

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

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20 **Abstract**

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

40 **Introduction**

41 Recruitment in fish is affected by a range of factors impacting on life stages from egg deposition
42 through to sexual maturity (Milner, Elliott, Armstrong, Gardiner, Welton, & Ladle, 2003).
43 Density-dependent factors acting on recruitment are usually functions of spawning stock biomass
44 or egg production in the previous year that influence the numbers of con- and hetero-specific
45 competitors during the cohort's early life stages (Subbey, Devine, Schaarschmidt, & Nash,
46 2014). Once these processes have reduced juvenile abundance to where food resources are no
47 longer limiting, the cohort is then more susceptible to density-independent factors that influence
48 their recruitment, such as the effects of variability in river discharge rates and water temperature
49 (Jonsson & Jonsson, 2009).

50

51 Discharge can impact salmonid recruitment directly by regulating food supply and thereby
52 mediating density-dependent competition in early life stages (Richard, Cattaneo, & Rubin,
53 2015); it can also act indirectly, for example by altering temperature conditions, sediment
54 structure, oxygen content and habitat availability (Warren, Dunbar, & Smith, 2015). Temperature
55 can influence salmonid recruitment directly through its effect on egg development and survival
56 rates (Saltveit & Braband, 2013), and indirectly via influencing larval emergence timing
57 (Skoglund, Einum, Forseth, & Barlaup, 2012) and juvenile growth (Jonsson & Jonsson, 2009).
58 Discharge and temperature can also interact to influence recruitment as observed for Arctic
59 grayling *Thymallus arcticus*, with recruitment being dependent on both discharge and
60 temperature during their early life. Specifically, recruitment was negatively correlated with mean
61 summer discharge and positively correlated with stream temperature (Deegan, Golden, Harvey,
62 & Peterson, 1999; Luecke & MacKinnon, 2008).

63

64 A potentially important issue with episodic spates or floods during the incubation and emergence
65 stages is the “wash out” of eggs and larvae from spawning gravels (Warren et al. 2015). For
66 example, 0+ trout population densities can be reduced in years when discharges were relatively
67 high during the cohort’s incubation and/ or emergence (Cattanéo, Lamouroux, Breil, & Capra,
68 2002). Conversely, high discharges can sometimes have a positive influence on recruitment, with
69 maximum daily discharges in the spawning period being positively related to recruitment,
70 possibly via reductions in fine sediment content within spawning gravels that increases egg
71 survival (Cattanéo et al., 2002). Low discharge conditions can also impact upon juvenile survival
72 and therefore recruitment. A long-term study on brook trout *Salvelinus fontinalis* revealed
73 consistent rates of reduced survival in summers of higher temperatures and lower discharges
74 (Letcher et al., 2015). In areas of low summer rainfall, as Southern England, the issues of low
75 discharges can become exaggerated when there is also high groundwater abstraction, such as in
76 many chalk streams, and thus results in potentially poor recruitment conditions in periods of
77 prolonged low rainfall (Gibbins & Heslop, 1998).

78

79 Given the importance of discharge and temperature for salmonid recruitment, climate change has
80 been identified as a major threat to riverine salmonid populations (Ruiz-Navarro, Gillingham, &
81 Britton, 2016). Predicted temperature increases could affect biochemical reactions, hence
82 impacting development, growth, behaviour and survival of salmonids (Jonsson & Jonsson,
83 2009), with salmonid populations in Southern England likely to be particularly heavily impacted
84 (UKCP09: Murphy et al., 2009). Furthermore, groundwater abstraction is forecast to increase
85 with human population expansion and so there will be less water for the locally adapted

86 salmonid populations (Crisp, 2000). Regarding precipitation, increased winter and spring flood
87 events could result in local population extinctions if they coincide with the critical periods of
88 salmonid incubation and emergence (Warren et al., 2015).

