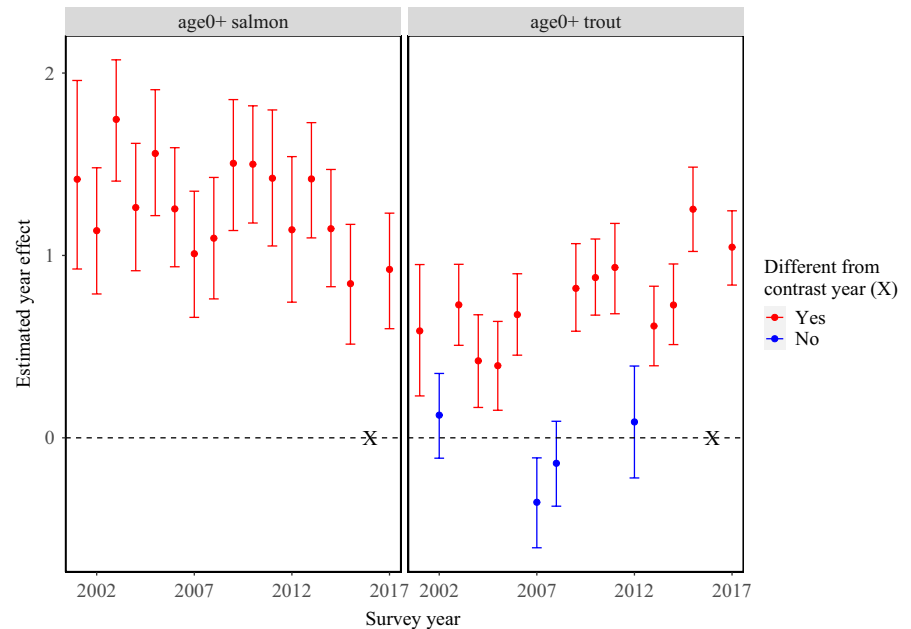
Using an extensive dataset spanning nearly 2 decades of juvenile salmonid recruitment across Wales, together with a data-driven statistical analysis, we found empirical evidence that Atlantic salmon recruitment in Welsh rivers was affected predictably by density-dependent and hypothesised density-independent factors. Moreover, we suggest that the 2016 recruitment crash was probably driven by high water temperature during spawning (between 1 November and 31 December) and low water temperature during emergence (approx. 87 days after peak spawning in 2016) and—to a lesser extent—by adverse high flow conditions (including floods) prior to emergence (between 1 January and approx. 86 days after peak spawning in 2016) and during emergence of alevins.

Results for trout were more ambiguous, suggesting that their recruitment is negatively influenced by high water flow, including floods, and high temperature during pre-spawning (between 1 September and 15 October), low water temperature during and around emergence (between 1 December and 30 June), and high water temperature during

the first summer (between 1 July and 31 August). Although trout recruitment was worse than average in 2016, it was not exceptional.

Overall, our analyses support strong empirical evidence for density-dependence in egg to juvenile salmon survival and density-independent effects of water temperature on spawning and emergence and flows on emergence of juvenile salmon and—to a lesser extent—trout. Our finding of density-dependence in salmon recruitment was consistent with our predictions. Density-dependence is a fundamental tenet of salmon recruitment (Milner et al., 2003) due to reoccurring and widespread empirical evidence of its existence (Grossman & Simon, 2020). In part, we attribute our ability to detect this effect to our use of data-driven statistical models that did not impose any strict form of density-dependence on the recruitment process (Dickey-Collas et al., 2015). Somewhat surprisingly, however, we did not detect any negative density-dependence in trout recruitment. This could be for a number of reasons, including that egg deposition was too low for juvenile trout to negatively affect one another or that they are more plastic in their behaviours—an idea that we discuss further below.

