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The effects of flow on Atlantic salmon (*Salmo salar*) redd distribution in a UK chalk stream between 1980 and 2015

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Abstract

Atlantic salmon are an ecologically and economically important migratory fish in the UK, whose stocks have been declining over the past 30 years. Future climate and water use changes have the potential to alter the reproductive behaviour and distribution of salmon within a river, by restricting times and ability to access suitable spawning areas. As the survival of emergent salmon juveniles is density dependent, understanding how climate-driven changes in flow affect the location of salmon redds is important for future conservation efforts. This study examined how flow conditions affect the distribution of redds within a UK chalk stream, the river Frome in Dorset. Sixteen years of redd distribution and flow data between 1980 and 2015 were analysed using Linear Mixed Effects modelling. Generally, highest redd densities occurred within middle reaches of the main river. Mean flow during the river Frome critical migration period (October – December) did not affect the density of redds directly but affected the relationship between redd density and distance from tidal limit: redd densities were spread more uniformly throughout the river under high flow conditions whereas redds were more aggregated in the middle river reaches under low flow conditions. Together, these findings suggest that access to upstream spawning grounds was limited under low flow conditions, which could have negative repercussions on juvenile survival. This study has revealed the distribution of redds along the river Frome for the first time and provided a basis for further study into the effects of redd distribution on subsequent juvenile life-stages.

Introduction

Migration between feeding grounds and suitable spawning areas is an important event in the life history of several fish species, having profound survival and fitness implications (Gross et al., 1988). For some species, such as the semelparous European eel (*Anguilla anguilla*), migration to spawning grounds is their only opportunity to contribute to the next generation. For other long distance migrants, such as the Atlantic salmon (*Salmo salar*; hereafter termed salmon), multi-annual spawning is possible and reproductive success is in part dependent on other factors, such as competition for spawning habitat and mates (Fleming, 1998). During salmonid migration, movements made to find habitat suitable for nest or redd construction is known as the search phase of migration (*sensu* Thorstad et al. 2008). Although several studies have investigated the influence of environmental conditions on the timing and success of migratory behaviour in the period preceding the search phase, (known as the upstream phase, see reviews by Thorstad et al. 2008; Jonsson & Jonsson 2009; Warren et al. 2015), fewer studies have investigated the role played by environmental conditions on the final distribution of redds throughout rivers, i.e. the outcome of the search phase (Chapman et al., 1986, Klett et al., 2013). This is somewhat surprising given the importance of the search phase for successful reproduction and fitness.

Studies to date have revealed that salmon construct redds in fine river gravels at the upstream part of riffles, which provide optimum oxygenation for incubating their eggs and embryos (Bardonnet and Baglinière 2000). Spawning close to deep pools or vegetative cover can also be advantageous as these habitats can reduce predation of breeding adults and developing juveniles (White, 1942 as cited in Armstrong et al., 2003). Other environmental factors, including temperature, sedimentation, river depth and water velocity can also affect the location of a salmon redd (Moir et al., 1998, Moir et al., 2002, Jonsson and Jonsson, 2009, Armstrong et al., 2003). For example, water velocity and depth, as well as gravel size, are important factors for Chinook salmon (*Oncorhynchus tshawytscha*) redd site selection (Groves and Chandler 1999; Kondolf and Wolman 1993).

Climate change is considered one of the greatest threats to biodiversity in the 21st century (Bellard et al., 2012, Thuiller, 2007). Rivers are less stable than marine ecosystems and therefore more prone to rapid changes in conditions, such as temperature or flow (Armstrong et al., 2003). Under current climate change predictions, the number of extreme weather events will increase over the next century, which may directly impact rivers through increases in extreme flow and temperature events (Hulme et al., 2002). Climate driven changes in extreme flow might affect salmon spawning success in a number of ways. Extreme high flow can result in gravel washout and damage to existing redds, while sedimentation of redds following high flows can negatively affect egg and embryo development and subsequent juvenile survival (Levasseur et al., 2006, Lapointe et al., 2000). On the other hand, at extreme low flow, factors such as reduced oxygen content and increased temperature may also hinder upstream migration (Solomon and Sandbrook, 2004). At the very extreme, drought conditions could result in the drying out of redds and subsequent mortality of developing embryos (Becker and Neitzel, 1985).

While the flow requirements and other preferences of spawning salmon have been studied extensively, little research has focused on the impact of flow on the overall distribution and density of redds along a river. It has been suggested that reduced flow during the period of peak migration can slow the upstream phase of migration, particularly of larger adults that preferentially spawn further upstream, leading to spawning aggregations below within-river barriers (Mitchell, et al. 2007; Solomon & Sambrook 1999). Studies on the river Tay and Dee in Scotland suggest that increased water discharge during the period of final migration, here assumed to be the search phase of migration, allowed salmon to access shallower spawning tributaries that did not provide suitable conditions for residence earlier in the season (Hawkins 1989; Webb 1989; Webb and Hawkins 1989). Aside from these studies, there are few studies that have directly investigated the effects of flows – and particularly extreme flows – on annual salmon redd distributions. Geist & Dauble (1998) examined the role of river geomorphology and its interaction with microhabitat variables in explaining Chinook salmon redd distributions, but their contrasts were different rivers. Chapman et al. (1986) examined the influence of flow on annual variation in the morphology and density of Chinook salmon redds on the Columbia river but their study was done at a single location. The findings from these studies should arguably be compared with caution, as the species and riverine hydrology can vary significantly compared to British or European rivers.

Using one of the longest running datasets on salmonid redds in the UK, we investigate how river flow affects the distribution of salmon redds on a British chalk stream. We build and compare statistical models to describe observed inter-annual changes in salmon redd densities at multiple survey locations on the river Frome, UK, from simple explanatory variables including river flow. Initial analysis of redds along the river Frome suggest that distribution is greatest within the middle reaches, due to the higher abundance of suitable flow conditions and habitat. We predict that low flows during the upstream and search migration phases will result in a higher redd density in the middle relative to the upper sections of the river (Fig. 1). We also predict that as flow increases, redd density will become more uniform across the river (Fig. 1). To our knowledge, this is the first example of how flow conditions during the search phase of Atlantic salmon spawning migration may directly affect the distribution of salmon redds along a British river. Our findings are important due to the density dependent survival of juvenile salmon, which may be governed by the location of redds along the river (Armstrong and Nislow, 2006). Our results may therefore have implications for the future recruitment and survival of salmon within UK rivers under current climate change predictions.

[Figure 1 here]

Methods

Site description and data collection

The river Frome, Dorset, UK, is one of 224 British chalk streams, comprising over 80km of braided channels, and is fed primarily by groundwater upwellings from the surrounding chalk and clay geology (Brunner et al., 2010, Sear et al., 1999). The river discharge is therefore alkaline, relatively stable and seldom prone to spates or flooding (National Rivers Authority, 1995). The river Frome has seen considerable anthropomorphic change over the past two centuries, including additions and removals of a number of weirs, fish passes and other modifications to river levels and discharge, such as abstraction (Solomon, 2000).

Salmon have been studied for over 50 years on the river Frome (Lauridsen et al., 2015). They reproduce in freshwater between November and February each year. Females excavate a redd in suitable gravel riverbed substrate, into which they deposit their eggs. A description of river Frome salmon redd structure and function (compared with those in other rivers) is given in Crisp & Carling (1989). Male(s) then fertilise the eggs after which the female buries them. Algae and aquatic macrophytes grow slowly in the cold winter water temperature in the river Frome so that redds can be identified from the river bank by their size and presence of clean (i.e., recently disturbed) gravel (Riedl & Peter 2013).

Redd surveys

River Frome salmonid redd surveys (hereafter *redd surveys*) were started by river wardens in the 1950's to monitor salmonid stocks. Initially, these surveys were irregular and inconsistent. Since the 1980's, however, the Centre for Ecology and Hydrology and the Environment Agency, with the support from the river Frome, Piddle and West Dorset Fishing Association and the Weld Estate, have carried out comparable salmonid redd surveys throughout the river Frome, from headwaters near Cattistock (section 14 in Fig. 2) downstream to Worgret (section 0 in Fig. 2).

[Figure 2 here]

Redd surveys were carried out in January or February, dependent on conditions. Two surveyors, equipped with polarised lenses, counted the number of redds within each survey section and estimated their length, width and the cleanliness of riverbed gravel, an indication of the age of the redd. The location of each salmonid redd was recorded; approximate locations were recorded on maps from 1980 to 1992, while the actual location of each redd was recorded on a handheld Global Positioning System for surveys after 2000. Maps indicating approximate redd locations were digitised and georeferenced, allowing the longitude and latitude of each redd to be extracted. Up to a total of 29 survey sections were surveyed in any one year (Fig. 2), although the proportion of sections surveyed in each year varied from 20-93% (mean 53%). Redds more than 110cm wide were deemed to be salmon redds, whereas redds less than 110cm wide were noted as trout (Wessex Water Authority, 1987). Trout redds were omitted from analysis and redd density was calculated as the number of salmon redds divided by the length of the survey section.