89
90 Most studies on the long-term recruitment drivers of salmonids have focused on salmon and/ or
91 trout, with a paucity of knowledge on other salmonids, such as European grayling, despite these
92 fish often being an important fisheries resource across Europe (Ibbotson et al. 2001), and with
93 apparent declines in many populations in recent years (Dawnay, Dawnay, Hughes, Cove, &
94 Taylor, 2011). Although there have been studies of many aspects of grayling ecology, including
95 their recruitment (reviewed in Ibbotson et al. 2001), these studies have tended to focus on the
96 recruitment process and were of short duration (e.g. Bardonnet, & Gaudin, 1990; Bardonnet, &
97 Gaudin, 1991; Bardonnet, Gaudin, & Thorpe, 1993). Grayling populations have similar
98 ecological requirements to other salmonids, with discharge and temperature tending to be
99 important determinants of recruitment (Charles, Mallet, & Persat, 2006; Ibbotson et al. 2001).
100 Density-dependence is thought to affect grayling recruitment, as it does other salmonids,
101 particularly because they are potamodromous, i.e. migrates within freshwater systems only, and
102 their juveniles do not move far from their place of emergence (Grimardias, Faivre, & Cattaneo,
103 2012; but see Leeuwen, Dokk, Haugen, Kiffney & Museth, 2017).

104
105 There are, however, important differences between their spawning behaviours with other
106 salmonids. Grayling reproduce later than other salmonids, generally in spring when temperatures
107 are warmer (Charles et al., 2006). They also lay their eggs relatively shallower in gravels
108 (Bardonnet & Gaudin, 1990) than do salmon and trout, and the thermal tolerance of their eggs is

109 narrower, the optimal range being: 4–18 °C vs 0–33 °C in salmon and 7–22 °C in trout (Ibbotson
110 et al. 2001; Jonsson & Jonsson, 2009). Given these characteristics, they can be considered to
111 represent a strong salmonid model species for testing the potential effects of warming and
112 flooding on recruitment processes in salmonids, particularly in relation to density-dependent
113 influences. The aim of the present study was to quantify the role of density- dependent and
114 independent factors affecting the annual recruitment of grayling over eight years using a
115 population in an English chalk stream near the southern edge of their range. The hypothesis
116 tested was that density-dependent and density-independent factors will significantly affect
117 grayling recruitment rates, but via impacts acting on different stages of their early development.

118

119 **Materials and Methods**

120 **Study species and locations**

121 The native range of grayling is northern Europe, ranging from Britain and France in the west to
122 the Ural Mountains in Russia in the east (Ibbotson et al. 2001). In Great Britain, their native
123 range is restricted to a relatively small number of rivers, including the Hampshire Avon and its
124 tributaries (Ibbotson et al. 2001). In general, grayling spawn in early spring when water
125 temperatures are 3–11 °C. Eggs are spawned in pockets on the gravel surface or buried at up to 5
126 cm depth, where they remain until hatching after \approx 180 degree-days. After hatching, larvae
127 remain in the gravel for another 4–5 days until emergence. Both eggs and larvae are susceptible
128 to various biotic and abiotic pressures, including predation, floods and droughts (Ibbotson et al.
129 2001).

130

131 The present study was undertaken on the River Wylde, a tributary chalk stream of the River
132 Avon in Hampshire (henceforth, Hampshire Avon). The Wyle is a typical chalk stream of ≈ 45
133 km length, with sequences of riffles and pools of depth rarely exceeding 1 m, channel widths up
134 to 8 m, and macrophytes are dominated by *Ranunculus* spp. As a chalk stream, the Wyle has
135 relatively invariable discharge and temperature regimes compared to rain-fed rivers with hard
136 bedrock; mean discharge is $4.05 \text{ m}^3 \text{ s}^{-1}$, Q95 is $1.11 \text{ m}^3 \text{ s}^{-1}$ and Q10 is $8.59 \text{ m}^3 \text{ s}^{-1}$ (NERC, 2017),
137 with increases in discharge January–May and stochastic episodes of elevated discharge ($5\text{--}30 \text{ m}^3$
138 s^{-1}), driven by local rainfall patterns (NERC, 2017). High discharge events have become more
139 frequent since the early 1990s, occurring in general every two to four years and last for at least
140 six months (NERC, 2017). Similarly, low discharge conditions can occur between these high
141 discharge events, with the recovery time following rainfall often prolonged due to groundwater
142 fed nature of the river.

