# Direct and indirect influences of macrophyte cover on abundance and growth of juvenile Atlantic salmon

Jessica E. Marsh[1,2,†*], J. Iwan Jones[1], Rasmus B. Lauridsen[2], James B Grace[3], Pavel Kratina[1]

[1]*School of Biological and Behavioural Sciences, Queen Mary University of London, Mile End Road, London, UK*

[2]*Salmon and Trout Research Centre, Game & Wildlife Conservation Trust, The River Laboratory, Wareham, UK*

[3]*U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, USA*

†Corresponding author: email jessicaelizabethmarsh@gmail.com

telephone: +44 (0) 7341 940988

List of ORCIDs:

JEM: 0000-0003-1154-4444; JBG: 0000-0001-6374-4726; PK: 0000-0002-9144-7937

**Keywords**: chalk stream, habitat heterogeneity, *Ranunculus*, path analysis, *Salmo salar*

**Running head:** Macrophytes indirectly influence salmon parr

* Present addresses: Centre for Environment, Fisheries and Aquaculture Science, Barrack Road, Weymouth DT4 8UB, UK; Department of Life and Environmental Sciences, Bournemouth University, BH15 5BB, UK.

## Abstract

1. The relationships between macrophytes and the physical and biological characteristics of the environments that aquatic organisms inhabit are complex. Previous studies have shown that the macrophytes, *Ranunculus* (subgenus *Batrachium*), which are dominant in lowland chalk streams and widespread across Europe, can enhance juvenile Atlantic salmon abundance and growth to a greater degree than other physical and biological habitat characteristics. However, mechanistic understanding of how this effect might arise requires consideration of the direct and indirect relationships among habitat characteristics that are likely to be influenced by the presence of macrophyte cover.
2. We applied structural equation modelling to data collected during a two-year in-river manipulative experiment in the river Frome (southern England, UK) designed to quantify the magnitude and the relative importance of direct and indirect influences of *Ranunculus* cover and other physical and biological variables, including water velocity, water depth, prey biomass and body size, and abundance of con- and hetero-specifics, on abundance and somatic growth of 0+ salmon.
3. Results indicated a strongly positive direct influence of *Ranunculus* cover on salmon abundance, as well as positive influences of *Ranunculus* on velocity heterogeneity and water depth that are indirectly related to decreased salmon abundance. Interestingly, there was no indication of a direct influence of *Ranunculus* cover on salmon growth, although *Ranunculus* was indirectly related to increased salmon growth through its positive influence on prey biomass, an effect mediated by velocity heterogeneity and proportion of fast velocities.

4. These findings provide novel mechanistic insights into the key role of *Ranunculus* in their native lowland rivers to enhance abundance and improve conditions for multiple food web components. Strategies to maintain or enhance naturally occurring *Ranunculus* in these rivers are therefore likely to return wide ranging ecosystem benefits, including for species of high conservation value, such as salmon. These mechanistic impacts on habitat heterogeneity and ecosystem productivity could generalise to native macrophytes in other river systems, particularly where habitat is dominated by vegetation in the absence of large substrates.

## 1. Introduction

Terrestrial and aquatic vegetation form key ecosystem structures that provide resources, shelter and physical conditions that benefit a variety of species and functional groups (Tews *et al.,* 2004; Teixeira de Mello *et al.,* 2015; Wilkinson *et al.,* 2021). Density and morphology of plants often underly habitat heterogeneity (Diehl & Kornijow, 1998; Tews *et al.,* 2004; Warfe & Barmuta, 2004), which is essential for resilient, abundant and diverse animal communities (Kovalenko, Thomaz & Warfe, 2012; Teixeira de Mello *et al.,* 2015). Macrophytes are considered to be such foundation species that strongly structure freshwater ecosystems (Scheffer *et al.,* 2015; Lürig, *et al.,* 2021) and their impacts on trophic interactions (e.g. Dionne & Folt, 1991; Warfe & Barmuta, 2004), water velocities and sediment retention (e.g. Wharton *et al.,* 2006) have been well studied. However, previous research has primarily focused on direct responses of animal abundances to macrophyte structures, with less consideration for how the habitat heterogeneity created by macrophytes modulates animal responses (Kovalenko, Thomaz & Warfe, 2012).

In lowland rivers, which are typically more stable and less dynamic than upland river systems (Berrie, 1992), macrophytes are particularly important for juvenile salmonids as they provide a key source of habitat heterogeneity in the absence of other large substrate structures (Berrie, 1992; Riley *et al.,* 2009). While not studied as extensively as other habitat characteristics, positive interactions between juvenile salmonids and macrophytes in lowland rivers have been demonstrated across a wide geographical scale, including southern England (e.g. Riley *et* al., 2009; Marsh *et al.,* 2021a), south-west Ireland (McCormick & Harrison, 2011), northern Finland (Maki-Petays *et al.* 2011), and north-eastern United States (Beland *et al.*

2004) and are unlikely to be limited to these areas. Atlantic salmon (*Salmo salar*, hereafter salmon) reach greater abundances and faster growth rates in habitats with high cover of the dominant lowland macrophytes known as water crowfoot, *Ranunculus* spp. (Marsh *et al*., 2020a, 2021a), although the mechanisms underlying these relationships remain unclear. Cover is important for juvenile salmon (Armstrong *et al.,* 2003; Marsh *et al.,* 2020a, 2021a), and so the vertical structure of *Ranunculus*, coupled with the floating canopy on the water surface, offers direct protection from both aerial and aquatic predators (Johnsson, Rydeborg & Sundstrom, 2004; Diehl & Kornijow, 1998), harsh environmental conditions (Gries & Juanes, 1998), and potential competitors (Venter *et al.,* 2008).