We calculated two types of explanatory variables for our analysis. Distance from tidal limit (in kilometres) of survey section start and end points were calculated by hand using QGIS software (www.qgis.org) and later verified by the online mapping system MAgiC (magic.defra.gov.uk). The UK Environment Agency has recorded flow at East Stoke on the river Frome every 15 mins since 1965 (ES on Fig. 2; see nrfa.ceh.ac.uk/data/station/info/44001). Flow measured at East Stoke was highly correlated with flow measured at Louds Mill, a flow gauge station located approximately 20km upstream (LM on Fig. 2; Pearson's r = 0.75, Confidence Intervals: 0.74 - 0.77), confirming that flow measured at East Stoke is representative of flow elsewhere in the catchment. Two flow variables were calculated for this analysis, chosen to represent the critical flow conditions available for spawning migration, shown to be an important determinant of migration success (e.g., Thorstad et al., 2008; Warren et al., 2015): (1) *mean flows* – average flow per year based on mean daily flow between 1st October to 31st December each year, and (2) *high flows* – the number of days between 1st October and 31st December that the daily flow exceeded the Q75 flow calculated for the same period in each year. The precise details of these variables, e.g., the dates, were agreed after extensive consultation with local experts about the patterns of spawning salmon migration (Fig. S1). These two flow variables were highly correlated (Pearson's r = 0.923) and were thus explored in separate models analysing the effect of flow on redd density.

Data analysis

A total of 16 years of redd surveys between 1980 and 2014 were chosen for analysis (see Table 1, Appendix). These 16 years were taken from a larger dataset of 22 years between 1957 and 2014 because they were surveyed using comparable methods and had the most complete redd survey and river discharge records. Plots of these redd density against distance from tidal limit are presented for these years in Supporting Information (Fig. S2). Of these 16 representative years, five years (1983, 1985, 2007, 2008, 2012) were both high flow years and years in which less than 50% of the sections were surveyed. To test whether inclusion of these years biased our results, we repeated our analysis excluding them and report the results in the Supporting Information. Not all sections were surveyed in all years and the proportion of survey sections surveyed varied from 20 (1985) to 94 % (2014; Table 1). Overall, however, more than 70 % of sections were surveyed in each year (Table 1) and the number of missing section surveys tended to decrease with increasing distance from the tidal limit and increase with increasing flow (Fig. S3).

[Table 1 here]

Linear Mixed Effects models were constructed within the statistical software package R (version 3.2.1, R Core Team, 2015). Models tested whether redd density varied with distance from tidal limit between years, and whether this distribution of redds was affected by flow during the previous year. The models compared are shown in Table 2. The saturated model was:

$$y \sim \alpha_i + \beta_1 Dist + \beta_2 Dist^2 + \beta_3 Flow + \beta_4 Dist \times Flow + \beta_5 Dist^2 \times Flow + \epsilon$$

where *y* is redd density during January/February, $Dist$ is distance from tidal limit (in km), $Flow$ is either mean flows or high flows, α_i is a random intercept for year i that is Gaussian distributed with mean 0 and variation σ^2_{year} to account for variation in redd density between years that could not be explained by our explanatory variables, $\beta_j \in [\beta_1, \ldots, \beta_J]$ is a coefficient relating the explanatory variable j to y, and ϵ is a Gaussian error term with mean 0 and variation σ^2. We assumed a Gaussian error term despite the possibility that could predict negative (<0) redd densities because it is more commonly used than a truncated Gaussian distribution, such as the Gamma distribution. In practice, negative redd densities were predicted only in the uppermost sections of the catchment.

Explanatory variables were standardised before entering the model. $Dist$ and $Flow$ were divided by their standard deviation calculated for all years combined; $Dist^2$ was then calculated as the $Dist$ raised to the power of 2. We standardised the explanatory variables to ensure the stability of coefficient estimates and thus the comparison of their effects on the response variable.

The models were fit by Maximum Likelihood using `R` package `lme4`, the estimated coefficient *p* values were calculated using Satterthwaite's approximations implemented in the `R` package `lmerTest`, and the conditional and marginal R squared values were calculated using the method of Nakagawa & Schielzeth (2013) implemented in `R` package `piecewiseSEM`. There is no "best practice" method to calculate standard errors for Linear Mixed Effects models and so we present model fits without standard error bands.

Results

We fitted and compared five models explaining inter-annual differences in salmon redd distribution along the river Frome that used linear and quadratic combinations of distance from tidal limit and mean flows during the “upstream phase” of the salmon migration period. Both linear and quadratic terms were included in analysis due to the curvilinear nature of redd density across the river Frome (Fig. 1). Final models were chosen based on factors including Akaike Information Criteria (AIC) and conditional and marginal R-squared values. Comparing the models by AIC suggested that the saturated model (QuadDFint in Table 2) was the “top-ranked” model. This model included linear terms for distance and mean flows and their interaction and a quadratic term for distance and its interaction with flow (Table 2).

[Table 2 here]

The difference in AIC (dAIC) between the “top-ranked” model and the second ranked model (the same model omitting the interaction between distance and flow; QuadDF) was 2.74, which exceeds the oft-cited threshold value of 2 AIC points (e.g., Burnham & Anderson, 2003) indicating a substantially better model, but not the more conservative threshold of 6 points (e.g., Richards, 2005). Moreover, the interaction between distance and mean flow in model QuadDFint was judged to be statistically significant ($t_{280.19}$ = 1.98, p < 0.05; Fig. 3a; Table S1) by Satterthwate's approximation. This suggests that mean flow may affect the distribution of redds within the river Frome. As this interaction was statistically significant, we retained the lower order mean flows term even though it was not statistically significant (Fig. 3a). Residuals from the “top-ranked” model were approximately normally distributed, suggesting that our assumption of Gaussian errors was appropriate (Fig. S4).

Random year effect estimates generally overlapped zero (Fig. 3b). Estimates for two years, however, were substantially different to zero, i.e., their standard errors did not overlap zero, suggesting that the random effect was non-negligible. Moreover, the assumption that the random effect was Gaussian was supported; the estimated year effects conformed to a theoretical Gaussian distribution (Fig. S5).

[Figure 3 here]

Marginal effect plots of each term suggested a concave quadratic relationship between redd density and distance (a positive effect of distance together with a negative effect of distance squared; Fig. 4), which was modified by a weakly convex quadratic relationship between redd density and the interaction between distance and flow (a negative effect of distance by flow together with a positive effect of distance squared by flow; Fig. 4). Combined, these relationships suggest that redd density was highest at intermediate distances from the tidal limit under low flow and more evenly distributed throughout the river during high flow. Plotting model fits to the observed redd densities ordered by increasing annual critical flow appear to support this pattern (Fig. 5).

[Figure 4 here]

[Figure 5 here]

We repeated this analysis using high flows as the measure of flow. For these models, the saturated model (QuadDFint in Table 2) was again the “top-ranked” model, although the dAIC between this and the second ranked model was slightly lower than for the models using mean flows as the measure of flow (Supporting Information; Table S2). Unlike the “top-ranked” model for mean flow, no significant relationship between high flows and redd density were observed; none of the terms including flow were statistically significant by Satterthwaite’s approximation (Table S2).

We repeated the analyses using mean flows and high flows as the measures of flow but omitted years with low survey coverage, namely years 1983, 2007, 2008 & 2012. For both measures of flow, the “top-ranked” model was the model including the quadratic effect of distance and the effect of flow but not including their interaction, i.e., model QuadDF (Tables S3 & S4). Again, however, the dAIC between the “top-ranked” and second ranked models were lower than for the models including all data, as were the marginal and conditional R^2 values, despite the additional variance present in the full datasets.

Discussion

Our analysis suggests that river flow limits the upstream distance that salmon can migrate to spawn and that low flows cause aggregated spawning in the middle sections of the river, with potentially detrimental consequences for emerging fry subject to strong density-dependent competition (Beall et al., 1994, Armstrong et al., 2003). To our knowledge, we are the first to demonstrate an inter-annual effect of flow on redd distribution in a UK chalk stream. This relationship was detected despite the relatively stable flow conditions in our groundwater-fed study river. The effect of flow on salmon redd distribution within freshet rivers may be far greater than those experienced in chalk streams, such as the river Frome.

