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Above parr: Lowland river habitat characteristics associated with higher juvenile Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) densities

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Abstract

Understanding juvenile salmonid habitat requirements is critical for their effective management, but little is known about these requirements in lowland rivers, which include important but unique salmonid habitats. We compared the relative influence of in-stream *Ranunculus* cover, water depth, prey abundance, distance upstream and two previously unexplored factors (water velocity heterogeneity and site colonisation potential) on summer densities of juvenile Atlantic salmon and brown trout. We applied electrofishing, habitat surveys and macroinvertebrate kick sampling, and calculated the site colonisation potential from salmon redd surveys across 18–22 sites in a lowland river in 2015–2017. Due to a recruitment crash in 2016, models including and excluding this unusual year were explored. Excluding 2016 data, juvenile salmon densities showed a positive association with *Ranunculus* cover and numbers of nearby upstream redds, and a negative association with distance upstream from the tidal limit. Trout densities were positively associated with velocity heterogeneity, indicating a potential indirect influence of *Ranunculus* mediated by water velocity. When including 2016, year had the largest effect on densities of both species, highlighting the impact of the recruitment failure. These findings uncover interspecific differences in the habitat requirements of juvenile salmonids in lowland rivers. Velocity heterogeneity and site colonisation potential had high explanatory power, highlighting that they should be considered in future studies of habitat use. These findings demonstrate that temporal replication and recruitment dynamics are important considerations when exploring species–habitat associations. We discuss potential management implications and argue that *Ranunculus* cover could be an important management tool in conservation of lowland salmonids.

KEYWORDS

Atlantic salmon, brown trout, habitat, parr, *Ranunculus*, salmonids

1 | INTRODUCTION

The degradation of freshwater habitats is a leading cause of species loss and declines in population densities (Dudgeon et al., 2006; Gordon et al., 2018; Reid et al., 2019). The population declines of some anadromous salmonids, such as Atlantic salmon (*Salmo salar*, hereafter salmon), in recent decades might be partly attributable to a change in freshwater conditions experienced by juveniles (Friedland et al., 2009; Gregory et al., 2017, 2019; Russell et al., 2012). An understanding of the freshwater habitat requirements of juvenile salmonids is therefore crucial to direct effective conservation and ensure viability of salmonid populations. Most studies relating densities of juvenile salmonid to habitat characteristics have considered in-stream cover, stream substrate, water depth and velocity as key factors (Heggenes, 1990), but have found variable and often contrasting relationships. Moreover, few of these studies have focused on lowland rivers (but see Riley, Ives, Pawon, & Maxwell, 2006; Riley, Pawson, Quayle, & Ives, 2009). Lowland rivers differ from many upland river systems because: (a) they are physically more stable habitats and typically have a smaller and more similar gradient throughout the river catchment, (b) they are low-energy systems, and (c) they lack the large substrate (i.e. rocks and boulders) typically used by juvenile salmonids as cover and refuge from high flows in upland rivers (Berrie, 1992; Ibbotson et al., 2013). Consequently, submerged macrophytes, such as the water crowfoots (*Ranunculus* subgenus *Batrachium*, hereafter *Ranunculus*), could play a particularly important structuring role in these rivers (McCormick & Harrison, 2011; Riley et al., 2006, 2009).

In-stream cover provides essential shelter for juvenile salmonids, including salmon and brown trout (*S. trutta*, hereafter trout), and is considered a key attribute in determining salmonid densities (Gries & Juanes, 1998; Milner, 1982). In upland rivers, an abundance of cobbles and boulders provides complex habitats with refugia from water flow, predators and competitors (Cunjak, 1998; Semple, 1991; Venter, Grant, Noel, & Kim, 2008). Aquatic vegetation, such as submerged macrophytes, can also be used as cover by smaller parr (Maki-Petays, Muotka, Huusko, Tikkanen, & Kreivi, 1997) and provide a night-time refuge (Riley et al., 2006). Very high macrophyte cover could reduce habitat heterogeneity and suitability for salmonid parr, but in the absence of large substrate, aquatic vegetation may provide essential shelter for both salmon and trout, particularly during summer and autumn.

Although there is some overlap in habitat preferences between the species, salmon parr are commonly associated with shallow to intermediate water depths and fast velocities, whereas trout parr are often associated with deeper, slower flowing river margins (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Heggenes, Bagliniere, & Cunjak, 1999; Heggenes, Saltviet, & Lingaee, 1996; Morantz, Sweeney, Shirvell, & Longard, 1987; Riley et al., 2006). Water velocity can influence salmonid foraging behaviour. Both salmon and trout are opportunistic feeders, seeking drifting and benthic prey depending on their availability (Gibson, 1993; Poff & Huryn, 1998), although trout actively search for prey more frequently than salmon (Bardonnnet & Bagliniere, 2000). Salmonids utilise heterogeneity in velocity to minimise the energetic cost of foraging by maintaining station in areas of low velocity adjacent

to fast flows that are carrying macroinvertebrate prey (Cunjak, 1998; McCormick & Harrison, 2011; Morantz et al., 1987). While causal relationships between habitat characteristics and changes in flow (e.g. boulders and low-velocity refuges in upland rivers) have been proposed (Cunjak, 1998; Venter et al., 2008), to our knowledge, no study of salmonid habitat use has related any measure of velocity heterogeneity or patchiness to juvenile salmonid densities.

Salmonids—particularly salmon—undergo ontogenetic shifts in both behaviour and habitat use during their freshwater stages (Folt, Nislow, & Power, 1998). Upon emergence from spawning nests (redds), fry often disperse downstream in search of habitat optimal for their growth and development. Maximum dispersal distances reported range from a few hundred metres (e.g. Crisp, 1995) to a few kilometres (e.g. Beall, Dumas, Claireaux, Barriere, & Marty, 1994), dependent on conspecific density and habitat availability (Bardonnnet & Bagliniere, 2000). Using fine-scale data, a positive relationship between estimated total salmonid redd area and local salmon parr densities was identified (Teichert et al., 2011), although these results might not be representative of all wild populations as salmon fry were considered to be limited dispersers in this study (<20 m). Although the presence and proximity of redds are likely to affect colonisation potential and the density of summer parr, no rigorous study has tested the influence of proximity among the habitats required for different salmonid life stages.

Here, we provided a comprehensive analysis of the relationships between characteristics of lowland river habitats and densities of salmon and trout parr. Habitat characteristics included in-stream vegetation (*Ranunculus*) cover, water depth, velocity and prey availability (macroinvertebrates). We also considered two hitherto overlooked characteristics, namely velocity heterogeneity, and the presence and proximity of salmon redds (colonisation potential), to draw a more complete picture of the habitat requirements of juvenile salmonids in lowland rivers. Additionally, distance from tidal limit was included to account for differences in the accessibility of sites to migrating adults, which could influence the distributions of juveniles the following summer. Based on the previous research, we hypothesised the following relationships for both species: (a) a strong positive influence of *Ranunculus* cover on salmonid densities (albeit to a threshold), (b) that fast water velocity had a strong positive effect on salmon densities, but a negative effect on trout, (c) a negative influence of water depth on salmon and a positive influence on trout densities, (d) a positive effect of prey abundance on salmonid densities, (e) a strong positive influence of velocity heterogeneity on salmonid densities and additionally for salmon and (f) a strong positive influence of the number of salmon redds found directly upstream on observed salmon densities.

2 | METHODS

2.1 | Study sites and sampling

The River Frome, Dorset, and its tributaries are the most westerly of the UK chalk streams. The lowland river is inhabited by salmon and

trout populations of regional significance (Berrie, 1992; Lauridsen et al., 2017), with salmon stock estimates annually reported to the International Council for the Exploration of the Seas (ICES, 2017). Trout populations in the River Frome (and therefore trout parr sampled in this study) represent individuals with resident and anadromous life histories (Goodwin, King, Jones, Ibbotson, & Stevens, 2016).

To determine the relationships between habitat characteristics and the summer density of juvenile salmonids, we sampled habitat characteristics, macroinvertebrates and juvenile salmonid populations at 18–22 sites on the River Frome (Figure 1). Sampling occurred during August and September for three years (2015–2017). Sampling sites were approximately 100 m in length, varied in physical characteristics and were selected to represent contrasting habitat, representing natural variation in *Ranunculus* cover throughout the river catchment (Table S1).

The habitat at each sampling site was surveyed using five evenly spaced quadrats (0.5 m × 0.5 m) distributed along each of ten evenly spaced transects across the wetted width of the river. Within each quadrat, water depth was measured, the cover of *Ranunculus* plants was estimated visually as a percentage, and the water velocity was estimated visually as one of five categories (1 = 0–25 cm/s; 2 = 25–50 cm/s; 3 = 50–75 cm/s; 4 = 75–100 cm/s; and 5 > 100+ cm/s). Specifically, water velocity was estimated by comparing visually the surface water changes around a wooden metre stick, that is how far up the stick the bow wave reached and the amount of turbulence the stick created. Although this measure was subjective, the estimates were all done by a single observer and were considered sufficiently objective to allow comparisons between quadrats within sites, between sites and over time. Percentage cover of other species of macrophytes, bryophytes and submerged riparian vegetation was also estimated in each quadrat, but they were not present with sufficient frequency or quantity to be considered in statistical analyses.

Aquatic macroinvertebrates were sampled with standardised effort once per site using a 180-s kick sample with a pond net (net size: 25 cm × 25 cm; mesh aperture: 1 mm). Kick samples covered the area of each site and sampled all habitats in proportion to their occurrence (Wright, 1997). The distribution of effort for the kick samples was determined a priori from water depth, velocity and macrophyte assemblages observed during habitat surveys. Kick samples were preserved in 70% ethanol solution and transported to the laboratory where they were washed with a 500-µm-pore sieve prior to sorting and identification. All specimens were identified to the lowest practical taxonomic level (usually species), except Oligochaeta (subclass), Hydrachnidae (family), Simuliidae (family) and Chironomidae (tribe). All habitat surveys and macroinvertebrate samples were collected at least two hours prior to the surveying of fish populations to limit disturbance to fish communities.

Standard quantitative k-pass depletion electrofishing was used to estimate densities of juvenile (0+) salmon and trout (Hilborn & Walters, 1992). There were too few older juvenile salmonids (1+) to be considered in this study, as the majority of anadromous individuals migrate to sea after their first year in the river in this system

(Ibbotson et al., 2013). We used between two and five fishing passes to achieve a depletion of >50% in the numbers of fish caught per pass. Pulsed DC was used where the output waveform was a square wave fished at 50 Hertz, ~200 volts and 25%–30% duty cycle. Electrofishing was carried out using a single anode (380 mm diameter) and cathode (3,000 mm long). These settings are known to return high salmonid parr capture rates and cause <1% mortality rates on the River Frome (W. Beaumont, personal communication, August 2015). We sedated captured fish, before identifying the species, measuring their fork length (L_F : to age fish) to the nearest mm, and taking a scale sample from between the dorsal fin and lateral line (used if ageing by L_F was inconclusive). After processing, all fish were released back into the river section where they were captured. Processing was carried out by licensed personnel under a UK Home Office A(SP)A Licence (PPL 30/3277). Additional data were available for salmon redds (but not for trout): GPS locations of redds on the main river, carriers (flood relief channels) and major tributaries for the 2014/15 and 2016/17 spawning seasons (River Frome salmon spawn around New Year) were collected by the Environment Agency (subcontractor, Casterbridge Fisheries, Ltd) in January/February 2015 and 2017. No data were available for the 2015/16 spawning season because surveys were prevented by high water levels and poor weather.

2.2 | Data preparation

Fish were aged using L_F distribution and scale samples where necessary (Figures S1 and S2; max 0+ salmon L_F : 129 mm; max 0+ trout L_F : 150 mm). The k-pass removal method used to calculate fish abundance estimates (and associated 95% confidence intervals) uses the maximum likelihood model of Carle and Strub (1978) and assumes that (a) the population is closed, (b) effort is constant between passes, and (c) the probability of capture for an animal is constant for all animals and samples. It was reasonable to assume constant capture probability within each site because the same personnel undertook all fishing within a site and fishing passes were undertaken successively. Fish density estimates were obtained by dividing the fish abundance estimate for a site by the site area (site length × mean channel width).