**FIGURE 6** Coefficient plot showing the estimated effect of individual years relative to 2016 on age 0+ juvenile salmon and trout counts in seven Welsh river catchments electrofished by Natural Resources Wales between 2001 and 2017 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**TABLE 6** Model performance and error family specific parameter estimates for a fit including only fixed effects of individual years to describe age 0+ Atlantic salmon and trout abundances collected across seven Welsh river catchments by Natural Resources Wales between 2001 and 2017. Conditional  $r^2$  is the variance explained by the model; marginal  $r^2$  is the amount of that explained by the fixed terms, i.e. the variables of interest.  $\theta$  is the overdispersion parameter of the negative binomial model;  $\omega$  is the zero-inflation parameter representing the proportion of values that were zero. Credible intervals give the lower and upper bounds of credible values;  $\hat{R}$  is the Rubin–Gelman statistic indicating convergence when  $<1.05$

Model	$r^2$		Error family parameter	Estimate	Credible interval		$\hat{R}$
	Conditional	Marginal			Lower	Upper	
Salmon	0.564	0.006	$\theta$	1.225	1.098	1.359	1.000
			$\omega$	0.073	0.052	0.095	1.001
Trout	0.608	0.122	$\theta$	1.788	1.627	1.959	1.000
			$\omega$	0.013	0.004	0.023	1.000

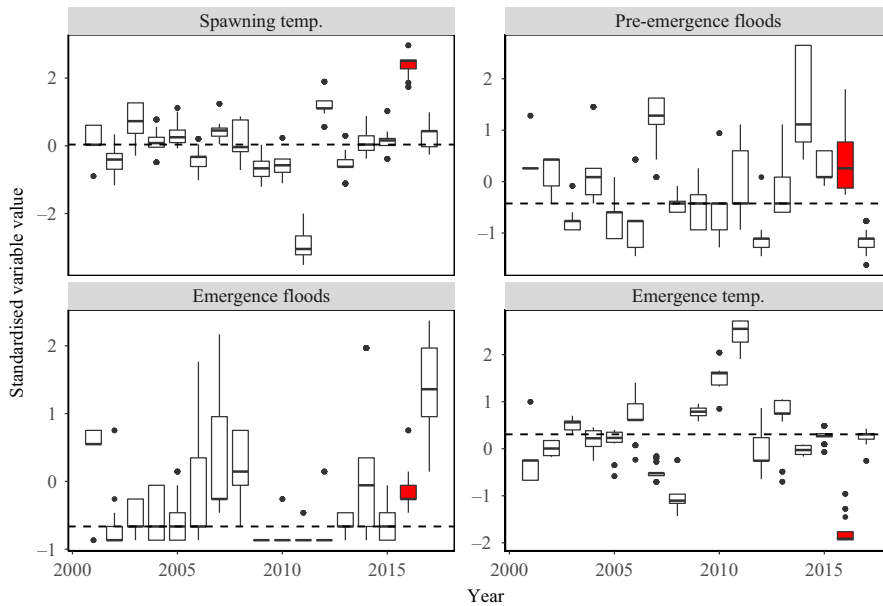
In contrast to the ubiquitous empirical evidence of density-dependence in salmon recruitment, evidence for density-independent effects of environmental variables on recruitment tend to be more ambiguous. Here, we consider each of our density-independent findings in the context of findings from other salmonid recruitment studies.

#### 4.1 | Temperature effects during the spawning period

Water temperature is thought to affect many aspects of salmonid spawning, including river entry (e.g. Solomon & Sambrook, 2004) and in-river migration (e.g. Erkinaro, Okland, Moen, Niemela, & Rahiala, 1999), both of which correspond to our pre-spawning period. In this study, the mean air temperature during the spawning period was positively associated with age 0+ salmon abundance at low to intermediate temperatures, beyond which the effect became

negative. This influence could be related to spawning behaviour or gamete production and viability.

It is a long-held adage that salmon spawning in the UK does not take place until after the first frost of autumn, which indicates that temperature might have an important influence on when and whether spawning takes place. Experimental work undertaken by Taranger and Hansen (1993) found that ovulation in multi-sea winter salmon was delayed by up to 5 weeks among fish held in warm water (increasing from 10°C to 13–14°C) compared to ambient temperature (decreasing from 10 to 8°C), and 43% of the fish did not ovulate within that time. There is, however, evidence to suggest that these experimental results might not translate well to natural conditions or might be modified by local adaptations: Baglinière, Maise, and Nihouarn (1990) found that spawning of female salmon in the river Oir (Normandy, France) was triggered by an increase in temperature from 6 to 9°C. Other studies have found no evidence that the initiation of spawning was temperature-related (e.g. Webb & McLay, 1996).