143

144 **Fish sampling**

145 Fish sampling was completed each October between 2009 and 2016 and covered six sites (Fig.
146 1). Sampling was completed by hand-held, single anode electric fishing, with between 3 and 5
147 passes completed per site until the depletion in captured grayling was $\geq 50 \%$ between the final
148 two passes. Sampling at each site involved fishing a 200 m stretch that was delimited with stop
149 nets set at both ends. The Wyle fish community is highly dominated by salmonids and
150 predominantly grayling and trout, but salmon and Eurasian dace *Leuciscus leuciscus* are rarely
151 captured. Following a UK Home Office licenced procedure (PPL 30/3277), all captured grayling
152 and trout were lightly anaesthetised (2-phenoxyethanol; 0.2 ml l^{-1}) and measured for fork length
153 (FL) to 1 mm and mass to 0.1 g. Young of year grayling (age 0+; identified by their FLs < 170

154 mm; Figure S1) were tagged using unique passive integrated transponder (PIT) tags inserted into
155 the peritoneal cavity, while individuals of age 1 year and over (age 1+) were tagged with a
156 unique Visible Implant (VI) tag inserted subcutaneously behind the eye. All tagged grayling also
157 had their adipose fin removed, to ensure recaptures could be identified despite potential tag loss,
158 and a scale sample taken for age validation, with a minimum number of three scales taken
159 between the dorsal fin and lateral line. VI tags were used for age 1+ grayling as they would
160 potentially lose a PIT tag during spawning (Summers, Roberts, Giles, & Stubbing, 2006).
161 Following recovery to normal swimming behaviour, all fish were returned alive to the site of
162 their capture.

163
164 Recruits were taken to be annual age 0+ grayling *T. thymallus* estimates from 2009 to 2016
165 (min–max numbers caught: 19–389). These were estimated using the general weighted *k*-pass
166 estimator proposed by Carle & Strub (1978) implemented in the function *removal()* in R package
167 FSA (Ogle, 2017; Figure S2). This estimator was appropriate for these data because they were
168 collected in a manner consistent with the assumptions of the underlying calculations.

169

170 FIGURE 1 HERE

171

172 **Explanatory variables for recruitment analysis**

173 Environmental variables measured included typical river discharge data (hereafter ‘discharge’),
174 taken from long-term records, where discharge was recorded every 15 min during the study
175 period (Stockton Park; 51°09'10.62"N, 2°02'13.65"W; National River Discharge Archive;
176 NERC, 2017). For analytical purposes, 15-min records were summarised to daily mean

177 discharges. Data were missing for some days due to equipment failures (Figure S3a). To
178 overcome this, missing daily mean discharges were imputed by minimising the covariance
179 between the daily mean discharges at Stockton Park and the nearby gauge station at South
180 Newton (Figure S3b) using function *impSeqRob()* of R package *rrcovNA* (Todorov & Filzmoser,
181 2009). River water temperature was taken from data collected every 15 minutes during the study
182 period at South Newton (51°11'00.4"N, 2°07'58.8"W). Where data was missing (some days in
183 2014 and 2016, several months in 2015 (Figure S4a), data were again imputed using data from
184 nearby recording stations as for discharge (Figure S4b). Different gauge stations were used for
185 discharge and temperature because the most complete data sets of river discharge and
186 temperature were not available from the same station. These discharge and temperature data
187 were then used to calculate the environmental variables suggested by literature to influence
188 grayling recruitment (Table 1 and S1; Figure 2).

