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

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, & Cattanéo, 2019; Bergerot & Cattanéo, 2017; Cattanéo, 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).
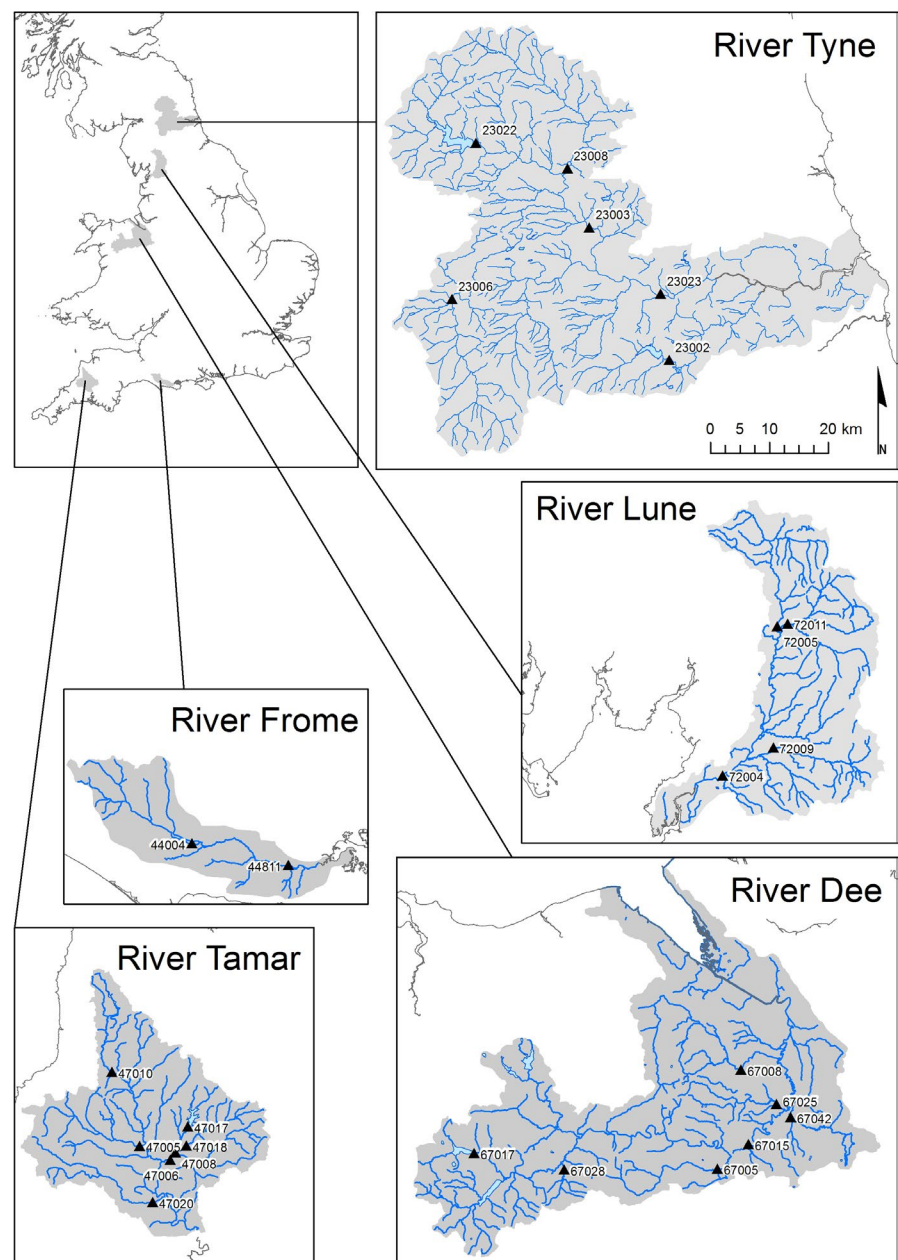

FIGURE 1 Location of five salmonid-producing rivers selected to investigate the effects of discharge variation on 0+ salmon and trout densities in England and Wales, United Kingdom. Discharge gauging stations (▲) shown in relation to the freshwater reaches of the Dee, Frome, Lune, Tamar and Tyne rivers.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

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 (km^2) bounded by watersheds draining into the river; Mean discharge = mean (±standard error) daily discharge (m^3/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 m^2) 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 m^2) 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 collated 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 ≥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:

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

$$\eta_{r:s,y} = \alpha + \theta X_{r:s,y} + \upsilon_{r:s} + \upsilon_y$$

$$\upsilon_{r:s} \sim \text{Normal}\left(0, \sigma_{r:s}\right)$$

$$\upsilon_y \sim \text{Normal}\left(0, \sigma_y\right)$$

(1)

where the probability that Density is 0 was modelled as logit (p); α is a constant intercept; $\theta = \beta 1, \beta 2,...,\beta k$ is a vector of K parameters relating $X = x1, x2,...,xk$ 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; $\upsilon_{r:s}$ 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 υ_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" (Lüdecke & 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.preemerge, np.gt.Q10.preemerge^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.postemerge	−1,271.50	51.09	2,543.00	−0.74	.001	.623
m13	rsd.preemerge, rsd.preemerge^2, np.gt.Q10. preemerge, np.gt.Q10.preemerge^2, mndur. gt.Q10.preemerge, mndur.gt.Q10.preemerge^2	−1,271.82	55.45	2,543.63	−1.06	.012	.622
m8	mndur.gt.Q10.preemerge, mndur.gt.Q10. preemerge^2	−1,272.21	53.01	2,544.43	−1.45	.001	.617
m3	rsd.postemerge	−1,272.29	51.30	2,544.57	−1.53	.000	.620
m9	mndur.gt.Q10.postemerge	−1,272.53	51.28	2,545.07	−1.77	.000	.622
m11	np.lt.Q90.postemerge, mndur.lt.Q90. postemerge	−1,273.10	53.02	2,546.21	−2.34	.001	.626

Note: Model terms include pre-emergence high discharge frequency (np.gt.Q10.preemerge), mean annual discharge (mean.annual), null model (none), post-emergence low discharge duration (mndur.lt.Q90.postemerge), pre-emergence discharge variability (rsd.preemerge), pre-emergence high discharge duration (mndur.gt.Q10.preemerge), post-emergence discharge variability (rsd.postemerge), post-emergence high discharge duration (mndur.gt.Q10.postemerge) and post-emergence low discharge frequency (np.lt.Q90.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 < 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
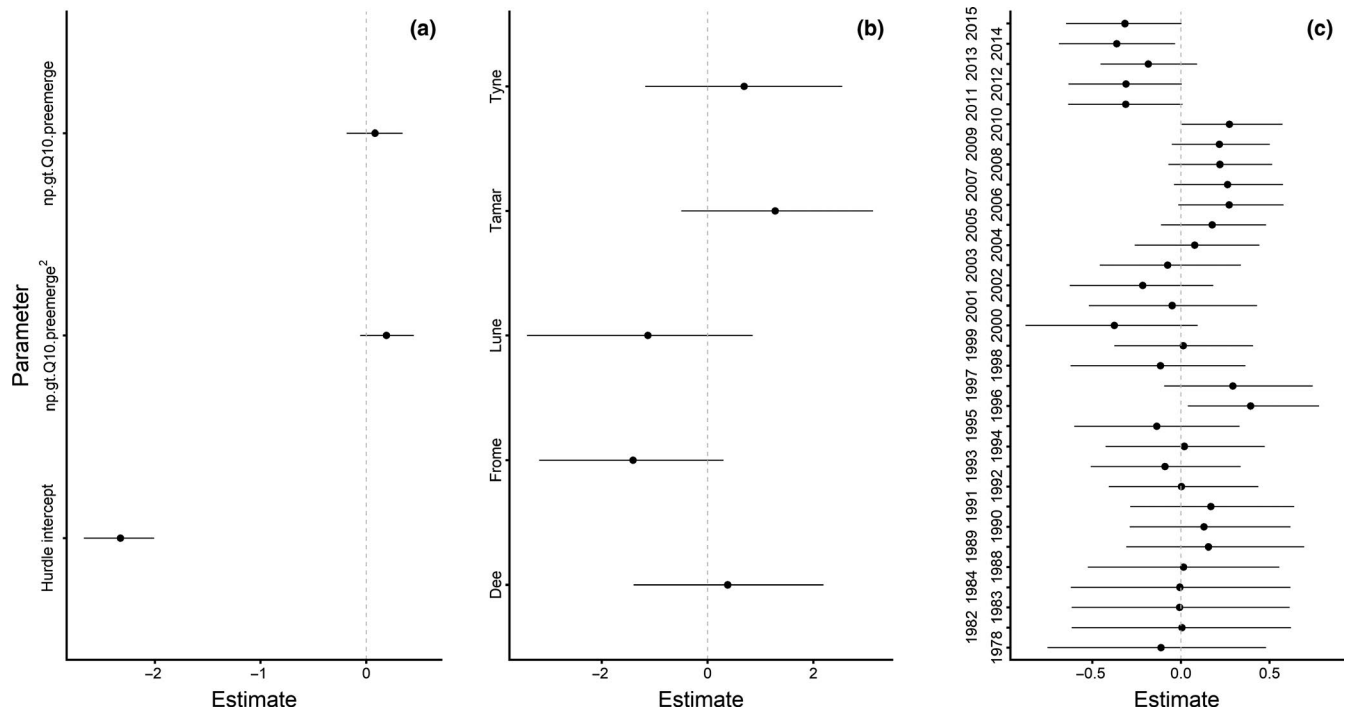
FIGURE 2 Caterpillar plots showing Bayesian estimates of (a) the population-level effects and (b–c) the group-level effects for the top-ranked 0+ salmon density model (Model 6). Points are the estimates, and lines are the 95% Bayesian credible intervals. The hydrological variable np.gt.Q10.preemerge is the standardised pre-emergence high discharge frequency. See Methods for a description of the standardisation
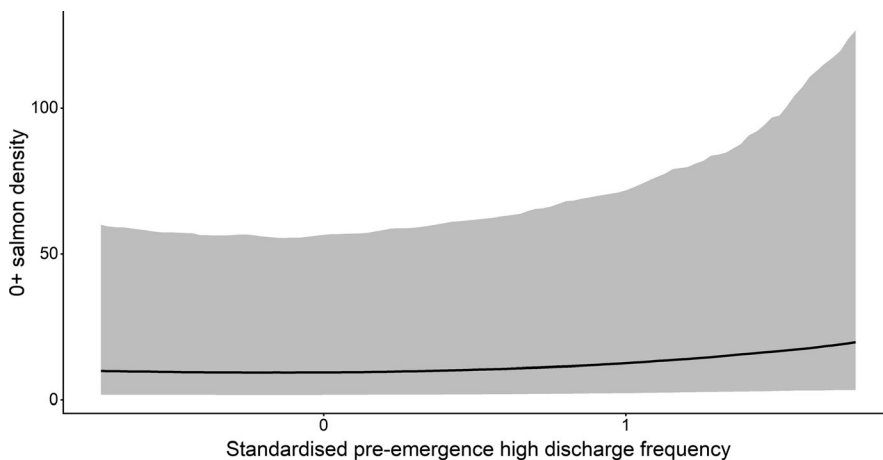

