

ARTICLE

Can aspects of the discharge regime associated with juvenile Atlantic salmon (*Salmo salar* L.) and trout (*S. trutta* L.) densities be identified using historical monitoring data from five UK rivers?

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Abstract

Understanding salmonid discharge requirements can help inform management to conserve wild populations in a changing climate. This study developed Bayesian hierarchical mixed-effects models relating 0+ Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) densities to different aspects of river discharge. Associations between these densities and nine hydrological variables representing the magnitude, frequency and duration of discharge events were evaluated using historical monitoring data from 36 sites on five rivers in England and Wales. All hydrological variables had weak associations with 0+ salmonid densities. More frequent high discharges between spawning and emergence were positively and negatively associated with 0+ salmon and trout densities, respectively. High discharges might increase spawning site availability for salmon and decrease egg-to-fry survival for trout. However, overall, only equivocal evidence was found regarding which discharge aspects affect juvenile salmonid densities. Therefore, a strategic review of juvenile salmonid monitoring programmes integrating environmental data collection is recommended.

KEYWORDS

electrofishing, high and low discharge, monitoring programme review, river flow, salmonids, spawning to emergence

1 | INTRODUCTION

Freshwater discharge is a “master variable” in rivers (sensu Power, Sun, Parker, Dietrich, & Wootton, 1995) that influences many environmental factors, such as geomorphology, sediment delivery, water temperature and dissolved oxygen (Arthington, 2012). Inter-annual variation in discharge is essential for maintaining the structure,

function and ecological integrity of rivers (Poff et al., 1997). Discharge can directly or indirectly regulate the quality and quantity of habitat available for aquatic species, including socio-economically important species, such as Atlantic salmon (*Salmo salar* L., hereafter salmon) and trout (*Salmo trutta* L.) (Pennell & Prouzet, 2009), and thereby their distributions and abundances (Bunn & Arthington, 2002). The effective management of freshwater habitats is therefore essential

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to maintain and enhance salmonid populations (Mainstone, Thomas, Bean, & Waterman, 2012), particularly given that fisheries managers have a limited ability to control factors influencing their survival at sea (Russell et al., 2012).

Every salmon and trout freshwater life stage is influenced by river discharge (Nislow & Armstrong, 2012), each with distinct requirements governing their growth and survival (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003). Consequently, the effects of discharge on the distributions and abundances of their different life stages have been well studied (Warren, Dunbar, & Smith, 2015). For example, discharges during incubation can affect salmonid eggs directly by washing them out of gravel nests, known as redds, at high discharges or desiccating them at low discharges (Malcolm, Gibbins, Soulsby, Tetzlaff, & Moir, 2012), and indirectly by altering sediment and oxygen supply and the removal of metabolic waste (Crisp, 1996; Lapointe, Bergeron, Bérubé, Pouliot, & Johnston, 2004). Newly emerged fry dispersing from redds are susceptible to downstream displacement during high discharges, and starvation during low discharges, due to their small body size and limited swimming capability (Heggenes & Traaen, 1988; Jensen & Johnsen, 1999). As fry develop into parr, their growth and survival are dependent on suitable discharges for summer rearing and subsequent overwintering (Gregory et al., 2017). In the spring, migrating juvenile salmon move downstream towards the ocean when discharge increases (Otero et al., 2014). During the latter part of the life cycle, discharge can affect the number and timing of returning anadromous adults migrating upstream by modifying the accessibility of spawning grounds (Milner, Solomon, & Smith, 2012).

Discharge can have strong or weak effects on salmonid populations (Milner et al., 2003). A review of discharge effects on salmonid distribution and abundance concluded that discharge affected all salmonid life stages, but empirical evidence was conflicting, particularly among studies seeking the subtle effects of discharge (Warren et al., 2015). Possible reasons for inconsistencies among studies include, *inter alia*, highly plastic life histories that promote local adaptation and the presence of confounding and interacting factors at local scales (Milner, Cowx, & Whelan, 2012). Another potentially important reason for this lack of consensus is that studies tend to be site-specific and of limited duration (Warren et al., 2015). For example, extreme high discharges during egg/embryo incubation and fry emergence decreased juvenile (hereafter 0+) trout densities in three study sites over a five-and-a-half-year period on the Rainy River in New Zealand (Hayes, Olsen, & Hay, 2010). Contrastingly, extreme high discharges after fry emergence were found to increase 0+ trout densities in nine study sites over a five-year period on the Upper Esopus Creek in the USA (George, Baldigo, Smith, & Robinson, 2015). To facilitate generalisation, Warren et al. (2015) recommended that future studies take a more broad-scale and long-term approach to investigate discharge effects on salmonid abundance. Such studies are necessary to confirm the attainability of general findings to reach a possible consensus on the efficacy of standard rules for salmonid discharge requirements. If

general findings can be established, more focussed studies can then elucidate specific mechanisms and derive targeted management actions (Rosenfeld, 2017).

In contrast to inconsistencies among studies seeking the subtle effects of discharge, the effects of comparatively rare extreme discharge events, such as floods and droughts, tend to be less ambiguous (Warren et al., 2015). Extreme discharge events disturb freshwater habitats beyond their typical limits, exposing aquatic organisms to unusual intensities and durations of disruption, to which they are not well adapted (Lytle & Poff, 2004). Indeed, floods and droughts have been identified as a main cause of severe reductions in 0+ salmonid abundance (Warren et al., 2015), including local extirpations (Jones et al., 2013). For example, high discharges into Teesdale streams in Northern England have a detrimental effect on 0+ trout densities by washing substantial quantities (12%–58%) of eggs downstream and reducing egg-to-fry survival (Ottaway, Clarke, & Forrest, 1981).

Relatively few rivers have retained their natural discharge regime (Poff et al., 1997). River headwaters have been diverted and channelled for drainage, middle reaches dammed, and floodplains developed (Boon, 1992). Modifications to discharge regimes have resulted from human activities including land use changes, such as agriculture/forestry and drainage practices, water abstraction, storage and transfer between catchments, impoundment and river regulation, and hydropower generation (Hendry, Cragg-Hine, O'Grady, Sambrook, & Stephen, 2003; Riley et al., 2018). Human modification of discharge regimes has affected anadromous salmonids that require connectivity between aquatic habitats to migrate from marine feeding areas into riverine spawning grounds (Gillson, 2011). Natural discharge regimes are expected to be further modified by climate change increasing the frequency and severity of flood and drought events (Schneider, Laizé, Acreman, & Flörke, 2013), and this could be exacerbated by human population growth increasing demand for water resources (Vörösmarty, Green, Salisbury, & Lammers, 2000). Understanding the effects of discharge on salmonid abundance has therefore never been more important.