The variable *depth* was normally distributed and required no transformation. *Ranunculus* cover was a proportion and was arcsine-transformed according to $(\arcsin(x/100) \times 2/\pi)$, where x is the explanatory variable. To select a summary statistic that best represented explanatory variables (measured at the quadrat level) at the site level, the mode, median and mean of the transformed explanatory variable were compared visually with its empirical distribution: the mean was chosen to represent *Ranunculus* cover and the median to summarise *depth*.

As trout parr inhabit slower water and have not been reported in habitats with velocities greater than 50 cm/s (Heggenes et al., 1996; Riley et al., 2006), we grouped velocity categories 3, 4 and 5 (50–100+ cm/s) to represent the faster velocities preferred by salmon

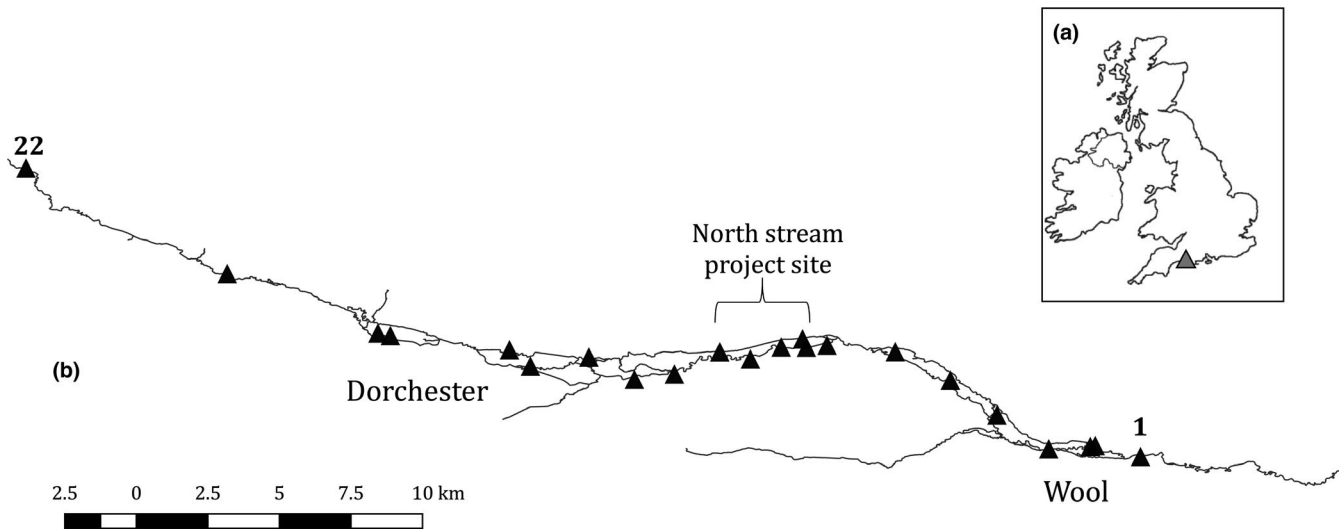


FIGURE 1 Study sites. (a) Location of River Frome in Dorset, UK; (b) study site locations along the River Frome (1 = most downstream site; 22 = most upstream site); section of river where juvenile salmonid diet sampling took place in a separate study on the North Stream

and avoided by trout. Site-level proportions of fast velocity were calculated as the proportions of quadrat measurements of the respective categories and arcsine-transformed as above. To represent heterogeneity in site-level velocity, we aimed to capture the difference in velocity between neighbouring quadrats. The mean steepness of gradients in velocity between adjacent quadrats was calculated for all quadrats with a complete set of eight neighbours (Figure 2), using the Terrain Ruggedness Index (TRI: Wilson, O'Connell, Brown, Guinan, & Grehan, 2007) and implemented in R package raster (Hijmans & van Etten, 2012). TRI was calculated as $\sum |x[-5] - x[5]| / 8$. values of TRI were averaged across all quadrats and used to represent velocity heterogeneity at the site level.

Abundance of aquatic macroinvertebrates is not the most representative measure of salmonid food availability (Folt et al., 1998) as taxa found frequently in kick samples but infrequently in the drift are less available to salmonids, for example, interstitial fauna (Poff & Huryn, 1998). Frequently consumed aquatic macroinvertebrate species were determined from a separate study undertaken on the North Stream of the River Frome (Figure 1) during June and August in 2016 and 2017, where gut contents were obtained from 0+ salmonids (204 salmon and 94 trout) across nine sites. Specimens in the gut contents were identified to the lowest possible taxonomic level (see above) and frequency of prey occurrence calculated for each fish species (Baker, Buckland, & Sheaves, 2014). Taxa that were present in at least 25% of all samples were considered to be "frequently consumed aquatic prey." For salmon, frequently consumed prey included *Baetis* spp, Simuliidae, Chironomidae and *Serratella ignita* (Ephemeroidea). The same taxa were frequently consumed by trout with the addition of *Gammarus pulex* group, *Hydrotilla* spp. and *Hydropsyche* spp. (Table S2). As the gut contents were sampled from a similar location in the catchment, and slightly earlier in the year than some of the kick samples, there was possible site-specific or seasonal bias in our measure of frequently consumed taxa. However, these taxa were present in all sites and

contributed >40% of the total abundance (except sites 8, 10 and 15 in 2015 and site 3 in 2017; Table S3), and thus arguably represent a common and available prey resource of salmonids. The total abundance of the frequently consumed taxa found in the kick samples was calculated to represent the variable *prey abundance*.

For data collected in 2015 and 2017, the GPS coordinates of salmon redd locations and study sites were used to calculate the distances along the river between the downstream starting point of each site and all upstream redds. A vector map of the River Frome was constructed using R package raster and the GRASS GIS functions *r.thin* and *r.to.vect*. Redds and study sites were positioned on the river using GRASS GIS function *v.net*, and least-cost (i.e. shortest) distances in km along the river between study sites and each upstream redd were calculated using GRASS GIS function *v.net.distance*. We used reported fish dispersal distances from Beall et al. (1994) as this study represents wild fish dispersal behaviour (using eggs reared in situ). Based on their estimates of summer downstream dispersal distances of 900 m by the majority of parr (68%), and an upper range of 2,400 m, we used a conservative limit of 1,100 m downstream to represent the majority of parr, while also capturing dispersal capabilities of fish that travelled further. We then calculated the number of redds present within 1,100 m upstream of a study site to represent the variable *number of nearby upstream redds* (colonisation potential).

We calculated distance between sites and the tidal limit (located approximately 3 km upstream from where the river enters Poole Harbour) using R package riverdist (Tyers, 2017). Across sites, averages of the explanatory variables did not differ between years, with the exception of *Ranunculus* cover in 2015 relative to 2017 (Figure 3 and Table S4).

2.3 | Statistical analysis

The analysis aimed to maximise the potential to draw interspecific comparisons in population density-habitat associations while

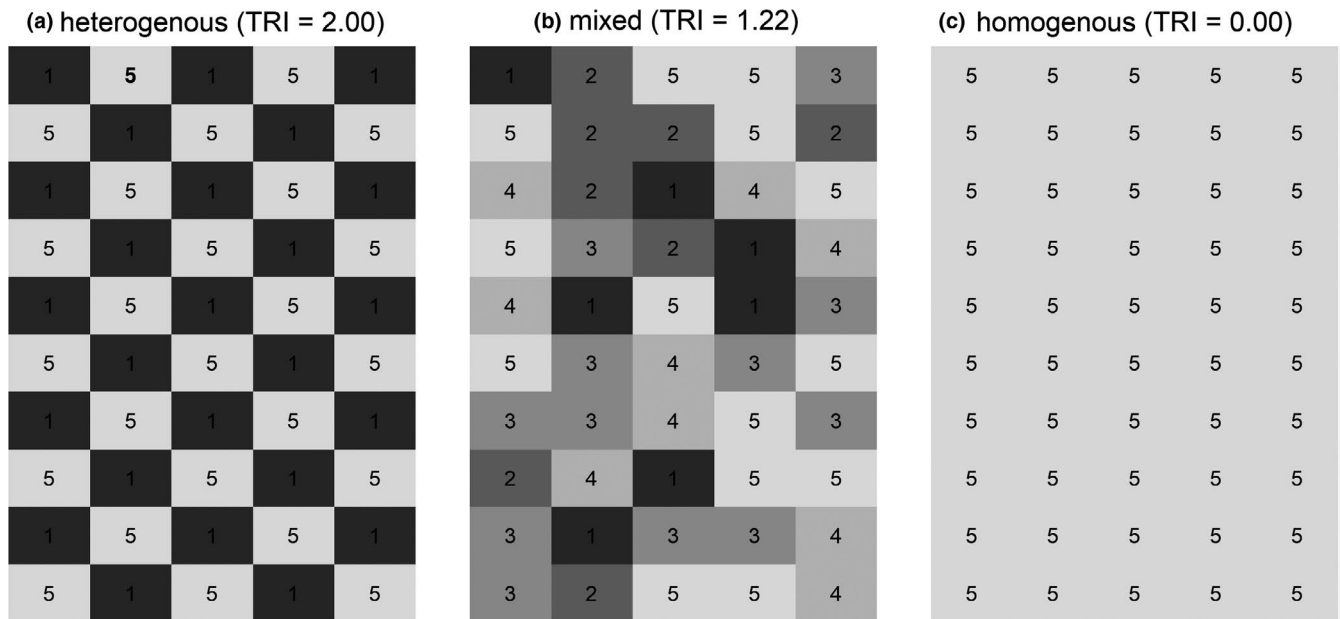


FIGURE 2 Example of the representation of site-level velocity heterogeneity using Terrain Ruggedness Index (TRI) calculations on matrices of fifty estimates (10 transects \times 5 quadrats) of velocity categories (1:5); (a) maximum heterogeneity between quadrats results in an average TRI value of 2.00; (b) a mixture of medium–fast velocity categories between quadrats results in a lower average TRI value of 0.81, as the average heterogeneity is lower; (c) maximum homogeneity between quadrats results in an average TRI value of 0.00, as the velocity category at all quadrats is identical

accounting for both an anomalous year (observed failure in salmonid recruitment in 2016 following high overwinter temperature in 2015–2016) and missing data (poor weather conditions prevented salmon redd counting in 2016 and collecting macroinvertebrate data at three sites across 2015 and 2016). We considered the following models to test our hypotheses: (a) models for each species including data from all 3 years but excluding cases with missing macroinvertebrate samples and the *number of upstream redds* explanatory variable, hereafter “3-year models” ($n = 56$); (b) models for each species excluding the anomalous 2016 data, two cases with missing macroinvertebrate samples and the *number of upstream redds* explanatory variable, hereafter “2-year models” ($n = 38$); and (c) models for salmon only excluding the anomalous 2016 data and two cases with missing macroinvertebrate samples but including the *number of nearby upstream redds* as an explanatory variable, hereafter “2-year salmon redds models” ($n = 38$). For each set of models, we considered the two species (salmon and trout) separately due to limiting sample sizes. Linear models tested the effect of the explanatory variables that were hypothesised to be important (Figure 3) on site-specific estimates of juvenile salmonid densities. The models took the general form:

$$y \sim \alpha + \beta X + \epsilon,$$

where y is salmon or trout density, α is an overall fish density, y is a vector of coefficients relating the matrix of explanatory variables X to y , and ϵ is an independent and identically distributed random normal variate representing model error.