**FIGURE 7** Boxplots of the spawning and emergence environmental variables used to describe age 0+ juvenile salmon counts in seven Welsh river catchments electrofished by Natural Resources Wales between 2001 and 2017. Median values are indicated by the thick lines, boxes delimit the 25–75% interquartile range (IQR) and open circles represent extreme values  $\geq 1.5 \times \text{IQR}$ . Red boxes highlight year 2016 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

There is also evidence to suggest that water temperature can affect egg survival and sperm motility in salmonids post-spawning. Survival of eyed salmon eggs was up to 15% higher at cold water temperatures (decreasing from 10 to 5°C) compared to ambient and warm water temperatures (Taranger & Hansen, 1993). Crisp (1993) reported that brown trout egg mortality increased from less than 5% at 1–10°C to 50% at 12°C and 100% above 16°C and speculated that salmon eggs would be affected similarly. Comparable findings have been seen in rainbow trout, *Oncorhynchus mykiss* (Pankhurst, Purser, Kraak, Thomas, & Forteach, 1996). Experimental evidence suggests that both salmon and trout sperm motility is optimum within a narrow temperature range, found to be 3–4°C under certain experimental conditions (Vladić & Jatrvi, 1997).

Although these studies highlight the singular importance of temperature on spawning success, it is widely accepted that the influences of water temperature on spawning migrations will be complex and confounded with other factors, including water flow and anthropogenic activities, such as dams (e.g. Malcolm, Gibbins, Soulsby, Tetzlaff, & Moir, 2012; Milner, Solomon, & Smith, 2012; Thorstad, Okland, Aarestrup, & Heggberget, 2008). We also note that our decision to use air temperature as a surrogate for water temperature (with corrections), and therefore limit our analysis to mean temperature variables, might have impacted our ability to detect subtle temperature effects.

#### 4.2 | Temperature effects during the emergence period

In contrast to the spawning period, mean temperature during the emergence period was positively correlated with age 0+ salmon abundance, while mean temperature during the emergence period in 2016 was exceptionally low. It has been suggested that temperature affects the survival and growth of newly emerged fry, known as alevins, through its effect on timing of emergence (related to

growing period) and post-emergence development (related to available food) (e.g. Elliott & Elliott, 2010; Jonsson & Jonsson, 2009; Solomon & Lightfoot, 2008).

Incubation temperature is negatively correlated with emergence timing, with alevins emerging from redds sooner at higher temperatures. This is commonly observed in salmonid breeding programmes, which have coined the terms *degree days* or *heat-sum* (reviewed for salmonids by Crisp, 1981). This relationship was used within this study to estimate the timing of peak emergence for each species in each year. Studies on wild salmonid stocks corroborate these results. Saltveit and Brabrand (2013) showed that salmon egg development and emergence occurred up to 40 days earlier in egg boxes situated nearest to warm groundwater seepages. Similarly, Skoglund, Einum, and Robertsen (2011) found that eggs incubated at a higher temperature in an ex-situ experiment produced larger and better surviving parr compared to those incubated at lower ambient temperatures. Generally, it is speculated that earlier alevin emergence due to increasingly warmer winter water temperatures might lengthen first-year growing periods, which could be advantageous to alevins and subsequent fry growth and survival (Elliott & Elliott, 2010; Gregory et al., 2017). It follows logically that cooler incubation temperatures could shorten the first-year growing period and reduce the growth potential and therefore, presumably, the survival of alevins. Jensen and Johnsen (1999) measured higher trout mortality in years with low water temperatures at emergence and high discharge during the alevin stage, but no effect on salmon mortality was observed, unlike in this study (although this could be due to differences in their thermal tolerances and the range of temperatures observed; Elliott & Elliott, 2010; Jensen & Johnsen, 1999; Jonsson & Jonsson, 2009). We note that although emergence timing was calculated as a function of probable peak spawning date and a year-specific measure of the incubation period,

we cannot be entirely sure how accurate these dates were and therefore whether they captured the behaviour or development of the majority of the spawning stock or alevins. As with spawning, the effects of temperature and flow at emergence are likely to be complex and to interact with themselves and other environmental variables (e.g. Elliott & Elliott, 2010; Jonsson & Jonsson, 2009).

### 4.3 | Flood effects during pre-emergence and emergence

One of the most sensitive salmonid life stages is the egg. Salmonids lay their eggs in gravels, in part to protect them from adverse environmental conditions, such as high flows. However, extreme high (flood) flows during the pre-emergence or emergence periods can be potentially harmful to salmonid recruitment (Bergerot, Bret, & Cattaneo, 2019).