In addition to the direct influence of macrophytes as shelter, the impacts of macrophyte cover on individual salmon and populations might be mediated by physical habitat characteristics, inter- and intra-specific competition, and resource quality and quantity. The structural complexity of submerged macrophytes, particularly those with dense canopies such as *Ranunculus* (Cotton *et al.,* 2006), dramatically increases the resistance to water flow. This provides refuges of low water velocity and increased water depths, the latter of which might be avoided by juvenile salmon due to increased presence of predators and larger conspecifics (Gibson, 1993; Wharton *et al.,* 2006, Marsh *et al.,* 2020a). As water velocities slow within the plant stands, water flow is accelerated around the plant beds, forming adjacent areas of fast velocities (Wharton *et al.,* 2006). This results in heterogeneous water velocities, a desirable habitat characteristic for juvenile salmonids to exploit for energy-efficient foraging opportunities, with low velocity refuges alongside fast water velocities providing increased supply of drifting prey, which might otherwise be energetically demanding environments to forage in (Wankowski & Thorpe, 1979; Morantz *et al.,* 1987).

Heterogeneity in water velocities and depths can promote more abundant and diverse macroinvertebrate communities, which juvenile salmon feed upon (Keeley & Grant, 1997;

100 Riley *et al.,* 2009). The reduced water velocities within plant stands result in increased
101 retention of fine sediment and organic material (Gregg and Rose 1982; Cotton *et al.,* 2006),
102 providing food for macroinvertebrate communities dominated by larger individuals. The
103 complexity provided by plant stands can also offer macroinvertebrates protection from
104 predators (Dionne & Folt, 1991) and thus, enables the coexistence of larger prey individuals
105 and their fish predators. Consequently, *Ranunculus* communities are often associated with
106 productive and abundant macroinvertebrate communities (Armitage & Cannan, 2000; Riley
107 *et al.,* 2009).

108 Teasing apart the direct and indirect influences of these habitat components to inform
109 fisheries management is challenging due to the interdependence among habitat factors
110 (Armstrong *et al.,* 2003), however, detailed understanding of the complex relationships
111 between *Ranunculus* and juvenile salmon populations is essential if we are to apply effective
112 management strategies. Populations of Atlantic salmon have suffered unprecedented declines
113 in the last few decades (ICES, 2021). Natural recovery of salmon populations is hindered by
114 a decline in both the numbers of juvenile salmon migrating to sea, and, in some regions, the
115 condition of the individuals prior to migrating. Recent works have quantified the relationship
116 between size of salmon pre-migration and the likelihood of individuals returning to
117 freshwater to reproduce (Armstrong *et al.,* 2018; Gregory *et al.,* 2019). Individual body
118 condition is strongly influenced by habitat conditions experienced during the first summer for
119 juvenile salmonids (Zabel & Achord, 2004), prompting calls for a better understanding of the
120 habitat conditions that maximise numbers and quality of juveniles (Armstrong *et al.,* 2018;
121 Gregory *et al.,* 2019). Macrophytes, such as *Ranunculus,* have also suffered population
122 crashes in lowland rivers within the last three decades, likely as a consequence of
123 anthropogenic impacts including flow modifications and increased agricultural inputs
124 (Cranston, 2004; Cotton *et al.,* 2006). There is, therefore, an urgency to understanding the

role of *Ranunculus* in promoting healthy juvenile salmon populations, to improve ecosystem management benefiting salmon and anticipate the implications of macrophyte declines on salmon productivity.

Here, we analysed detailed data from an in-field *Ranunculus* manipulation experiment designed to quantify ecological mechanisms governing the previously observed positive impact of *Ranunculus* cover on salmon abundances and somatic growth (Figure 1, Marsh *et al.,* 2021a). We aimed to determine whether these relationships represent direct influences through a source of cover, or indirect via influences on the wider ecosystem dynamics through impacts on physical habitat, food resources and/or competition. We hypothesised that abundant *Ranunculus* positively influences heterogenous physical habitat characteristcs (increased water depth and velocity heterogeneity), the amount of basal resources and prey (organic material and macroinvertebrate prey biomass and body size), but also increases the potential for intra- and inter-specific competition via increased abundance of juvenile salmon and brown trout (*Salmo trutta*) respectively (Figure 2). We subsequently postulated indirect influences of *Ranunculus* on salmon abundance through a positive influence of velocity heterogeneity, fast velocities and prey biomass, and a negative influence of increased water depths (and associated higher predation risk) on salmon abundance (Figure 2a). We also hypothesised indirect influences of *Ranunculus* on salmon growth through a positive influence of velocity heterogeneity and prey biomass and body size, as well as a negative influence of fast velocities (and associated reduced foraging efficiency) and higher abundances of salmon and trout competitors (Figure 2b).