This study aimed to determine which aspects of river discharge were associated with inter-annual variation in 0+ salmon and trout densities using historical monitoring data. Following the recommendations of Warren et al. (2015) and Rosenfeld (2017), 0+ salmon and trout density data collected at 36 sites on five rivers in England and Wales between 1971 and 2015 were used to parameterise and compare *a priori* candidate sets of statistical models designed to identify broad spatial and temporal associations with hydrological variables representing different aspects of the discharge regime. These models aim to make best use of existing monitoring data and were tailored to the data, allowing for zero-inflation and accounting for spatial and temporal variation. Similar approaches have proven valuable for identifying that high discharges between spawning and emergence drive reductions in 0+ trout densities across rivers (Bergerot, Bret, & Cattaneo, 2019; Bergerot & Cattaneo, 2017; Cattaneo, Lamouroux, Breil, & Capra, 2002). Two hypotheses were explored: (a) hydrological

variables capturing high and low discharge events will better describe variation in 0+ salmon and trout density data than those representing more general conditions, such as mean annual discharge; and (b) hydrological variables representing discharge variability will have weak effects and explain small amounts of variation in 0+ salmon and trout density data, given the inconsistencies in discharge–abundance relationships across time and space (*sensu* Rosenfeld, 2017).

2 | METHODS

Associations between 0+ salmonids surveyed during summer/autumn and river discharge were the focus of this analysis because: (a) 0+ salmonids represent a substantial proportion of populations in most rivers (Gibson & Cutting, 1993), (b) hydrological variation is

expected to more strongly influence the growth and survival of 0+ fish than older salmonids (Nislow & Armstrong, 2012), and (c) part or all of the older cohorts may have already departed the river as smolts.

2.1 | Study areas

Five rivers in England and Wales with the longest, most detailed and complete salmonid fisheries time-series data were selected (Figure 1). These were the rivers and tributaries of the Dee, Frome, Lune, Tamar and Tyne (Table 1). Juvenile population dynamics in these rivers have been monitored using river-specific methods for over 20 years, and they report salmonid stock status estimates to the International Council for the Exploration of the Sea (ICES).

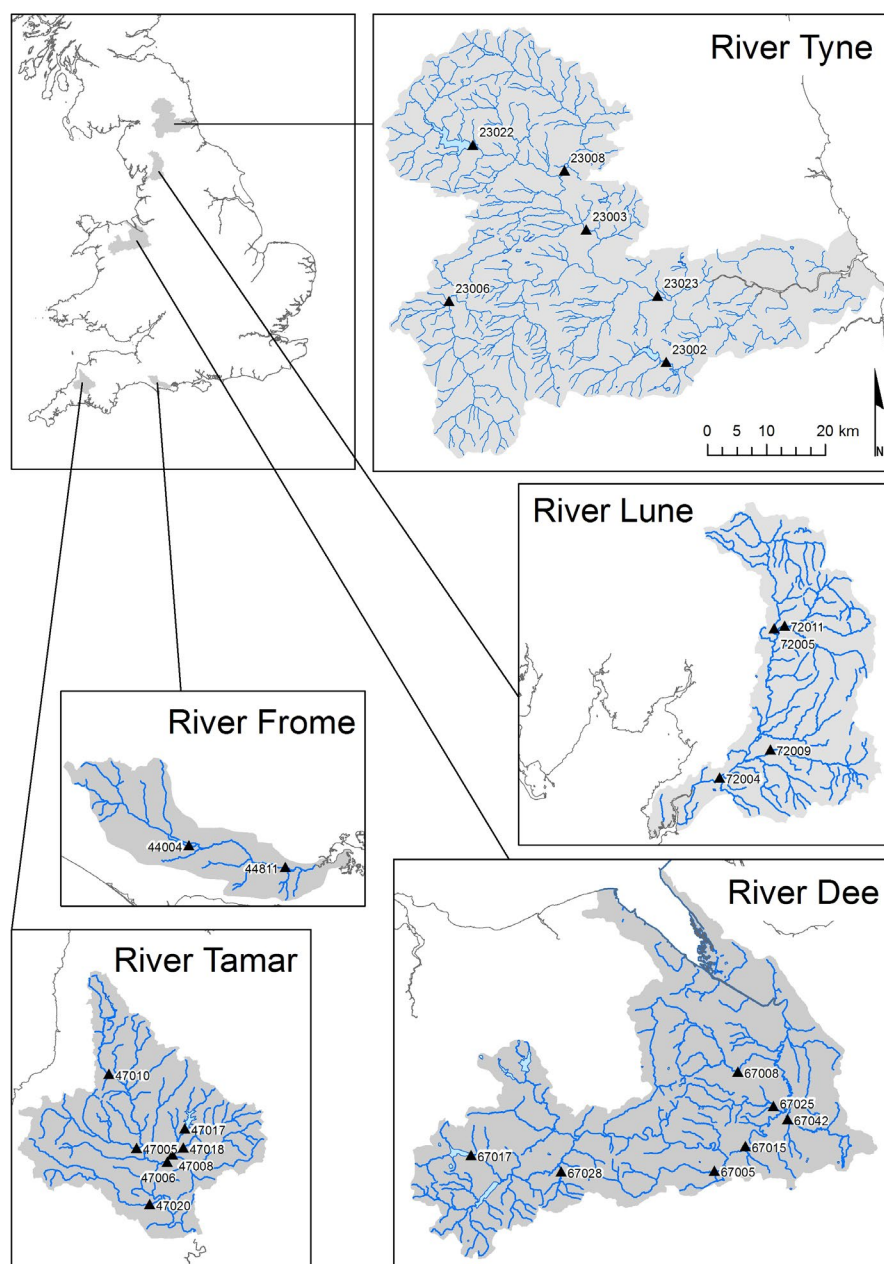


FIGURE 1 Location of five salmonid-producing rivers selected to investigate the effects of discharge variation on 0+ salmon and trout densities in England and Wales, United Kingdom. Discharge gauging stations (▲) shown in relation to the freshwater reaches of the Dee, Frome, Lune, Tamar and Tyne rivers. Gauging station names are detailed in Table S2. Note that the panels presenting the five rivers are all at the same cartographic scale [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 1** Rivers selected to investigate the effects of discharge variation on 0+ salmon and trout densities

River	Lat./Long.	River type	Length	Basin area	Mean discharge	River reg.	Catch 2015
Dee	53°32'83"N, 3°21'61"W	Spate river from an upland source	110	1,817	34.08 ± 0.46	Moderate	244 (39:61)
Frome	50°68'85"N, 2°07'68"W	Lowland river and chalk stream	49	454	1.21 ± 0.01	High	124 (52:48)
Lune	53°98'52"N, 2°87'88"W	Spate river from an upland source	71	1,300	36.11 ± 0.35	Low	316 (51:49)
Tamar	50°31'79"N, 4°15'54"W	Spate river from an upland source	98	1,800	22.78 ± 0.20	Low	275 (59:41)
Tyne	55°01'29"N, 1°40'15"W	Spate river from an upland source	118	2,936	36.50 ± 0.38	Moderate	1838 (47:53)