Compared to years of high flow, we found that the difference in redd density between the middle and upper sections of the river was accentuated in years when river flow was low during the search phase of spawning migration, taken to be 1st October to 31st December on the river Frome. This was characterised by a pronounced humped (or quadratic) relationship between redd density and distance in the middle river sections, which might represent spawning aggregations. Conversely, we found that relative to years of low flow, the difference in redd density between the middle and upper sections of the river was smaller. Redds were more evenly distributed throughout the river and the quadratic relationship between redd density and distance was less pronounced in years of higher flow. Furthermore, when we repeated our analysis omitting years of limited survey coverage due to high flows, the “top-ranked” models omitted the distance-flow interaction, providing circumstantial evidence that the distance-flow interaction captured the difference in patterns of redd density between high and low river flow years.

The increased redd density observed within the middle reaches under low flow may have occurred due to two factors. Under extreme low flow, potential barriers to migration may have become difficult to pass, leading to aggregations directly downstream. Salmon gathering below various weirs along the river Frome has been documented since 1913 (Solomon, 2000). Aggregation below power stations, weirs and other barriers have also been documented across Europe, and the ability to pass these barriers within the river can be exacerbated under low flow (Thorstad et al., 2003, Ugedal et al., 2008, Klett et al., 2013). Secondly, tributaries used for spawning and upstream passage might become unfavourable under low flow, resulting in an increase in individuals within the middle reaches of the main river. Studies on the Tay and Dee in Scotland suggest that higher water discharge towards the period of final spawning migration allows salmon to access spawning tributaries that are otherwise inaccessible because of insufficient water (Webb 1989, Webb & Hawkins 1989). Assuming that these salmon construct redds in these otherwise inaccessible tributaries, then these results would support our finding of relatively higher redd density in higher river sections in high flow years. In contrast, salmon migration through the main river stem of the Tay and Dee was scarcely affected by water discharge, suggesting that these deeper waters were always accessible to spawning salmon (Hawkins 1989). Again assuming that these fish construct redds, then these results would support our finding that redds tend to be aggregated in the middle river sections, as characterised by the quadratic relationship between redd density and distance.

Climate change predictions forecast changing rainfall patterns across the UK, characterised by an increasing mean temperature and more variable precipitation. For rivers, these predictions will likely manifest in extreme flow events, including increasing incidences of droughts and floods. There are many studies hypothesising how these predictions might impact salmonids in the UK and elsewhere (see reviews Jonsson and Jonsson 2009; Isaak, et al. 2012). From the perspective of our findings, the forecast extreme flow events and their effect on salmon spawning behaviour could have significant negative impacts on spawning success. One feasible negative outcome could be large spawning aggregations due to sustained low flows during the search phase of migration would result in a highly competitive environment for emerging fry (Jonsson and Jonsson, 1998). Another potential negative outcome might be that high flows during the search phase of migration facilitate salmon entry into upstream spawning habitat that subsequently dries out under drought conditions, resulting in unsuccessful redds (Becker et al., 1983, Reiser and White, 1983).

Any effect of flow on redd distribution might cause a shift in the behaviour and ultimately survival of juvenile parr. Previous research on parr survival and movement in the river Frome revealed that some parr move past the smolt monitoring station in Autumn (October – January) prior to the main Spring smolt migration between March and May (Ibbotson et al., 2013). While parr that remain in their natal river site have a higher probability to smoltify with increasing distance upstream, it is currently unknown whether autumn migration make a significant contribution to spawning stock and success (Riley et al., 2009). Under extreme low flow a higher proportion of redds might occur within the middle reaches, which might lead to a higher proportion of autumn migrating parr. Moreover, competition for limited resources in the middle to lower reaches of the river might increase during low flow years, with detrimental consequences for individual parr survival.

A significant challenge in this study was to decide how best to represent flow conditions, so that they accurately corresponded to the search time frame of southern UK salmon. To avoid subjectivity, we followed expert opinion to define the period of final migration and summarised the flow data for that period in two ways: (1) mean flows, and (2) high flows, supposed to represent mean and extreme flow events, respectively. We repeated our analyses with each measure of flow separately. We found that the models including the distance-flow interaction were “top-ranked” for both measures of flow. The most parsimonious explanation for this finding is that the two variables were highly related, i.e., were measuring the same effect. Indeed, the Pearson’s correlation coefficient between the variables was > 0.9. Nevertheless, it is reassuring that the “top-ranked” models with two highly – but not perfectly – related variables included the distance-flow interaction, particularly since these “top-ranked” models were not different from the second-ranked models at the more conservative dAIC level of 6 (Richards 2005).

Although we have taken care to ensure our findings are robust, we acknowledge some study limitations, several of which relate to pitfalls in redd surveying methods. Regards the statistical analysis, we used AIC for model selection, which can favour more complex models compared to, for example, Bayesian Information Criteria (BIC; Burnham & Anderson, 2003). We argue that more complex models will better capture the reality of redd distribution patterns. Thus reality should be favoured over parsimony and AIC over BIC. Moreover, we argue that AIC should be preferred when the possibility of making false negative result is considered more harmful than the possibility of making a false positive result, which we consider the case with this small but valuable dataset. We had a limited number of predictors to explain the inter-annual patterns of salmon redd density, primarily because data on other factors are limited or have not been collected. For example, locations of groundwater upwellings are believed to influence redd site selection (Saltveit, 2013) and sedimentation may also affect redd success, but we do not have these data for the river Frome.

Aside from the statistical limitations of our findings, there are some well-known issues with redd surveys that deserve mention. First, there is growing evidence that multiple males and females are involved in spawning on any individual redd and that individual fish can construct multiple redds, frequently >1km apart (Taggart, et al. 2001). Second, redd superimposition (the construction of one redd over another) was not uncommon in the Girnock Burn, a tributary of the river Dee in Scotland (Taggart, et al. 2001). Finally, there are several issues that question the accuracy of redd surveys. They are measured without an assessment of their associated uncertainty (e.g., Dunham et al., 2001). A number of factors may affect a redd census such as the redd age, size, and colour, the vegetation cover in the survey section and observer experience. Most importantly, the river depth, flow and turbidity are also thought to affect the survey accuracy. To investigate the possible effect of flow conditions on redd survey accuracy, we repeated our analyses omitting low survey coverage years, which tended to occur in high flow years. We found that the top-ranked models for these reduced data omitted the distance-flow interaction. While this could be interpreted as evidence for the importance of the interaction term to describe the difference in redd distributions in low and high flow years, it doesn't clarify the potential bias from poor survey accuracy because low survey coverage is confounded with high flows. To better understand this potential bias requires further work. In the meantime, we hold some confidence in the accuracy of the redd survey data because it is often significantly correlated with spawner abundances (Beland, 1996; Dunham et al., 2001; Gallagher and Gallagher, 2005).

While our study focused on a single UK chalk stream, and a single species, Atlantic salmon, we feel that our results could generalise to other systems and fish species. There are several fish species that undertake spawning migrations, including diadromous species, such as salmon and sea trout (*Salmo trutta*) that migrate between fresh- and sea- waters, and potamodromous species, such as European grayling (*Thymallus thymallus*) that migrate within the freshwater only. We see no reason why migrations of these species could not also be influenced by flow conditions. Indeed, for some species, such as the European grayling, the effects of flow on recruitment might be more severe than for salmon because they construct comparatively shallow redds that will be less resilient to extreme events which may further increase their highly variable recruitment (Crisp, 1996, Ibbotson, et al. 2001). We believe our results can also be generalised to other systems, i.e., rivers. Chalk streams are fed by groundwater upwellings and have stable flow regimes compared to rain-fed rivers. That we were able to detect an effect of flow on redd distributions in a stable southern UK chalk stream suggests that the effects of flow on the search phase of salmonid migration might be more pronounced on rain-fed rivers.

Conclusion

In conclusion, this study has – for the first time - revealed the multi-annual effect of flow conditions on chalk stream salmon spawning behaviour. Our results suggest that under low flow, densities become aggregated within the middle reaches which could have a negative impact on juvenile survival and overall recruitment. As human populations continue to grow, balancing the abstraction needs of the UK with the flow requirements of salmon, all under increased climate change, is an issue which will need to be addressed if we are to preserve this ecologically and economically important species. Managing habitat and potentially removing weirs still present on the Frome may also improve the movement of spawning salmon upstream, leading to fewer spawning aggregations under extreme low flow. Our findings could also be used to revise current abstraction practices during this key migration period, to improve the spawning success of salmon and other salmonids under adverse flow conditions and potentially aid in future conservation of Atlantic salmon within the river Frome and other chalk stream rivers.

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Tables

Table 1. Summary of redd, flow and survey site data each survey year, and an indication of whether it was considered a "high flow year".