## 2. Methods

### Experimental design

149 The in-field *Ranunculus* manipulation experiment took place over two years (2016-2017) on
150 the North Stream, an anabranch of the river Frome, a lowland river situated in Dorset, UK
151 (Figure 3). Three blocks, approximately 100 m in length, were selected on the North Stream
152 in locations with similar physical habitat, existing *Ranunculus* beds and no riparian canopy.
153 At each block, three sites, 20 m in length, were designated and each assigned a different
154 *Ranunculus* treatment, which was achieved by digging out and replanting *Ranunculus* plants
155 between sites. To simulate the natural mosaic of *Ranunculus* beds, we replanted plants in
156 random patches within the site.Following manipulation of the existing *Ranunculus* plant
157 cover in spring (March/April) of each year, the treatments of low (<10%), medium (30-40%)
158 and high (>60%) cover were maintained throughout the year, producing a gradient of
159 *Ranunculus* cover until the plants began natural senescence in autumn (see Marsh et al.,
160 2021a for full details of the manipulation procedure). On four sample occasions between June
161 and October of each year, juvenile salmonid populations, aquatic macroinvertebrates and
162 basal resources were sampled, and *Ranunculus* cover, water velocity and depths were
163 quantified. Previous findings from this experiment showed that both salmon abundance and
164 growth were enhanced by *Ranunculus* during summer months (Marsh *et al.,* 2021a, Figure 1).
165 We used these data to investigate potential direct or indirect effects of *Ranunculus* cover on
166 juvenile salmon (Figure 2).

167 Salmon abundance and growth

168 Juvenile salmon (0+ or young-of-the-year) abundance and biometric data were collected
169 between June and October of each year at each of the nine sites (see Marsh et al., 2021a for
170 full fish sampling procedure). We repeatedly electrofished each site in a upstream direction,
171 capturing and removing all juvenile salmonids encountered, until two consecutive fishing
172 passes yielded zero salmonid captures. We set stop nets at the downstream and upstream site
173 limits to maximise capture efficiency. Captured individuals were sedated, identified to

174 species, weighed (to nearest 0.2 g), and marked with a Passive Integrated Transponder (PIT)
175 tag (12.5 mm length, 2.12 mm diameter, Biomark, Idaho, USA), which was inserted into the
176 body cavity, and the adipose fin clipped to indicate a tagged individual. Growth of individual
177 salmon was calculated using change in the weight (g) measurements of tagged individuals
178 that were recaptured in the same site, with the assumption that the individuals had been
179 exposed to the site-specific *Ranunculus* cover for the duration of the growing period
180 measured.

181 Physical habitat variables

182 Physical habitat variables were recorded at 25 evenly spaced quadrats (0.5 x 0.5 m) per site,
183 on each sample occasion. *Ranunculus* cover was estimated as the percentage quadrat cover,
184 water depth was measured (cm), and water surface velocity was estimated visually as one of
185 five categories [1 = 0-25 cm $s^{-1}$; 2 = 25-50 cm $s^{-1}$; 3 = 50-75 cm $s^{-1}$; 4 = 75-100 cm $s^{-1}$; 5
186 >100 cm $s^{-1}$]. We calculated the site-level proportion of fast velocities as the proportion of
187 velocity categories 3, 4 and 5 recorded in quadrats at a site. Measures of *Ranunculus* cover,
188 water depth and proportion of fast velocities were averaged to create a site-level measure of
189 each variable. The steepness in velocity gradients between a quadrat and its neighbouring
190 quadrats was calculated using the Terrain Ruggedness Index (TRI, see Marsh et al., 2020a for
191 details). Absolute values of TRI were averaged to represent site-level velocity heterogeneity.

192 Prey and basal resources

193 To determine biomass and size of macroinvertebrate prey, and the resources potentially used
194 by the prey (basal resources), we sampled the benthos at three randomly selected locations
195 per site, on each sample occasion. Using a Surber sample (0.25 m x 0.25 m, mesh aperture
196 250 µm), we disturbed the substrate by hand for 30 seconds to collect macroinvertebrates and
197 organic material. Samples were preserved in 70 % ethanol solution for sorting, identification
198 and measuring individual macroinvertebrates, and processing of the organic material. All

199 macroinvertebrate specimens were identified to the lowest practical taxonomic level (usually
200 species), counted and measured. We used macroinvertebrate measurements to estimate
201 biomass of each taxon (Table S1) and multiplied the mean biomass by the abundance of each
202 taxon to generate a measure of prey biomass. We summed the biomass of each taxon and
203 calculated the average biomass of measured individuals within each Surber sample to
204 produce measures of total prey biomass and mean prey size, respectively. After
205 macroinvertebrate specimens had been picked from the sample, the remaining organic
206 material was dried to constant mass (70°C, 72 h) and weighed, prior to being combusted
207 (550°C, 4 h) and re-weighed. The ash-free dry mass of organic material was calculated by
208 subtracting the combusted weight from the dried weight, producing a measure of basal
209 resources. Measures of total prey biomass, mean prey size, and basal resources were averaged
210 across the three Surber samples to create a site-level variable of each.