Note: Lat./Long. = latitude and longitude of the river mouth; River type = hydro-geomorphological classification; Length = distance (km) from the source to the river mouth; Basin area = land area (km²) bounded by watersheds draining into the river; Mean discharge = mean (±standard error) daily discharge (m³/s) for available data at the gauging station closest to the river mouth (Table S2); River reg. = relative measure of the degree of human influence on the natural discharge regime based on factors affecting NRFA gauging station runoff codes from the UK Hydrometric register (Marsh & Hannaford, 2008) and other discharge-regulation features; and Catch 2015 = estimated number of one-sea-winter (1SW) and multi-sea-winter (MSW) salmon caught in rod fisheries in 2015 with sea-age ratio (1SW:MSW) shown in parenthesis (Cefas, Environment Agency, & Natural Resources Wales, 2016).

TABLE 2 Fisheries and hydrological data sources and formats

Variable	Source	Format	River	Period
Density estimates from multiple-pass electrofishing surveys	EA NFPD	Annual 0+ densities (numbers per 100 m ²)	All (39)	1971–2015
Density estimates from five-minute electrofishing point-samples	NRW RMP	Annual 0+ densities (numbers per 100 m ²)	Dee (6)	1992–2015
A relative index of density from single electrofishing passes	GWCT	Annual 0+ densities (numbers per 100 m)	Frome (27)	2003–2015
Discharge (observed)	NRFA/EA/NRW	Annual, seasonal, monthly, and pre- and post-emergence river discharge (m ³ /s)	All (45)	1971–2015
Discharge (modelled)	Derived from flow accumulation model	Annual, seasonal, monthly, and pre- and post-emergence river discharge estimates (m ³ /s)	Frome (27)	2003–2015

Note: Flow accumulation model = the flow accumulation function, Arc Hydro Tools v2.0 (Esri, 2011b); River = rivers for which the source supplied 0+ density or hydrological data, along with the number of sites in parenthesis; and Period = data year range.

Abbreviations: EA NFPD, Environment Agency National Fish Population Database; EA, Environment Agency; GWCT, Game and Wildlife Conservation Trust; NRFA, National River Flow Archive; NRW RMP, Natural Resources Wales index River Monitoring Programme; NRW, Natural Resources Wales.

2.2 | Fisheries data

Salmon and trout 0+ density estimates (numbers per 100 m²) were compiled for the Rivers Lune, Tamar and Tyne from 1971 to 2015 by the Environment Agency (EA) (Table 2). They were collected using standardised multiple-pass (≥three passes) electrofishing surveys undertaken at 45 sites in spawning, nursery and rearing areas to monitor juvenile salmonid population dynamics for the EA's National Salmon Strategy. Separate density estimates (numbers per 100 m²) collected during five-minute electrofishing surveys were obtained from Natural Resources Wales' (NRW) monitoring programme for the River Dee between 1992 and 2015. For the River Frome, a relative index of 0+ salmon densities (numbers per 100 m) was derived

from the first electrofishing pass on 27 long-term monitoring sites from 2003 to 2015 as part of the Game and Wildlife Conservation Trust (GWCT) salmon monitoring programme. This monitoring programme samples 0+ salmonids in all available habitat using electrofishing surveys at 50–150 m sections throughout the catchment. Within rivers, only spatially independent sites that were separated by at least 1 km downstream distance were used, which exceeds the reported dispersal distance of newly emerged fry (Beall, Dumas, Claireaux, Barriere, & Marty, 1994; Webb, Fryer, Taggart, Thompson, & Youngson, 2001).

Measures were undertaken to ensure the fisheries data collected from different sources were comparable. First, the models included river and site-within-river group-level effects that control for



river-specific differences (e.g. different survey methods) while accounting for unexplained random noise among sites (e.g. inter-annual variation in electrofishing inefficiencies). Second, no electrofishing capture probabilities were supplied, but it was assumed that most factors affecting them (Millar, Fryer, Millidine, & Malcolm, 2016) were negated because the surveys were standardised (i.e. fish were surveyed under relative benign river conditions by trained personnel at the same time of year when their size rendered them susceptible to electrofishing). Third, having controlled for possible systematic biases, any consistent signal from ecological processes at this large spatial and temporal scale was expected to prevail over local noise due to observation processes.

2.3 | Hydrological data

Local fisheries officers provided approximate spawning and fry emergence timings on each river that allowed the hydrological variables to be tailored to account for latitudinal variation in spawning and emergence. Using these data, hydrological variables characterising five distinct temporal periods were defined: (a) annual, (b) seasonal, (c) monthly, (d) pre-fry emergence and (e) post-fry emergence. The annual period spanned the time interval between fish surveys, which was defined as the period from 1 September to 31 August. Seasonal periods were classified as: autumn (September to November), winter (December to February), spring (March to May) and summer (June to August). Pre-emergence was defined as the river-specific period from peak autumn to winter adult spawning to spring fry emergence, and post-emergence was defined as the river-specific period from spring fry emergence to the summer to autumn survey sampling date when the 0+ density estimates were collected (Table S1). The pre- and post-emergence period definitions included key events around emergence because: (a) considerable uncertainty existed on the timings of some key events (e.g. spawning) for each species in all rivers and years; (b) these broad periods avoided the possibility of finding spurious effects or missing real effects in poorly-defined shorter periods; and (c) sessile egg/embryo and free-living stages could be differentiated into two clearly dichotomous periods.

To match fish survey sites to locations of UK National River Flow Archive (NRFA) data, discharge gauging stations had to be less than 1 km upstream or downstream from the fish survey site and within the same river reach. Using these criteria, 45 fish survey sites were matched to 26 NRFA gauging stations using ArcMap (Esri, 2011a) (Table S2). Gauged daily flow (GDF) data for each station were extracted for the period 1971 to 2015 from the UK NRFA website (<https://nrfa.ceh.ac.uk/data>). In cases where GDF data were unavailable, an alternative matched station was used and GDF data were obtained directly from the EA and NRW. As there are few NRFA gauging stations in the River Frome catchment, a flow accumulation method was used to estimate discharges at fish survey sites located over 1 km away from a gauging station. Arc Hydro Tools (Esri, 2011b) was used to derive a flow accumulation model for subcatchments defined by the downstream locations of the gauging stations, the

latter of which were designated as catchment outlets. Observed discharge at those outlets was substituted as the maximum discharge per subcatchment and the flow accumulation model apportioned upstream discharge values throughout each subcatchment.