Survey Year	Mean daily flow m^3/s		Percentage of Sites Surveyed	Total redds	High flow year	Included in analysis
	October - December	January - February				
1980-81	5.14	5.41	87	376	N	Y
1982-83	7.28	8.05	87	139	N	Y
1983-84	3.97	9.34	40	101	Y	N
1985-86	4.00	9.71	20	67	N	N
1988-89	3.57	3.65	76	308	N	Y
1991-92	5.78	3.72	73	167	N	Y
2001-02	4.04	6.40	93	335	N	Y
2004-05	4.33	4.55	47	189	N	Y
2005-06	5.91	4.25	80	345	N	Y
2007-08	5.97	8.90	37	141	Y	N
2008-09	5.58	8.24	40	237	Y	N
2009-10	6.88	8.03	67	182	N	Y
2010-11	4.34	6.86	67	129	N	Y
2011-12	2.94	3.41	93	492	N	Y
2012-13	10.82	12.67	33	60	Y	N
2014-15	4.60	6.68	94	256	N	Y

Table 2. A table presenting the Maximum Likelihood model comparison statistics comparing fits for models in which *Flow* is measured as *mean flows*: the mean daily flow from October to December in the year previous to the redd survey. The table is ordered by difference in Akaike Information Criteria (dAIC) from the "top-ranked" model (i.e., the model with the lowest AIC). Marginal and conditional R^2 were calculated according to the method of Nakagawa & Schielzeth (2013).

Model name	**Model terms**	**Model fit**			**Comparison**		**R^2**	
		Sigma	**logLik**	**Deviance**	**AIC**	**dAIC**	**Marginal**	**Conditional**
QuadDFint	$Dist, Dist^2, Flow, Dist \times Flow, Dist^2 \times Flow$	3.33	-775.0	1550.0	1566.0	0	0.26	0.34
QuadDF	$Dist, Dist^2, Flow$	3.37	-778.4	1556.8	1568.8	2.74	0.24	0.33
LinDF	$Dist, Flow$	3.73	-805.6	1611.2	1621.2	55.20	0.10	0.17
LinDFint	$Dist, Flow, Dist \times Flow$	3.73	-805.3	1610.6	1622.6	56.52	0.10	0.16
LinD	$Dist$	3.73	-807.4	1614.8	1622.8	56.80	0.07	0.17

Figures

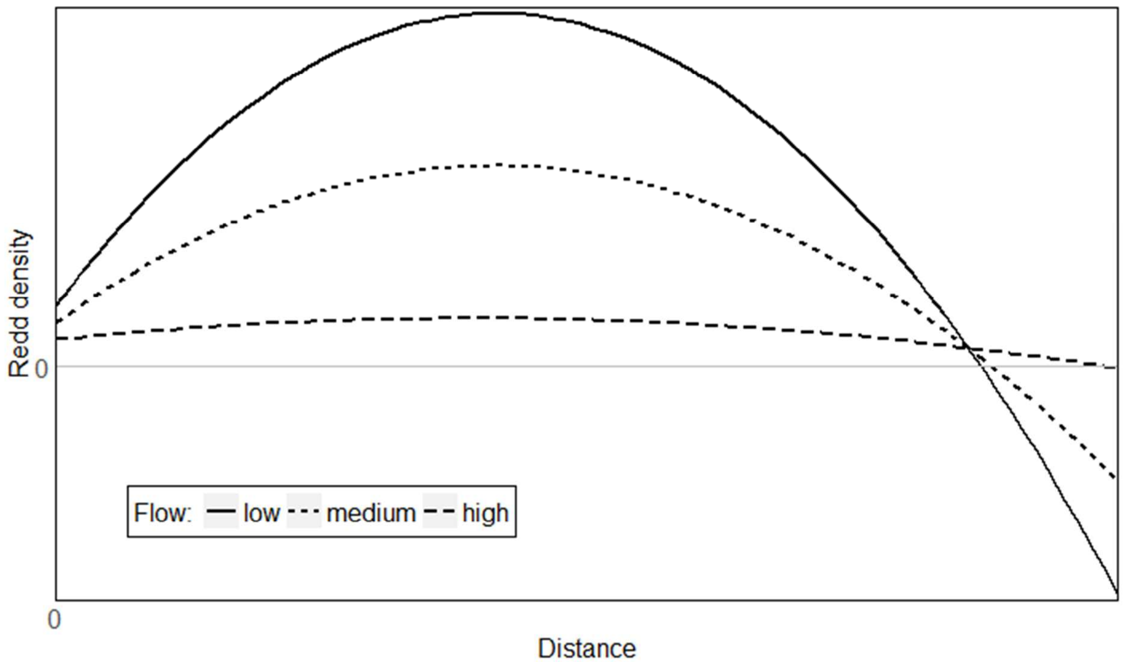


Figure 1. Diagram showing how the density of redds is predicted to change with distance from the tidal limit under low, medium and high flow conditions.

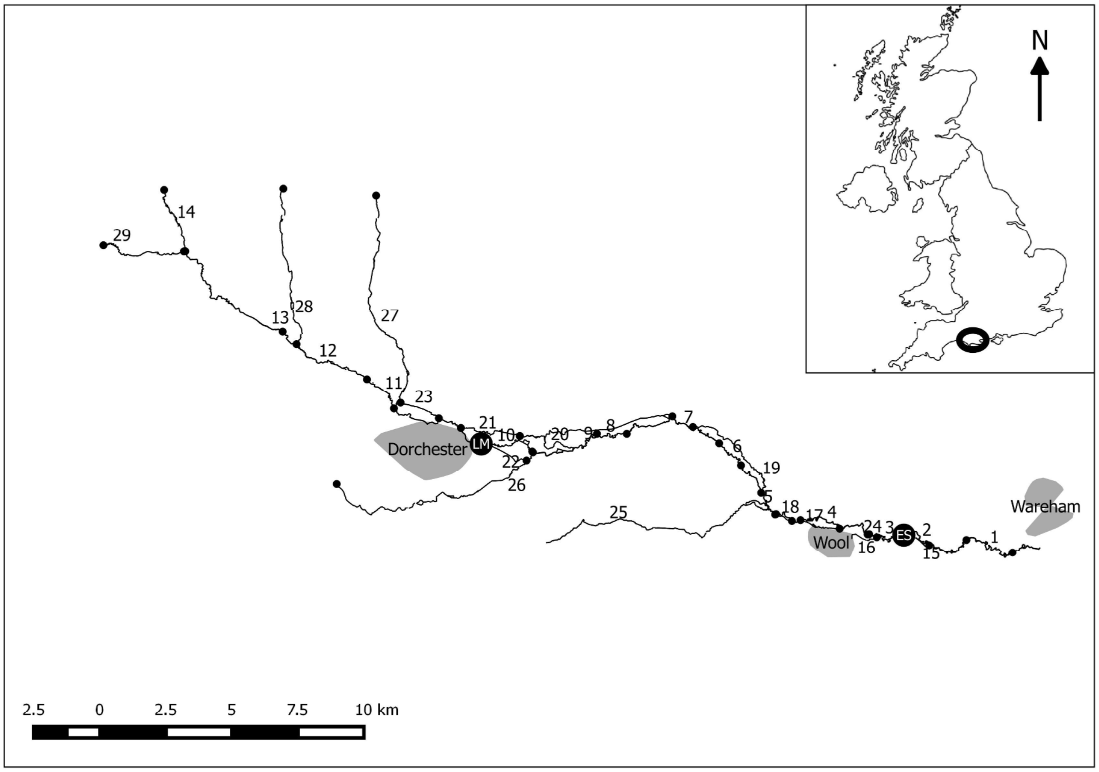
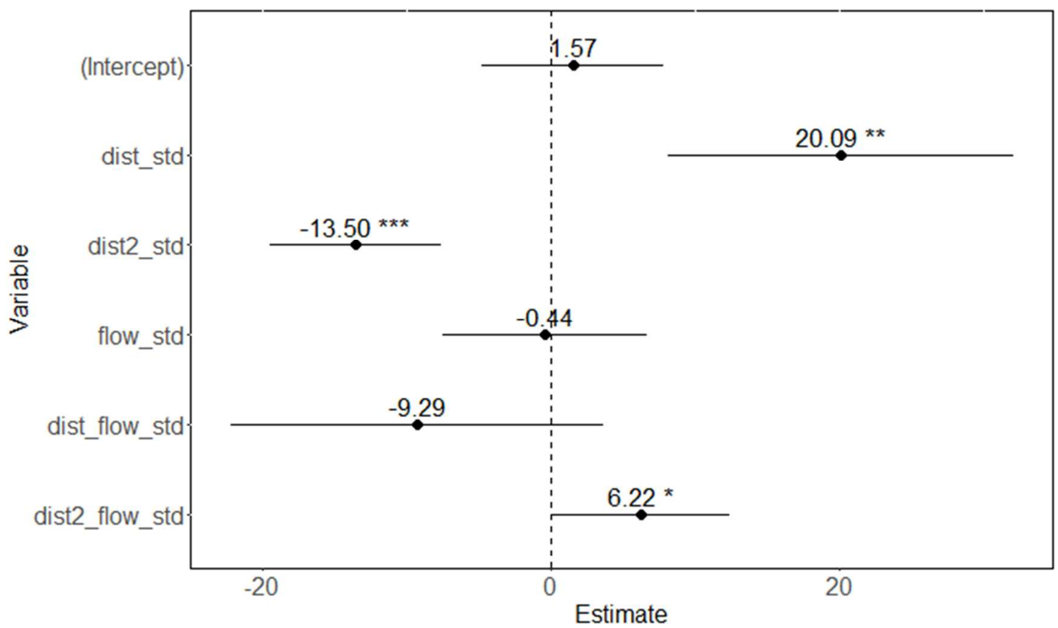
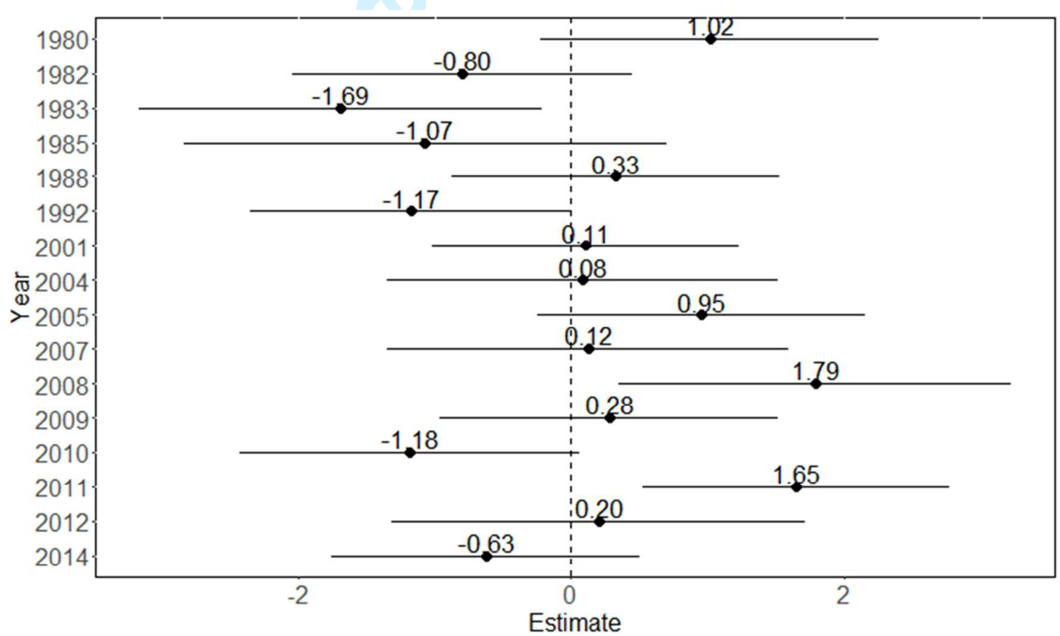