FIGURE 3 Marginal effect of the standardised pre-emergence high discharge frequency on 0+ salmon density. See Methods for a description of the standardisation. The shaded grey area is the standard error of the estimated effect

fry emergence have a marked effect on 0+ salmonid densities (Bergerot & Cattanéo, 2017; Cattanéo 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.preemerge², np.gt.Q10. preemerge, mndur.gt.Q10.preemerge	−325.32	29.40	650.64	0.00	.084	.238
m10	rsd.preemerge, rsd.preemerge², 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.preemerge²	−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.preemerge², 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 (δlooic) 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.
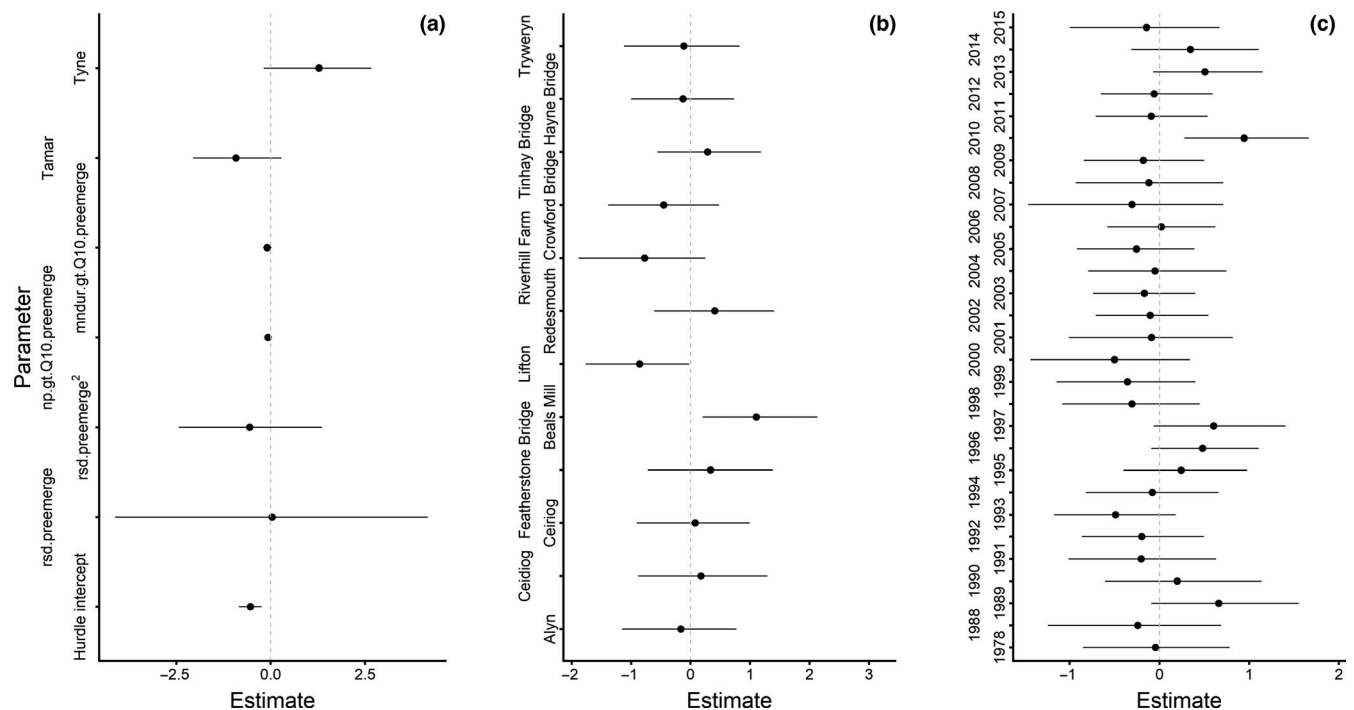

FIGURE 4 Caterpillar plots showing Bayesian estimates of (a) the population-level effects and (b–c) the group-level effects for the top-ranked 0+ trout density model (Model 13). Points are the estimates, and lines are the 95% Bayesian credible intervals. The hydrological variable rsd.preemerge is the 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,
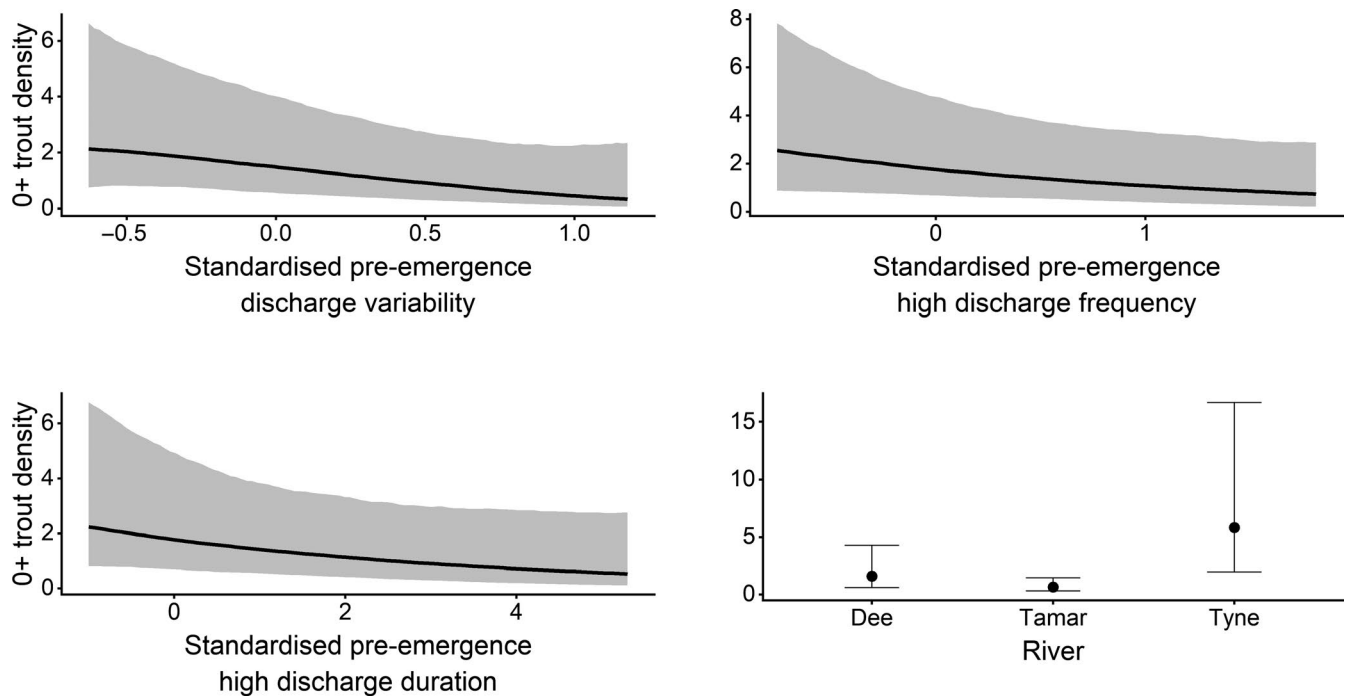
FIGURE 5 Marginal effect of the standardised pre-emergence discharge variability, the pre-emergence high discharge frequency, the pre-emergence high discharge duration and river on 0+ trout density. See Methods for a description of the standardisation. The shaded grey area is the standard error of the 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 0+ 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 0+ 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 0+ trout densities in years with high discharges between spawning and fry emergence (Bergerot et al., 2019; Bergerot & Cattanéo, 2017; Cattanéo 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 0+ 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 0+ 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.

Supporting information

Supporting methods

Table S1. Peak spawning and fry emergence dates used to define the pre- and post-emergence periods for salmon and trout in the Dee, Frome, Lune, Tamar and Tyne rivers. Dates shown in day-month format for autumn-winter peak adult spawning and spring fry emergence were acquired from EA and NRW fisheries officers for the respective rivers.