Fourteen hydrological variables were selected to measure discharge variation for each of the five aforementioned temporal periods. These were based on the indicators of hydrological alteration approach developed by Richter, Baumgartner, Powell, and Braun (1996) and were chosen to capture the magnitude, timing, duration, frequency and rate of change in the discharge regime (Table S3). High (Q10) and low (Q90) discharge percentiles were used to measure the frequency and severity of high and low discharge events, respectively (UK Centre for Ecology and Hydrology definitions at <https://nrfa.ceh.ac.uk/derived-flow-statistics>). These discharge percentiles were chosen because: (a) they capture discharges observed regularly but infrequently in rivers; more extreme high and low discharges are episodic events that have a low probability of occurrence, which makes it difficult to study their effects (Altwegg, Visser, Bailey, & Erni, 2017); and (b) uncertainty in discharge estimates is greatest when extreme high discharges overflow river banks and inundate the surrounding land bypassing the gauging station (Bates, Pappenberger, & Romanowicz, 2014). High pulses were defined as periods where discharge exceeded Q10 of long-term daily discharge, while low pulses were classified as periods where discharge fell below Q90 of long-term daily discharge. The number of rises and falls measured the frequency of positive and negative changes in discharge from one day to the next, while the means of all positive and negative differences among consecutive daily means measured the mean positive and negative change in discharge over successive days.

2.4 | 0+ salmonid density and hydrological data fulfilling the selection criteria for analysis

Twenty-six NRFA gauging stations were matched to 45 fish survey sites. However, only 15 out of 45 (33%) of the sites on the Rivers Dee, Lune, Tamar and Tyne and 21 out of 27 (78%) of the River Frome sites had matching 0+ survey data. Further consideration was therefore given to 36 unique site-station combinations (Table S4).

2.5 | Data analysis

The data comprised annual 0+ salmon and trout densities at fish survey sites with matched hydrological variables. To avoid the potential of drawing spurious conclusions from inadequate data, the data had to meet specific criteria to be included in the analysis. Fish survey sites with $\geq 75\%$ zeros and years with ≥ 15 days of missing hydrological data were removed. This did not preclude surveys finding no 0+ salmonids, which were present in 14%–67% of the examined time series (Figures S1–S2), nor years with unusual hydrological features in the rivers (Figure S3).



For each species, separate candidate sets of statistical models designed to explore the influence of individual and combinations of hydrological variables on inter-annual variation in 0+ densities were defined. Any outliers in 0+ densities were identified statistically using the *grubbs.test()* function of the R package "outliers" (Komsta, 2011) and removed from the data set (two observations, 0+ salmon densities for 2012 and 2014 at Redesmouth in the River Tyne, possibly due to an increase in the number of hatchery-reared juvenile salmon stocked since 2011 (J. Anson, personal communication, 18 September 2018)). To facilitate effect size comparisons, hydrological variables were standardised across rivers by subtracting the mean and dividing by two standard deviations (Gelman, 2008). Collinearity among the standardised hydrological variables was inspected using Pearson's correlation coefficients (Figure S4). Where variables were strongly correlated ($|r| \geq 0.7$), the perceived most ecologically important variable was retained for analysis (Figures S5–S6; Dormann et al., 2013). Monthly and seasonal hydrological variables were omitted from the analysis due to strong correlations with other independent variables. From the 14 hydrological variables considered, a reduced set of nine variables were selected for further investigation (Table S5).

Bayesian hierarchical mixed-effects models with a hurdle gamma error distribution were used to relate the nine hydrological variables to positively skewed 0+ densities. The models took the form:

$$\text{Density}_{r,s,y} = \begin{cases} 0 & \text{with probability } p \text{ and} \\ \text{Gamma}(\mu_{r,s,y}, \varphi) & \text{with probability } 1-p \end{cases} \quad (1)$$

$$\eta_{r,s,y} = \alpha + \theta X_{r,s,y} + v_{r,s} + v_y$$

$$v_{r,s} \sim \text{Normal}(0, \sigma_{r,s})$$

$$v_y \sim \text{Normal}(0, \sigma_y)$$

where the probability that Density is 0 was modelled as logit (p); α is a constant intercept; $\theta = \beta_1, \beta_2, \dots, \beta_k$ is a vector of K parameters relating $X = x_1, x_2, \dots, x_k$ hydrological variables to Density measured at site s , nested within river r , in year y . Density was modelled as Gamma distributed with mean $\mu_{r,s,y}$ fitted via a log link with linear predictor $\eta_{r,s,y}$ and shape parameter φ ; $v_{r,s}$ is a river:site group-level effect with mean zero and river-specific variance term $\sigma_{r,s}$ allowing a random intercept by river to be represented by a nested group-level effect of site, and v_y is a year group-level effect with mean zero and variance σ_y . The model structure for 0+ trout was simplified to include river as a population-level effect because a nested river:site group-level effect could not be robustly estimated from the data, which were limited to three rivers (Harrison et al., 2018). Model parameters were estimated by MCMC using Stan (Carpenter et al., 2017) run using the function *brm()* of R package "brms" (Bürkner, 2018). Three parallel MCMC chains were run for 2000 iterations, and all parameter estimates were presented with their 95% Bayesian credible intervals. Convergence was assessed by visually examining MCMC trace plots and the Gelman–Rubin statistic (Brooks & Gelman, 1998), and was considered stable if

the chains were mixing and non-convergent, that is the Gelman–Rubin test statistic < 1.05 for all parameters. Default weakly informative priors were used for all parameters: improper flat priors over the reals for covariate effects, Student $t(\mu = 1, \sigma = 10, \nu = 3)$ for the intercept, Student $t(\mu = 0, \sigma = 10, \nu = 3)$ for the standard deviation terms, Gamma (0.01, 0.01) for φ and logistic (0,1) for the zero Density probability parameter.

Exploratory analyses examined whether pre-emergence hydrological variables should be fitted as a linear or quadratic term in the models because salmonid eggs and embryos are sessile and more susceptible to high and low discharges than post-emergence life stages (Warren et al., 2015). By contrast, post-emergence hydrological variables were represented as a linear term in the models, because fry and parr exhibit behavioural adaptations and seek refugia habitat to limit the physiological costs of extreme discharges (Armstrong, Braithwaite, & Fox, 1998).

Candidate models were compared by their goodness of fit using a combination of the approximate leave-one-out (LOO) cross-validation procedure in the *loo()* function of R package "loo" (Vehtari, Gelman, & Gabry, 2017), and conditional and marginal R^2 values were calculated using the method of Gelman, Goodrich, Gabry, and Vehtari (2019) and implemented in the function *r2_bayes()* of R package "performance" (Lüdtke & Makowski, 2019). Model checks for violation of assumptions of normality and homogeneity of variance included density histograms of residuals, normal quantile–quantile plots and plots of Pearson's residuals versus fitted values. Autocorrelation in the data was checked using the *acf()* function of R package "ggfortify" (Tang, Horikoshi, & Li, 2016).