211 Using data from the summer months in which *Ranunculus* had a positive relationship with
212 both salmon abundance and growth, led to the use of August and September data to
213 investigate salmon abundance ($n$ = 36, i.e., abundance measures in three sites in each of the
214 three blocks at two months for two years, treated as independent data points), and June and
215 August data to investigate salmon growth ($n$ = 71). Explanatory variables used in the growth
216 analysis were averaged across June and August to represent average conditions during the
217 growth period.

218 Data analyses

219 To investigate whether and how the effects of *Ranunculus* cover on salmon abundance and
220 growth were mediated by changes in the physical habitat, prey resources and/or competition,
221 we applied confirmatory path analysis (Grace, 2006) in a piecewise structural equation
222 modelling (SEM) framework (Lefcheck, 2016). SEM is a quantitative framework able to

223 quantify and partition the relative direct and indirect conditional associations of key habitat
224 characteristics on natural populations (Grace, 2006). This approach has been commonly
225 applied to investigating complex theory-supported hypotheses about ecosystems and
226 ecological scenarios. Piecewise SEM fits multiple component sub-models within a global
227 model to allow for testing of direct and indirect effects within a single causal network
228 (Shipley, 2009; Lefcheck, 2016). The component models are solved separately and are
229 therefore appropriate for conventional requirements of generalised mixed models (Shipley,
230 2000; Shipley, 2009). We constructed the global path model for each main response variable
231 (abundance and growth) based on previously determined relationships (Marsh et al., 2021a),
232 and other hypothesised drivers of salmon abundance and growth (Table 1).

233 Firstly, we tested whether the observed positive influence of *Ranunculus* cover on salmon
234 abundance was best represented as a direct effect of cover, or an indirect effect operating
235 through changes to the physical environment and prey resources associated with *Ranunculus*
236 cover (Figure 2a). The path model consisted of a set of linear regressions (identity-link
237 function), describing the variation in variables representing physical environment or prey
238 sources, and a negative binomial regression (log-link function), describing the variation in
239 salmon abundance. A negative binomial distribution was used to account for potential
240 overdispersion in the abundance data with log site area ($m^2$) included in the model as an
241 offset to account for variation in abundance that might be due to differences in habitat size
242 (O'Hara & Kotze, 2010). Model residuals were inspected to ensure assumptions of
243 homogeneity, normality and independence were not violated.

244 Secondly, we investigated whether the observed positive effect of *Ranunculus* cover on
245 salmon growth in weight was best represented as a direct effect of cover, or an indirect effect
246 operating through changes to the physical environment, prey resources and/or abundance of
247 competitors (Figure 2b). This path model consisted of a set of linear and negative binomial

248 regressions to describe physical habitat, prey resource and salmonid abundance variables as
249 described above, and a linear mixed effect model (identity link function) to describe variation
250 in salmon growth in weight. The growth model included an offset term of log initial weight to
251 account for the influence of initial weight on growth potential and a random intercept of site
252 to account for multiple measures (individuals) at each site.

253 Path models for both salmon abundance and growth were fitted and model performance was
254 evaluated using R package piecewiseSEM (Lefcheck et al., 2018), which applies Shipley's
255 (2000) directed-separation test to determine if all variables are conditionally independent and
256 identify any important missing links in the path model. Any missing links that were indicated
257 by the analyses and ecologically justifiable were incorporated into the model. Non-significant
258 links were dropped to ensure they did not have an undue influence on the remaining paths in
259 the system before refitting the model (Tables S2 – 3 outline the specific process of removal
260 and addition of links). The goodness-of-fit of models fitted to individual response variables
261 were summarized using marginal $R^2$ (and conditional $R^2$ where random effects were
262 included), and overall SEM adequacy was evaluated with the approximately distributed Chi-
263 squared Fisher's C-statistic (Shipley, 2009). Prior to model fitting: (1) collinearity of
264 explanatory variables was assessed using Pearson's correlation, none of which were highly
265 correlated ($r \geq |0.7|$, Dormann *et al.,* 2013, Figures S1 –2); and (2) all numerical explanatory
266 variables were standardised prior to analyses by subtracting their mean and dividing by their
267 standard deviation. All statistical analyses were performed in R version 4.0.5 (R
268 Development Core Team, 2021), using R packages lmerTest (Kuznetsova, Brockhoff &
269 Christensen, 2017) and MASS (Venables & Ripley, 2002), in addition to those previously
270 mentioned.

271 We of course recognize that scientific inferences based on quantitative models, as applied in
272 this study, depend on a number of mechanistic assumptions, as recently described by Grace

and Irvine (2020). In this study, the most general and vital assumptions associated with network structure that we have included in our models are consistent with both known and plausible mechanisms whereby *Ranunculus* can influence physical and other biological system components. The use of experimental data in this study is a great asset in supporting interpretations. As with all ecological studies, estimates are assumed to be approximate and the confirmation of conclusions dependent on subsequent studies.