River	Peak spawning for salmon	Fry emergence for salmon	Peak spawning for trout	Fry emergence for trout
Dee	01–12	01–04	01–11	01–03
Frome	01–01	01–04	01–11	01–03
Lune	15–11	01–04	21–10	01–04
Tamar	21–12	15–04	21–11	21–03
Tyne	01–12	01–04	15–11	01–03

Table S2. NRFA gauging stations matched to fish survey sites in the Dee, Frome, Lune, Tamar and Tyne rivers. Selected NRFA gauging stations were located less than 1 km from the fish survey site where the 0+ salmonid density estimates were collected and within the same river reach. Station number indicates the NRFA gauging station number. Gauging stations in italics are closest to the river mouth.

River	Main-river stem/tributary	Station name	Station number	National grid reference
Dee	Tryweryn	Llyn Celyn Outflow	67017	SH8807739939
	Ceidiog	Llandrillo	67028	SJ0348437154
	Ceiriog	Brynkinalt Weir	67005	SJ2950337318
	Alyn	Pont-y-Capel	67008	SJ3352654047
	Clywedog	Bowling Bank	67025	SJ3958048249
	Emral Brook	Worthenbury Manor	67042	SJ4200645976
	Dee	Manley Hall	67015	SJ3482241459
	Dee	*Chester suspension bridge*	*67033*	*SJ4100065900*
Frome	Frome	Dorchester Total	44004	SY7084890331
	Frome	*East Stoke Weir*	*44811*	*SY8723286688*
Lune	Lune	Killington	72005	SD6220590633
	Wenning	Wennington	72009	SD6154270082
	Rawthey	Brigflatts	72011	SD6394591114
	Lune	*Caton*	*72004*	*SD5293565318*
Tamar	Inny	Beals Mill	47020	SX3591177075
	Lyd	Lifton Park	47006	SX3889684249
	Ottery	Werrington Park	47005	SX3372186613
	Tamar	Crowford Bridge	47010	SX2900699099
	Thrushel	Tinhay	47008	SX3978385516
	Thrushel	Hayne Bridge	47018	SX4162586663
	Wolf	Combe Park Farm	47017	SX4189089810
	Tamar	*Gunnislake*	*47001*	*SX4260072500*
Tyne	Rede	Rede Bridge	23008	NY8683783213
	North Tyne	Reaverhill	23003	NY9055573231
	South Tyne	Featherstone	23006	NY6721661064
	North Tyne	Ugly Dub	23022	NY7126287574
	Derwent	Eddy's Bridge	23002	NZ0410750791
	South Tyne	*Riding Mill*	*23023*	*NZ0269861956*

Table S3. Hydrological metrics calculated to derive annual, seasonal, and monthly hydrological variables, some of which were used to evaluate the effects of discharge variation on 0+ salmon and trout densities. These hydrological metrics were based on the indicators of hydrological alteration approach proposed by Richter et al. (1996). Abbreviation = metric name used in the hydrological variable; and Measurement = hydrological metric description.

Metric	Abbreviation	Measurement
Minimum discharge	min	Lowest daily discharge
Low discharge	Q90	Daily discharge equalled or exceeded 90% of the time
Mean discharge	mean	Average daily discharge
Maximum discharge	max	Highest daily discharge
High discharge	Q10	Daily discharge equalled or exceeded 10% of the time
Discharge variability	rsd	Relative standard deviation of discharge
High discharge frequency	np.gt.allQ10	Frequency of high pulses equal or above Q10
Low discharge frequency	np.lt.allQ90	Frequency of low pulses equal or below Q90
High discharge duration	mndur.gt.allQ10	Mean duration of high pulses equal or above Q10
Low discharge duration	mndur.lt.allQ90	Mean duration of low pulses equal or below Q90
Mean discharge increase	mn.pos.dif	Average daily discharge increase measured over successive days
Mean discharge decrease	mn.neg.dif	Average daily discharge decrease measured over successive days
Number of rises	n.rises	Frequency of daily discharge increases
Number of falls	n.falls	Frequency of daily discharge decreases

Supporting results

Table S4. Fish survey sites and NRFA gauging stations selected for analysis. Site = fish survey site; station name = NRFA gauging station; and distance (m) = the distance between the fish survey site and the NRFA gauging station. Fulfilled criteria indicates whether the fish survey site and the NRFA gauging station had data fulfilling the five temporal and spatial selection criteria for analysis: (1) the NRFA gauging station must be located less than 1 km from the fish survey site and within the same river reach; (2) each year was required to have more than 350 days of discharge data and less than 14 missing days during the life-history period between spawning and the survey sampling date; (3) sites must be located at a distance of more than 1 km away from each other and matched to a unique NRFA gauging station; (4) 0+ density estimates had to be from a single electrofishing survey method in each river; and (5) each site was required to have six or more observations of hydrological variables and 0+ salmonid densities including less than 75% zeros. The 36 unique site–station combinations fulfilling the temporal and spatial selection criteria for analysis were denoted as 'S' for salmon and 'T' for trout. Note that the 27 long-term monitoring sites on the River Frome have no NRFA gauging station information because these sites were located over 1 km away from the gauging stations and GDF estimates were derived from a flow accumulation model.

River	Site	Station name	Distance (m)	Fulfilled criteria
Dee	AY3_ALYN	Pont-y-Capel	137	S/T
	CD1.1_CEIDIOG	Llandrillo	327	S/T
	CE1.1_CEIRIOG1	Brynkinalt Weir	224	S/T
	CL1_CLYWEDOG	Bowling Bank	48	S
	Eel site 2	Emral Brook	754	N
	Old Eel site	Emral Brook	479	N
	Old eel site	Bowling Bank	30	N
	TR1.3_TRYWERYN	Llyn Celyn outflow	296	S/T
	WB1_WORTHENBURY BROOK1	Emral Brook	539	S
	117	Manley Hall	349	N
	143	Llyn Celyn outflow	293	N
	151	Emral Brook	550	N
	164	Llandrillo	283	N
	175	Bowling Bank	64	N
	215	Emral Brook	638	N
	244	Pont-y-Capel	91	N
Frome	Greys Bridge Meadow	Dorchester Total	701	N
	d/s Louds Mill	Dorchester Total	84	N
	Greys Bridge d/s bridge	Dorchester Total	840	N
	Mill Stream at East Stoke	East Stoke Weir	51	N
	Opposite Ambulance Station	Dorchester Total	699	N
	Bhompston Hatches to Bockhampton Bridge			S
	Bockhampton Bridge to Louds Mill			S
	Bradford Peveril Bridge to Muckleford			N
	Broompound Farm Bridge to Moreton Weir			S
	Clyffe Farm			N
	Dairy House			S
	East Burton Eel Rack to Broompound Farm Bridge			S
	East Burton Ford to East Burton Sleeper Bridge			S
	East Burton Sleeper Bridge to Eel Rack			S

	Grayling Run to Bindon Mill Hatches			N
	Greys Bridge Carrier below Bockhampton Bridge			N
	Greys Bridge Carrier By-pass to Offtake			S
	Hurst Bridge to top of Moreton Carrier			S
	Moreton Ford			S
	Moreton Ford to Hurst Bridge			S
	Muckleford			S
	Nine Hatches to Lewell Mill			S
	North Stream Clyffe Farm			S
	North Stream Duddle Farm			N
	North Stream Nine Hatches			S
	North Stream Norris Mill			S
	Sturts Weir to Nine Hatches			S
	Top of Moreton Carrier to D/S Pallington			S
	U/S Lewell Mill Bridge			N
	Whitfield Hatches			S
	Woodsford Road Bridge to Sturts Weir			S
	Wool Bridge			S
Lune	Above Broadraine Counter	Killington	104	N
	Ingmire Stickle	Brigflatts	132	N
	Low Mill at Caton	Caton	622	N
	Near Stangerthwaite	Killington	887	N
	Stakes Dub	Killington	842	N
	U/S Wennington	Wennington	496	N
	Wennington	Wennington	131	S
Tamar	INNY14_Beals Mill	Bealsmill	229	S/T
	LYD2_u/s Gatherley	Lifton Park	807	N
	LYD3_Lifton Park	Lifton Park	155	N
	LYD4_Lifton Playing Field	Lifton Park	635	S/T
	OTTERY13_Werrington Park	Werrington Park	304	N
	TAMAR10_Crowford Bridge	Crowford Bridge	429	T
	THRUSHEL1_Tinhay Bridge	Tinhay	433	S/T
	THRUSHEL2_Tinhay	Tinhay	482	N
	THRUSHEL3_d/s Hayne Bridge	Hayne Bridge	68	S/T
	WOLF9_d/s Roadford Dam	Combe Park Farm	22	N
Tyne	River Rede at Redesmouth	Rede Bridge	39	S/T
	North Tyne at Riverhill farm	Reaverhill	88	S/T
	North Tyne at Yarrow	Uglydub	364	N
	Riding Mill Smolt Trap	Riding Mill	44	N
	River Derwent at Eddy's Bridge	Eddys Bridge	320	N
	River Rede at Rede Bridge	Rede Bridge	97	N
	South Tyne at Featherstone Bridge	Featherstone	129	S/T

Table S5. Hydrological variables selected to investigate the effects of discharge variation on 0+ salmon and trout densities along with their hypothesised influence.