3 | RESULTS

3.1 | Temporal trends in river discharge

Distinct monthly, seasonal and inter-annual discharge trends were evident in all rivers between 1971 and 2015 (Figure S3). The largely chalk aquifer-fed River Frome had lower magnitude fluctuations than the other rivers, and its highest discharges occurred from winter to spring, rather than from autumn to winter.

3.2 | Relationships between river discharge and 0+ salmonid densities

A set of 16 candidate models describing relationships between 0+ salmonid densities and hydrological variables representing different aspects of the discharge regime were chosen a priori, fitted and compared for each species. All models converged without issue, all Gelman–Rubin R statistics < 1.05 (Figures S7 – S8), and the 95% credible intervals of the hurdle parameter estimates did not intercept zero (Tables S6 – S7), justifying the added model complexity.

TABLE 3 Statistics comparing fits for 0+ salmon density models with different combinations of hydrological variables as population-level effects and year and site nested within river as group-level effects on the intercept using approximate leave-one-out (LOO) cross-validation [expected log pointwise predictive density (ELPD)] presented as an information criterion statistic on the deviance scale [LOO information criterion (LOOIC)]

Model	Model terms	ELPD	np	LOOIC	δ looic	Marginal R^2	Conditional R^2
m6	np.gt.Q10.preemergence, np.gt.Q10.preemergence ²	-1,270.76	51.32	2,541.52	0.00	.001	.624
m1	mean.annual	-1,271.15	50.00	2,542.30	-0.39	.001	.621
m0	none	-1,271.21	50.35	2,542.42	-0.45	.000	.620
m5	mndur.lt.Q90.postemergence	-1,271.50	51.09	2,543.00	-0.74	.001	.623
m13	rsd.preemergence, rsd.preemergence ² , np.gt.Q10.preemergence, np.gt.Q10.preemergence ² , mndur.gt.Q10.preemergence, mndur.gt.Q10.preemergence ²	-1,271.82	55.45	2,543.63	-1.06	.012	.622
m8	mndur.gt.Q10.preemergence, mndur.gt.Q10.preemergence ²	-1,272.21	53.01	2,544.43	-1.45	.001	.617
m3	rsd.postemergence	-1,272.29	51.30	2,544.57	-1.53	.000	.620
m9	mndur.gt.Q10.postemergence	-1,272.53	51.28	2,545.07	-1.77	.000	.622
m11	np.lt.Q90.postemergence, mndur.lt.Q90.postemergence	-1,273.10	53.02	2,546.21	-2.34	.001	.626

Note: Model terms include pre-emergence high discharge frequency (np.gt.Q10.preemergence), mean annual discharge (mean.annual), null model (none), post-emergence low discharge duration (mndur.lt.Q90.postemergence), pre-emergence discharge variability (rsd.preemergence), pre-emergence high discharge duration (mndur.gt.Q10.preemergence), post-emergence discharge variability (rsd.postemergence), post-emergence high discharge duration (mndur.gt.Q10.postemergence) and post-emergence low discharge frequency (np.lt.Q90.postemergence). Also given are the effective number of parameters (np) and the difference in LOOIC (δ looic) between the top-ranked and other models. Marginal and conditional R^2 were calculated according to the method of Gelman et al. (2019). Statistics for models with δ looic < 2.35 are presented. A complete list of statistics for the full range of models is shown in Table S6.

Eight models for 0+ salmon were statistically indistinguishable, differing from the top-ranked model by δ looic < 2. However, pre-emergence high discharge frequency and duration were retained in 3 out of 8 (38%) of the models and were present in Model 6, which was the top-ranked model, and Model 13, which had the highest marginal R^2 (Table 3). The top-ranked Model 6 included a positive quadratic term for pre-emergence high discharge frequency, although the estimated population-level effect was weak with 95% credible intervals that overlapped zero (Figure 2a) and had high uncertainty (Figure 3). There was some evidence of heteroscedasticity in the residuals of Model 6 (Figure S9) (which was less than when assuming Gaussian errors; results not shown), but the possible violation of this assumption was judged acceptable given the large number of observations analysed. The group-level effects were approximately Gaussian (Figure 2b–2c). A model including post-emergence low discharge duration received little support and ranked below the null model.

Exploratory analyses for 0+ trout revealed the additional complexity required to represent pre-emergence high discharge frequency and duration as quadratic terms was not supported, and therefore, these were assumed linear in subsequent analyses. Five models for 0+ trout were statistically indistinguishable, and most of these included hydrological variables representing pre-emergence discharges, among which Model 13 was top-ranked (Table 4). Unlike for salmon, however, Model 1 had the highest marginal R^2 and included only mean annual discharge. The top-ranked Model

13 included a negative quadratic term for pre-emergence discharge variability and negative linear terms for pre-emergence high discharge frequency and duration, although their 95% credible intervals overlapped zero and considerable uncertainty existed around most of their estimates (Figure 4a) and marginal effects (Figure 5). Again, there was some heteroscedasticity in the residuals of Model 13 (Figure S10) that was accepted. The group-level effects were approximately Gaussian (Figure 4b–4c). Models including pre- and post-emergence low discharge frequency and duration were poorly supported with δ looic > 2.

4 | DISCUSSION

Following the recommendations of Warren et al. (2015) and Rosenfeld (2017) for a broad spatial and temporal investigation of associations between salmonid abundance and river discharge, the current analysis confirmed the expectation that hydrological variables representing high discharge events affect 0+ salmon and trout densities. Hydrological variables representing low discharge events were not discernibly associated with 0+ salmonid densities and those representing discharge variability had weak effects, explaining only small amounts of the variation in 0+ salmon and trout densities, even after accounting for variance due to the large spatial and temporal sampling protocol.

The findings from this study add to the growing body of evidence suggesting that high discharges between spawning and