# 3. Results

## 3.1. Salmon abundance

Results indicate a strong and positive direct influence of *Ranunculus* cover on salmon abundances ($\gamma = 0.52$, $p < 0.001$) and an overall positive influence of *Ranunculus* (Table 2a), which was mediated through water velocities and depths (Figure 4a). *Ranunculus* cover was positively associated with increased velocity heterogeneity ($\gamma = 0.46$, $p < 0.01$), which had a weakly supported, negative association with the proportion of fast velocities ($\beta = -0.30$, $p = 0.08$). Proportion of fast velocities in turn had a strongly supported, positive influence on salmon abundances ($\beta = 0.34$, $p < 0.01$). *Ranunculus* cover was also positively associated with increased water depths ($\gamma = 0.40$, $p = 0.02$), which was negatively related to salmon abundance ($\beta = -0.29$, $p = 0.02$). There was no significant influence of velocity heterogeneity or prey biomass on salmon abundance, and *Ranunculus* cover was not related to basal resources or prey biomass. Consequently, these pathways were not retained in the final model, though there was a positive relationship between basal resources and prey biomass ($\beta = 0.31$, $p = 0.06$). The model was an adequate representation of the data (i.e. all paths were judged to be independent: Fisher's $C_8 = 6.97$, $p$ value = 0.54), and explained a high amount of

297 variation in salmon abundance (marginal $R^2 = 0.70$). Model residuals did not violate
298 assumptions of homogeneity, normality or independence.

299 3.2. Salmon growth

300 The direct positive influence of *Ranunculus* cover on salmon growth was not retained in the
301 path model. Instead, there were multiple indirect influences of *Ranunculus* cover on growth
302 via physical habitat and prey resource variables (Figure 4b). *Ranunculus* cover was positively
303 directly related to prey biomass ($\gamma = 0.84$, $p < 0.001$) and velocity heterogeneity ($\gamma = 0.53$, $p$
304 $< 0.001$). Prey biomass had a strong, positive influence on salmon growth ($\beta = 0.81$, $p <$
305 0.001). Velocity heterogeneity was negatively related to proportion of fast velocities ($\beta = -$
306 0.59, $p = < 0.001$), which in turn was strongly, positively related to prey biomass ($\beta = 0.75$, $p$
307 $= < 0.001$). This latter relationship between proportion of fast velocities and prey biomass
308 was identified as an important missing link in the initial model. The influences of prey size,
309 salmon abundance and trout abundance on salmon growth were not significant, and so these
310 variables were not retained in the final model. Velocity heterogeneity and proportion of fast
311 velocities did not directly affect salmon growth, so these pathways were also removed. The
312 overall effect of *Ranunculus* cover on growth was positive (Table 2b), and the data were
313 judged to be consistent with the model (Fisher's $C_{10} = 10.27$, $p = 0.42$). The model explained
314 a high proportion of the variance in salmon growth in weight (marginal $R^2 = 0.56$, conditional
315 $R^2 = 0.66$). Model residuals did not violate assumptions of homogeneity, normality or
316 independence.

317

318 # 4. Discussion

319 This study uncovered evidence that the positive influences of *Ranunculus* cover on salmon
320 abundance and growth during summer (Marsh *et al.,* 2021a), are likely driven by a direct

effect of cover, and indirect effects operating through multiple pathways, respectively. These findings provide mechanistic understanding of the key influence that macrophytes have on salmon communities in lowland rivers. Salmon abundance was strongly influenced by a direct effect of *Ranunculus* and indirectly, through influences on water depths and velocities. By contrast, salmon growth appears to not be substantially affected by a direct effect of *Ranunculus,* but instead predominantly influenced indirectly via impacts of *Ranunculus* on prey resources and water velocities. Multiple indirect pathways were identified in each analysis, via physical habitat and food resource variables, highlighting the potential of *Ranunculus* to influence multiple ecosystem components in lowland rivers.

Higher *Ranunculus* cover was directly associated with higher salmon abundance, supporting the hypothesis that densities of juvenile salmonids are determined by availability of shelter, not just food resources (Riley *et al*., 2009). Greater plant cover increases the area of shelter afforded by both the floating canopy on the water surface, to protect salmon from aerial predators (Johnsson, Rydeborg & Sundstrom, 2004), and a complex vertical structure throughout the water column to shield or aid evasion from aquatic predators (Dionne & Folt, 1991; Diehl & Kornijow, 1998). Such structural complexity could result in plant cover being preferable habitat, attracting more individuals and resulting in reduced mortality rates from predation. Higher salmon abundance in patches with high *Ranunculus* cover might also result from visual isolation among competitors, which can reduce aggressive behaviour, and consequently the territory size defended by an individual (Venter *et al.,* 2008), increasing the effective carrying capacity of a site (Venter *et al.,* 2008). The presence and use of shelters by salmon (e.g. boulders, tree roots, aquatic vegetation) can also lead to lower metabolic rates (Millidine, Armstrong & Metcalfe, 2006), sheltering them from extreme daytime summer temperatures (Gries & Juanes, 1998) and allowing rest out of fast water flows during night (Riley *et al.,* 2006).