Prior to model fitting, explanatory variables were examined for collinearity (Figures S3 and S4): Pearson's correlations between

pairs of potential explanatory variables $r \geq |.6|$ were considered highly correlated (Dormann et al., 2013), and models including highly correlated variables were further investigated to decide which explanatory variables to exclude. To compare the effects of variables measured at different scales, numerical explanatory variables were standardised prior to analyses by subtracting their mean and dividing by their standard deviation. We also explored whether the effect of *Ranunculus* was best represented by a linear or quadratic relationship, by comparing univariate models with Akaike's information criteria model selection (AICc), corrected for small sample size (Figure S5). Models containing a linear or quadratic term of *Ranunculus* were statistically indistinguishable; thus, we included *Ranunculus* as a linear term. Where *Ranunculus* was retained in the best-fit model, we implemented post-candidate model comparisons (post-tests), using all best models and additional models fit with a quadratic *Ranunculus* term (replacing the linear *Ranunculus* term, where applicable). This allowed for the selection of the overall best model and to consider whether there was a threshold effect of cover, where *Ranunculus* was important.

Candidate models for the 3-year and 2-year analyses represented hypotheses of the effects of different combinations of explanatory variables based on predictions and field observations. Starting with a global model (including all explanatory variables), we removed variables one at a time to compare their relative importance. Subsequent simpler models included only the variables important for one or both species (designated as important if the difference in $\Delta AICc$ between initial models was >1), and finally, we tested each variable individually (see Tables S5 and S6 for full process).

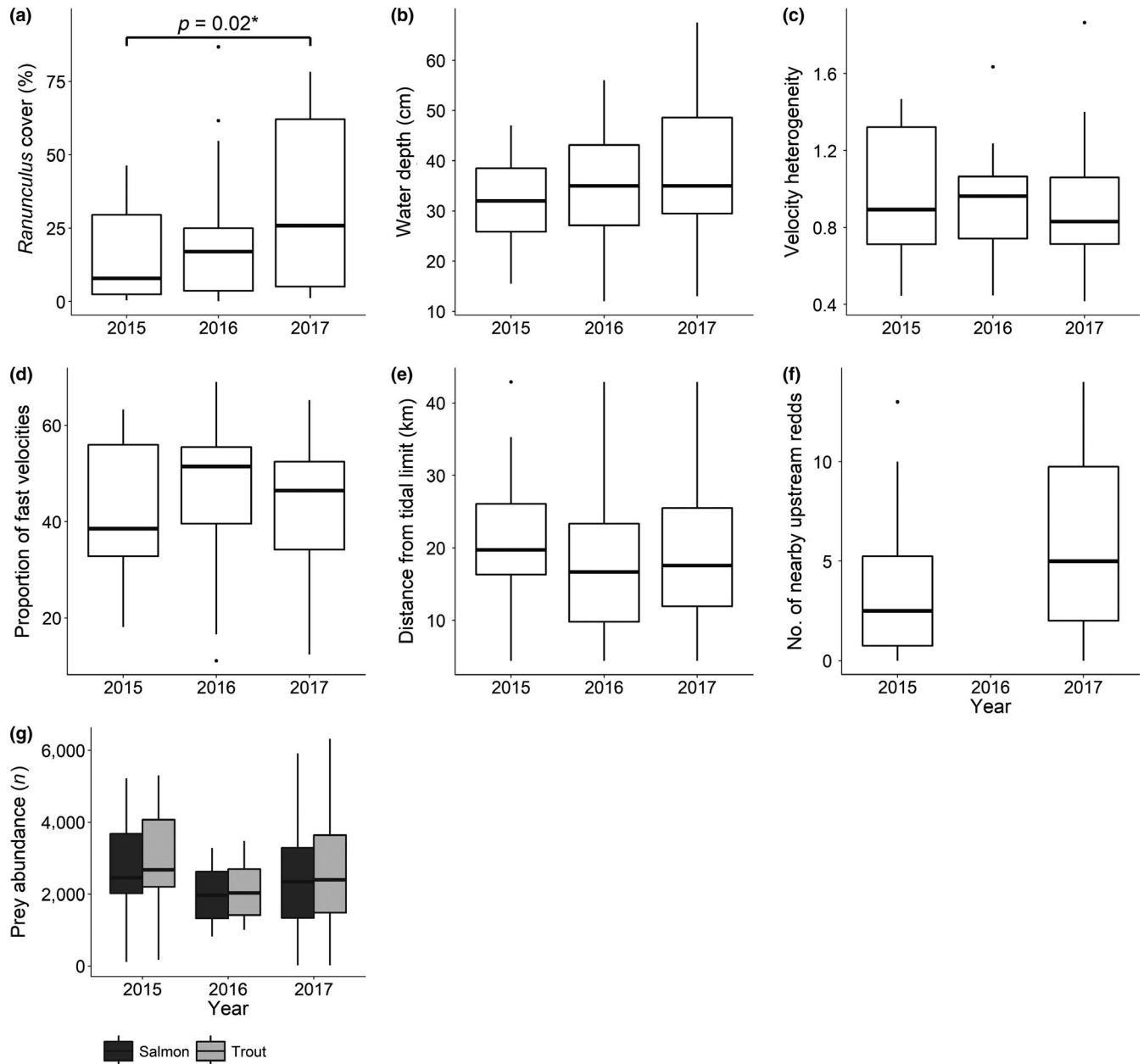


FIGURE 3 Median and range of environmental variables recorded across all study sites included in subsequent analyses for each year: 2015 ($n = 16$); 2016 ($n = 18$); and 2017 ($n = 22$). (a–f) represent environmental variables common to a site; (g) shows abundance of preferred prey items for each fish species. All variables were tested for differences between years; significant differences between years are marked with a p -value

Models were fitted using maximum likelihood, and the model with the lowest AICc was selected as the final best model. If the difference between two models with the lowest ΔAICc was <2 , the models were deemed to be statistically indistinguishable (Burnham & Anderson, 2002), and the most parsimonious model was selected. To understand the balance between the generality and specificity of the models, we also calculated the predictive performance using leave-one-out cross-validation (LOO CV). The model with the smallest prediction error ($\Delta\text{LOO CV}$) was assumed to have the greatest predictive ability.

To test for the importance of redds in the 2-year salmon redd analysis, we included the redd variable to the best performing model(s) of the 2-year salmon analysis to construct a global candidate model. We then constructed a set of candidate models including different combinations of variables in the global model. Models were fitted and compared as above. Model residuals of the best performing 2-year models for salmon and trout were inspected to ensure they did not violate assumptions of homogeneity, normality and independence. All statistical analyses were conducted in R version 3.4.4 (R Development Core Team, 2018).

3 | RESULTS

3.1 | 3-year models

Mean densities of juvenile salmon were higher than densities of juvenile trout across all years and the lowest mean densities for both species occurred in 2016 (Figure 4). Eighteen candidate models were fitted to the 3-year fish data and compared (Table 1). The four best models at predicting juvenile salmon densities were statistically indistinguishable ($\Delta AICc < 2$), all of which included a *year* effect. As *Ranunculus* was retained in two of these models, six post-test comparisons were implemented (Table 1). The most parsimonious of the post-test models, and therefore the best overall model, was Model PS6, which included the effects of *year* and *distance from tidal limit* and explained 29% of variance in salmon densities (Table 1). Extending the *Ranunculus* term from a linear term (Model PS3) to a quadratic term (Model PS4) explained more variance ($R^2_{adj} = .30$ and $.33$ respectively), and a combination of a quadratic *Ranunculus* term and *prey abundance* explained the most variance ($R^2_{adj} = .34$), although the prediction error for all six models was equal ($\Delta LOO CV = 0.004$). The parameters *proportion of fast velocities*, *velocity heterogeneity* and *depth* were not retained in the best-fit salmon models (Table 1).

Juvenile trout densities were best described by Model 17, which contained the terms *year* and *velocity heterogeneity* and explained 36% of the variance in densities (Table 1). As *Ranunculus* was not retained in the best model, no post-test comparisons were performed. No other candidate models explained more variance or had a lower

prediction error ($\Delta LOO CV < 0.0004$). The parameters *proportion of fast velocities*, *depth*, *prey abundance* and *distance from tidal limit* were not retained in the best-fit trout models (Table 1).

Both salmon and trout densities were strongly influenced by *year*, whereby the effect was driven by the negative influence of 2016 when juvenile salmonid populations were unusually low, relative to 2015 and 2017 (Figures 4 and 5). Salmon density was negatively associated with *distance from tidal limit*, with density estimates decreasing the further upstream the sites were located (Figure 5a). Juvenile trout density increased with increasing *heterogeneity in velocity* (Figure 5b).

3.2 | 2-year models

When omitting 2016 data, *depth* was strongly correlated with *Ranunculus* ($r = .63$). As *Ranunculus* is likely to be important juvenile salmonid habitat and because its presence is associated with increased water depths (Franklin, Dunbar, & Whitehead, 2008), *depth* was excluded and *Ranunculus* was retained in the model selection.

Subsequently, 19 candidate models were fitted to the 2-year fish data and compared (Table 2). Model 13, including the effects of *Ranunculus* and *distance from tidal limit*, was the best model at explaining salmon densities. Post-test comparisons included this model with and without a quadratic *Ranunculus* term. The two post-test models were statistically indistinguishable, but Model P15 was the most parsimonious, and thus the best overall performing model (Table 2). Including *Ranunculus* as a quadratic term explained more variance in salmon densities than Model P15 ($R^2_{adj} = .25$ and $.19$ respectively), but the prediction error was identical for both models ($\Delta LOO CV = 0.005$). The parameters *proportion of fast velocities*, *prey abundance*, *velocity heterogeneity* and *year* were not retained in the best models (Table 2).

The juvenile trout densities were best described by Model 18, with *velocity heterogeneity* as the only model term (Table 2). As *Ranunculus* was not retained in the best model, no post-test comparison was performed. Model 18 explained 22% of the variance in trout densities and had the lowest prediction error of all candidate models tested ($\Delta LOO CV = 0.0004$).

3.3 | 2-year salmon redd model

Eight candidate models that included *number of upstream redds* as an explanatory variable were fitted to the 2-year salmon data and compared (Table 3). The six best models were statistically indistinguishable ($\Delta AICc < 2$), and all included an effect of *Ranunculus*. The two most parsimonious models, Models 1 and 2, performed equally well ($R^2_{adj} = .19$, $\Delta LOO CV = 0.005$) and, in addition to a linear *Ranunculus* term, included *distance from tidal limit* and *number of nearby upstream redds* respectively. Model 1 was the same best model in the 2-year analysis. Including *Ranunculus* as a quadratic term rather than a linear term explained more variance in salmon density (Table 3). The most variation was explained by Model 4 ($R^2_{adj} = .28$), which included