Figure 2. Map showing the redd survey sections on the river Frome, Dorset, UK. Major settlements Wareham, Wool and Dorchester are shown in grey. Black dots indicate the start and end points of each survey section. Black circles are locations of flow gauging stations East Stoke (ES) and Louds Mill (LM).



(a)



(b)

Figure 3. Caterpillar plots showing Maximum Likelihood estimates of (a) the fixed effects and (b) the random effect for the "top-ranked" 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 <0.001, ** p <0.01, and * p <0.05. Explanatory variable definitions are: dist_std = standardised distance; dist2_std = standardised distance squared; flow_std = standardised flow;

dist_flow_std = standardised distance and flow interaction; dist2_flow_std = standardised distance squared and flow interaction. As flow and distance were standardised, no units are specified for these variables.

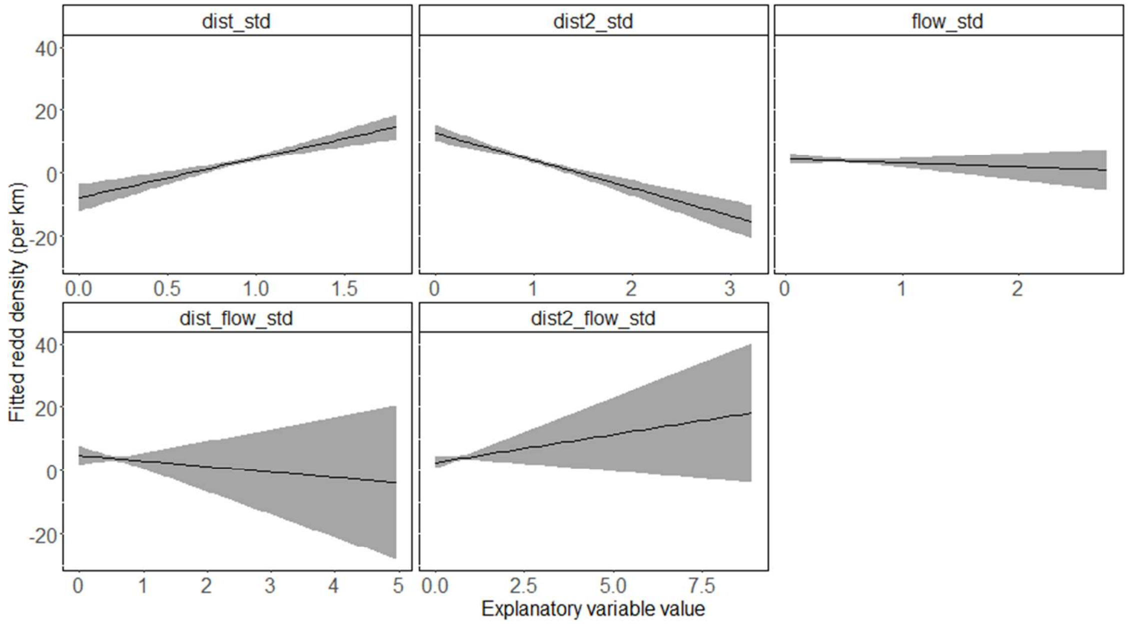


Figure 4. Line plots showing the marginal effects of each of the explanatory variables: dist_std = standardised distance; dist2_std = standardised distance squared; flow_std = standardised flow; dist_flow_std = standardised distance and flow interaction; dist2_flow_std = standardised distance squared and flow interaction. X axis is the explanatory variable value, e.g., standardised distance for the first panel. The shaded grey area is the standard error of the estimated effect. As flow and distance were standardised, no units are specified for these variables.

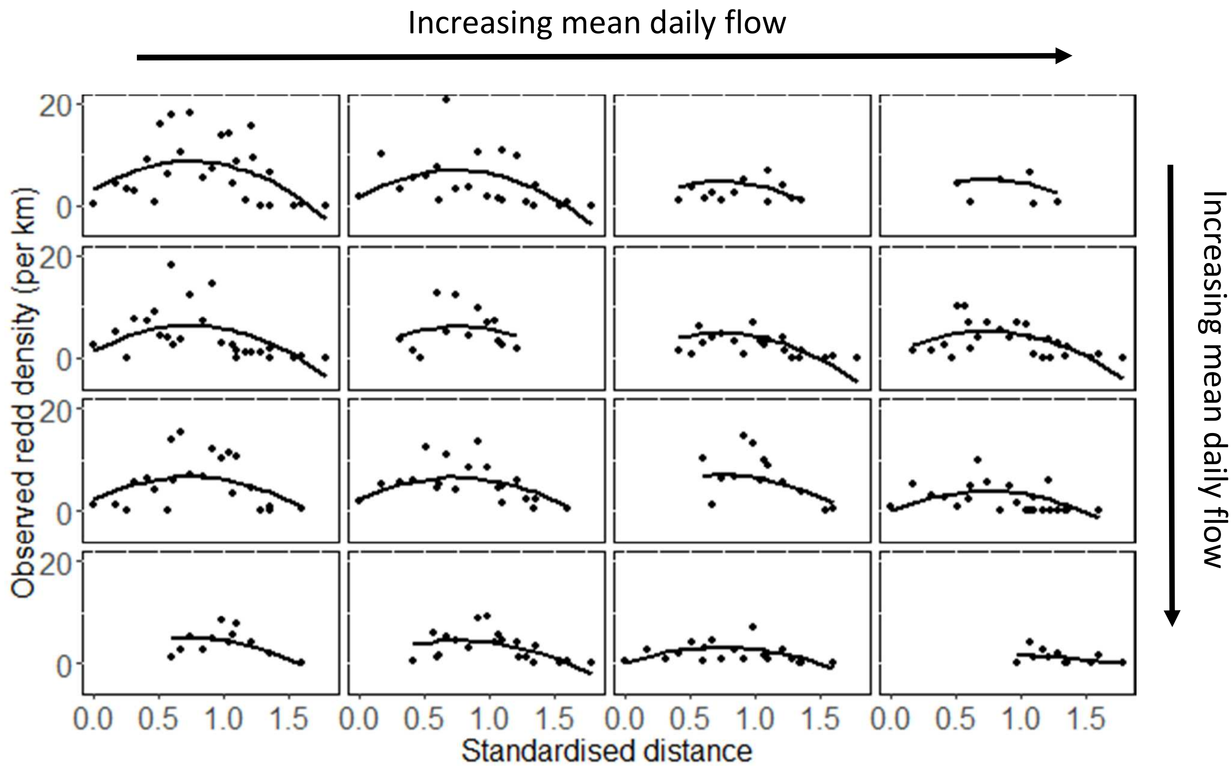


Figure 5. Scatter plots showing observed redd densities as a function of standardised distance from the tidal limit. Each panel represents a different year characterised by a measure of mean daily flow from 1st October to 31st December and panels are ordered from low (top left) to high (bottom right) flow. Lines are the “top-ranked” model fits. As flow and distance were standardised, no units are specified for these variables.