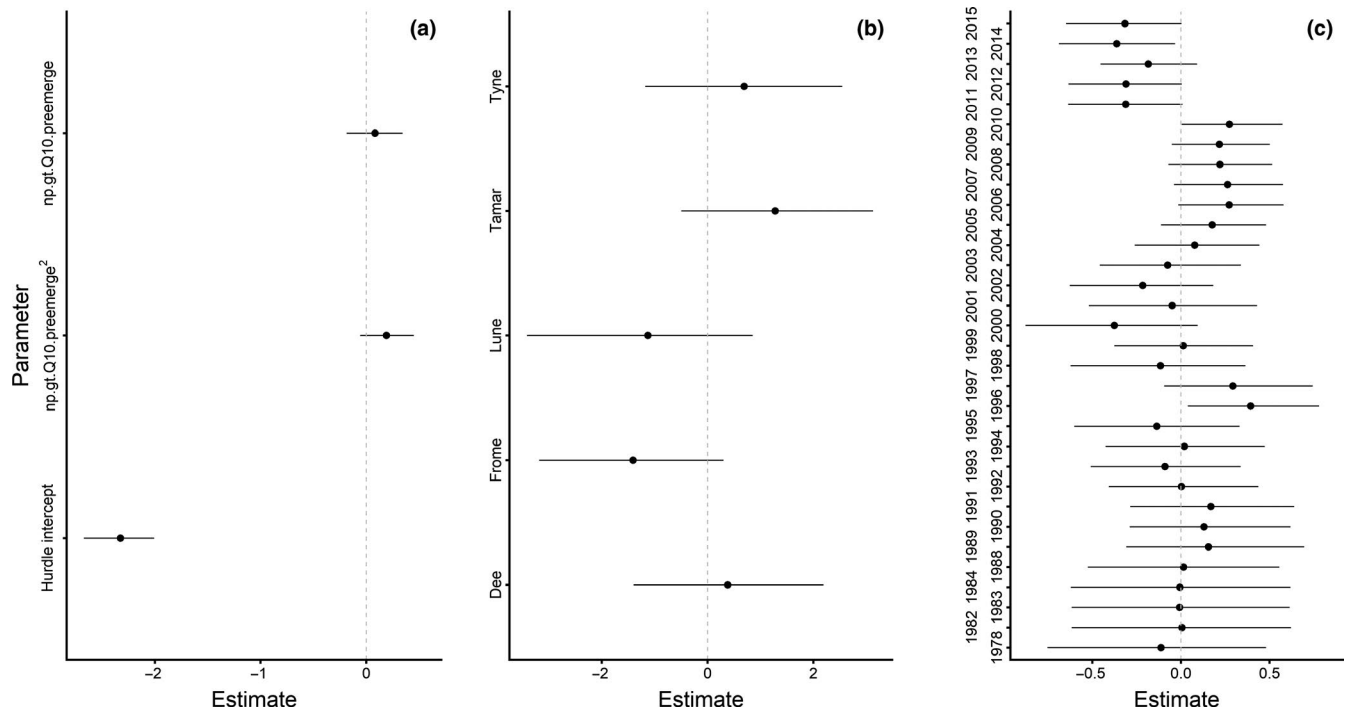


FIGURE 2 Caterpillar plots showing Bayesian estimates of (a) the population-level effects and (b–c) the group-level effects for the top-ranked 0+ salmon density model (Model 6). Points are the estimates, and lines are the 95% Bayesian credible intervals. The hydrological variable np.gt.Q10.premerge is the standardised pre-emergence high discharge frequency. See Methods for a description of the standardisation

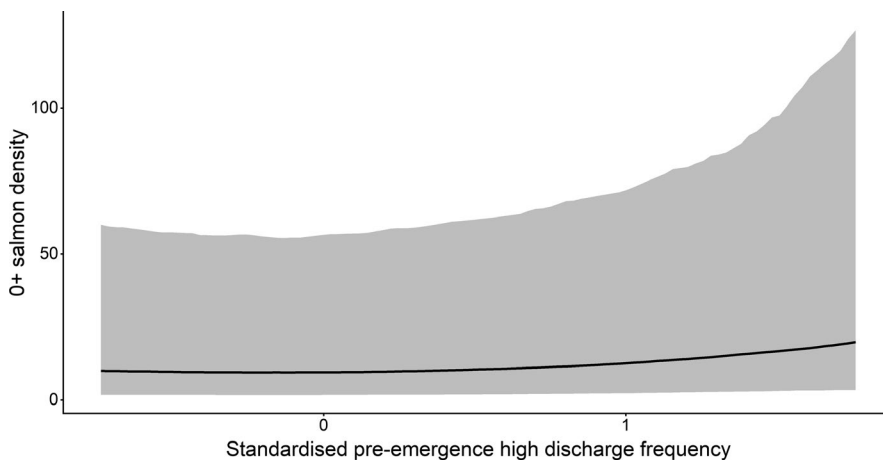


FIGURE 3 Marginal effect of the standardised pre-emergence high discharge frequency on 0+ salmon density. See Methods for a description of the standardisation. The shaded grey area is the standard error of the estimated effect

fry emergence have a marked effect on 0+ salmonid densities (Bergerot & Cattaneo, 2017; Cattaneo et al., 2002; Malcolm et al., 2012). Specifically, pre-emergence high discharge frequency driven mainly by natural variation was found to be positively and non-linearly associated with 0+ salmon densities. As the number of high discharge events rose from zero to four, the density marginal effect initially decreased from 10 (± 6.7) to 9.5 (± 6.4), followed by a subsequent increase to 19.9 (± 14.3) as the number of high discharge events peaked at 18. Glover, Soulsby, Fryer, Birkel, and Malcolm (2020) showed that high discharges between spawning and emergence enhance 0+ salmon densities. Pre-emergence covered the river-specific period from peak

autumn to winter adult spawning to spring fry emergence. Several mechanisms operating on spawning migration and site selection, egg development and fry emergence could underlie this result. Salmon are anadromous and use high discharges to migrate upstream to spawning grounds (Milner, Solomon, et al., 2012). High discharges allow salmon to access rivers earlier in the spawning season, penetrate further upstream and disperse their offspring more uniformly throughout the catchment (Jonsson, Jonsson, & Hansen, 2007; Parry, Gregory, Lauridsen, & Griffiths, 2018), which can increase the growth and survival of emerging fry by lowering intra-specific competition for food and territories (Einum, Nislow, Mckelvey, & Armstrong, 2008; Moir, Soulsby, & Youngson, 1998).

TABLE 4 Statistics comparing fits for 0+ trout density models with different combinations of hydrological variables and river as population-level effects and year and site as group-level effects on the intercept using approximate leave-one-out (LOO) cross-validation [expected log pointwise predictive density (ELPD)] presented as an information criterion statistic on the deviance scale [LOO information criterion (LOOIC)]

Model	Model terms	ELPD	np	LOOIC	δ looic	Marginal R^2	Conditional R^2
m13	rsd.preemerge, rsd.preemerge ² , np.gt.Q10.preemerge, preemerge, mndur.gt.Q10.preemerge	-325.32	29.40	650.64	0.00	.084	.238
m10	rsd.preemerge, rsd.preemerge ² , rsd.postemerge	-326.26	29.89	652.52	-0.94	.072	.215
m1	mean.annual	-326.40	25.15	652.79	-1.08	.180	.226
m2	rsd.preemerge, rsd.preemerge ²	-326.96	28.99	653.92	-1.64	.067	.217
m3	rsd.postemerge	-327.16	27.80	654.31	-1.84	.066	.204
m15	mean.annual, rsd.preemerge, rsd.preemerge ² , np.gt.Q10.preemerge, mndur.gt.Q10.preemerge, rsd.postemerge, np.lt.Q90.postemerge, mndur.lt.Q90.postemerge, np.gt.Q10.postemerge, mndur.gt.Q10.postemerge	-328.43	31.27	656.86	-3.11	.221	.297