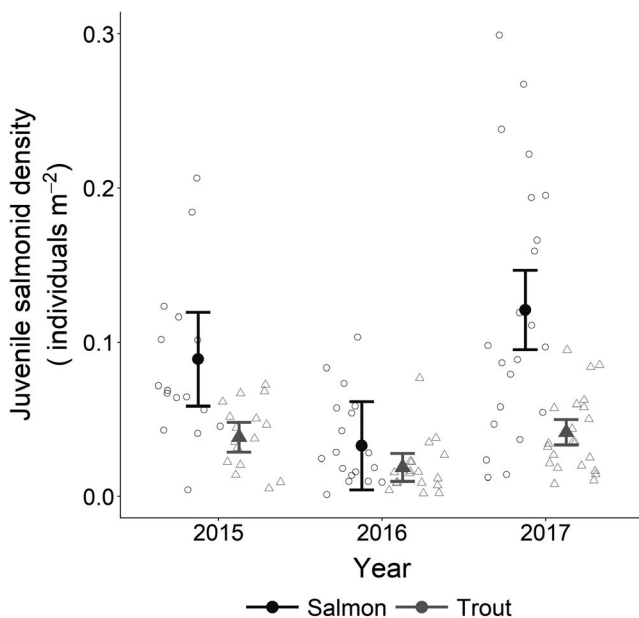


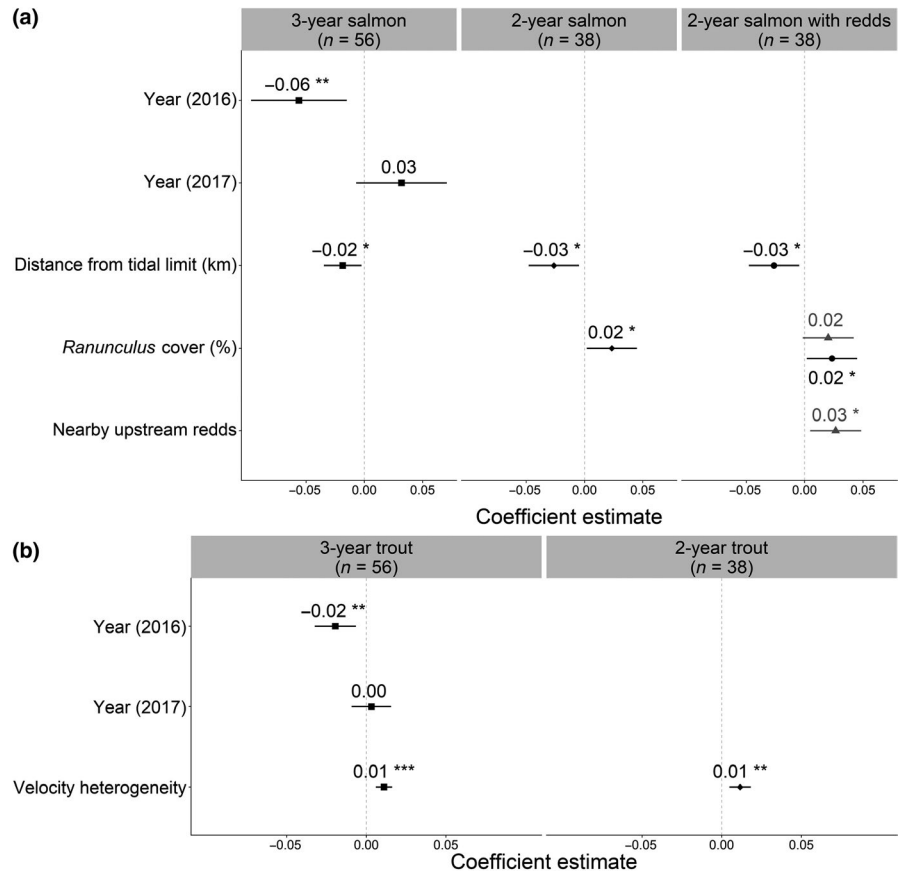
FIGURE 4 Marginal effect of year on estimated juvenile salmon (circles) and trout (triangles) densities in the top-performing 3-year models (PS6, 17) as determined by AICc model selection. Points are mean estimates, and error bars are the 95% confident interval. Raw density estimates are illustrated as jittered open circles and triangles for salmon and trout, respectively

TABLE 1 3-year models: Information statistic summary for the fit of 18 candidate models to the 3-year juvenile salmon and trout density data

Hypothesis tested	Candidate models		Salmon					Trout				
	Model no.	Model terms	AICc	Δ AICc	K	σ	R^2_{adj}	AICc	Δ AICc	K	σ	R^2_{adj}
Candidate model selection												
Global model	Global	Y + R + D + FV + VH + P + DS	-140.4	8.54	8	0.06	.28	-268.6	8.42	8	0.02	.35
DS is not important	1	Y + R + D + FV + VH + P	-138.9	10.03	7	0.06	.24	-267.7	9.25	7	0.02	.32
P is not important	2	Y + R + D + FV + VH + DS	-141.5	7.49	7	0.06	.27	-270.1	6.88	7	0.02	.35
VH is not important	3	Y + R + D + FV + P + DS	-143.2	5.75	7	0.06	.29	-258.8	18.13	7	0.02	.21
FV is not important	4	Y + R + D + VH + P + DS	-143.1	5.82	7	0.06	.29	-270.5	6.47	7	0.02	.36
D is not important	5	Y + R + FV + VH + P + DS	-142.3	6.63	7	0.06	.28	-271.0	5.96	7	0.02	.36
R is not important	6	Y + D + FV + VH + P + DS	-142.2	6.77	7	0.06	.28	-269.7	7.27	7	0.02	.35
Y is not important	7	R + D + FV + VH + P + DS	-130.9	18.04	6	0.07	.09	-258.4	18.61	6	0.02	.17
VH and A both important	8	Y + R + DS + VH + P	-144.9	4.00	6	0.06	.29	-272.8	4.18	6	0.02	.36
VH not as important as P	9	Y + R + DS + P	-147.3	1.67	5	0.06	.30	-263.5	13.44	5	0.02	.23
P not as important as VH	10	Y + R + DS + VH	-146.5	2.42	5	0.06	.29	-274.3	2.62	5	0.02	.36
VH and P not important	11	Y + R + DS	-148.9	0.00	4	0.06	.30	-263.4	13.58	4	0.02	.20
R most important	12	Y + R	-145.2	3.78	3	0.06	.24	-261.5	15.44	3	0.02	.15
D most important	13	Y + D	-147.3	1.61	3	0.06	.27	-261.0	15.93	3	0.02	.15
FV most important	14	Y + FV	-145.0	3.95	3	0.06	.23	-265.8	11.15	3	0.02	.22
DS most important	15	Y + DS	-148.9	0.05	3	0.06	.29	-263.7	13.22	3	0.02	.19
P most important	16	Y + P	-143.9	5.07	3	0.06	.22	-262.0	14.96	3	0.02	.16
VH most important	17	Y + VH	-143.7	5.22	3	0.06	.22	-277.0	0.00	3	0.02	.36
Post-candidate model comparisons on top-performing model/s (post-tests)												
Mod S9: R performs better than R ²	PS1	Y + R + DS + P	-147.3	2.32	5	0.06	.30	—	—	—	—	—
Mod S9: R ² performs better than R	PS2	Y + R ² + DS + P	-148.6	0.94	6	0.06	.34	—	—	—	—	—
Mod S11: R performs better than R ²	PS3	Y + R + DS	-148.9	0.65	4	0.06	.30	—	—	—	—	—
Mod S11: R ² performs better than R	PS4	Y + R ² + DS	-149.6	0.00	5	0.06	.33	—	—	—	—	—
Mod S13: D most important	PS5	Y + D	-147.3	2.26	3	0.06	.27	—	—	—	—	—
Mod S15: DS most important	PS6	Y + DS	-148.9	0.70	3	0.06	.29	—	—	—	—	—

Note: Model parameters include: Y, year; R, *Ranunculus*; D, depth; FV, fast velocity; VH, velocity heterogeneity; P, prey abundance; DS, distance from tidal limit. K is the number of model parameters. Rows in bold represent the best-fitting models selected by AICc for each species.

FIGURE 5 Coefficient estimates for explanatory variables retained in the best 3-year and 2-year model for (a) salmon and (b) trout. Best-fit 2-year redd models are also shown for salmon. 2015 is the reference level for year estimates. Points illustrate mean estimates (■, 3-year model; ◆, 2-year model; ●, 2-year salmon redd [Model 1]; ▲, 2-year salmon redd [Model 2]), lines are 95% confidence limits, and values denote the estimate and significance levels (* $p < .05$, ** $p < .01$, *** $p < .001$)



distance from tidal limit, number of upstream redds and a quadratic *Ranunculus* term, though the prediction error for all candidate models was equal ($\Delta\text{LOO CV} = 0.005$).

3.4 | Direction and strength of habitat effects

Marginal effects plots visualise the relationships between salmonid densities and individual habitat characteristics, while holding the effects of other model parameters constant (Figures 6 and 7). The best 2-year salmon redd models and 2-year trout model were used to assess habitat effects on fish densities in years of regular recruitment (i.e. excluding the unusual year). The residuals of the best models did not violate the assumptions of homogeneity, normality or independence (Figure S6).

The first 2-year salmon redd model (Model 1) showed that *Ranunculus* was positively associated, whereas distance from tidal limit was negatively associated with salmon density (Figure 6). The 95% confidence intervals of the effects *Ranunculus* and distance from tidal limit did not overlap with zero (Figure 5a). The second 2-year salmon redd model (Model 2) showed that *Ranunculus* and number of nearby upstream redds were positively associated with salmon density, though the 95% confidence interval of the *Ranunculus* effect did intercept zero (Figure 5a). Salmon density was higher in sites with higher *Ranunculus* cover and more redds upstream, but was lower in sites located further upstream of the tidal limit (Figure 6). The 2-year trout model showed a strong

positive association between velocity heterogeneity and trout density (Figure 7), and the 95% confidence interval of the effect did not overlap with zero (Figure 5b).

4 | DISCUSSION

Juvenile salmon and trout densities were associated with different summer habitat characteristics. Salmon density was positively associated with *Ranunculus* and site colonisation potential, and negatively associated with distance upstream, whereas trout density was strongly positively associated with velocity heterogeneity. These findings highlight the different habitat requirements of each species in lowland rivers and indicate how juvenile summer habitat might be managed to increase their salmonid populations.

When incorporating a poor recruitment year in the analyses, year had the largest effect on both salmon and trout densities. This emphasises the importance of recruitment dynamics in studies of species–habitat associations and of temporal replication to identify potential effects of habitat characteristics. The low juvenile salmonid densities recorded on the River Frome in 2016 corresponded with a juvenile salmon recruitment crash across England and Wales following an unusually wet and warm winter thought to have caused high egg and alevin (pre-emerged salmonid) mortality (ICES, 2017).

The importance of recruitment is further emphasised, as proximity to salmon redds had a positive influence on juvenile salmon densities suggesting that, in addition to habitat characteristics, the

TABLE 2 2-year models: Information statistic summary for the fit of 19 candidate models to the 2-year juvenile salmon and trout density data

Hypothesis tested	Candidate models			Salmon					Trout				
	Model no.	Model terms		AICc	Δ AICc	K	σ	R^2_{adj}	AICc	Δ AICc	K	σ	R^2_{adj}
Candidate model selection													
Global model	Global	Y + R + FV + VH + P + DS		-81.1	10.58	6	0.07	.11	-173.9	8.13	6	0.02	.23
DS is not important	1	Y + R + FV + VH + P		-80.7	11.00	5	0.07	.06	-173.5	8.53	5	0.02	.18
P is not important	2	Y + R + FV + VH + DS		-84.1	7.64	5	0.07	.14	-174.3	7.70	5	0.02	.20
VH is not important	3	Y + R + FV + P + DS		-84.1	7.61	5	0.07	.14	-167.9	14.08	5	0.02	.05
FV is not important	4	Y + R + VH + P + DS		-84.3	7.39	5	0.07	.14	-175.0	7.00	5	0.02	.21
Y is not important	5	R + FV + VH + P + DS		-83.9	7.86	5	0.07	.13	-176.2	5.75	5	0.02	.24
R is not important	6	Y + FV + VH + P + DS		-80.6	11.13	5	0.07	.05	-175.2	6.75	5	0.02	.22
VH and P important	7	R + DS + VH + P		-86.9	4.86	4	0.07	.16	-177.3	4.72	4	0.02	.22
FV and P important	8	R + DS + FV + P		-86.7	5.06	4	0.07	.15	-170.5	11.54	4	0.02	.07
VH and FV important	9	R + DS + VH + FV		-86.6	5.14	4	0.07	.15	-176.4	5.63	4	0.02	.20
VH important	10	R + DS + VH		-89.1	2.57	3	0.07	.17	-178.8	3.15	3	0.02	.22
P important	11	R + DS + P		-89.5	2.24	3	0.07	.18	-173.3	8.74	3	0.02	.09
FV important	12	R + DS + FV		-89.1	2.59	3	0.07	.17	-171.5	10.45	3	0.02	.05
DS important	13	R + DS		-91.7	0.00	2	0.07	.19	-173.0	9.01	2	0.02	.05
R most important	14	R		-88.5	3.21	1	0.07	.09	-173.0	9.01	1	0.02	.01
FV most important	15	FV		-86.0	5.75	1	0.07	.03	-174.6	7.42	1	0.02	.05
DS most important	16	DS		-89.6	2.14	1	0.07	.11	-174.1	7.89	1	0.02	.04
P most important	17	P		-84.1	7.64	1	0.08	<.01	-173.5	8.54	1	0.02	.02
VH most important	18	VH		-84.3	7.39	1	0.08	<.01	-182.0	0.00	1	0.02	.22
Post-candidate model comparisons on top-performing model/s													
Mod S13: R performs better than R^2	P1S	R + DS		-91.7	1.30	2	0.07	.19	—	—	—	—	—
Mod S13: R^2 performs better than R	P2S	R^2 + DS		-93.0	0.00	3	0.06	.25	—	—	—	—	—