Variable	Abbreviation	Description	Influence	References
Mean annual discharge	mean.annual	Annual average discharge magnitude	Adult abundance and distribution; juvenile growth and survival	Armstrong et al. (2003) Parry et al. (2018)
Pre-emergence discharge variability	rsd.preemerge	Temporal variation in discharge during the pre-emergence period	Adult abundance and distribution; egg and embryo survival and development	Armstrong et al. (2003) Malcolm et al. (2012) Gibson & Cutting (1993)
Post-emergence discharge variability	rsd.postemerge	Temporal variation in discharge during the post-emergence period	Juvenile growth and survival	Warren et al. (2015)
Post-emergence low discharge frequency	np.lt.Q90.postemerge	Frequency of low pulses equal or below Q90 discharge during post-emergence	Juvenile growth and survival	Riley et al. (2009) Gregory et al. (2017)
Post-emergence low discharge duration	mndur.lt.Q90.postemerge	Severity of low pulses equal or below Q90 discharge during post-emergence	Juvenile growth and survival	Riley et al. (2009) Gregory et al. (2017)
Pre-emergence high discharge frequency	np.gt.Q10.preemerge	Frequency of high pulses equal or above Q10 discharge during pre-emergence	Adult abundance and distribution; egg washout; recruitment	Armstrong et al. (2003) Parry et al. (2018) Milner et al. (2012)
Post-emergence high discharge frequency	np.gt.Q10.postemerge	Frequency of high pulses equal or above Q10 discharge during post-emergence	Fry emergence and dispersal; juvenile growth and survival	Jensen & Johnsen (1999) Warren et al. (2015)
Pre-emergence high discharge duration	mndur.gt.Q10.preemerge	Severity of high pulses equal or above Q10 discharge during pre-emergence	Adult abundance and distribution; egg washout; recruitment	Armstrong et al. (2003) Parry et al. (2018) Malcolm et al. (2012) Milner et al. (2012)
Post-emergence high discharge duration	mndur.gt.Q10.postemerge	Severity of high pulses equal or above Q10 discharge during post-emergence	Fry emergence and dispersal; juvenile growth and survival	Jensen & Johnsen (1999) Warren et al. (2015)