Note: Model terms include pre-emergence discharge variability (rsd.preemerge), pre-emergence high discharge frequency (np.gt.Q10.preemerge), pre-emergence high discharge duration (mndur.gt.Q10.preemerge), post-emergence discharge variability (rsd.postemerge), mean annual discharge (mean.annual), pre-emergence high discharge duration (mndur.gt.Q10.preemerge), post-emergence low discharge frequency (np.lt.Q90.postemerge), post-emergence low discharge duration (mndur.lt.Q90.postemerge), post-emergence high discharge frequency (np.gt.Q10.postemerge) and post-emergence high discharge duration (mndur.gt.Q10.postemerge). Also given are the effective number of parameters (np) and the difference in LOOIC (δ looic) between the top-ranked and other models. Marginal and conditional R^2 were calculated according to the method of Gelman et al. (2019). Statistics for models with δ looic < 3.12 are presented. A complete list of statistics for the full range of models is shown in Table S7.

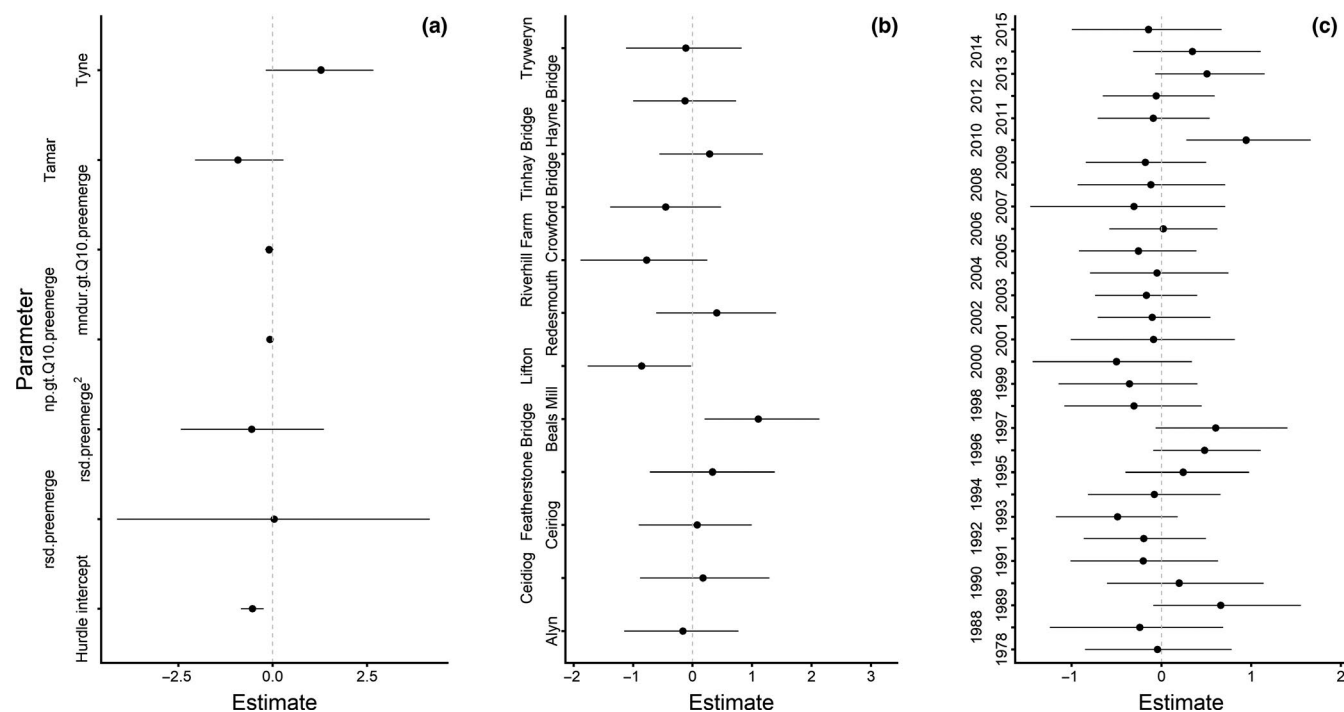


FIGURE 4 Caterpillar plots showing Bayesian estimates of (a) the population-level effects and (b-c) the group-level effects for the top-ranked 0+ trout density model (Model 13). Points are the estimates, and lines are the 95% Bayesian credible intervals. The hydrological variable rsd.preemerge is the standardised pre-emergence discharge variability, np.gt.Q10.preemerge is the standardised pre-emergence high discharge frequency, and mndur.gt.Q10.preemerge is the standardised pre-emergence high discharge duration. See Methods for a description of the standardisation

After spawning, high discharges can also increase egg survival by washing out organic sediments depleting available oxygen and removing metabolic waste (Crisp, 1996). However, high discharges

beyond an optimum threshold can impede spawner passage (Milner, Solomon, et al., 2012), decrease egg survival due to streambed scour or fine sediment intrusion (Gibbins, Shellberg,