Supporting Information

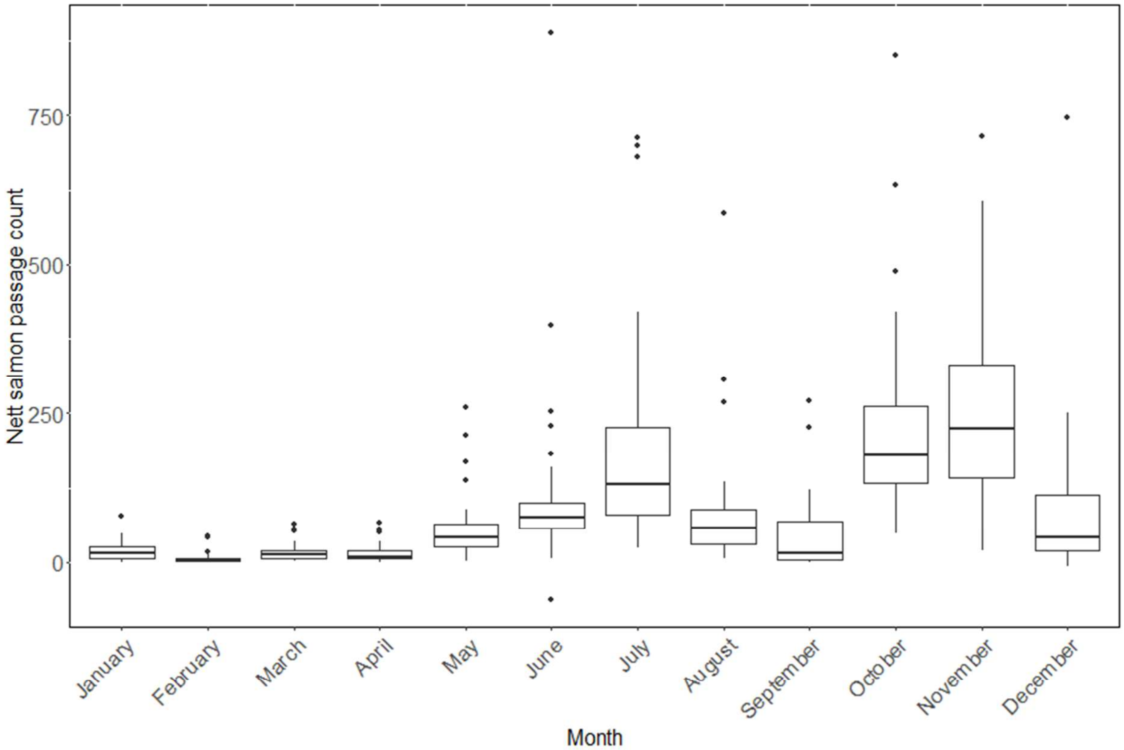


Figure S1. Boxplot of mean monthly Atlantic salmon counts on the Frome, from 2009 to 2014, illustrating the high numbers of adults returning to the river during October – December each year to breed.

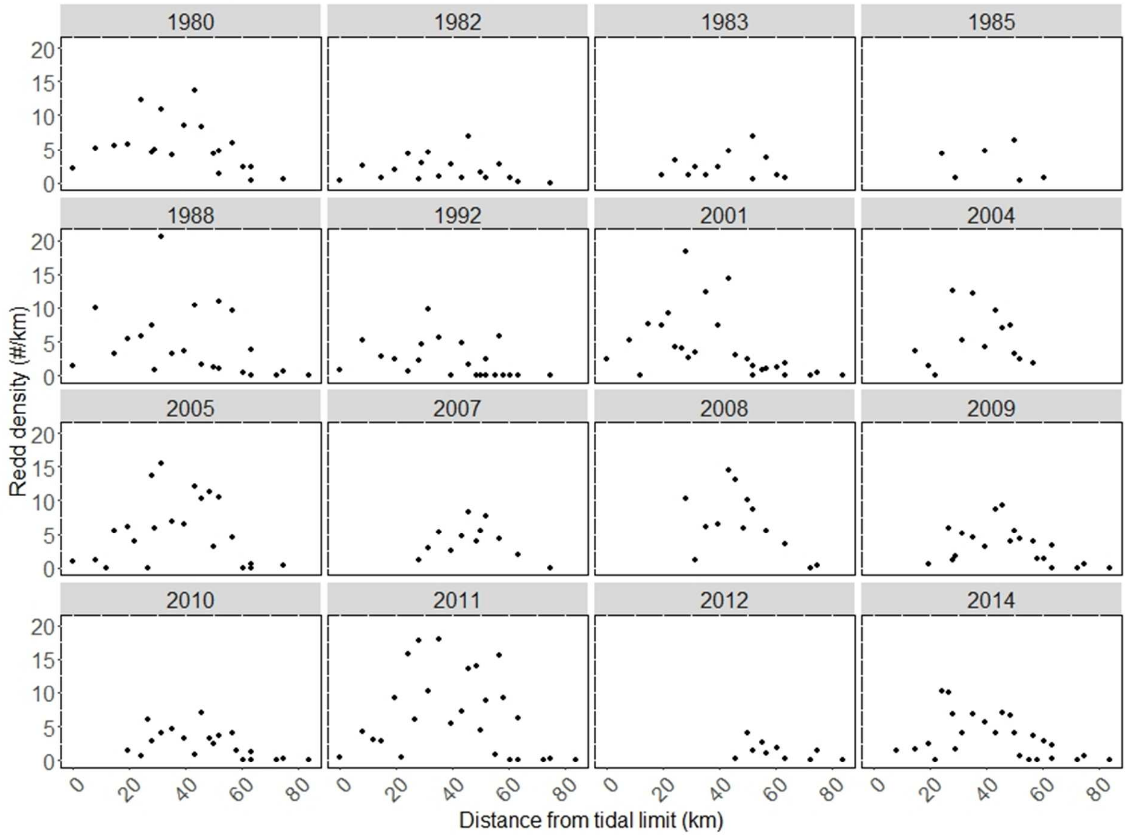
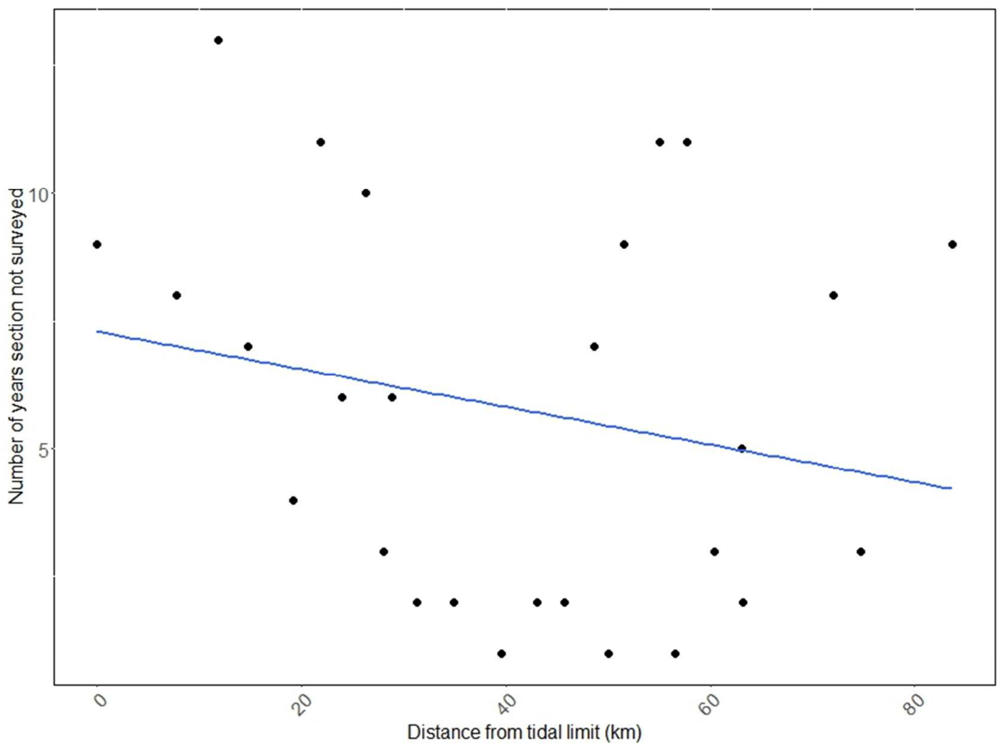
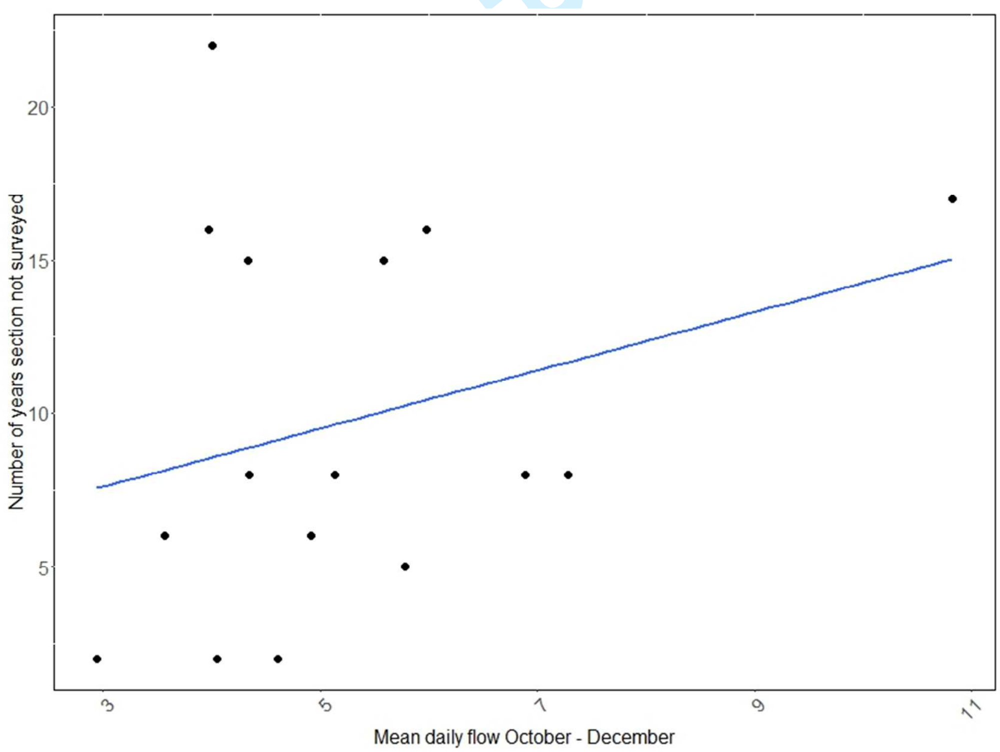