189

190 FIGURE 2 HERE

191

192 **Conspecific and heterospecific densities**

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

199 model representing density dependent recruitment from eggs to age 0+ (Equation 2; Beverton &
200 Holt, 1957). They were given by:

201

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

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

$$\alpha \geq 0$$

202

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

207

$$R \sim Normal(\phi_y, \sigma^2) \quad \text{Eq. 2}$$

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

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

208

209 where the variables and parameters are the same as in Eq. 1 with the addition of parameter β
210 representing the negative effect of additional eggs on egg survival when the number of eggs
211 reaches an unknown threshold, i.e., an estimate of negative density-dependence on egg survival.

212

213 The estimated numbers of eggs produced in years 2010 to 2016 (see below for details on 2009)
214 were calculated by summing the mean weight of spawning individuals for each age class, site

215 and year combination (i.e., the site- and year-specific spawning stock biomass), and multiplying
216 it by a coefficient relating grayling weight to the numbers of eggs produced. Where individual
217 weight was missing, it was imputed from a linear regression of log length on log weight for 1046
218 individuals measured throughout the survey ($F_{1,1044} = 65643.0$, $r^2 = 0.98$, $P < 0.01$; Figure S5).
219 (Note: individuals were pooled over years, as there was no evidence for a difference in the
220 weight-length slopes between years.) The coefficient relating grayling weight to number of eggs
221 produced was estimated using data from a separate study in which 42 mature grayling were
222 captured on the River Wylfe in 2002, euthanized, measured (nearest 1 mm), weighed (nearest
223 0.1 g) and dissected. For each dissection, the grayling sex was recorded and gonads removed
224 and, in the case of females, the eggs were counted. The coefficient was estimated from a linear
225 regression of log egg number on log weight for 17 female grayling ($F_{1,15} = 123$, $r^2 = 0.89$, $P <$
226 0.01 ; Figure S6). It was assumed that 0+ grayling are immature and do not spawn and that only
227 60% of 1+ adults spawned, as estimated from the fecundity data. As sex ratio was assumed to be
228 1M:1F and thus the number of eggs was divided by two (Ibbotson et al. 2001).

229
230 For 2009, the total numbers of grayling eggs could not be estimated as above because only
231 single-pass quantitative surveys were done in 2008. This was resolved by using the ratio of site-
232 specific first-pass and multiple-pass spawning stock biomass estimates for years 2009 to 2016 to
233 estimate site-specific empirical Gaussian kernel densities, using the *density()* function in R, from
234 which a random value was drawn and used to calculate a possible site-specific spawning stock
235 biomass for 2008. This was repeated 10000 times to produce 10000 datasets. For each dataset,
236 the linear and non-linear stock-recruitment model fits were compared by Akaike information
237 criteria (AIC) and the non-linear model was selected where its AIC value was a minimum of 2

238 points lower than that of the linear model (Burnham & Anderson, 2002). The model used to
239 describe stock-recruitment relationship was then taken to be that which provided the “best” fit to
240 the majority of the 10000 datasets. Model residuals were then extracted from the 10000 model
241 fits and averaged to give an index of survival conditioned for any effect of conspecific density
242 and incorporating the uncertainty of the 2008 spawning biomass (hereafter, *survival index*; Table
243 1).

244

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

250

251 **Recruitment models**

252 Survival index of age 0+ grayling (SI) was the response variable in a candidate set of statistical
253 models designed to compare the influence of individual and combinations of environmental
254 explanatory variables on inter-annual variation in SI. The full set of environmental explanatory
255 variables investigated is presented in Tables 1 and S1. Prior to analysis, explanatory variables
256 were rescaled by subtracting their mean and dividing by their standard deviation using the *scale()*
257 function in R and examined for collinearity (Figure S8). Where explanatory variables were
258 correlated $r \geq |0.7|$, the perceived most ecologically important variable was retained for analysis
259 (Figure 2 and S9; Dormann et al., 2013). The statistical models took the form:

260

$$SI_{s,y} \sim \text{Normal}(\mu_{s,y}, \sigma^2) \quad \text{Eq. 3}$$

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

261

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

269 Candidate models were compared by their goodness-of-fit using a combination of Information
270 Theory, e.g., Akaike Information Criteria, and conditional and marginal R^2 values calculated
271 using the method of Nakagawa & Schielzeth (2013) and implemented in function *rsquared()* in
272 R package piecewiseSEM (Lefcheck, 2015).