If flood conditions occur during the pre-emergence period, then high velocity water can wash eggs out of redds into unsuitable habitat, including estuaries, causing them to die (Crisp & Carling, 1989). This effect—known as *egg washout*—is likely to be more severe in rivers with steep gradients draining impermeable geology where discharge responds rapidly to rainfall events, as is often a feature of rivers in Wales. Conversely, a relatively low magnitude or long duration flood could wash sediments out of redds that would otherwise asphyxiate the developing eggs, thereby improving egg survival (Greig, Sear, & Carling, 2005).

Eggs that survive flooding or other threats during the incubation phase go on to hatch and become alevins. Following emergence, alevins tend to stay in the shallow, protected waters at the edges of river channels because they are not strong swimmers (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003). High flows during, or shortly after emergence have been associated with high alevin mortality (Jensen & Johnsen, 1999): they too can be washed out of the river and die, whether down the river channel into unsuitable saline water downstream, or over the edge of the channel onto adjoining land (Heggenes & Traaen, 1988). For example, salmon mortality increased significantly in years with high discharge during the alevin stage as well as the first week after emergence, whereas high discharges during the egg stage and more than 1 week after emergence seemed to be of minor importance (Jensen & Johnsen, 1999). However, alevin swimming ability increases quickly with size and so the timing of the flood is critical to alevin survival (Heggenes & Traaen, 1988); a well-timed flood might actually improve conditions for alevins by refreshing food supplies (Warren, Dunbar, & Smith, 2015).

### 4.4 | Insights into the 2016 recruitment crash

From these analyses, it appears that a combination of high water temperature during spawning, and low water temperature together

with high flows during emergence might have led to the 2016 juvenile salmon crash in Welsh rivers. It is noteworthy that although egg deposition overall was not especially low for the 2016 year-class, five of the seven rivers examined in this study recorded egg deposition levels below their conservation limit. Although the extreme high temperature and, in some cases, high flows probably impacted Welsh salmon recruitment success in 2016, the exact causes remain uncertain.

Our findings were more ambiguous for trout. First, 2016 did not appear to be a recruitment crash: although it was a poor year, it was within the range of inter-annual recruitment levels observed among these stocks since 2001. Moreover, the number of environmental variables affecting age 0+ trout recruitment was greater, but their effects were weaker than for salmon, suggesting that trout recruitment is influenced by a suite of more subtle effects, although we note that some environmental variables had a similar influence on recruitment for both species, such as water temperature during the emergence period and flow during the pre-emergence period.

The findings for trout may be more ambiguous than salmon because, as a species, they are more plastic in their behaviour (Klemetsen et al., 2003). For example, depending on whether they are sea trout or resident brown trout, trout spawn in a wider variety of locations within a river than salmon (Birnie-Gauvin, Thorstad, & Aarestrup, 2019), and other biological differences between trout and salmon might also be important. Heggberget, Haukebo, Mork, and Stahl (1988) found that there were differences in spawning behaviour in terms of both timing and site selection between sympatric populations of salmon and trout. Skoglund, Einum, Forseth, and Barlaup (2012) also highlighted differences in the competitive abilities of sympatric salmon and trout alevins, in which trout were generally better competitors, although this depended on emergence timing.

### 4.5 | Generalisation across and beyond Wales

Our statistical analyses were carefully designed to treat sites as representative of their catchments, and the seven Welsh catchments included in this analysis were assumed to be representative (e.g. in terms of geographical range) of salmonid rivers in Wales. Consequently, without further information on important differences between rivers or salmonid stocks, we would expect our findings to generalise to salmonid stocks in other rivers across Wales, although this would need to be done carefully to overcome the low explanatory power of these models.

It is also likely that these results might generalise to neighbouring rivers in England (and possibly beyond) with similar catchment characteristics, such as those in the south-west and north-west. The chalk streams of southern England, such as the Hampshire Avon or Dorset Frome, are renowned to have more stable flow and temperature regimes than more rain-fed rivers and are likely to behave quite differently (Basic et al., 2018; Solomon & Paterson, 1980).

By opting to treat our sample rivers as random representatives of Wales, we precluded making river-specific inferences because our river-specific estimates will have reduced variance due to shrinkage (Harrison et al., 2018). Nevertheless, we would encourage managers of specific rivers to review the local information available to them, including data and expert opinion, and use it in a more targeted (and potentially nuanced) analysis, rather than necessarily drawing inferences from a large-scale and general analysis such as this.