This subset of hydrological variables was selected from a larger list of hydrological variables that was refined based on their perceived ecological importance and collinearity with other hydrological variables (Table S3). The annual timescale was defined as the period between 1 September and 31 August, pre-emergence was the river-specific period from peak autumn-winter adult spawning to spring fry emergence, and post-emergence was the river-specific period from spring fry emergence to the survey sampling date when the juvenile density estimates were collected (Table S1).
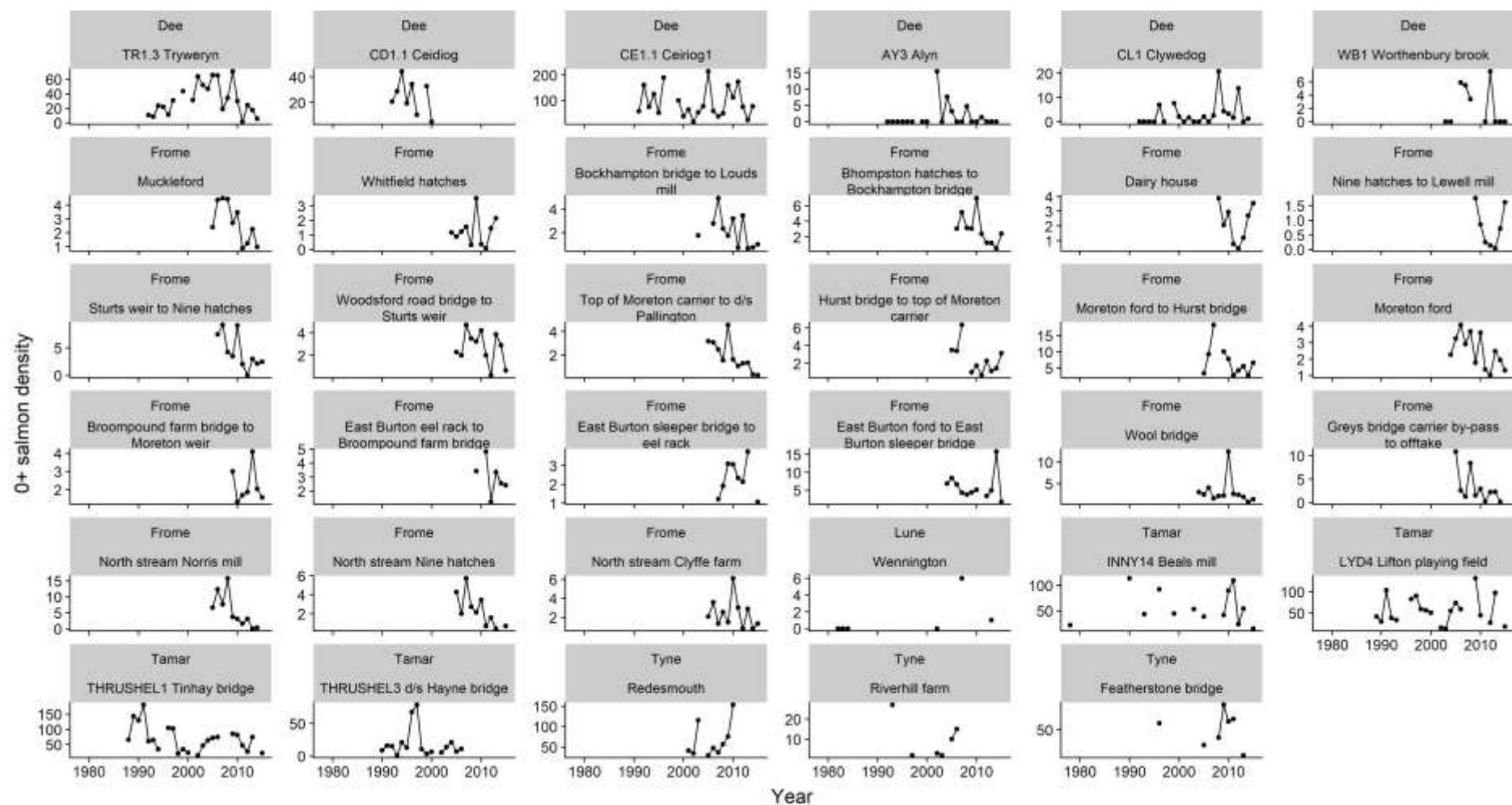
Figure S1. Time series plots of annual 0+ salmon density estimates from 1978 to 2015 at 35 fish survey sites on five UK rivers. River and site names are shown in the grey panels on top of each plot. A continuous line indicates 0+ density estimates over consecutive years. Plots are presented in an upstream to downstream order based on site distance from the river mouth.
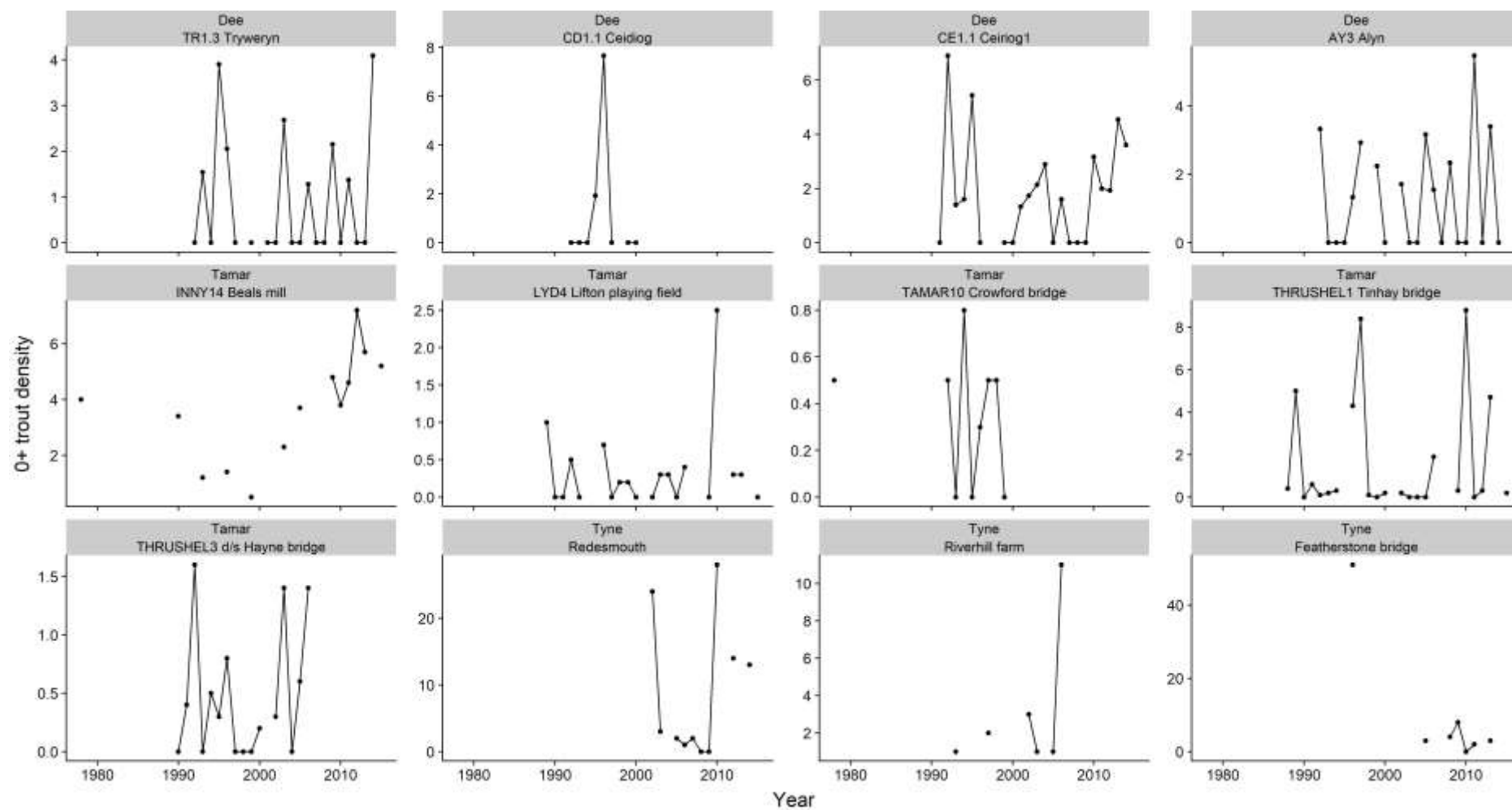
Figure S2. Time series plots of annual 0+ trout density estimates from 1978 to 2015 at 12 fish survey sites on three UK rivers. River and site names are shown in the grey panels on top of each plot. A continuous line indicates 0+ density estimates over consecutive years. Plots are presented in an upstream to downstream order based on site distance from the river mouth.
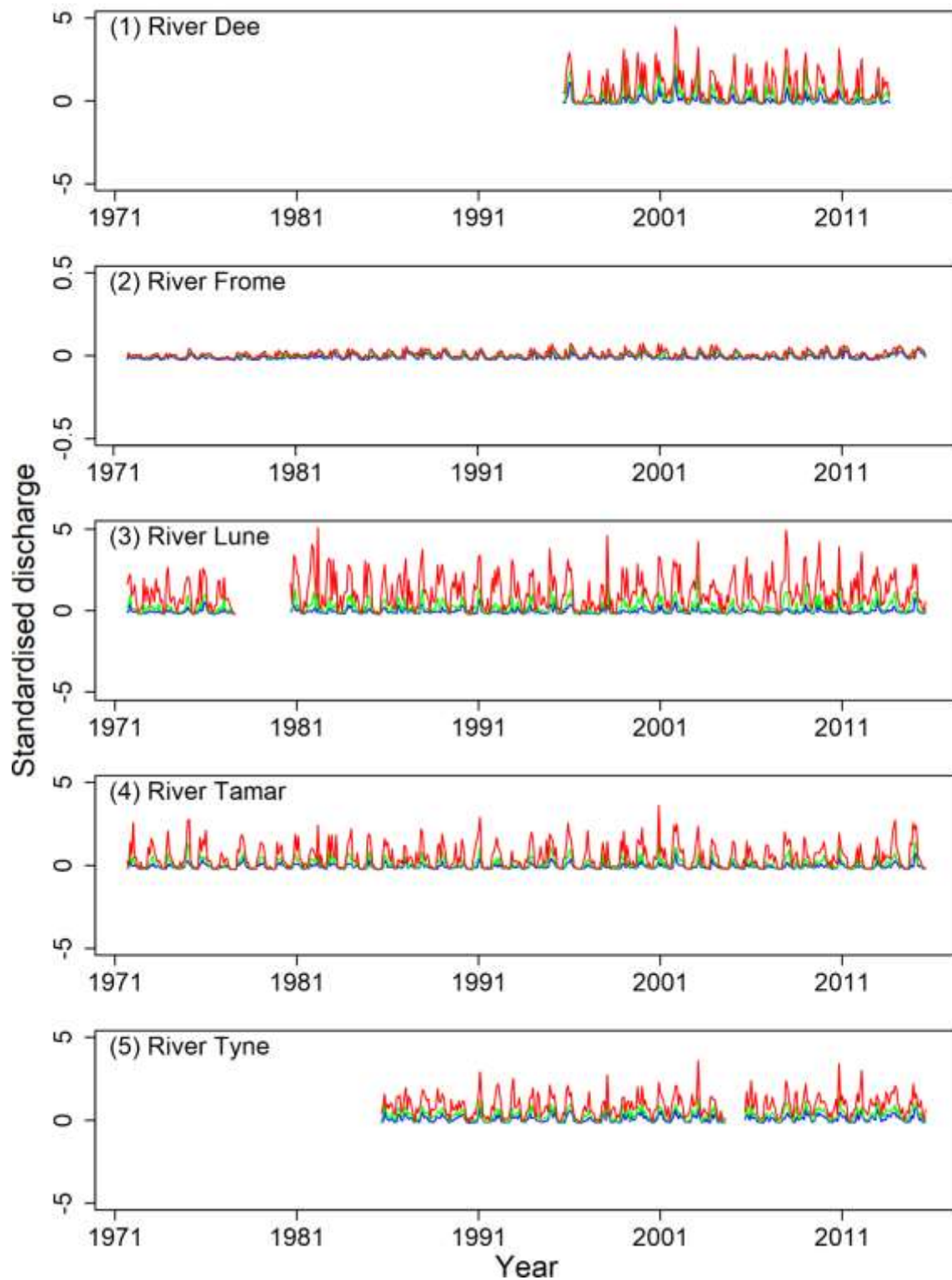
Figure S3. Temporal trends in standardised discharge for the Dee (1), Frome (2), Lune (3), Tamar (4) and Tyne (5) rivers between September 1971 and August 2015. Monthly Q90 (lower blue line), Q50 (middle green line), and Q10 (upper red line) discharge. Discharge trends presented for illustrative purposes from the following NRFA gauging stations located closest to the river mouth: (1) Chester Suspension Bridge, (2) East Stoke Weir, (3) Caton, (4) Gunnislake, and (5) Riding Mill. Differences in the duration of the discharge time series compared to those presented in Table 2 result from the shorter reporting periods of these NRFA gauging stations. The y-axis for the River Frome differs from the other rivers to ensure that the discharge trends are visible.
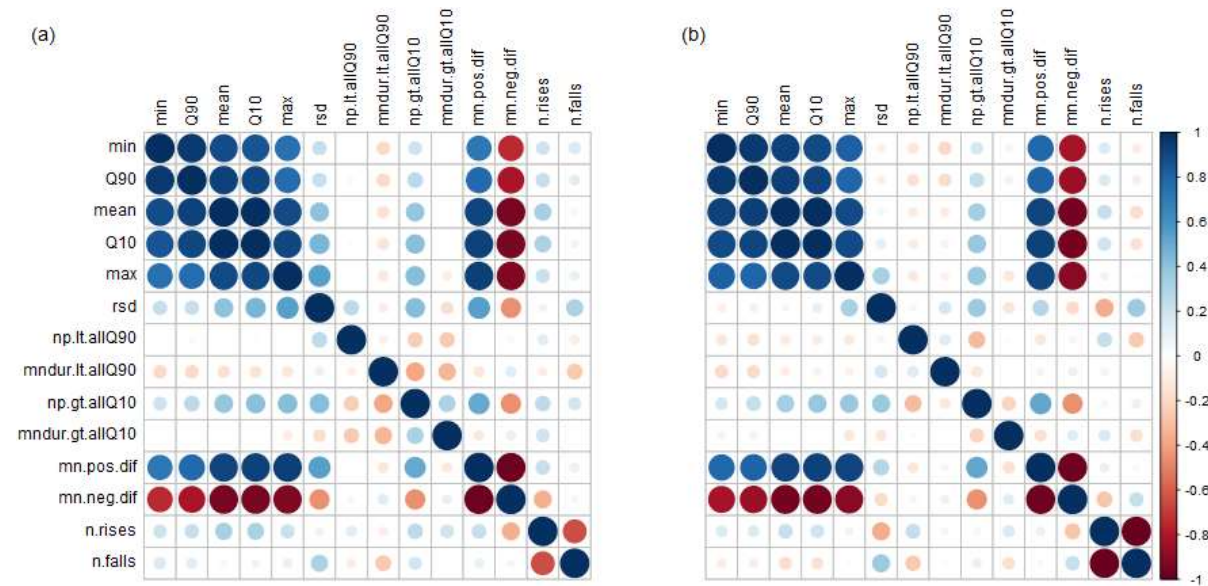
10