273

274 Parameters representing the influence of each environmental variable on SI were estimated from
275 the "best" model. Parameter p values were calculated using Satterthwaite's approximations
276 (Satterthwaite, 1946) implemented in the function *lmer()* in R package lmerTest (Kuznetsova,
277 Brockhoff, & Christensen, 2015). There is no "best practice" method to calculate standard errors
278 for linear mixed-effect models and so parameter estimates are presented without standard error
279 bands. Plots of the parameter estimates and their partial (or marginal) effects on SI were
280 constructed using the function *ggplot()* in R package ggplot2 (Wickham, 2009). Residuals from
281 the "best" model were tested against the assumptions of normality, homogeneity and

282 independence using standard graphical validations for linear mixed-effect models in R (Figure
283 S11; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

284

285 **Results**

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

296

297 In terms of conspecific densities, non-linear stock-recruitment model fits to the site- and year-
298 specific grayling data were better than linear model fits in 98.1 % of the cases (Figure 3).
299 Consequently, model residuals were extracted from 10000 Beverton-Holt stock-recruitment
300 models and their mean value was taken as an index of age 0+ grayling survival conditioned on
301 conspecific density (SI; Table 1).

302

303 **FIGURE 3 HERE**

304

305 Among all the explanatory environmental variables, only post-incubation temperature anomaly
306 was included as a quadratic term in the multivariate models because of its curvilinear
307 relationship with survival index; all other explanatory variables were included in the multivariate
308 models as linear terms (Figure S10). Six candidate multivariate mixed effect models were chosen
309 *a priori*. Among those, the “best” model was Model 2, which omitted a linear effect of days of
310 high discharge compared to the saturated model (Model 1), although the difference in AIC
311 (Δ AIC) was less than 2. It included a quadratic term for post-incubation temperature anomaly
312 and linear terms for incubation temperature anomaly, number of days with low discharge and
313 estimated age 0+ *S. trutta* numbers (Table 2). The conditional and marginal R^2 values for Model
314 2 were high, with only Model 1 (the saturated model) explaining more variation in the response
315 variable (Table 2). All explanatory variables in the “best” Model 2 were statistically significant
316 according to the Satterthwaite’s approximation and had 95% confidence intervals that did not
317 overlap zero (Figure 4a). The “best” model was validated against the assumptions of linear
318 mixed effect models and indicated no severe violations of normality, homogeneity or
319 independence in model residuals (Figure S11). In addition, random site effect estimates did not
320 differ from a theoretical Gaussian distribution, confirming the assumption of a Gaussian
321 distribution of random effects (Figure 4b).

322

323 FIGURE 4 HERE

324

325 Marginal effect plots revealed a concave quadratic relationship between age 0+ grayling survival
326 index and post-incubation temperature anomaly, indicating positive effect of post-incubation
327 temperature on 0+ grayling survival up to a threshold temperature of 13.5 °C beyond which it

328 has a negative effect (Figure 5). In contrast, incubation temperature anomaly had a linear
329 relationship with age 0+ grayling survival, with the increase of incubation temperature
330 suggesting higher survival of age 0+ grayling in the river Wylfe for the studied period (Figure
331 5). Similarly, increasing age 0+ trout numbers had a positive effect on age 0+ grayling survival
332 (Figure 5). However, increasing number of days with low discharge had a negative effect on age
333 0+ grayling survival in this study (Figure 5).