Our decision to concentrate on only age 0+ juveniles, however, restricts our analysis to only this component of salmonid populations. In Wales and elsewhere around salmon and trout native ranges, older juveniles make up an oftentimes non-negligible component of the juvenile population. So, although, our results could generalise spatially across Wales and beyond, they will still be restricted to only the youngest juvenile component of any of those populations.

#### 4.6 | Looking to the future

Using abundant spatio-temporal historical data and a flexible statistical approach, we have found that juvenile salmonid recruitment—and particularly salmon recruitment—is density-dependent and influenced by temperatures and flows during spawning and emergence. Most notably, extreme flow and temperature conditions experienced during the winter of 2015/16 appear to be the cause of the crash in juvenile salmon recruitment widely reported in the 2016 survey season. We note that we cannot infer causation because our results are based on historical data and are therefore necessarily correlative. Nevertheless, long-term trends in temperature and flow, and the occurrence of unusual events such as that in 2016, suggest that the resilience of salmonid populations—in Wales and neighbouring jurisdictions—might be seriously compromised under future climate change scenarios, which will probably see an increase in the frequency and intensity of extreme events outside the range of conditions to which these populations are adapted, particularly during winters (UKCP09). Elliott and Elliott (2010) highlighted that both salmon and trout are cold-water adapted species and that their egg stages were most susceptible to changes in thermal regimes. They suggested that continued increases in water temperatures during spawning and early egg development could render rivers too hostile for subsequent recruitment (Elliott & Elliott, 2010). Indeed, it has been suggested that some stocks in warmer regions, such as Spain, might have already been extirpated due to recent climate change (Parrish et al., 1998). Several possible mitigation measures would provide a precautionary response to help slow any negative impact of forecast climate change, including tree planting to shade water bodies and lower river water temperatures, wetland creation to help prevent extreme low and high flows and improved river connectivity through barrier removal and fish passage schemes (Palmer et al., 2009), although the efficacy of these measures would have to be validated on a case-by-case basis.

Alongside measures such as the above, there is a need to use studies such as this as the impetus for more detailed examination

of the causal mechanisms of long-term recruitment decline. For example, current salmon, and to a lesser extent sea trout, assessment and management strategies in England and Wales (and elsewhere) are largely centred around the use of conservation limits and the density dependent stock-recruitment relationships that underpin them (Centre for the Environment, Fisheries, & Aquatic Science, Environment Agency and Natural Resources Wales, 2019). Our findings are supportive of these density-dependent relationships, but also suggest that annual deviations from a density-dependent stock-recruitment relationship could be explained (in part) by density-independent variables, such as environmental conditions. Including environmental variables in stock-recruitment models could improve how well they describe highly variable stock-recruitment data and, in doing so, better inform understanding of recruitment failure and help to refine management responses. Developing models with capacity to include environmental factors affecting recruitment in future stock assessments could improve their predictive power and suggest where mitigation might reduce their negative impacts (Tonkin et al., 2019), especially if the future climate is characterised by more frequent and intense events, such as the latest record-breaking high oceanic temperatures in the winter of 2019 (Cheng et al., 2020).

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#### DATA AVAILABILITY STATEMENT

Data, including summaries of site-specific catches and year-specific environmental variables, are available from the authors upon request.

#### ORCID

Stephen D. Gregory  <https://orcid.org/0000-0002-8230-0191>

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#### SUPPORTING INFORMATION

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

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## Supplementary material

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**Table S1** Potential environmental variables from which the final set was taken forward for statistical analysis based on expert opinion and the need for explanatory variables to be statistically independent.