Figure S4. A graphical display of the correlation matrices for the annual hydrological variables investigated to evaluate the effects of discharge variation on 0+ salmon (a) and trout (b) densities. Positive correlations are displayed in blue and negative correlations in red. The intensity of the colour and the size of the circle are proportional to the correlation coefficients.
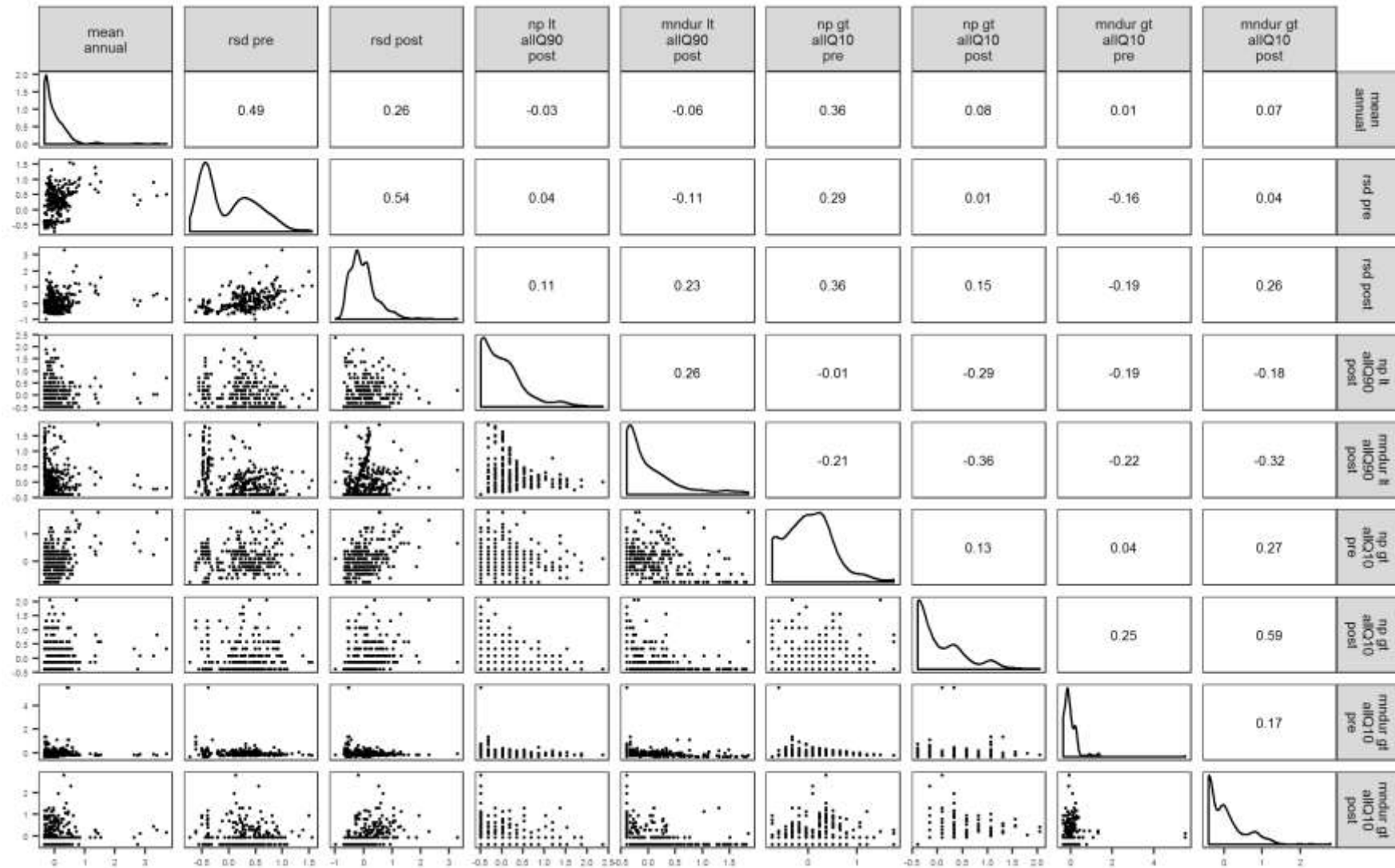
Figure S5. Pairs plots showing correlations among the nine hydrological variables selected to investigate the effects of discharge variation on 0+ salmon densities in the Dee, Frome, Lune, Tamar and Tyne rivers. Abbreviations for the hydrological variables are shown in Table S5.
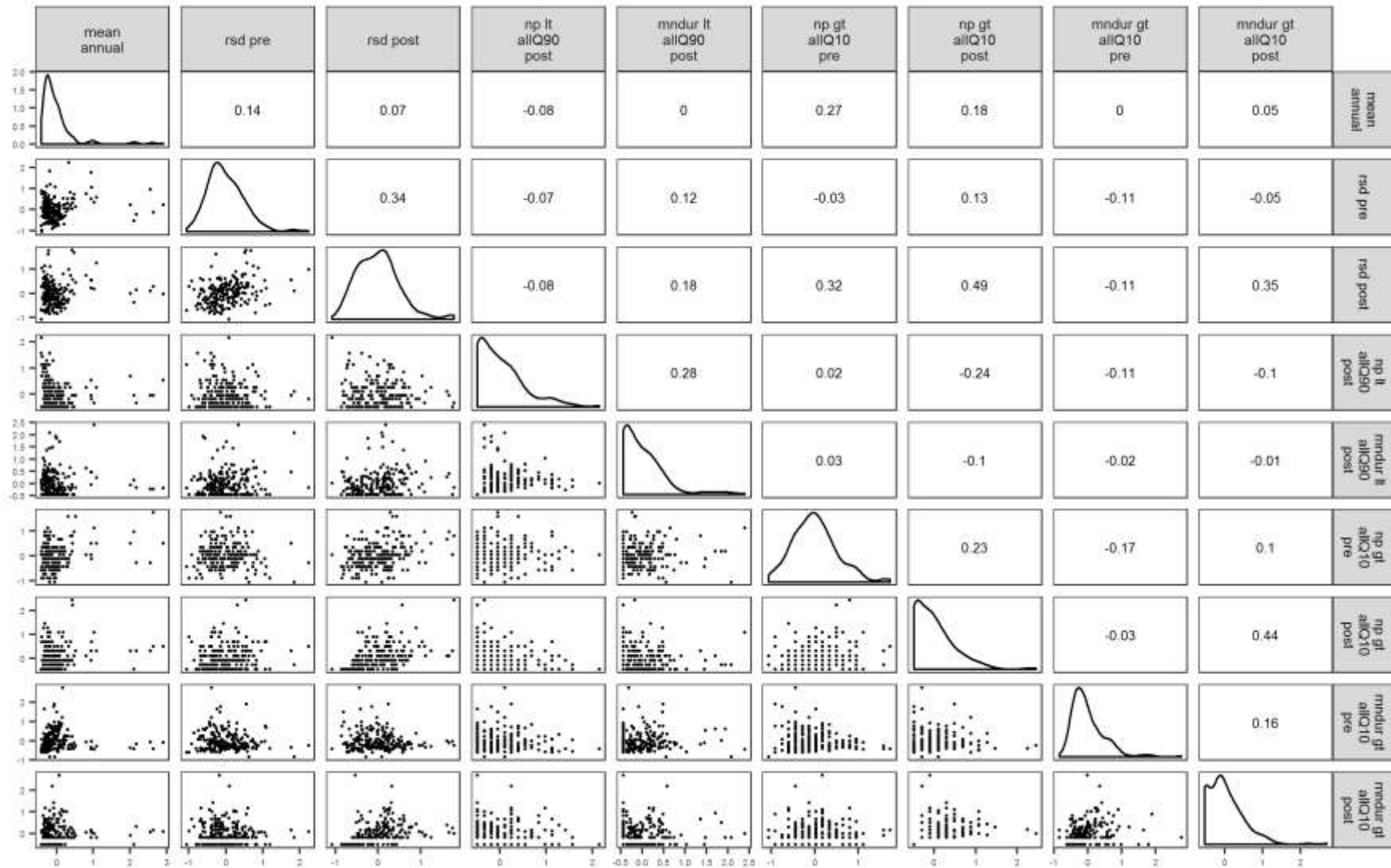
Figure S6. Pairs plots showing correlations among the nine hydrological variables selected to investigate the effects of discharge variation on 0+ trout densities in the Dee, Tamar and Tyne rivers. Abbreviations for the hydrological variables are detailed in Table S5.

13

Table S6. 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	δlooic	Marginal R^2	Conditional R^2
m6	np.gt.Q10.preemerge, np.gt.Q10.preemerge^2	−1270.76	51.32	2541.52	0.00	0.001	0.624
m1	mean.annual	−1271.15	50.00	2542.30	−0.39	0.001	0.621
m0	None	−1271.21	50.35	2542.42	−0.45	0.000	0.620
m5	mndur.lt.Q90.postemerge	−1271.50	51.09	2543.00	−0.74	0.001	0.623
m13	rsd.preemerge, rsd.preemerge^2, np.gt.Q10.preemerge, np.gt.Q10.preemerge^2, mndur.gt.Q10.preemerge, mndur.gt.Q10.preemerge^2	−1271.82	55.45	2543.63	−1.06	0.012	0.622
m8	mndur.gt.Q10.preemerge, mndur.gt.Q10.preemerge^2	−1272.21	53.01	2544.43	−1.45	0.001	0.617
m3	rsd.postemerge	−1272.29	51.30	2544.57	−1.53	0.000	0.620
m9	mndur.gt.Q10.postemerge	−1272.53	51.28	2545.07	−1.77	0.000	0.622
m11	np.lt.Q90.postemerge, mndur.lt.Q90.postemerge	−1273.10	53.02	2546.21	−2.34	0.001	0.626
m12	np.gt.Q10.preemerge, np.gt.Q10.preemerge^2, mndur.gt.Q10.preemerge, mndur.gt.Q10.preemerge^2, np.gt.Q10.postemerge, mndur.gt.Q10.postemerge	−1273.13	55.64	2546.27	−2.37	0.003	0.628
m4	np.lt.Q90.postemerge	−1273.14	52.32	2546.29	−2.38	0.000	0.623
m7	np.gt.Q10.postemerge	−1273.21	51.12	2546.42	−2.45	0.000	0.621
m2	rsd.preemerge, rsd.preemerge^2	−1273.57	51.80	2547.13	−2.81	0.006	0.616
m10	rsd.preemerge, rsd.preemerge^2, rsd.postemerge	−1274.30	52.87	2548.61	−3.54	0.006	0.619
m14	rsd.postemerge, np.lt.Q90.postemerge, mndur.lt.Q90.postemerge, np.gt.Q10.postemerge, mndur.gt.Q10.postemerge	−1275.84	55.16	2551.68	−5.08	0.003	0.628
m15	mean.annual, rsd.preemerge, rsd.preemerge^2, np.gt.Q10.preemerge, np.gt.Q10.preemerge^2, mndur.gt.Q10.preemerge, mndur.gt.Q10.preemerge^2, rsd.postemerge, np.lt.Q90.postemerge, mndur.lt.Q90.postemerge, np.gt.Q10.postemerge, mndur.gt.Q10.postemerge	−1276.79	60.01	2553.58	−6.03	0.017	0.629

Model terms include the selected hydrological variables (Table S5) and the null model (none, m0). Also given are the effective number of parameters (np) and the difference in LOOIC (δlooic) between the top-ranked and other models. Marginal and conditional R^2 were calculated according to the method of Gelman et al. (2019).