346 We found evidence of a strong, positive effect of fast velocities on salmon abundance, which
347 is consistent with suggestions that water velocity is a key determinant of juvenile salmon
348 habitat selection (Morantz *et al.,* 1987; Armstrong *et al.,* 2003; Girard, Grant &
349 Steingrimsson, 2004). Body morphology can influence habitat choice by fish (Armstrong *et*
350 *al.,* 2003), and the large pectoral fins and streamlined body assist juvenile salmon to maintain
351 position near the riverbed in fast flowing water (Arnold, Webb & Holford, 1991). Fast
352 velocities might be preferred by individual fish due to the continuous supply of drifting prey.
353 In the study stream, salmon prey heavily on three taxonomic groups, *Baetis* sp. and *Serratella*
354 *ignita* (Ephemeroptera), and Simuliidae (Diptera), which are characteristic of drift taxa
355 (Waters, 1972; Marsh *et al.,* 2020b). Faster water velocity might therefore support a greater
356 number of salmon by providing an adequate supply of drifting invertebrates, to ensure
357 sufficient resources for greater number of individuals. *Ranunculus* cover mediates this effect
358 by its strong influence on velocity heterogeneity, that is, the steepness of adjacent velocity
359 gradients in and around plant stands (Wharton *et al.,* 2006). *Ranunculus* cover thus can be
360 particularly beneficial in habitats with fast water velocities as it offers a low velocity refuge.

361 The negative effect of water depth on salmon abundance suggests that shallower habitats are
362 preferred during the summer feeding period. Ontogenetic shifts in habitat selection occur in
363 salmonid species, and older and larger fish tend to shift to deeper habitats (Morantz *et al.,*
364 1987; Armstrong *et al.,* 2003). Subsequently, increased water depths are associated with
365 greater abundance of older, and potentially more successful, competitors and predators
366 (Gibson, 1993; Keeley & Grant, 1995). Therefore, juvenile salmon individuals might either
367 not select for, or suffer higher mortality rates in deeper water, and so are recorded in lower
368 abundance in these habitats. In contrast, juvenile salmonids in upland rivers avoid shallow
369 water in favour for intermediate depths (Morantz *et al.,* 1987; Girard, Grant & Steingrimsson,
370 2004), as depth benefits include increased prey encounter rates for drift-feeding salmonids

371 and protection from aerial predators and high flows (Gregory, 1993; Piccolo *et al.,* 2007).
372 *Ranunculus* can provide comparable habitat conditions, i.e. greater foraging opportunities and
373 shelter from high velocities and predators, in lowland rivers, which might diminish the
374 advantages of occupying deeper water over shallow habitats.

375 Velocity heterogeneity and prey biomass were not identified as important drivers of salmon
376 abundance, suggesting that shelter has a greater influence than access to prey resources. The
377 strong relationships between *Ranunculus* and velocity heterogeneity and water depth
378 illustrate how macrophytes can influence the physical environment, predominately through
379 altering water flow dynamics. *Ranunculus* had little influence on basal resources, contrasting
380 with existing knowledge on the ability of *Ranunculus* stands to retain substantial amounts of
381 organic material (Gregg & Rose, 1982; Cotton *et al.,* 2006). However, this finding should be
382 considered with caution as it could also indicate a limitation of the benthic sampling
383 procedure, i.e. not enough samples were collected to capture average levels of organic matter
384 associated with site-level *Ranunculus* cover accurately, due to patchy distributions (Downes,
385 Lake & Schreiber, 1993).

386 Salmon growth was not directly affected by *Ranunculus* cover in our models, suggesting that
387 the previously observed positive influence of cover on salmon growth (Marsh *et al.,* 2021a)
388 was mediated by the physical habitat and food resources associated with *Ranunculus* cover.
389 The influence of *Ranunculus* operated through positive impacts on velocity heterogeneity and
390 prey biomass, the latter of which in turn was related to greater growth. This finding supports
391 the expectation that higher *Ranunculus* cover allows for greater abundance and biomass of
392 macroinvertebrate prey. The strong association between *Ranunculus* cover and
393 macroinvertebrate prey in the growth model was not retained in the abundance model that
394 was parameterised on data collected later in the year when macroinvertebrate abundance
395 declines and *Ranunculus* plants begin to die back (Marsh et al. 2021a). Macrophytes provide

396 microhabitats that invertebrates can occupy (Hutchens *et al.,* 2004), and plants with complex
397 architectures are purported to support greater macroinvertebrate biomass due to increased
398 surface area for colonisation and protection from predators (Heck and Crowder 1991; Diehl
399 & Kornijow, 1998). Structural complexity from highly dissected *Ranunculus* leaves enhances
400 ability to trap detritus and support epiphytic biomass (Gregg and Rose 1982), that form food
401 resources for macroinvertebrates. These increased resources might therefore support greater
402 numbers of individuals and explain why prey biomass was greater in higher *Ranunculus*
403 cover.

404 High velocities were expected to be detrimental to salmon growth due to the increased
405 energetic demands of inhabiting fast flowing water (Wankowski & Thorpe, 1979), but a
406 direct influence of the proportion of fast velocities was not found to be important. Although
407 drift feeding in salmonids can be considered as energetically expensive (Puckett & Dill,
408 1985), behavioural responses to foraging in habitats with increased velocities, such as
409 reducing attack distances, can negate any additional energy costs (Godin & Rangeley, 1989).
410 The proportion of fast velocities indirectly influenced salmon growth through a positive
411 association with prey biomass, a relationship that was not originally hypothesised but
412 identified from the model fit. This could represent the habitat preferences of
413 macroinvertebrate taxa that were highly abundant in the Surber samples, particularly
414 rheophilic fauna, such as Baetidae, Simuliidae, Ephemerellidae, Elmidae and
415 Hydropsychidae (Marsh *et al.,* 2020b). High velocity conditions can afford benefits through
416 predator evasion and increasing oxygen supply, particularly for larger macroinvertebrate
417 individuals with greater resource requirements (Sagnes, Merigoux & Peru, 2008).

