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

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## **Abstract**

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

# Introduction

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

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

## Materials and Methods

### 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 ℃. Eggs are spawned in pockets on the gravel surface or buried at up to 5

126    cm depth, where they remain until hatching after ≈ 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 Wylye, 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 Wylye has

135     relatively invariable discharge and temperature regimes compared to rain-fed rivers with hard

136     bedrock; mean discharge is 4.05 m$^3$ s$^{-1}$, Q95 is 1.11 m$^3$ s$^{-1}$ and Q10 is 8.59 m$^3$ s$^{-1}$ (NERC, 2017),

137     with increases in discharge January–May and stochastic episodes of elevated discharge (5–30 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 ≥ 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 Wylye 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

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


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


FIGURE 1 HERE


**Explanatory variables for recruitment analysis**

Environmental variables measured included typical river discharge data (hereafter 'discharge'), taken from long-term records, where discharge was recorded every 15 min during the study period (Stockton Park; 51°09′10.62″N, 2°02′13.65″W; National River Discharge Archive; 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$^o$11'00.4"N, 2$^o$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

$$R \sim Normal\left(\phi_y, \sigma^2\right)$$                 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), $\phi_y$ is the expected

204     density of recruits surviving from Eggs deposited in year $y$ after suffering a temporally invariant

205     density-independent mortality $\alpha$, and $\sigma^2$ is an independent and identically distributed (i.i.d.)

206     error term; and

207

$$R \sim Normal\left(\phi_y, \sigma^2\right)$$                 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 $\beta$

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 Wylye 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

$$SI_{s,y} \sim \text{Normal}(\mu_{s,y}, \sigma^2)$$ <span style="float:right">Eq. 3</span>

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

261

262    where $\theta = \beta_1, \beta_2, \ldots, \beta_k$ is a vector of $K$ parameters relating explanatory variables $X =$

263    $x_1, x_2, \ldots, x_k$ to SI measured at site $s$ in year $y$, accounting for a Site random effect $\upsilon_s$ with a

264    zero mean and variance $\tau_s$ 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

## 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    (ΔAIC) 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 Wylye 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 $^{o}$C; at higher temperatures, the effect

387  became negative. The Wylye's mean water temperature was found to be already close to 13.5 $^{o}$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 (1.38–4.73 $m^3$ $s^{-1}$) 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 75–232 $m^3$

407 $s^{-1}$ and Mundahl (2017) who recorded impacts at 100–200 $m^3$ $s^{-1}$. 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 Wylye. 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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# Tables

**Table 1** List of explanatory variables used to describe inter-annual changes in age 0+ juvenile *Thymallus thymallus* numbers on the river Wylye 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 1st March and 30th 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 1st April and 31st 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 1st March and 30th 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 1st April and 31st 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+ *T. thymallus* (recruits) regressed on estimated numbers of eggs in previous year (spawning stock) | Juvenile survival / growth | de Eyto et al., 2016<br><br>Grant & Imre, 2005<br><br>Gregory et al., 2017 |
| Heterospecific density | Nt | *S. trutta* 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 (ΔAIC) 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 | | | | | $R^2$ | |
|---|---|---|---|---|---|---|---|---|
| | | Sigma | LogLik | Deviance | AIC | ΔAIC | 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 Wylye in the UK (inset map) and numbered sites on the Wylye 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 (°C); Ianom = incubation temperature anomaly (°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.