Type	Period	Life-stage	Event	Variable	Description	Hypothesised influence	References
Egg deposition		Fry	Density dependence	Estimated egg deposition as a percent of river Conservation Limit	Estimated egg deposition as a percent of river Conservation Limit	+/-	Milner et al. (2003)
Flow	Annual	All	General	Mean annual flow	Annual average flow between 1st October and 31st September (lagged by one year for parr).	+	Jonsson et al. (1991) Warren et al. (2015)
Flow	Annual	Spawning adult	General	Mean annual flow	Annual average flow between 1st February y0 and 31st January y1	+	Jonsson et al. (1991) Armstrong et al. (2003) Parry et al. (2017)
Flow	Pre-spawning	Spawning adult	General	Mean flow during pre-spawning	Mean flow during the pre-spawning period	+/-	Malcolm et al. (2012) Parry et al. (2018)
Flow	Pre-spawning	Spawning adult	Variation	Standard deviation of flow during pre-spawning	Temporal variation in flow during the pre-emergence period for each specific catchment	+/-	Armstrong et al. (2003) Malcolm et al. (2012)
Flow	Pre-spawning	Spawning adult	Flood	Number of high flow pulses between 3 and 5 times long-term Q50 during pre-spawning	Frequency of mild severity high flow events. Calculate as number of times flows exceed 3xQ50 minus the number of times flows exceed 5xQ50.	+/-	Malcolm et al. (2012) Parry et al. (2018)
Flow	Pre-spawning	Spawning adult	Flood	Number of high flow pulses between 5 and 7 times magnitude of long-term Q50 during pre-spawning	Frequency of medium severity high flow events. Calculate as number of times flows exceed 5xQ50 minus the number of times flows exceed 7xQ50.	+/-	Armstrong et al. (2003) Parry et al. (2017) Malcolm et al. (2012) Milner et al. (2012)
Flow	Pre-spawning	Spawning adult	Flood	Number of high flow pulses >7 times magnitude of long-term Q50 during pre-spawning	Frequency of high severity high flow events. Calculate as number of times flows exceed 7xQ50.	+/-	Armstrong et al. (2003) Parry et al. (2017) Malcolm et al. (2012) Milner et al. (2012)
Flow	Spawning	Spawning adult	General	Mean flow during spawning	Mean flow during the spawning period	+/-	Malcolm et al. (2012) Parry et al. (2018)
Flow	Pre-emergence	Egg & embryo	General	Mean flow during pre-emergence	Mean flow during the pre-emergence period	+	Malcolm et al. (2012) Warren et al. (2015)
Flow	Pre-emergence	Egg & embryo	Variation	Standard deviation of flow during pre-emergence	Temporal variation in flow during the pre-emergence period for each specific catchment	+/-	Armstrong et al. (2003) Malcolm et al. (2012)
Flow	Pre-emergence	Egg & embryo	Flood	Number of high flow pulses between 3 and 5 times long-term Q50 during pre-emergence	Frequency of mild severity high flow events. Calculate as number of times flows exceed 3xQ50 minus the number of times flows exceed 5xQ50.	-	Crisp (1989) Warren et al. (2015)