418 There was no significant influence of salmon or trout abundance on salmon growth detected,
419 suggesting that growth (and competition for resources) was not negatively impacted by the
420 abundance of con- or hetero-specifics in this experiment. This finding is likely context

421 specific, however, as other studies have shown negative effects of competitor densities
422 (salmon or trout) on juvenile salmon growth, linked to individuals competing for similar and
423 limited resources (e.g. Bal *et al.,* 2011; Gregory *et al.,* 2017). Additionally, due to the
424 recruitment crash in the river Frome catchment in 2016 (Marsh *et al.,* 2021b), there might
425 have been insufficient densities of con- or hetero-specifics to detect any influence of
426 competition on growth. In line with previous works that observed the territory sizes of
427 juvenile salmon to be within a few square metres (Armstrong et al. 1994; Venter et al. 2008),
428 in this study we assumed that the home ranges of juvenile salmon were mostly limited to the
429 individual 20 m study sites and thus, exposure to the *Ranunculus* treatments. Extending the
430 scale of the study, both temporally and spatially, would be required to discern whether the
431 relationships between *Ranunculus* and salmon abundance and growth sustained across larger
432 scales and, ultimately, resulted in a change at the population level. This work would be an
433 interesting future research direction.

434 Direct and indirect influences of *Ranunculus* underlie greater abundance of faster growing
435 salmon at a reach-scale. Even in these relatively simple path analyses, the important links
436 retained for the two salmon responses demonstrate the complex interactions, which govern
437 the impact of *Ranunculus* cover on multiple abiotic and biotic variables. This highlights the
438 role of *Ranunculus* as a key aquatic structure that mediates environmental conditions in
439 lowland streams promoting abundance, and growth conditions in individuals of species at
440 multiple trophic levels by creating suitable physical habitat with abundant resources. The
441 analytical approach taken in the study allowed us to test for salmon responses to varying level
442 of macrophyte cover as well as associated changes in habitat heterogeneity, providing new
443 mechanistic insights into how *Ranunculus* benefits juvenile salmon in lowland rivers. The
444 impact of macrophytes on habitat and ecosystem productivity could generalise to native
445 macrophytes and fish communities in river systems where large substrates that provide

446 structural complexity are infrequent. Only by elucidating the mechanisms driving change in
447 population dynamics, can we design and undertake effective restoration of ecosystems
448 degraded by anthropogenic activity. This study suggests that strategies to maintain or
449 enhance naturally occurring *Ranunculus* will likely return wide ranging ecosystem benefits,
450 including for species of high conservation value, such as salmon.

## Acknowledgements

We are grateful to S. Gregory, L. Scott, D. Cooling, J. Pretty, W. Beaumont, J. Murphy, A. Arnold, T. Porteus, J. Picken, and C. Little for their helpful input and field assistance, A. Daniell for providing the location for the experimental sites, and local farmers for permitting access to the river.

## Author contribution statement

Conceptualisation: JM, JIJ, RL, PK. Developing methods; data interpretation; writing: JM, JIJ, RL, JG, PK. Conducting the research, data analysis, preparation of figures and tables: JM.

## Conflict of interest statement

The authors declare that they have no conflict of interest.

## Data availability statement

The data supporting the original experiment and used in this study are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.612jm643t (Marsh et al., 2021c); additional data are available from the authors upon reasonable request.

## Funding information

This work was funded by the G & K Boyes Charitable Trust (Charity No: 1166015) through a PhD studentship awarded to JM. This study was supported in part by the USGS Climate R&D and Ecosystems Programs. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

References

Armitage, P. D. & Cannan, C. E. (2000). Annual changes in summer patterns of mesohabitat distribution and associated macroinvertebrate assemblages. *Hydrological Processes*, 14, 3161-3179.

Armstrong, J. D., Shackley, P. E. & Gardiner, R. (1994). Redistribution of juvenile salmonid fishes after localised catastrophic depletion. *Journal of Fish Biology*, 45, 1027-1039.

Armstrong, J. D., Kemp, P. S., Kennedy, G. J. A., Ladle, M. & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research,* 62, 143-170.

Armstrong, J. D., McKelvey, S., Smith, G. W., Rycroft, P. & Fryer, R. J. (2018). Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology,* 92, 569-578.

Arnold, G. P., Webb, P.W. & Holford, B. H. (1991). The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *Journal of Experimental Biology,* 156, 625-629.

Bal, G., Rivot, E., Prйvost, E., Piou, C. & Baglinиre, J. L. (2011). Effect of water temperature and density of juvenile salmonids on growth of young-of-the-year Atlantic salmon *Salmo salar. Journal of Fish Biology*, 78, 1002-1022.

Beland, K. F., Trial, J. G. and Kocik, J. F. (2004). Use of riffle and run habitats with aquatic vegetation by juvenile Atlantic salmon. *North American Journal of Fisheries Management* 24:525–533.

Berrie, A. D. (1992). The chalk-stream environment. *Hydrobiologia,* 248, 3-9.