Figure S2. Scatter plots of redd density (#/km) as a function of distance from tidal limit (km) for the years that were included in the model fitting.



(a)



(b)

Figure S3. Scatter plots of number of years a section was not surveyed as a function of **(a)** distance from tidal limit and **(b)** mean daily flow. Blue lines are fitted linear regression predictions.

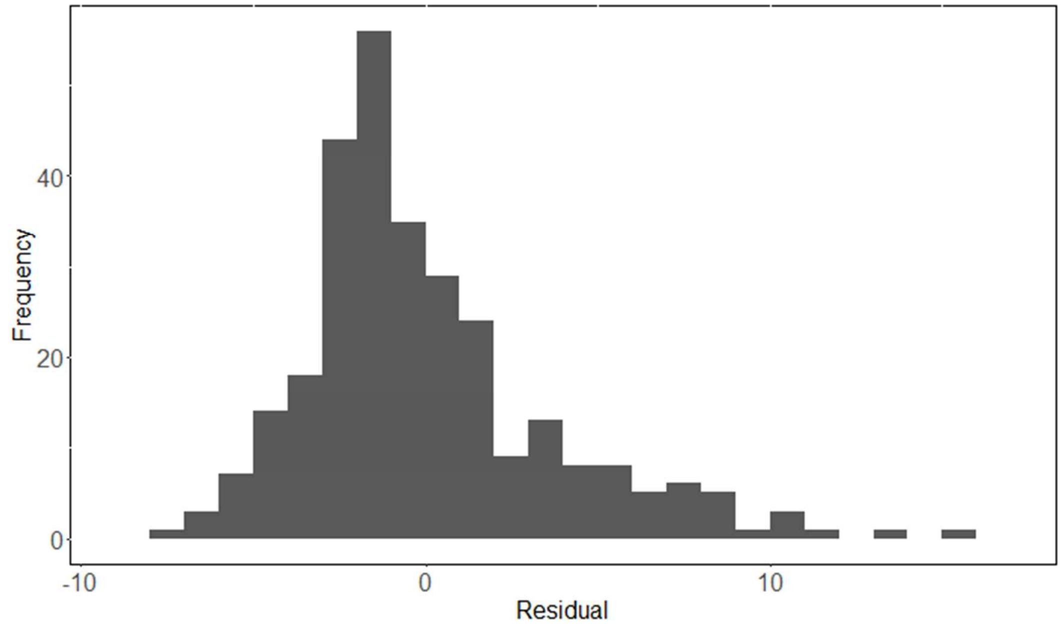


Figure S4. A histogram of the “top-ranked” model residuals suggesting that the assumption of normally distributed (Gaussian) errors was supported.

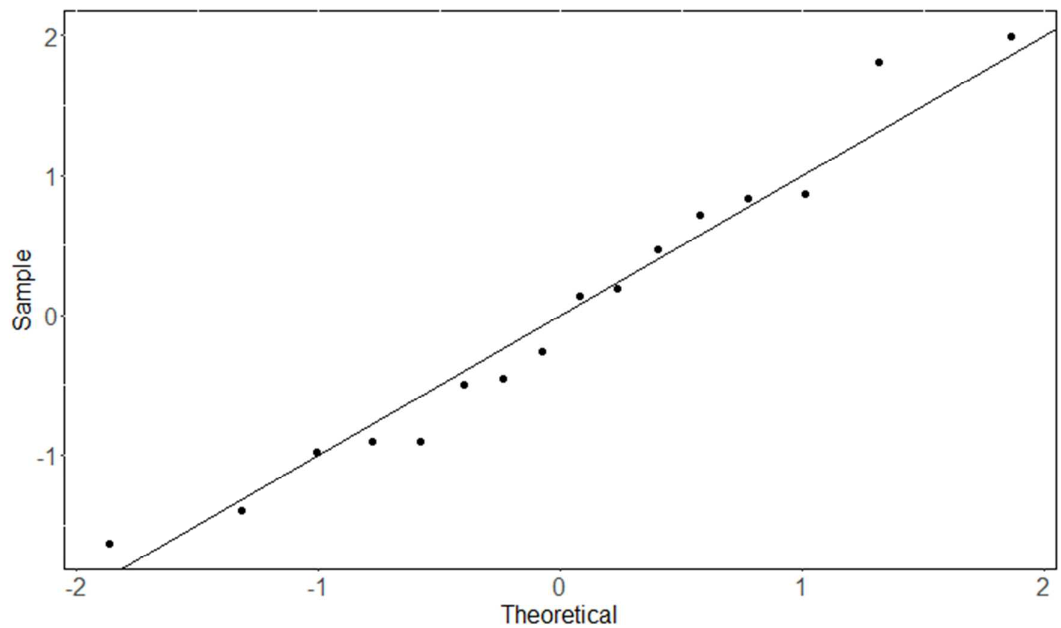


Figure S5. A quantile-quantile plot showing that the sample of years analysed as a random effect conform to a theoretical normal distribution, suggesting that the assumption of normally distributed year effects was supported.

Table S1. A table presenting the coefficient estimates of the top-ranking models (as assessed by AIC) when the flow predictor is either (i) *mean flows*: the mean daily flow from 1st October to 31st December or (ii) *high flows*: the number days from 1st October to 31st December that the daily flow exceeded the Q75 flow in the year previous to the redd survey.