334

335 FIGURE 5 HERE

336

337 **Discussion**

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

350

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

361

362 The number of days with low discharge was tested against grayling recruitment to capture the
363 effect of low summer discharge rates as an important stressor of the 0+ fish, given that several
364 studies have demonstrated that juvenile salmonid growth and even survival are depressed when
365 summer discharge rates are reduced and vice versa (Davidson, Letcher, & Nislow, 2010;
366 Gregory et al., 2017; Xu, Letcher & Nislow 2010). Both Charles et al. (2006) and Letcher et al.
367 (2015) revealed that survival of 0+ grayling and brook trout survival was reduced during years of
368 low summer discharges and higher water temperatures. Moreover, Letcher et al. (2015) revealed
369 these results were consistent spatially and affected different age-classes similarly. Thus, the
370 significant relationship between reduced summer discharges and low grayling recruitment
371 detected here provides further evidence that low summer discharges have substantial impacts on

372 salmonid population persistence and thus there is an urgent requirement for natural discharge
373 regimes to be promoted in salmonid rivers wherever possible (Enders, Scruton & Clarke, 2009).

374

375 There were two temperature-related variables that significantly influenced grayling recruitment,
376 incubation temperature anomaly and post-incubation temperature anomaly. The former had a
377 positive influence on grayling recruitment, with similar findings reported in other salmonid
378 fishes. For example, Skoglund, Einum & Robertsen (2011) revealed salmon eggs incubated at a
379 higher temperature produced larger eggs with higher survival rates versus those incubated at
380 lower temperatures. The general pattern is warmer winters can result in the production of larger
381 juveniles, perhaps due to a more prolonged growth season (Gregory et al., 2017), with these
382 larger individuals then potentially having higher survival rates via greater access to better
383 feeding areas than smaller conspecifics that might be more easily displaced by other foraging
384 salmonids (Huntingford, Metcalfe, Thorpe, Graham, & Adams, 1990). The post-incubation
385 temperature anomaly was parameterised as a quadratic effect and had significant and positive
386 effect on post-incubation survival up to a threshold of 13.5 °C; at higher temperatures, the effect
387 became negative. The Wylfe's mean water temperature was found to be already close to 13.5 °C,
388 suggesting that the population might be locally adapted to these conditions (Haugen & Vollestad,
389 2000), but also highlights its vulnerability to future temperature increases via warming processes
390 (Ruiz-Navarro et al., 2016). Similar patterns of the effect of temperature on post-incubation
391 survival have been detected in other salmonid fishes. For example, Letcher et al. (2014) revealed
392 that brook trout survival in a network of streams in western Massachusetts, USA, was related to
393 summer temperatures, with survival generally reduced at both high and low summer

394 temperatures. Equally, age 0+ grayling survival increased with temperature up to a threshold
395 limit, above which survival rates then reduce once more (Charles et al. 2006).

396

397 Days with high discharge was expected to negatively affect recruitment patterns because
398 elevated spring discharges could displace eggs from gravels (“egg washout”), particularly due to
399 the propensity of grayling to lay their eggs relatively shallow or even on the gravel surface
400 (Warren et al., 2015). The non-significant relationship detected here suggests that the spring
401 discharges were never sufficient to have a detectable impact, perhaps due to the underlying chalk
402 geology and groundwater influence of the study river resulting in relatively stable discharge and
403 temperature regimes compared to other salmonid rivers. For example, the spring discharges
404 detected during the study period ($1.38\text{--}4.73\text{ m}^3\text{ s}^{-1}$) might have lacked the energy to displace
405 eggs and/ or recently emerged larvae versus other studies where such impacts have been
406 recorded, such as Jensen & Johnsen (1999) where impacts occurred at discharges of $75\text{--}232\text{ m}^3$
407 s^{-1} and Mundahl (2017) who recorded impacts at $100\text{--}200\text{ m}^3\text{ s}^{-1}$. Indeed, the stable discharge
408 conditions afforded by chalk stream rivers have resulted in the recruitment of other fishes being
409 more dependent on environmental factors other than periods of elevated discharge rates, even in
410 non-salmonid fishes, such as roach *Rutilus rutilus* (Beardsley & Britton, 2012). Consequently,
411 the deleterious impacts of high discharge events on age 0+ salmonids might be limited to less
412 stable rivers that are prone to high discharge events (Warren et al., 2015), especially during
413 critical life-stage periods such as emergence, given that even extreme floods in late summer can
414 result in minimal impacts on salmonid populations (George, Baldigo, Smith, & Robinson, 2015).