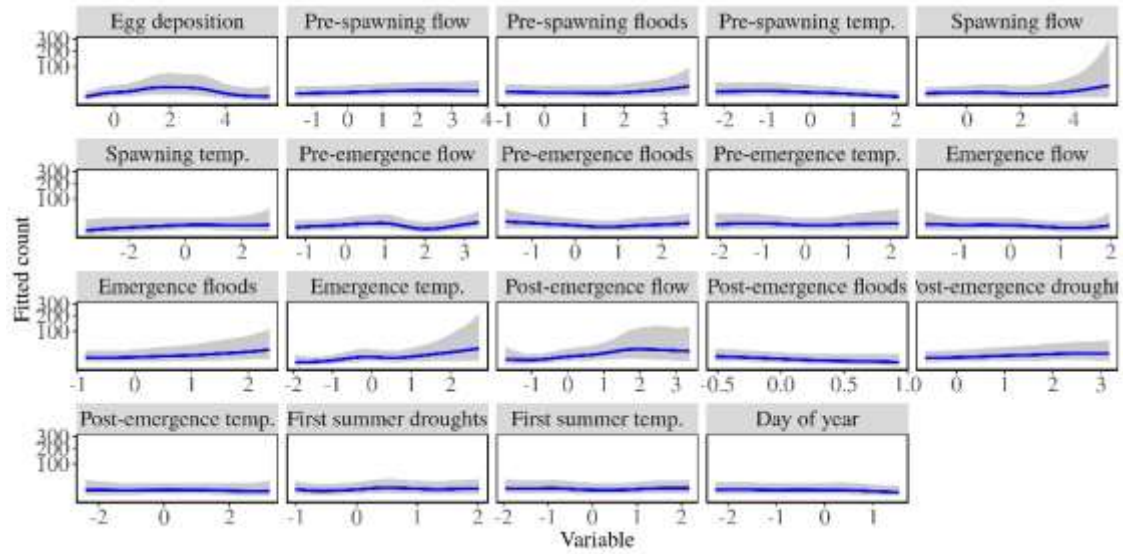
Flow	Pre-emergence	Egg & embryo	Flood	Number of high flow pulses between 5 and 7 times long-term Q50 during pre-emergence	Frequency of medium severity high flow events. Calculate as number of times flows exceed 5xQ50 minus the number of times flows exceed 7xQ50.	+/-	Armstrong et al. (2003) Parry et al. (2017) Malcolm et al. (2012) Milner et al. (2012)
Flow	Pre-emergence	Egg & embryo	Flood	Number of high flow pulses >7 times long-term Q50 during pre-emergence	Frequency of high severity high flow events. Calculate as number of times flows exceed 7xQ50.	-	Armstrong et al. (2003) Parry et al. (2017) Malcolm et al. (2012) Milner et al. (2012)
Flow	Emergence	Fry	General	Mean flow during emergence	Mean flow during the emergence period	+	Malcolm et al. (2012) Warren et al. (2015)
Flow	Emergence	Fry	Flood	Number of high flow pulses between 3 and 5 times long-term Q50 during emergence	Frequency of mild severity high flow events. Calculate as number of times flows exceed 3xQ50 minus the number of times flows exceed 5xQ50.	-	Crisp (1989) Warren et al. (2015)
Flow	Post-emergence	Fry	General	Mean flow during post-emergence	Mean flow during the post-emergence period	+/-	Jonsson et al. (1991) Warren et al. (2015)
Flow	Post-emergence	Fry	Variation	Standard deviation of flow during post-emergence	Temporal variation in flow during the post-emergence period for each specific catchment	+/-	Warren et al. (2015)
Flow	Post-emergence	Fry	Drought	Number of days below long-term Q90 flow during post-emergence	Duration of low flows during post-emergence	-	Riley et al. (2009) Warren et al. (2015)
Flow	Post-emergence	Fry	Drought	Minimum daily flow during post-emergence	Severity of low flows during post-emergence	-	Gregory et al. (2017) Basic et al. (2017)
Flow	Post-emergence	Fry	Flood	Number of high flow pulses between 3 and 5 times long-term Q50 during post-emergence	Frequency of mild severity high flow events. Calculate as number of times flows exceed 3xQ50 minus the number of times flows exceed 5xQ50.	-	Jonsson et al. (1991) Warren et al. (2015)
Flow	Post-emergence	Fry	Flood	Number of high flow pulses between 5 and 7 times long-term Q50 during post-emergence	Frequency of medium severity high flow events. Calculate as number of times flows exceed 5xQ50 minus the number of times flows exceed 7xQ50.	-	Armstrong et al. (2003) Parry et al. (2017) Malcolm et al. (2012) Milner et al. (2012)
Flow	Post-emergence	Fry	Flood	Number of high flow pulses >7 times long-term Q50 during post-emergence	Frequency of high severity high flow events. Calculate as number of times flows exceed 7xQ50.	-	Armstrong et al. (2003) Parry et al. (2017) Malcolm et al. (2012) Milner et al. (2012)
Flow	First summer	Fry	Drought	Number of days below long-term Q90 during first summer	Frequency of low pulses equal or below Q90 flow during spring to summer	-	Nislow et al. (2004) Warren et al. (2015)
Flow	First summer	Fry	Drought	Minimum daily flow during first summer		-	Armstrong et al. (2003) Parry et al. (2017) Milner et al. (2003) Milner et al. (2012)

Temperature	Annual	All	General	Mean annual temperature	Annual average temperature between 1st October and 31st September (lagged by one year for parr).	+/-	Elliott and Elliott (2010) Todd et al. (2011)
Temperature	Pre-spawning	Spawning adult	General	Mean temperature during pre-spawning	Mean temperature during pre-spawning	+/-	Taranger and Hansen (1993)
Temperature	Spawning	Spawning adult	General	Mean temperature during spawning	Mean temperature during spawning	+/-	Taranger and Hansen (1993)
Temperature	Pre-emergence	Egg & embryo	General	Mean temperature during pre-emergence	Mean temperature during pre-emergence	+/-	Basic et al. (2018) Jonsson and Jonsson (2009)
Temperature	Pre-emergence	Egg & embryo	Warming	Number of days with mean daily temperature >11degC during pre-emergence	Duration of periods with elevated temperatures	-	Solomon & Lightfoot (2008)
Temperature	Emergence	Fry	General	Mean temperature during emergence	Mean temperature during emergence	+/-	Elliott (1991)
Temperature	Post-emergence	Fry	General	Mean temperature during post-emergence	Mean temperature during post-emergence	+/-	Elliott and Elliott (2010) Basic et al. (2018)
Temperature	Post-emergence	Fry	Warming	Number of days with mean daily temperature >20degC during post-emergence	Duration of periods with elevated temperatures	-	Solomon & Lightfoot (2008)
Temperature	First summer	Fry	General	Mean temperature during first summer	Mean temperature during summer	+/-	Elliott (1991) Elliott and Elliott (2010)
Day of year		Fry	Natural mortality	Day of year of the survey	Day of year of the survey	-	