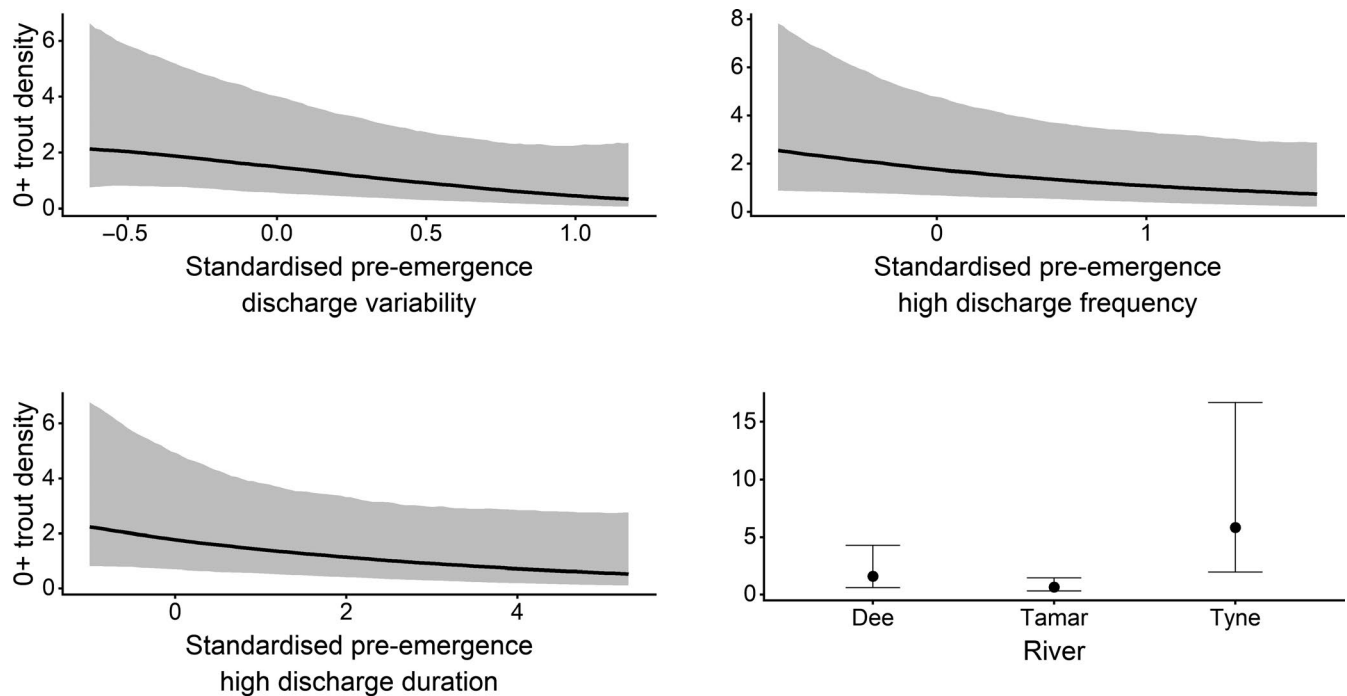


FIGURE 5 Marginal effect of the standardised pre-emergence discharge variability, the pre-emergence high discharge frequency, the pre-emergence high discharge duration and river on O+ trout density. See Methods for a description of the standardisation. The shaded grey area is the standard error of the estimated effect

Moir, & Soulsby, 2008), and displace fry downstream away from suitable habitat, increasing mortality (Heggenes, 1990). High discharges can therefore have positive and negative effects on O+ salmon densities that vary over short periods and with local site conditions, making the net effect hard to predict.

In contrast to salmon, pre-emergence high discharge frequency was negatively associated with O+ trout densities. As the number of high discharge events increased from zero to 18, the density marginal effect decreased from 2.6 (± 1.3) to 0.7 (± 0.5). Similar associations were found for pre-emergence high discharge duration and discharge variability. These results are consistent with other studies showing reductions in O+ trout densities in years with high discharges between spawning and fry emergence (Bergerot et al., 2019; Bergerot & Cattaneo, 2017; Cattaneo et al., 2002). Unlike these studies, however, the current investigation could not pinpoint the life-history event affected by high discharges because the pre-emergence period included multiple ontogenetic stages. Trout have more plastic life histories than salmon (Klemetsen et al., 2003), and many of the O+ trout in this study were likely offspring of freshwater-resident parents that do not require high discharges to migrate to spawning grounds. They tend to spawn in slower-flowing, shallower areas in the smaller tributaries of rivers compared with salmon (Louhi, Mäki-Petäys, & Erkinaro, 2008), which are prone to flash flooding (Petersen, 2001). Trout typically bury their eggs at shallower depths (0–25 cm) than salmon (10–30 cm) (DeVries, 1997), making them more susceptible to washout, scouring and sediment entombment during high discharges (Crisp, 1996; Sear, 1993). As discharge does not affect salmonid fry emergence timing (Riley & Moore, 2000), trout fry emerging under high discharges will face a

greater displacement risk than salmon because they are less able to hold station in fast water velocities due to their smaller pectoral fins generating less negative lift (Arnold, Webb, & Holford, 1991). High discharges might therefore impair spawning and reduce the egg-to-fry survival of trout.

None of the other hydrological variables considered had discernible associations with O+ salmonid densities. Several possible explanations exist for this finding. Salmonids might not be affected by these hydrological variables because they have evolved life-history strategies in response to the discharge regime of their natal river (Bunn & Arthington, 2002; Lytle & Poff, 2004). Perhaps these hydrological variables operated at local spatial and temporal scales or interacted with variables not considered in this analysis, such as water temperature (Gibson & Myers, 1988), habitat availability (Armstrong et al., 2003), geomorphology (Moir, Gibbins, Soulsby, & Webb, 2004), within-catchment location (Vollset et al., 2014), and adult abundance or egg deposition (Glover et al., 2020), for which comparable data were incomplete or unavailable. Definitions of hydrological variables used in this analysis might have differed from other studies. For example, the pre- and post-emergence periods were necessarily broad to overcome uncertainty in the timings of key life-history events. Partitioning these periods into finer, more biologically relevant time intervals might have provided better insight into the underlying mechanisms. Similarly, high discharges based on Q10 ranged from elevated flows to extreme flood events and a finer discrimination might have revealed stronger effects of more extreme events. Finally, despite careful alignment to the data, including the capacity to cope with unbalanced sample sizes, perhaps the models were unable to discern weak effects that might be apparent in targeted

river-specific studies. Such local effects were not the focus of this analysis and cannot be reliably inferred from the models because the estimation of group-level effects can alter the strength around other effects due to shrinkage (Harrison et al., 2018). Despite these caveats, this analysis identified a high discharge effect between spawning and fry emergence on 0+ salmon and trout densities, consistent with other studies (e.g. Bergerot et al., 2019; Glover et al., 2020), and thereby contributing to the development of a conceptual model of hydro-ecological processes.

Only equivocal evidence was found regarding which aspects of river discharge are associated with inter-annual variation in 0+ salmonid densities. Nevertheless, there was some empirical support that high discharges between spawning and fry emergence were positively and negatively associated with 0+ salmon and trout densities, respectively. Mechanisms underlying the species-specific associations with high discharges could not be elucidated. Further studies considering a wider range of abiotic variables at finer spatial and temporal scales are required to validate these findings. Attention should focus on the effects of extreme high discharges on 0+ salmonids. With climate change projected to increase the frequency and severity of floods in rivers (Schneider et al., 2013), improved knowledge of the effects of extreme high discharges on 0+ salmonids is vital for the development of effective management strategies (Jonsson & Jonsson, 2009). Possible strategies to restore the natural capacity of rivers to buffer the effects of floods include wetland creation and improving river connectivity (Palmer et al., 2009). General findings on salmonid discharge requirements are emerging, but more detailed analyses using better monitoring data are necessary. Finding only weak species-specific associations with high discharges suggests that developing stock-recruitment models including the environmental drivers of recruitment may prove challenging using existing monitoring data. More extensive and strategic monitoring of 0+ salmonids with discharge, temperature, habitat, geomorphology and within-catchment location along important salmonid rivers will aid future analyses. Undertaking a strategic review of juvenile salmonid monitoring programmes guided by a conceptual model of hydro-ecological processes to improve the efficacy and consistency of biological and environmental data collection within and between rivers in England and Wales is recommended.

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SUPPORTING INFORMATION

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

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