415

416 The present study uncovered evidence to support a negative impact of intra-specific density-
417 dependence on grayling recruitment, which is supported by a number of studies demonstrating
418 that salmonid growth and survival can be related to conspecific density. For example, de Eyto et
419 al. (2016) found that a Beverton-Holt model was a better fit to trout stock-recruitment data than a
420 density-independent model in the River Burrishoole, Ireland, although the opposite was true for
421 salmon. This result was anticipated for grayling because, as previously mentioned, grayling is
422 potamodromous and juveniles remain close to their place of emergence (Grimardias, et al.,
423 2012). Although the Beverton-Holt fit to the grayling data was not strong, it was a better fit than
424 the density-independent model. However, the high variance in the number of recruits was not
425 sufficiently captured in the model, suggesting that the population was not closed, perhaps
426 because juvenile (Leeuwen et al., 2017) and adult grayling (Ovidio, Parkinson, Sonny &
427 Philippart, 2004) can undertake considerable in-river migrations. If these movements were
428 apparent in the study river, then this would undermine the relationship between spawning stock
429 size and the number of recruits at a site level and thus have impacted the model fit. In addition,
430 low temporal resolution could have impacted the observed fit, and if more data were available
431 the importance of conspecific density could have diminished.

432

433 In the present study, and as with all such correlative studies completed using field data, there
434 were potential issues around the choice of explanatory variables that were explored within
435 analyses. Environmental variables explored here were all derived from water discharge and
436 temperature data and, although these are all generally considered as important determinants of
437 fish population dynamics, they are also the most commonly available parameters of in-river
438 environmental conditions. The impact of grayling removal (culling) on grayling recruitment was

439 excluded from the analysis, because it has not been applied in Southern English chalk streams
440 since the early 1990s (Ibbotson et al., 2001), so it was not considered to affect population
441 dynamics in the River Wylde. Although it was beyond the scope of the present study, other
442 variables could have been considered for measurement and testing, including in-river vegetation
443 cover (Riley & Pawson, 2010), water quality (Whitehead, Wilby, Battarbee, Kernan, & Wade,
444 2009) and substratum composition (Kemp, Sear, Collins, Naden, & Jones, 2011). These issues,
445 combined with the generalities of some of the results reported here (i.e. several significant
446 correlates of environmental variables with recruitment), suggest that the relationships between
447 recruitment and biotic and abiotic variables might be context-dependent at the site level. Any
448 such context dependency could be important because it would inhibit the results being readily
449 transferable to other sites and rivers (Warren et al., 2015). Nevertheless, the general pattern of
450 the results presented here were that the early life stages of grayling were susceptible to several
451 aspects of discharge and water temperature, and this was manifested in their annually variable
452 recruitment success. These outcomes thus do retain high management utility, especially in this
453 era of declines in salmonid populations (Northcote, 1995), and so emphasise the importance of
454 management interventions that seek to increase population resilience via restoring natural
455 discharge regimes (Vehanen, Huusko, Yrjänä, Lahti, & Mäki-Petäys, 2003) and limiting future
456 temperature increases (Ruiz-Navarro et al., 2016).

457

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463

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Tables

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

Name	Symbol	Description	Influence	Reference
Days with high discharge	Dhf	Number of days between 1 st March and 30 th April with discharge equal or above Q10 (the 90th percentile discharge in the period 2009-2016)	Egg washout	Clausen & Biggs, 2000 Jensen & Johnsen, 1999 Warren et al., 2015
Days with low discharge	Dlf	Number of days between 1 st April and 31 st of August with discharge equal or below Q90 (the 10th percentile discharge in the period 2009-2016)	Juvenile survival	Mantua, Tohver, & Hamlet, 2010 Pyrce, 2004 Riley et al., 2009 Warren et al., 2015
Incubation temperature anomaly	Ianom	Mean temperature between 1 st March and 30 th April subtracted from mean temperature in that monthly period from 2009-2016	Egg survival / development	Mattern et al., 2017
Post-incubation temperature anomaly	Panom	Mean temperature between 1 st April and 31 st August subtracted from mean temperature in that monthly period from 2009-2016	Juvenile survival / growth	Mattern et al., 2017