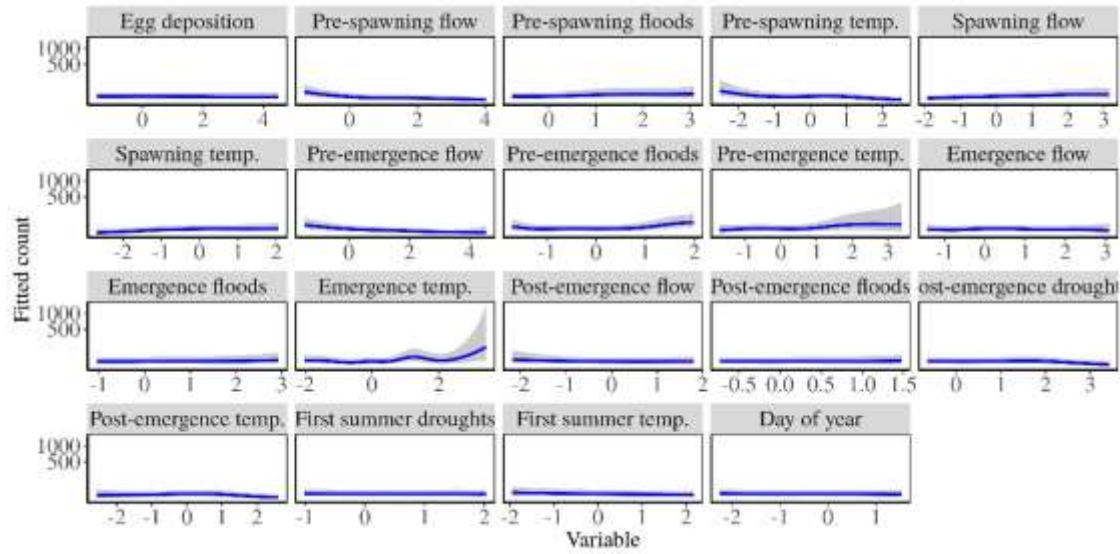
**Table S2** Fixed year model coefficients for GLMM fit to each species.

Species	Year	Estimate	Credible interval	
			Lower	Upper
Salmon	2001	1.418	0.263	0.926
	2002	1.136	0.176	0.789
	2003	1.746	0.170	1.407
	2004	1.263	0.179	0.916
	2005	1.559	0.176	1.218
	2006	1.255	0.167	0.938
	2007	1.009	0.174	0.660
	2008	1.095	0.172	0.762
	2009	1.505	0.183	1.137
	2010	1.500	0.164	1.178
	2011	1.423	0.189	1.052
	2012	1.141	0.203	0.744
	2013	1.419	0.162	1.096
	2014	1.146	0.167	0.829
	2015	0.845	0.166	0.514
	2017	0.923	0.160	0.598
	Trout	2001	0.586	0.183
2002		0.124	0.121	-0.112
2003		0.729	0.115	0.507
2004		0.422	0.129	0.167
2005		0.395	0.126	0.151
2006		0.676	0.114	0.453
2007		-0.353	0.124	-0.603
2008		-0.140	0.118	-0.375
2009		0.820	0.122	0.584
2010		0.879	0.106	0.673
2011		0.934	0.128	0.680
2012		0.087	0.155	-0.220
2013		0.613	0.112	0.395
2014		0.728	0.115	0.511
2015		1.253	0.118	1.022
2017		1.045	0.104	0.838





**Figure S1** Smooth representations of environmental variable effects on age0+ salmon counts when treating sites as representing catchments and catchments as a sample of a wider area, i.e., Wales.



**Figure S2** Smooth representations of environmental variable effects on age0+ trout counts when treating sites as representing catchments and catchments as a sample of a wider area, i.e., Wales.