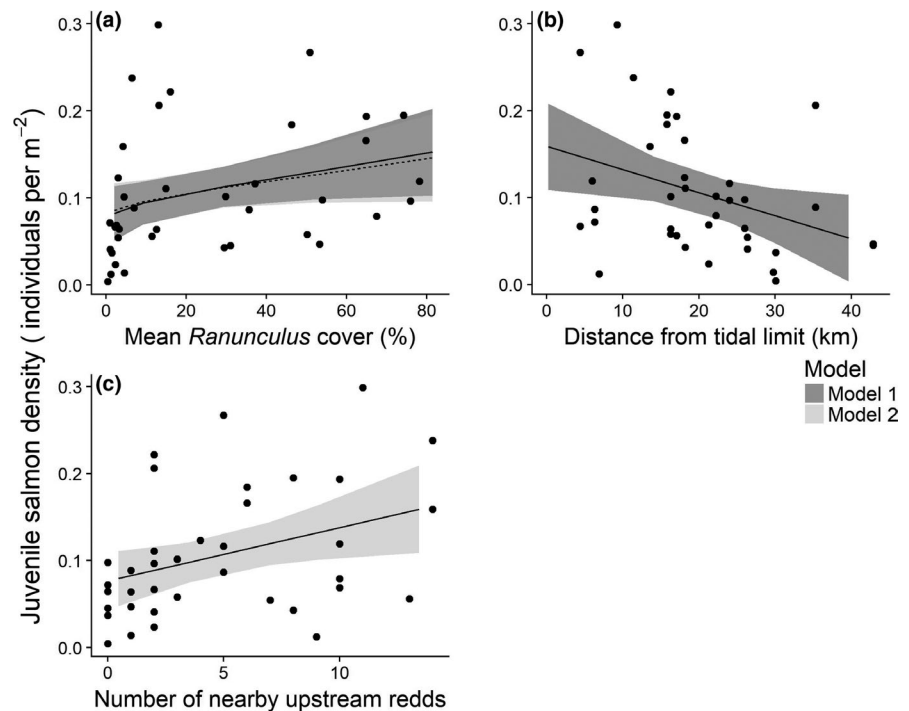
Note: Model parameters include: Y, year; R, *Ranunculus*; FV, fast velocity; VH, velocity heterogeneity; P, prey abundance; DS, distance from tidal limit. K is the number of model parameters. Rows in bold represent the best-fitting models selected by AICc for each species.

TABLE 3 2-year salmon redd models: Information statistic summary for the fit of 8 candidate models to the 2-year juvenile salmon density data, including number of nearby upstream redds as an explanatory variable

Hypothesis tested	Candidate models		Salmon				
	Model no.	Model terms	AICc	Δ AICc	K	σ	R^2_{adj}
Global model	Global	R + DS + RD	-91.3	1.68	3	0.07	.22
RD not important	1	R + DS	-91.7	1.30	2	0.07	.19
DS not important	2	R + RD	-91.7	1.31	2	0.07	.19
RD most important	3	RD	-90.8	2.22	1	0.07	.14
R^2 performs better than R	4	R^2 + DS + RD	-92.6	0.39	4	0.06	.28
RD not important, R^2 performs better than R	5	R^2 + DS	-93.0	0.00	3	0.06	.25
DS not important, R^2 performs better than R	6	R^2 + RD	-92.2	0.85	3	0.07	.23
R not important	7	DS + RD	-90.2	2.84	2	0.07	.16

Note: Model parameters include: R, *Ranunculus*; DS, distance from tidal limit and RD, number of nearby upstream redds. K is the number of model parameters. Rows in bold represent the best-fitting models selected by AICc.

FIGURE 6 Relationships between juvenile salmon density and (a) mean *Ranunculus* cover, (b) distance from tidal limit and (c) number of upstream redds, the explanatory variables retained in the top two performing 2-year salmon redds models (Models 1 and 2), as determined by AICc. The black line is the mean estimated effect, the shaded grey area is the standard error of the estimated effect, and black points are observed salmon densities at individual sites



colonisation potential of a site influences juvenile population sizes. Although salmon fry are capable of considerable dispersal distances from redds to summer habitats (Beall et al., 1994), the results of the current investigation suggest that fry move downstream only as far as adequate feeding grounds. Hence, maintaining appropriate summer habitats close to suitable spawning areas would have the greatest benefit. It further suggests that knowledge of salmon redd distributions would allow for more focused habitat conservation and improvements at sites with high colonisation potential.

A recent long-term study of salmon redd distribution on the River Frome found the highest densities of redds within the middle

reaches of the river. These aggregations increased under low-flow conditions, when access to upper reaches might be limited (Parry, Gregory, Lauridsen, & Griffiths, 2017). Although salmon fry can move to summer habitats upstream of their redd, the majority of juveniles disperse downstream (Beall et al., 1994). If most recruitment occurs in the middle reaches, it is plausible to expect higher juvenile densities at sites located in the lower to middle reaches of the river. Recruitment distribution, therefore, could explain the importance of distance from tidal limit at describing salmon densities and why lower densities were associated with sites further upstream.

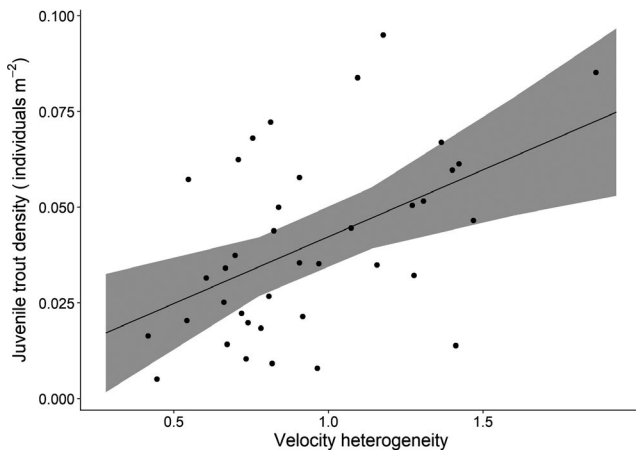


FIGURE 7 Relationship between juvenile trout density and velocity heterogeneity, the explanatory variable retained in the top-performing 2-year trout model (Model 18), as determined by AICc. x-axis scales from 0 (indicating constant velocity) to 2 (indicating high-velocity heterogeneity): see Figure 2. The black line is the mean estimated effect, the shaded grey area is the standard error of the estimated effect, and black points are observed trout densities

Ranunculus cover was positively associated with juvenile salmon density. Several potential mechanisms could drive this relationship. When comparing juvenile salmonid densities between open canopy sites with macrophytes and shaded sites without macrophytes but extensive canopy cover, higher densities of juvenile (0+) salmon (McCormick & Harrison, 2011; Riley et al., 2009) and trout (Riley et al., 2009) were found in the open canopy sites. While canopy cover can protect stream fish from aerial predators, thereby maximising foraging and minimising vigilance behaviour (Johnsson, Rydeborg, & Sundstrom, 2004), Riley et al. (2009) and McCormick and Harrison's (2011) results suggest that macrophytes afford adequate protection from aerial predators. Moreover, *Ranunculus* can provide necessary structural complexity throughout the water column to reduce predation (Diehl & Kornijow, 1998) and reduce the visual capacity of competitors, thereby promoting smaller, more numerous young-of-year salmonid territories (Imre, Grant, & Keeley, 2002). For example, an in-river experiment found that increasing habitat complexity (through addition of boulders) increased young-of-year salmon population densities via decreases in territory size (Venter et al., 2008). As larger substrates, such as boulders, are absent from lowland rivers, *Ranunculus* can perhaps provide a comparable level of habitat complexity.

Our results are consistent with findings from other river systems that highlight the importance of mixed water velocities for juvenile salmonids, which promote energy-efficient foraging (McCormick & Harrison, 2011; Morantz et al., 1987). Velocity heterogeneity influenced trout density in all years (including 2016), suggesting that it could be an important habitat requirement, irrespective of conspecific density. However, salmon densities were not influenced by heterogeneity in velocity and perhaps instead

utilise the structure and prey resources of *Ranunculus* in lowland rivers. As trout are more active predators than salmon (Bardonnnet & Bagliniere, 2000), they might be more likely to use different velocities while foraging.

Several habitat characteristics previously associated with higher juvenile salmonid densities (Heggenes, 1990) were not important in this study, suggesting that their relative influence differs between lowland rivers and other river types. For example, deeper water and in-stream cover are thought to be essential for juvenile trout (Heggenes et al., 1999; Milner, 1982), yet we found no association between water depth nor *Ranunculus* cover and higher trout densities. Large substrates act as important velocity refuges (Cunjak, 1998) and increase habitat heterogeneity (Venter et al., 2008). Lowland rivers, however, lack coarse substrate, and sediment is generally finer than in other river systems (Armstrong et al., 2003). In the absence of coarse substrate, the ability of *Ranunculus* beds to slow water through hydraulic drag within the plant stands (Franklin et al., 2008) might enhance velocity heterogeneity in lowland rivers and therefore indirectly influence trout densities. Neither salmon nor trout densities were influenced by fast water velocities in this study, in contrast to suggestions that juvenile salmon prefer faster flowing water, and juvenile trout prefer slower flowing water (McCormick & Harrison, 2011; Riley et al., 2006). The lack of influence of these measures of water velocity and depth on either species suggests opportunistic habitat use based on availability, which might occur more readily in rivers with fewer multi-cohort assemblages (Gibson, 1993; Maki-Petays et al., 1997).

Macroinvertebrate prey abundance was not important in describing observed densities of either fish species. Riley et al. (2009) suggested that habitat that offers refuge might be more imperative than prey resource, as densities of juvenile salmon and trout in their study were associated with increases in aquatic and marginal vegetation, rather than increases in macroinvertebrate biomass. Alternatively, the measure of macroinvertebrate prey availability used in this study might have differed from measures used in other studies, perhaps because benthic sampling under-represented prey accessible to drift-feeding salmonids (McCormick & Harrison, 2011). Although not directly quantified in this study, competitors and predators could also influence the density of juvenile salmonids. While some studies report that competition between salmon and trout alters habitat use of juvenile salmonids (Bardonnnet & Bagliniere, 2000), others suggest these species have different niches (Davidson, Letcher, & Nislow, 2010). Density-dependent effects on juvenile salmonids are thought to be most influential within the first three months post-redd emergence, as juveniles establish feeding territories (Pender & Kwak, 2002). However, this study was performed approximately five to six months postemergence, thus after an earlier phase of intraspecific competition. This study also assumed that summer habitat associated with higher densities of juvenile salmonids allows for predator avoidance. If predation caused high mortality at a particular site, there would be lower juvenile densities present and the findings from that site would indicate habitat unsuitable to support high juvenile density.

In conclusion, this study (i) describes summer habitat characteristics that promote high densities of juvenile salmon and trout in a lowland river, (ii) highlights how juvenile salmonid density-habitat relationships might be dynamic associations dependent on context and (iii) demonstrates the potential of previously unexplored habitat characteristics, velocity heterogeneity and salmon redds, to better describe juvenile salmonid densities. Both an unexpected recruitment crash during this study and the importance of proximity to redds further demonstrate the need to consider the influence of recruitment to habitat patches when exploring species-habitat associations, to avoid misrepresenting the importance of habitat characteristics. Most importantly, this finding, together with the strong influence of distance upstream, stresses the importance of the spatial configuration of habitats for different life stages. This conclusion is pertinent to the conservation of the fish populations studied here, and more widely. Whether acting directly or indirectly to influence their densities, *Ranunculus* appears to be a key habitat characteristic for juvenile salmonids in low-energy, lowland rivers where macrophytes play a pivotal role in structuring aquatic habitats. This finding has possible implications for management of both riparian and aquatic vegetation. Restoration of riparian vegetation might mitigate against rising temperatures and create a buffer to protect the river from agricultural runoffs and nutrient enrichment, but dense canopy cover tends to reduce macrophyte growth (McCormick & Harrison, 2011; Riley et al., 2009). Macrophyte cutting in lowland rivers is undertaken to promote suitable recreational fisheries and prevent flooding of adjacent farmland, but these practices can disrupt macrophyte communities and potentially negatively influence densities of juvenile salmon. We suggest that land managers consider maintaining a heterogeneous river ecosystem, and avoid full canopy closure or excessive macrophyte cutting, particularly in areas downstream of habitual salmonid spawning sites. Further study to ascertain the mechanisms driving the observed relationships between *Ranunculus* and densities of juvenile salmonids would aid our understanding of its potential as a conservation tool for lowland salmonid populations.