Table S7. 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	δlooic	Marginal R^2	Conditional R^2
m13	rsd.preemerge, rsd.preemerge^2, np.gt.Q10.preemerge, mndur.gt.Q10.preemerge	−325.32	29.40	650.64	0.00	0.084	0.238
m10	rsd.preemerge, rsd.preemerge^2, rsd.postemerge	−326.26	29.89	652.52	−0.94	0.072	0.215
m1	mean.annual	−326.40	25.15	652.79	−1.08	0.180	0.226
m2	rsd.preemerge, rsd.preemerge^2	−326.96	28.99	653.92	−1.64	0.067	0.217
m3	rsd.postemerge	−327.16	27.80	654.31	−1.84	0.066	0.204
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	0.221	0.297
m8	mndur.gt.Q10.preemerge	−329.21	28.46	658.43	−3.89	0.068	0.213
m9	mndur.gt.Q10.postemerge	−329.40	26.99	658.80	−4.08	0.069	0.213
m12	np.gt.Q10.preemerge, mndur.gt.Q10.preemerge, np.gt.Q10.postemerge, mndur.gt.Q10.postemerge	−329.92	29.24	659.83	−4.60	0.095	0.244
m0	None	−330.30	27.47	660.60	−4.98	0.063	0.204
m7	np.gt.Q10.postemerge	−330.41	27.72	660.83	−5.09	0.084	0.223
m4	np.lt.Q90.postemerge	−330.46	27.84	660.93	−5.14	0.086	0.209
m6	np.gt.Q10.preemerge	−330.54	27.31	661.07	−5.22	0.074	0.209
m5	mndur.lt.Q90.postemerge	−331.23	27.55	662.45	−5.91	0.072	0.208
m11	np.lt.Q90.postemerge, mndur.lt.Q90.postemerge	−331.26	28.24	662.52	−5.94	0.090	0.212
m14	rsd.postemerge, np.lt.Q90.postemerge, mndur.lt.Q90.postemerge, np.gt.Q10.postemerge, mndur.gt.Q10.postemerge	−331.99	31.30	663.98	−6.67	0.114	0.233