Conspecific density	SI	Survival index; residuals from a non-linear stock-recruitment model of 0+ <i>T. thymallus</i> (recruits) regressed on estimated numbers of eggs in previous year (spawning stock)	Juvenile survival / growth	de Eyto et al., 2016 Grant & Imre, 2005 Gregory et al., 2017
Heterospecific density	Nt	<i>S. trutta</i> 0+ numbers at site and time of capture	Juvenile survival / growth	Degerman et al., 2000

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

Model	Model term	Model fit			Comparison		R^2	
		Sigma	LogLik	Deviance	AIC	Δ AIC	Marginal	Conditional
2	Panom, Panom ² , Ianom, Dlf, Nt	0.70	-51.7	103.3	119.3	0.0	0.48	0.50
1	Panom, Panom ² , Ianom, Dlf, Dhf, Nt	0.70	-51.3	102.6	120.6	1.3	0.49	0.51
3	Panom, Panom ² , Ianom, Dlf	0.71	-54.2	108.4	122.4	3.1	0.41	0.48
4	Panom, Panom ² , Ianom, Dhf, Nt	0.73	-53.3	106.6	122.6	3.3	0.45	0.46
5	Ianom, Dlf, Dhf, Nt	0.78	-55.9	111.9	125.9	6.6	0.39	0.39
6	Panom, Panom ² , Dlf, Dhf, Nt	0.78	-56.5	113.0	129.0	9.7	0.37	0.38

Figure captions

Figure 1 A map showing the location of the River Wylfe in the UK (inset map) and numbered sites on the Wylfe since 2009, starting from the upstream site: 1) Below viaduct (lower Parsonage), 2) Lower Knook, 3) Upton Lovell, 4) Heronry, 5) Below Boyton, and 6) Stockton (Ordnance survey, 2005; Ordnance survey, 2015). Stars indicate locations of discharge (Stockton Park) and temperature (South Newton) stations.

Figure 2 Line plots showing the mean and standard error (error bars) of the standardized response variable (SI = survival index) and one of the explanatory variables (Nt = number of 0+ *Salmo trutta*) and standardized environmental variables (Dhf = number of days with high discharge during incubation, Dlf = number of days with low discharge during post-incubation, Ianom = incubation temperature anomaly, Panom = post-incubation temperature anomaly) plotted across investigated years (2009–2016).

Figure 3 Scatter plot of recruitment (estimated 0+ *Thymallus thymallus* numbers) as a function of spawning stock biomass (estimated number of eggs produced). Lines are fitted linear regression (solid line) and non-linear regression (dashed line) predictions. Black points represent data for years 2009–2016 for all sites combined, and grey points represent predicted data for year 2008 with the range of variability around the estimates presented as standard error.

Figure 4 Caterpillar plots showing maximum-likelihood estimates of (a) the fixed effects and (b) the random effect for the “best” model. Points are the estimates; lines are the estimate standard errors; labels are the estimate values followed by an indication of their statistical

significance, whereby: *** $p < .001$, ** $p < .01$ and * $p < .05$. Explanatory variable definitions are as follows: Panom = post-incubation temperature anomaly ($^{\circ}\text{C}$); Ianom = incubation temperature anomaly ($^{\circ}\text{C}$); Nt = age 0+ *Salmo trutta* abundance; Dlf = number of days with low discharge during post-incubation.

Figure 5 Line plots showing the marginal effects of each of the standardized explanatory variables, where Panom = post-incubation temperature anomaly, Ianom = incubation temperature anomaly, Nt = age 0+ *Salmo trutta* abundance; Dlf = Dlf = number of days with low discharge during post-incubation, X-axis is the explanatory variable value and Y-axis is the response variable. The shaded grey area is the standard error of the estimated effect.