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AUTHOR CONTRIBUTIONS

RL and IJ conceived the study and designed the investigation with input from all authors. JM, RL, SG, WB and LS collected data in the field, and JM performed the laboratory work. JM led the analysis and writing of the paper with contributions from all authors.

DATA AVAILABILITY STATEMENT

The data are available upon reasonable request from the corresponding author.

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SUPPORTING INFORMATION

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

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Supporting Tables

Study sites

Table S1. Sites sampled in 2015 ($n = 18$), 2016 ($n = 19$), and 2017 ($n = 22$). Sites are ordered in ascending distance from the tidal limit.

Site	Length (m)			Average width (m)			Average Ranunculus cover (%)			Missing data
	2015	2016	2017	2015	2016	2017	2015	2016	2017	
1	100	100	100	14.8	16.5	19.8	7	10	51	
2	NA	91	91	NA	10.6	11.7	NA	58	71	
3	100	100	100	17.1	15.6	20.0	4	32	42	
4	60	60	60	14.0	12.5	14.1	0	2	6	2015: No macroinvertebrate data
5	NA	60	60	NA	7.1	7.6	NA	1	20	
6	NA	90	85	NA	8.8	7.5	NA	32	16	
7	60	60	60	11.6	9.6	11.5	39	15	10	2015: No macroinvertebrate data
8	100	NA	100	8.3	NA	8.3	49	NA	65	
9	114	114	85	7.5	14.6	11.4	7	12	23	
10	100	100	100	5.7	7.3	7.2	19	33	50	
11	100	100	100	12.0	12.2	12.7	17	18	61	
12	74	74	55	9.2	11.3	10.5	6	27	59	
13	50	50	50	5.5	5.6	5.6	34	8	23	
14	100	100	100	14.5	14.5	14.2	8	4	8	
15	100	NA	100	8.8	NA	9.9	36	NA	62	
16	100	100	100	10.7	11.3	11.8	41	77	67	
17	95	95	95	11.3	10.9	12.0	9	55	54	
18	110	110	110	5.6	5.4	5.1	5	31	10	
19	NA	90	90	NA	10.2	10.3	NA	25	12	
20	90	NA	90	7.8	NA	7.9	2	NA	7	
21	80	80	75	11.7	10.0	10.2	21	11	17	2016: No macroinvertebrate data
22	85	85	85	8.0	8.1	8.8	38	50	52	

Frequency of occurrence of macroinvertebrate prey taxa

Table S2a. Frequency of occurrence of prey taxa found in at least 25% of salmon parr gut samples (n = 204)

Prey species in salmon gut contents	Frequency of occurrence (%)
<i>Baetis</i> sp.	86.7
Simuliidae	86.7
Chironomidae	67.6
<i>Serratella ignita</i>	51.6

Table S2b. Frequency of occurrence of prey taxa found in at least 25% of trout gut samples (n = 94)

Prey species in trout gut contents	Frequency of occurrence (%)
<i>Baetis</i> sp.	85.3
Simuliidae	81.4
Chironomidae	68.6
<i>Serratella ignita</i>	50.0
<i>Gammarus pulex</i> group	33.3
<i>Hydropsyche</i> sp.	31.4
<i>Hydroptila</i> sp.	28.4

Macroinvertebrate abundances

Table S3. Abundance of macroinvertebrates in kick samples per site (1 – 22) and year (2015 – 2017): total macroinvertebrate abundance; abundance of frequently consumed prey (FCP) for salmon and trout, and percentage contribution of FCP taxa to total abundance.

Site	2015						2016						2017					
	Total Abundance	FCP Abundance		% contribution of FCP to Total Abundance		Total Abundance	FCP Abundance		% contribution of FCP to Total Abundance		Total Abundance	FCP Abundance		% contribution of FCP to Total Abundance		Total Abundance	FCP Abundance	
		Salmon	Trout	Salmon	Trout		Salmon	Trout	Salmon	Trout		Salmon	Trout	Salmon	Trout		Salmon	Trout
1	7201	3614	4100	50.1	56.9	2481	1428	1553	57.6	62.6	3364	2335	2391	69.4	71.1			
2	NA	NA	NA	NA	NA	2014	1297	1371	64.4	68.1	3299	2351	2380	71.3	72.1			
3	7322	5224	5306	71.3	72.5	2472	1656	1707	67.0	69.1	199	21	25	10.6	12.6			
4	NA	NA	NA	NA	NA	1695	1072	1109	63.2	65.4	4026	2198	2322	54.6	57.7			
5	NA	NA	NA	NA	NA	1872	821	1007	43.9	53.8	2435	1229	1376	50.5	56.5			
6	NA	NA	NA	NA	NA	3315	2303	2379	69.5	71.8	4495	2399	2549	53.4	56.7			
7	NA	NA	NA	NA	NA	3215	1722	1823	53.6	56.7	7125	3854	4350	54.1	61.1			
8	6366	2274	2607	35.7	41.0	NA	NA	NA	NA	NA	4226	2934	3021	69.4	71.5			
9	4776	2085	2311	43.7	48.4	4325	2990	3115	69.1	72.0	4033	1684	2401	41.8	59.5			
10	915	111	168	12.1	18.3	4565	3279	3464	71.8	75.9	5688	3135	3705	55.1	65.1			
11	4162	2582	2757	62.0	66.2	2644	1825	1863	69.0	70.5	4367	3337	3450	76.4	79.0			
12	7571	4292	4376	56.7	57.8	2209	1157	1224	52.4	55.4	2333	1727	1793	74.0	76.9			
13	3219	1837	1976	57.1	61.4	4804	3265	3482	68.0	72.5	7540	5140	5850	68.2	77.6			
14	5783	4823	4885	83.4	84.5	4294	2931	3013	68.3	70.2	2505	1783	1948	71.2	77.8			
15	2451	816	940	33.3	38.4	NA	NA	NA	NA	NA	584	292	320	50.0	54.8			
16	3714	2202	2278	59.3	61.3	3116	2261	2339	72.6	75.1	5495	4553	4695	82.9	85.4			
17	4404	3387	3433	76.9	78.0	2473	1066	1102	43.1	44.6	4132	2634	2718	63.7	65.8			
18	4142	2337	2362	56.4	57.0	4716	2518	2589	53.4	54.9	2306	1079	1138	46.8	49.3			
19	NA	NA	NA	NA	NA	3036	2109	2201	69.5	72.5	6557	3762	3933	57.4	60.0			
20	5531	3295	3386	59.6	61.2	NA	NA	NA	NA	NA	2139	1027	1147	48.0	53.6			
21	5595	3868	4056	69.1	72.5	NA	NA	NA	NA	NA	8255	5909	6316	71.6	76.5			
22	1802	990	1082	54.9	60.0	3244	2664	2737	82.1	84.4	596	292	316	49.0	53.0			

Statistical testing for differences in explanatory variables between years

Table S4. Linear models were used to test for differences in the explanatory variables between years. We report the p -values to show statistical significance.

Variable	Comparison years		
	2015:2016	2015:2017	2016:2017
<i>Ranunculus</i> cover	0.31	0.02*	0.17
Depth	0.45	0.11	0.40
Velocity heterogeneity	0.68	0.51	0.81
Fast velocities	0.35	0.83	0.43
Distance from tidal limit	0.27	0.48	0.63
Salmon prey abundance	0.12	0.50	0.32
Trout prey abundance	0.72	0.72	0.24
Salmon redds	-	0.18	-

Candidate model selection process for 3-year analysis

Table S5. Full candidate model selection process for 3-year analysis. AIC statistics are supplied for initial Stage 1 to determine which variables should be retained for further analyses.

Stages of model development	Hypothesis tested	Candidate models		Salmon		Trout	
		Model no.	Model Terms	AICc	$\Delta AICc$	AICc	$\Delta AICc$
Stage 1: Identify most important ($\Delta AICc > 1$) and least important ($\Delta AICc < 1$) variable/s for both species.	Global model	Global	Year, Ranunc, Depth, FastVelocity, VelocityHet, Abundance, Distance	-140.4	2.79	-268.6	2.46
	Distance is not important	1	Year, Ranunc, Depth, FastVelocity, VelocityHet, Abundance	-138.9	4.28	-267.7	3.28
	Prey abundance is not important	2	Year, Ranunc, Depth, FastVelocity, VelocityHet, Distance	-141.5	1.74	-270.1	0.92
	Velocity heterogeneity is not important	3	Year, Ranunc, Depth, FastVelocity, Abundance, Distance	-143.2	0.00	-258.8	12.17
	Fast velocity is not important	4	Year, Ranunc, Depth, VelocityHet, Abundance, Distance	-143.1	0.06	-270.5	0.51
	Depth is not important	5	Year, Ranunc, FastVelocity, VelocityHet, Abundance, Distance	-142.3	0.88	-271.0	0.00
	Ranunculus is not important	6	Year, Depth, FastVelocity, VelocityHet, Abundance, Distance	-142.2	1.02	-269.7	1.30
	Year is not important	7	Ranunc, Depth, FastVelocity, VelocityHet, Abundance, Distance	-130.9	12.29	-258.4	12.65
Keep Year, Distance & Ranunc in all subsequent models as important for both species and omit Depth and Fast Velocity from all subsequent candidate models because not important for either species. Test combinations of remaining variables, i.e. Abundance and Velocity heterogeneity, which are considered to be important for one of the species.							

Stage 2: Test different combinations of most important variables	Velocity heterogeneity and abundance both important	6	Year, Ranunc, Distance, VelocityHet, Abundance
	Velocity heterogeneity not as important as abundance	7	Year, Ranunc, Distance, Abundance
	Abundance not as important as velocity heterogeneity	8	Year, Ranunc, Distance, VelocityHet
	Velocity heterogeneity and abundance not important	9	Year, Ranunc, Distance
Test all variables individually alongside Year to test for importance of Ranunculus vs other variables.			
Stage 3: Test all variables individually alongside Year to test for importance of Ranunculus vs other variables	Ranunculus most important	10	Year, Ranunc
	Depth most important	11	Year, Depth
	Fast velocity most important	12	Year, FastVelocity
	Distance most important	13	Year, Distance
	Prey abundance most important	14	Year, Abundance
	Velocity heterogeneity most important	15	Year, VelocityHet
If Ranunculus included in the best performing model, test model with quadratic effect & test without Year for all best performing model			
Stage 4: Post model selection test	e.g. Quadratic Ranunc performs better than linear	P1_s	e.g. Year, Ranunc ² , Distance

Candidate model selection process for 2-year analysis

Table S6. Full candidate model selection process for 3-year analysis. AIC statistics are supplied for initial Stage 1 to determine which variables should be retained for further analyses.