Model name	Coefficient	Estimate (SE)	*df*	*t*	*p*
Mean flows	$Intercept$	1.57 (3.17)	214.26	0.50	ns
	$Dist$	20.09 (6.05)	286.50	3.32	<0.05
	$Dist^2$	-13.50 (3.00)	281.54	-4.50	<0.001
	$Flow$	-0.44 (3.54)	229.47	-0.13	ns
	$Dist \times Flow$	-9.29 (6.54)	286.92	-1.42	ns
	$Dist^2 \times Flow$	6.22 (3.15)	280.19	1.98	<0.05
High flows	$Intercept$	1.68 (1.07)	177.95	1.57	ns
	$Dist$	12.99 (2.25)	282.65	5.77	<0.001
	$Dist^2$	-9.00 (1.22)	282.35	-7.41	<0.001
	$Flow$	-1.25 (1.50)	237.67	-0.83	ns
	$Dist \times Flow$	-1.79 (2.81)	285.76	-0.64	ns
	$Dist^2 \times Flow$	1.78 (1.36)	281.01	1.30	ns

High flows results

Table S2. Tables of (a) Maximum Likelihood model comparison statistics comparing fits for models in which *Flow* is measured as *high flows*: the Q75 daily flow from October to December in the year previous to the redd survey. The table is ordered by difference in Akaike Information Criteria (dAIC) from the "top-ranked" model (i.e., the model with the lowest AIC). Marginal and conditional R^2 were calculated according to the method of Nakagawa & Schielzeth (2013). (b) Coefficient estimates of the top-ranking model fitted to the same data, as assessed by AIC.

(a)

Model name	**Model terms**	**Model fit**			**Comparison**		**R^2**	
		Sigma	**logLik**	**Deviance**	**AIC**	**dAIC**	**Marginal**	**Conditional**
QuadDFint	$Dist, Dist^2, Flow, Dist \times Flow, Dist^2 \times Flow$	3.33	-775.4	1550.8	1566.8	0.0	0.25	0.35
QuadDF	$Dist, Dist^2, Flow$	3.37	-778.7	1557.3	1569.3	2.5	0.23	0.33
LinDF	$Dist, Flow$	3.73	-806.1	1612.2	1622.2	55.4	0.09	0.17
LinD	$Dist, Flow, Dist \times Flow$	3.73	-807.4	1614.8	1622.8	56.0	0.07	0.17
LinDFint	$Dist$	3.72	-805.8	1611.5	1623.5	56.7	0.10	0.17

(b)

Model	**Coefficient**	**Estimate**	**SE**	***df***	***t***	***p***	***p* level**
QuadDFint	$Intercept$	1.68	1.07	177.95	1.57	0.12	ns
	$dist\_std$	12.99	2.25	282.65	5.77	0.00	<0.001
	$dist2\_std$	-9.00	1.22	282.35	-7.41	0.00	<0.001
	$flow\_std$	-1.25	1.50	237.67	-0.83	0.41	ns
	$dist\_flow\_std$	-1.79	2.81	285.76	-0.64	0.52	ns
	$dist2\_flow\_std$	1.78	1.36	281.01	1.30	0.19	ns

Removing "odd" years

Mean flows results

Table S3. Tables of (a) Maximum Likelihood model comparison statistics comparing fits for models in which *Flow* is measured as *high flows*: the Q75 daily flow from October to December in the year previous to the redd survey and years with low survey coverage (1983, 2007, 2008 & 2012) have been removed. The table is ordered by difference in Akaike Information Criteria (dAIC) from the "top-ranked" model (i.e., the model with the lowest AIC). Marginal and conditional R^2 were calculated according to the method of Nakagawa & Schielzeth (2013). (b) Coefficient estimates of the top-ranking model fitted to the same data, as assessed by AIC.

(a)

Model name	Model terms	Model fit			Comparison		R^2	
		Sigma	logLik	Deviance	AIC	dAIC	Marginal	Conditional
QuadDF	$Dist, Dist^2, Flow$	3.49	-655.79	1311.6	1323.6	0.00	0.27	0.31
QuadDFint	$Dist, Dist^2, Flow, Dist \times Flow, Dist^2 \times Flow$	3.46	-654.09	1308.2	1324.2	0.62	0.28	0.32
LinDF	$Dist, Flow$	3.88	-679.59	1359.2	1369.2	45.60	0.12	0.15
LinDFint	$Dist, Flow, Dist \times Flow$	3.87	-679.15	1358.3	1370.3	46.73	0.12	0.15
LinD	$Dist$	3.87	-682.78	1365.6	1373.6	49.99	0.07	0.14

(b)

Model	Coefficient	Estimate	SE	*df*	*t*	*p*	*p* level
QuadDF	$Intercept$	5.36	1.55	18.44	3.47	0.00	<0.05
QuadDF	$dist\_std$	11.46	1.99	236.58	5.75	0.00	<0.001
QuadDF	$dist2\_std$	-7.92	1.09	236.61	-7.29	0.00	<0.001
QuadDF	$flow\_std$	-4.46	1.49	10.66	-2.99	0.01	<0.05

High flows results

Table S4. Tables of (a) Maximum Likelihood model comparison statistics comparing fits for models in which *Flow* is measured as *high flows*: the Q75 daily flow from October to December in the year previous to the redd survey and years with low survey coverage (1983, 2007, 2008 & 2012) have been removed. The table is ordered by difference in Akaike Information Criteria (dAIC) from the "top-ranked" model (i.e., the model with the lowest AIC). Marginal and conditional R^2 were calculated according to the method of Nakagawa & Schielzeth (2013). (b) Coefficient estimates of the top-ranking model fitted to the same data, as assessed by AIC.

(a)

Model name	Model terms	Model fit			Comparison		R^2	
		Sigma	logLik	Deviance	AIC	dAIC	Marginal	Conditional
QuadDF	$Dist, Dist^2, Flow$	3.48	-657.73	1315.47	1327.47	0.00	0.24	0.32
QuadDFint	$Dist, Dist^2, Flow, Dist \times Flow, Dist^2 \times Flow$	3.47	-656.47	1312.93	1328.93	1.47	0.25	0.32
LinDF	$Dist, Flow$	3.87	-681.58	1363.16	1373.16	45.69	0.09	0.15
LinD	$Dist$	3.87	-682.78	1365.56	1373.56	46.09	0.07	0.14
LinDFint	$Dist, Flow, Dist \times Flow$	3.87	-681.13	1362.26	1374.26	46.80	0.09	0.15

(b)

Model	Coefficient	Estimate	SE	*df*	*t*	*p*	*p* level
QuadDF	$Intercept$	1.95	0.96	101.44	2.02	0.05	<0.05
QuadDF	$dist\_std$	11.52	1.99	236.28	5.78	0.00	<0.001
QuadDF	$dist2\_std$	-7.93	1.09	236.41	-7.31	0.00	<0.001
QuadDF	$flow\_std$	-1.17	0.72	11.95	-1.61	0.13	ns

Table S5. Survey section details including survey section length (calculated using GIS) and distance from tidal limit. The location of the start and end points of each survey section are illustrated in figure 2.

Survey Section Number and Name	Section Length (in kilometres)	Start point distance from tidal limit (in kilometres)
1 Worgret - Holme Bridge	7.78	0
2 Holme Bridge - East Stoke Weir	3.50	7.80
15 East Stoke Mill Stream	1.0	11.80
3 East Stoke Weir - Bindon Hatches	2.50	14.70
16 Bindon Mill Stream	0.25	18.50
24 Wool Stream	1.75	18.70
4 Bindon Hatches - East Burton Hatches	4.50	19.20
17 Waterbarn Stream	1.75	21.80
19 Moreton North Stream	3.25	23.90
18 Trout Stream	0.50	26.30
5 E Burton Hatches - Moreton House Weir	1.75	28.0
25 Tadnoll Brook	8.0	28.80
6 Moreton House Weir - Hurst Weir	1.75	31.30
7 Hurst Weir - Woodsford Weir	4.50	34.90
20 North Stream	5.0	39.50
8 Woodsford Weir - Nine Hatches	1.25	43.0
9 Nine Hatches - Stafford House Weir	3.0	45.70
20a North Stream south arm	1.50	48.60
21 Greys Bridge Carrier	2.50	50.0
10 Stafford House Weir - Louds Mill	2.75	51.50
26 South Winterbourne	8.50	51.50
22 South Winterbourne Carrier	2.25	55.0
11 Louds Mill - Whitfield Hatches	3.75	56.60
23a Dorchester Mill Stream	1.41	57.70
23 North Dorchester Carrier	6.0	60.40
27 River Cerne	14.50	63.10
12 Whitfield Hatches - Frampton Weir	4.75	63.20
28 Sydling Brook	72.10	72.10
13 Frampton Weir - Hooke confluence	6.25	74.70
14 Hooke confluence - Cattistock	1.75	83.70
29 River Hooke	3.62	83.70