Model terms include the selected hydrological variables (Table S5) and the null model (none, m0). Also given are the effective number of parameters (np) and the difference in LOOIC (δlooic) between the top-ranked and other models. Marginal and conditional R^2 were calculated according to the method of Gelman et al. (2019).
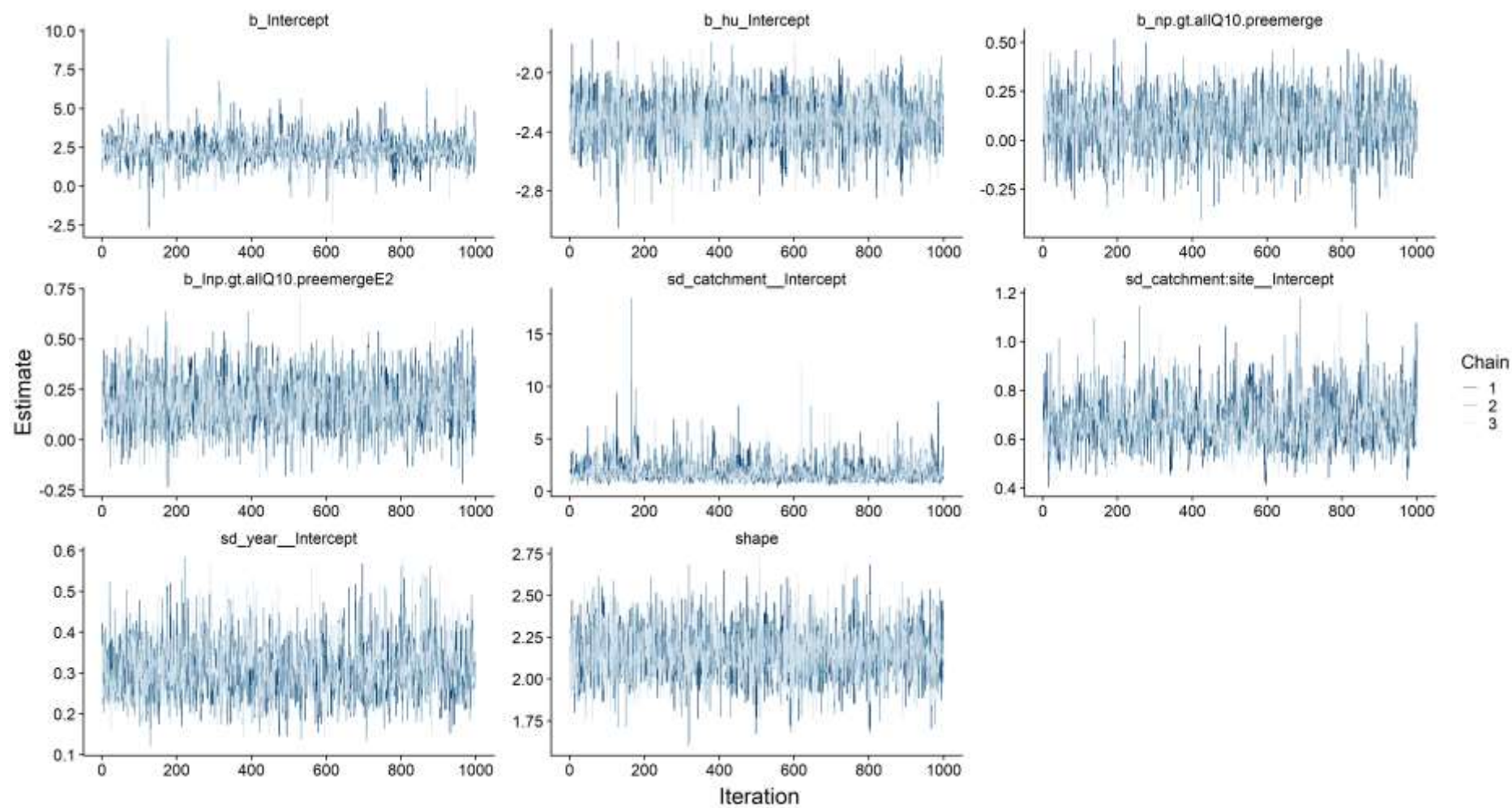
Figure S7. Trace plots of parameters for the top-ranked 0+ salmon density model (Model 6).
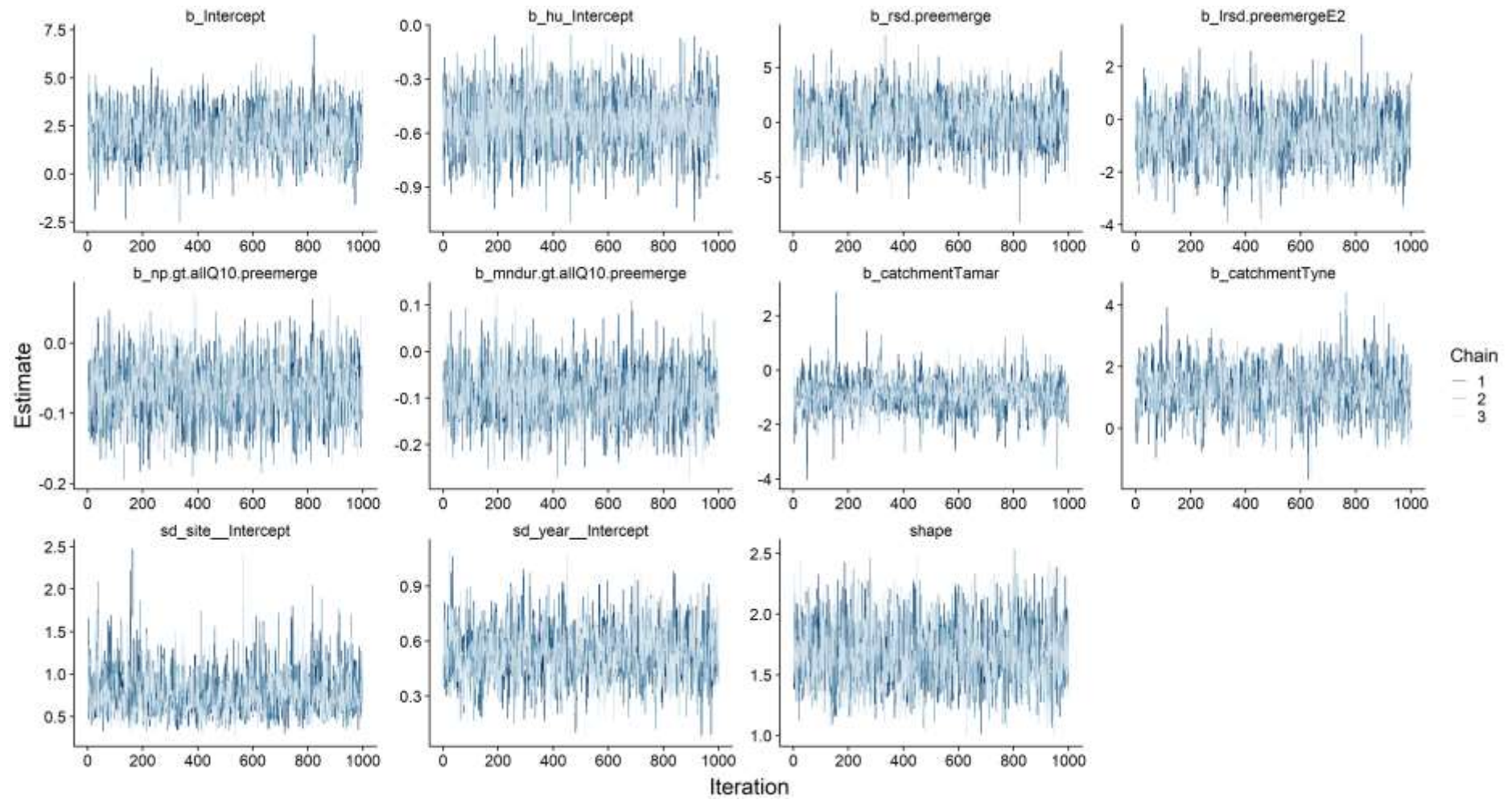
Figure S8. Trace plots of parameters for the top-ranked 0+ trout density model (Model 13).
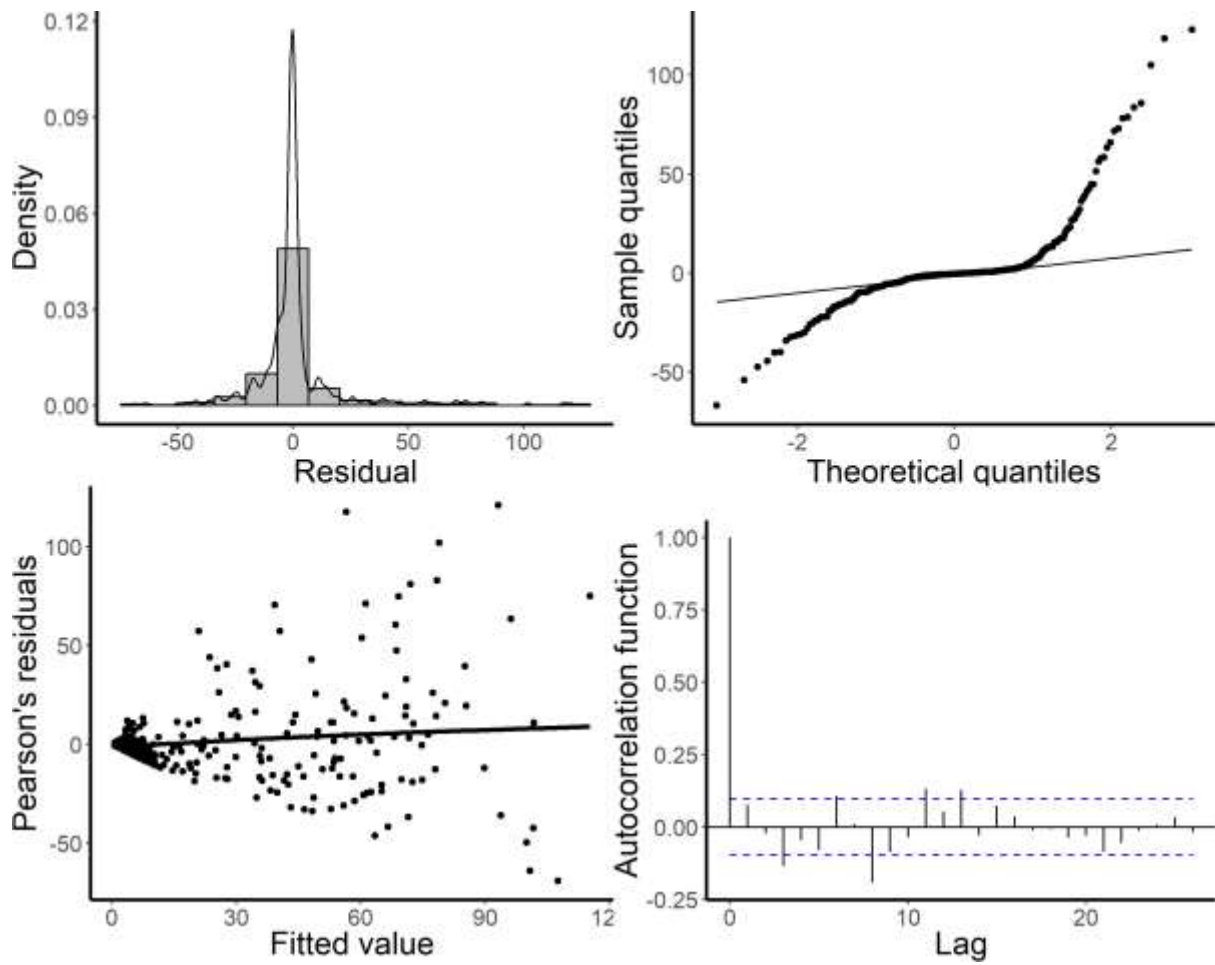
Figure S9. Diagnostic plots for the top-ranked 0+ salmon density model (Model 6). Plots are a density histogram of residuals (top-left), normal quantile-quantile plot (top-right), Pearson's residuals against fitted values (bottom-left) and the autocorrelation function (bottom-right).
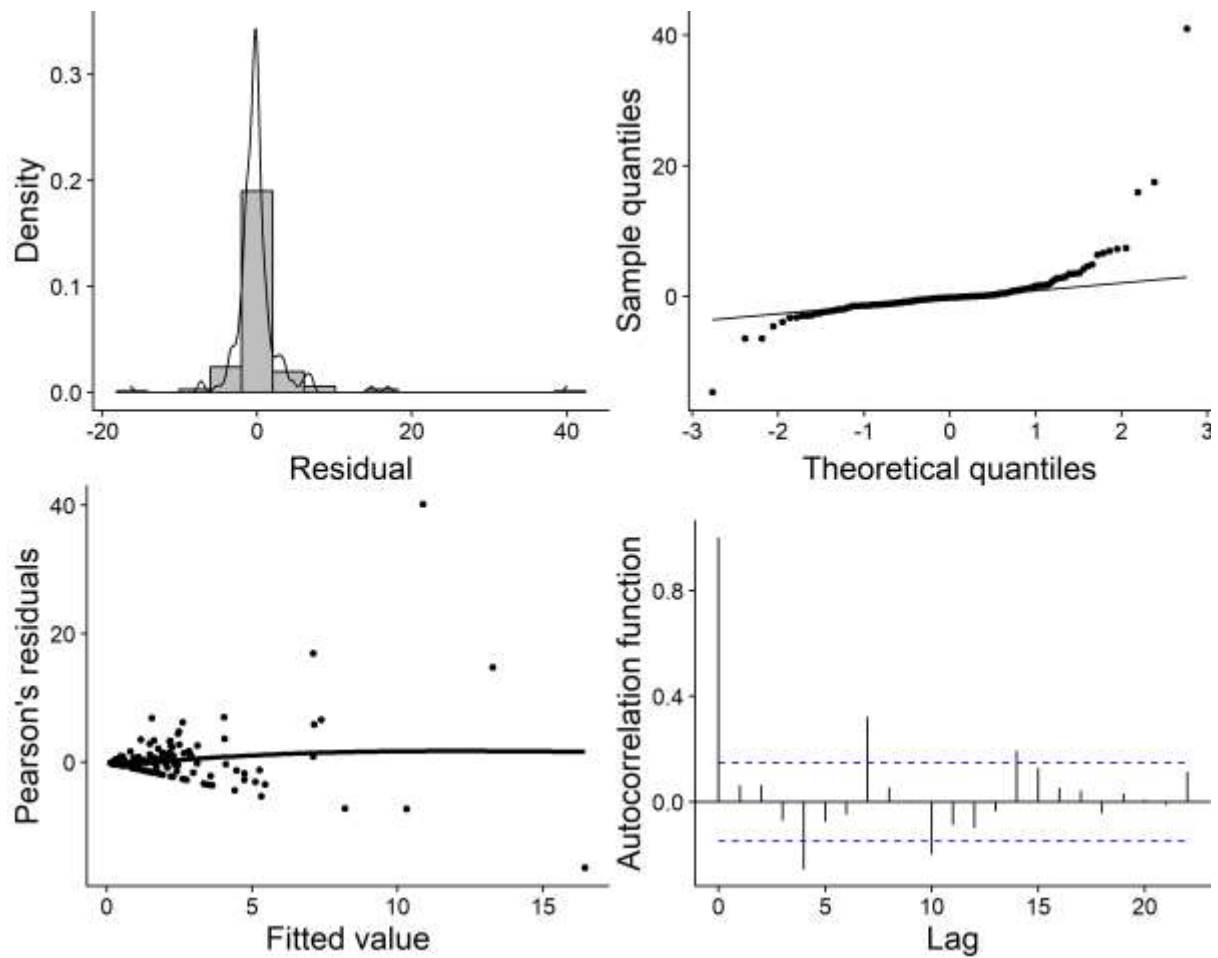
Figure S10. Diagnostic plots for the top-ranked 0+ trout density model (Model 13). Plots are a density histogram of residuals (top-left), normal quantile-quantile plot (top-right), Pearson's residuals against fitted values (bottom-left) and the autocorrelation function (bottom-right).

19

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