Stages of model development	Hypothesis tested	Candidate models		Salmon		Trout	
		Model no.	Model Terms	AICc	$\Delta AICc$	AICc	$\Delta AICc$
Stage 1: Identify most important ($\Delta AICc > 1$) and least important ($\Delta AICc < 1$) variable/s for both species	Global model	Global	Year, Ranunc, FastVelocity, VelocityHet, Abundance, Distance	-81.1	3.19	-173.9	2.37
	Distance is not important	1	Year, Ranunc, FastVelocity, VelocityHet, Abundance	-80.7	3.61	-173.5	2.78
	Prey abundance is not important	2	Year, Ranunc, FastVelocity, VelocityHet, Distance	-84.1	0.25	-174.3	1.95
	Velocity heterogeneity is not important	3	Year, Ranunc, FastVelocity, Abundance, Distance	-84.1	0.22	-167.9	8.32
	Fast velocity is not important	4	Year, Ranunc, VelocityHet, Abundance, Distance	-84.3	0.00	-175.0	1.25
	Year is not important	5	Ranunc, FastVelocity, VelocityHet, Abundance, Distance	-83.9	0.47	-176.2	0.00
	Ranunculus is not important	6	Year, FastVelocity, VelocityHet, Abundance, Distance	-80.6	3.74	-175.2	1.00
Keep Ranunc & Distance in all subsequent models as important for both species and omit Year from all subsequent candidate models because not important for either species. Test combinations of remaining variables, i.e. Abundance, Fast Velocity & Velocity heterogeneity, as variables are considered to be important for one of the species.							
Stage 2: Test different combinations of most important variables	Velocity heterogeneity and abundance most important	6	Ranunc, Distance, VelocityHet, Abundance				
	Fast velocity and abundance most important	7	Ranunc, Distance, FastVelocity, Abundance				
	Velocity heterogeneity and fast velocity most important	8	Ranunc, Distance, VelocityHet, FastVelocity				
	Velocity heterogeneity most important	9	Ranunc, Distance, VelocityHet				
	Abundance most important	10	Ranunc, Distance, Abundance				
	Fast velocity most important	11	Ranunc, Distance, FastVelocity				
	Distance most important	12	Ranunc, Distance				

Test all variables individually test for importance of Ranunculus vs other variables.			
Stage 3: Test all variables individually to test for importance of Ranunculus vs other variables	Ranunculus most important	13	Ranunc
	Fast velocity most important	14	FastVelocity
	Distance most important	15	Distance
	Prey abundance most important	16	Abundance
	Velocity heterogeneity most important	17	VelocityHet
If Ranunculus included in the top performing model, test quadratic effect of Ranunc			
Stage 4: Post model selection test	As above		

Supporting Figures

Salmon length histogram

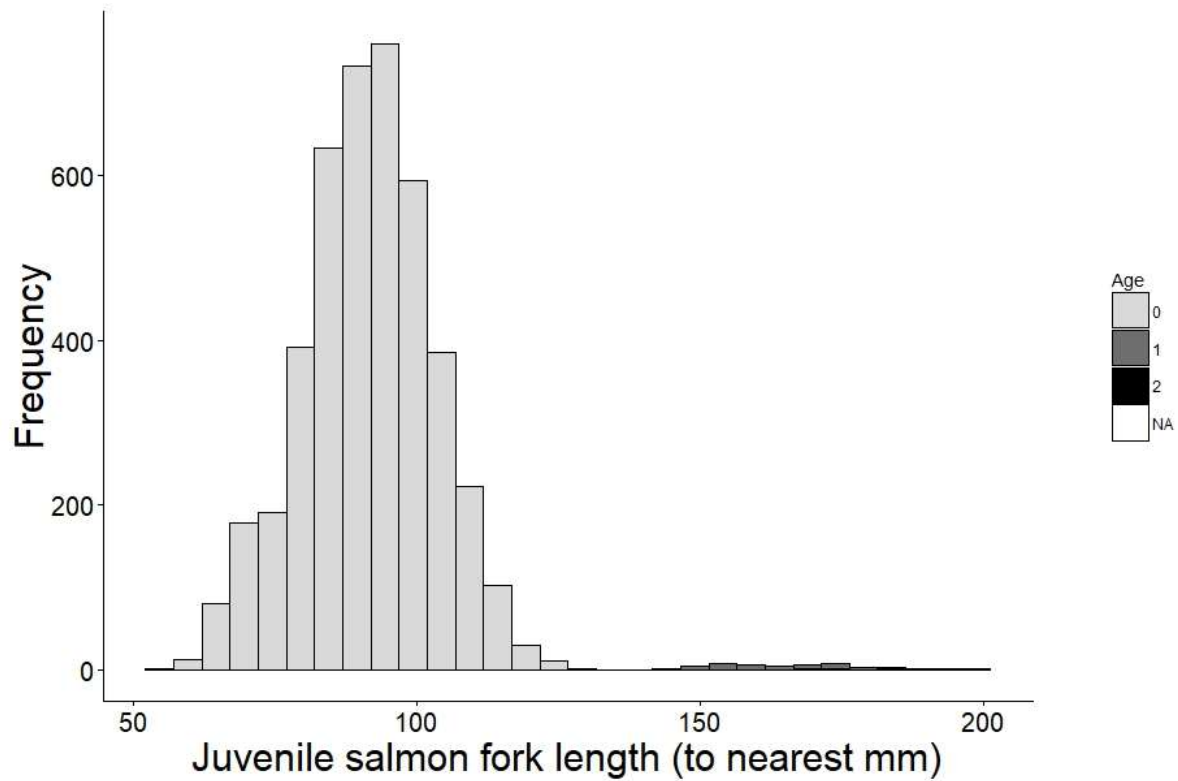


Figure S1. Fork length-frequency histogram for juvenile salmon. Maximum length of juvenile salmon (Age 0) is 129mm, classified by fork length and verified using scale samples. NA values represent older salmon of which age could not be verified using scale samples.

Trout length histogram

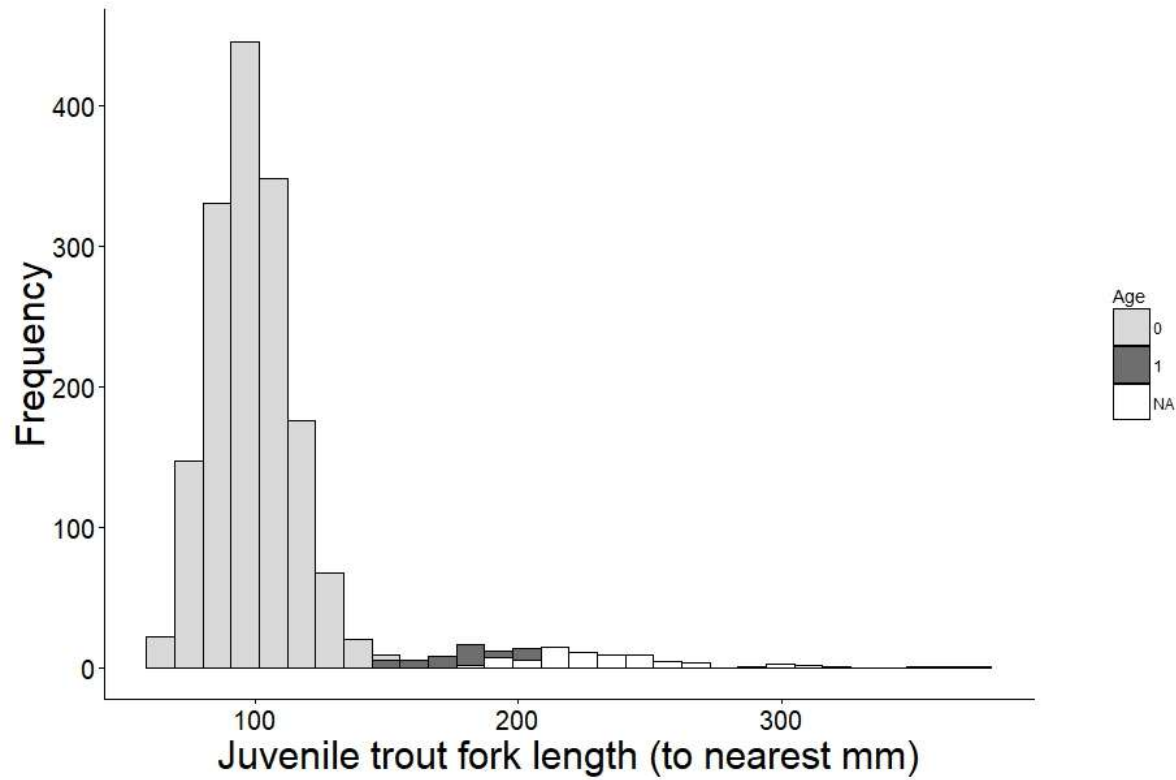


Figure S2. Fork length-frequency histogram for juvenile trout. Maximum length of juvenile trout (Age 0) is 150mm, classified by fork length and verified using scale samples. NA values represent older trout of which age could not be verified using scale samples.

Correlation matrices: Explanatory variables in 3-year and 2-year analyses

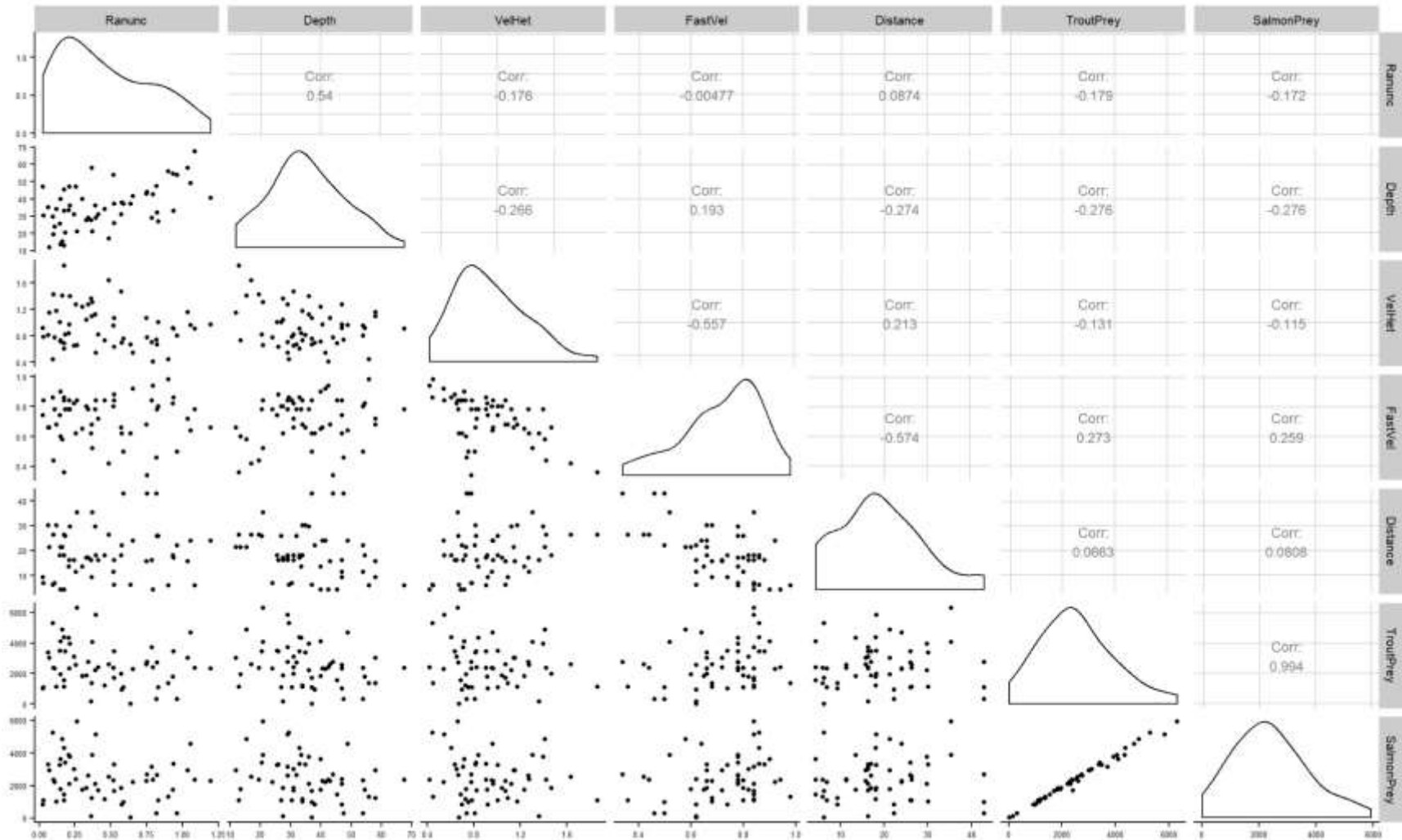


Figure S3. Pearson's pairwise correlation of all explanatory variables considered in the 3-year analysis; Ranunc = *Ranunculus* cover; Depth = water depth; VelHet = velocity heterogeneity; FastVel = proportion of fast velocities; Distance = distance from tidal limit; TroutPrey = Abundance of preferred prey of trout; SalmonPrey = Abundance of preferred prey of salmon.

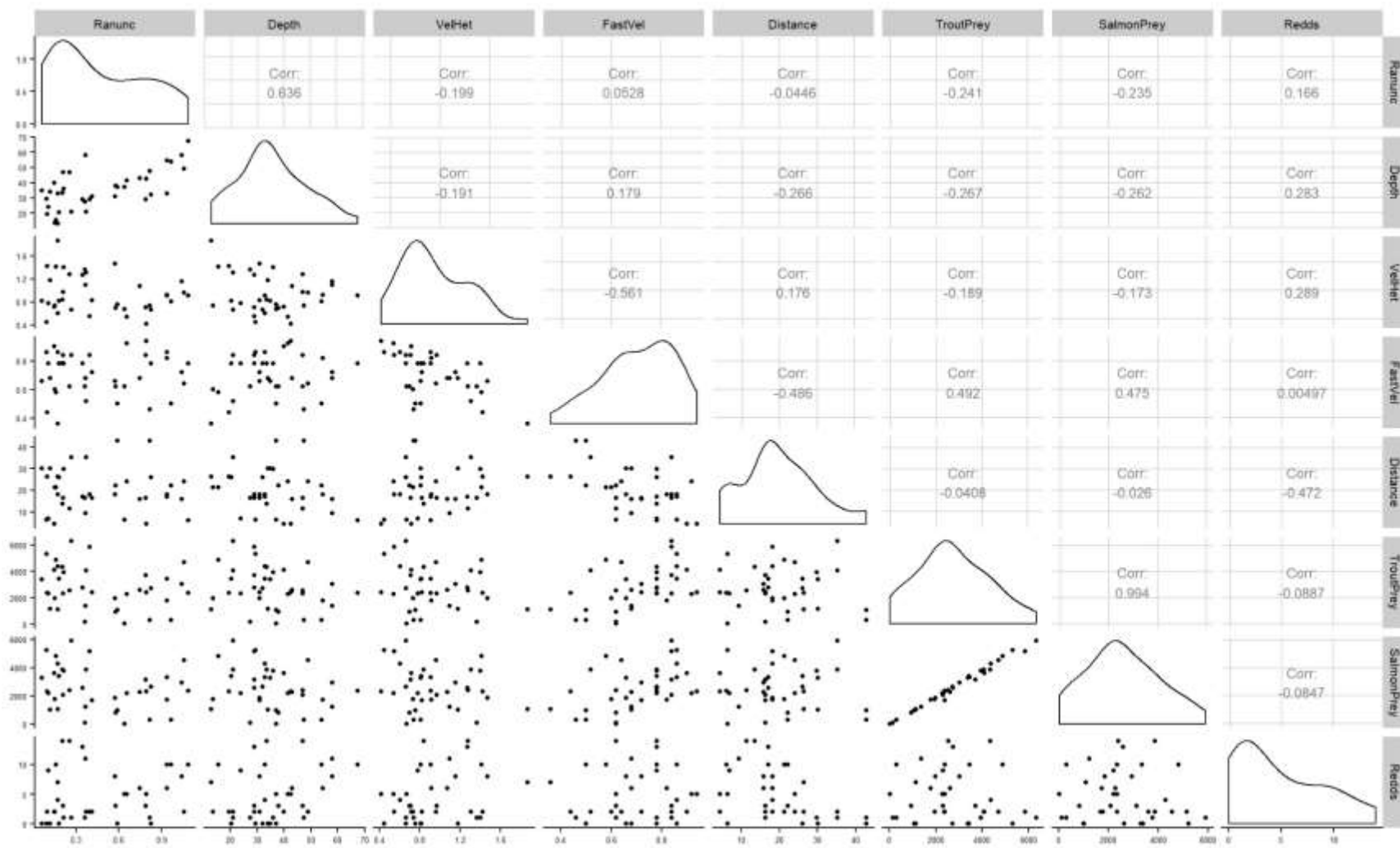
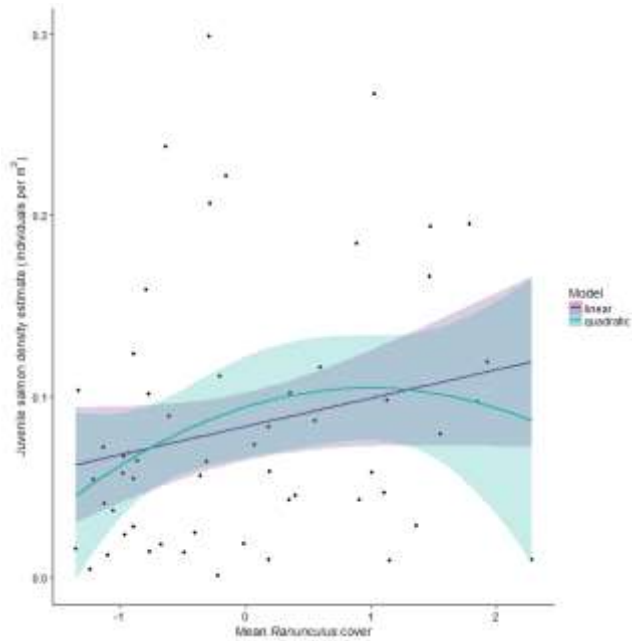


Figure S4 Pearson's pairwise correlation of all explanatory variables considered in the 2-year analysis and 2-year salmon redd analysis; Ranunc = Ranunculus cover; Depth = Water depth; VelHet = Velocity Heterogeneity; FastVel = Proportion of fast velocities; Distance = distance from tidal limit; TroutPrey = Abundance of preferred prey of trout; SalmonPrey = Abundance of preferred prey of salmon; Redds = Number of nearby upstream redds (only in 2-year salmon redd analysis).

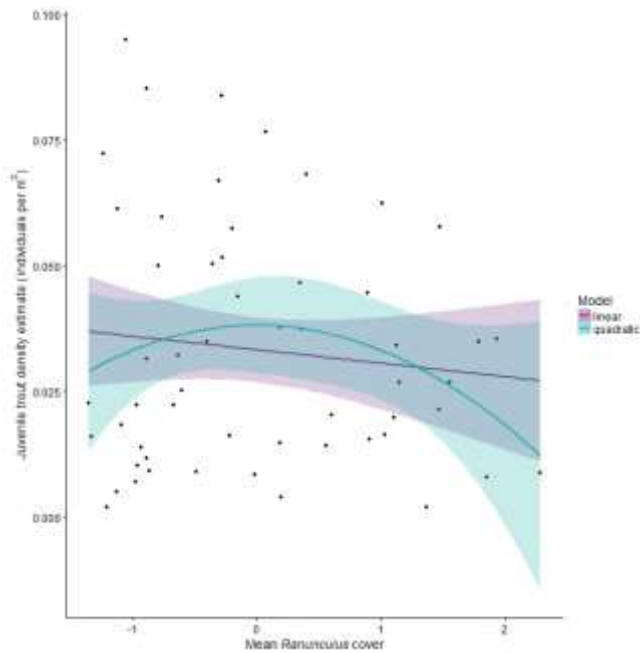
Pre-test of linear and quadratic *Ranunculus* terms

a)



(Salmon: Linear model $\Delta AICc = 0.00$. Quadratic model - $\Delta AICc = 1.21$)

b)



(Trout: Linear model - $\Delta AICc = 0.00$. Quadratic model - $\Delta AICc = 0.29$)

Figure S5. Scatter plots of a) salmon, and b) trout density as a function of *Ranunculus* cover. Lines are fitted linear regression (purple) and quadratic regression (green) predictions.

“Best” salmon and trout model diagnostics

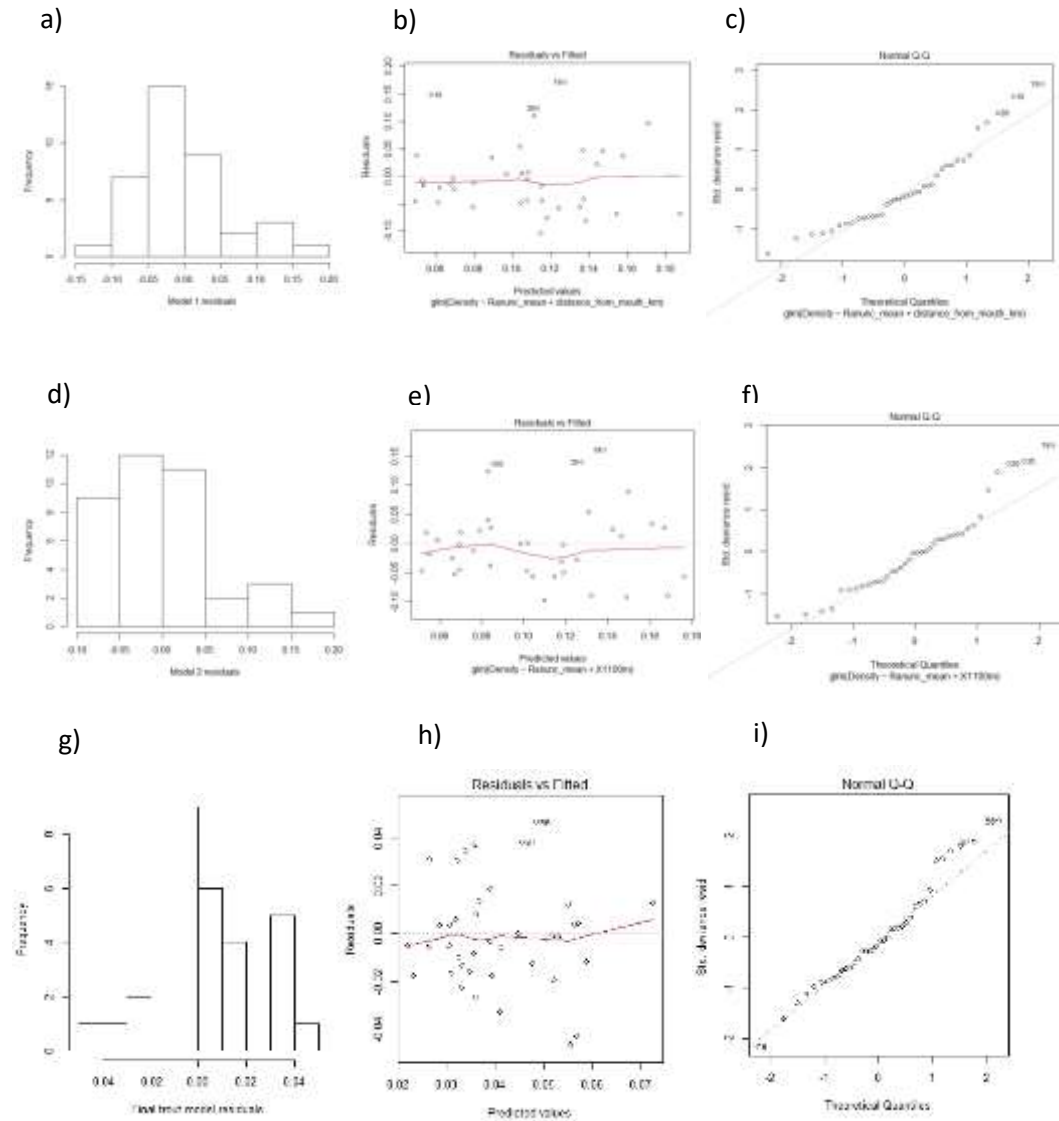


Figure S6. Model diagnostic plots for the best performing 2-year salmon and trout models: (a-c) salmon 2-year redd model (Model 1), (d-f) salmon 2-year redd model (Model 2), (g-i) trout 2-year model (Model 18).