Cotton, J. A., Wharton, G., Bass, J. A. B., Heppell, C. M. & Wotton, R. S. (2006). The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology,* 77, 320-334.

Cranston, E. (2004). *Ranunculus in Chalk rivers: phase 2*. Environment Agency, Bristol, UK.

Diehl, S. & Kornijow, R. (1998). Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates in E. Jeppesen, M. Sondergaard, M. Sondergaard & K. Christoffersen (eds). *The structuring role of submerged macrophytes in lakes*. Springer New York, pp. 24-46.

Dionne, M. & Folt, C. L. (1991). An experimental analysis of macrophyte growth forms as fish foraging habitat. *Canadian Journal of Fisheries and Aquatic Sciences,* 48, 123-131.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carrй, G., Marquйz, J. R. G... & Lautenbach, S. (2012). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography,* 36, 27-46.

Downes, B.J., Lake, P.S. & Schreiber, E.S.G. (1993). Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. *Freshwater Biology,* 30, 119-132.

Gibson, R. J. (1993). The Atlantic salmon in fresh water: spawning, rearing and production. *Reviews in Fish Biology and Fisheries,* 3, 39-73.

Girard, I. L., Grant, J. W. A. & Steingrimsson, S.O (2004). Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to habitat use in Catamaran Brook, New Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences,* 61, 2339-2349.

Godin, J.-G. J. & Rangeley, R. W. (1989). Living in the fast lane: effects of cost of locomotion on foraging behaviour in juvenile Atlantic salmon. *Animal Behaviour,* 37, 943-954.

Grace, J. B. (2006). *Structural Equation Modeling and Natural Systems*, Cambridge University Press.

Grace, J. B., & Irvine, K. M. (2020). Scientist's guide to developing explanatory statistical models using causal analysis principles. *Ecology*, *101*(*4*), e02962. https://doi.org/10.1002/ecy.2962.

Gregg, W. W. & Rose, F. L. (1982). The effects of aquatic macrophytes on the stream microenvironment. *Aquatic Botany,* 14, 309-324.

Gregory, R. S. (1993). Effect of turbidity on the predator avoidance behaviour of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences,* 50, 241-246.

Gregory, S. D., Nevoux, M., Riley, W. D., Beaumont, W. R. C., Jeannot, N., Lauridsen, R. B… & Roussel, J.-M. (2017). Patterns on a parr: Drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. *Freshwater Biology*, 62, 1117-1129.

Gregory, S. D., Ibbotson, A. T., Riley, W. D., Nevoux, M., Lauridsen, R. B., Russell, I. C., Britton, J. R… & Rivot, E. (2019). Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*, fsz066.

Gries, G. & Juanes, F. (1998). Microhabitat use by juvenile Atlantic salmon (*Salmo salar*) sheltering during the day in summer. *Canadian Journal of Zoology,* 76, 1441-1449.

Heck K.L., Crowder L.B. (1991). Habitat structure and predator—prey interactions in vegetated aquatic systems. *In*: Bell S.S., McCoy E.D., Mushinsky H.R. (eds) *Habitat Structure.* Population and Community Biology Series, vol 8. Springer, Dordrecht.

Hutchens, J. J., Wallace, J. B. & Romaniszyn, E. D. (2004). Role of *Podostemum ceratophyllum Michx*. in structuring benthic macroinvertebrate assemblages in a southern Appalachian river. *Journal of the North American Benthological Society,* 23, 713-727.

ICES. (2021). Working Group on North Atlantic Salmon (WGNAS). ICES Scientific Reports. 3:29. 407 pp. https://doi.org/10.17895/ices.pub.7923.

Johnsson, J., Rydeborg, A. & Sundstr:om, L. F. (2004). Predation risk and the territory value of cover: an experimental study. *Behavioral Ecology and Sociobiology,* 56, 388-392.

Keeley, E. R. & Grant, J. W. A. (1995). Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences,* 52, 186-196.

Keeley, E. R. & Grant, J. W. A. (1997). Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences,* 54, 1894-1902.

Kovalenko, K. E., Thomaz, S. M. & Warfe, D. M. (2012). Habitat complexity: approaches and future directions. *Hydrobiologia,* 685, 1-17.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1-26.

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution,* 7, 573-579.

Lefcheck, J. S, Byrnes, J. E. K., & Grace, J. B. (2018) piecewiseSEM: Piecewise structural equation modeling. An r package. version 2.1. 0. https://cran.r-project.org/web/packages/piecewiseSEM/piecewiseSEM.pdf.

Lürig,M. D., Narwani, A., Penson, H., Wehrli, B., Spaak, P., & Matthews, B. 2021. Non-additive effects of foundation species determine the response of aquatic ecosystems to nutrient perturbation. *Ecology*, 102, e03371.

Maki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P. and Kreivi, P. (1997). Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a

northern boreal river. *Canadian Journal of Fisheries and Aquatic Sciences* 54:520–530.

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Beaumont, W. R. C., Scott, L. J., Kratina, P. & Jones, J. I. (2020a). Above parr: Lowland river habitat characteristics associated with higher juvenile Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) densities. *Ecology of Freshwater Fish*, 29, 542-556.

Marsh, J. E. (2020b). The importance of *Ranunculus* spp. for juvenile salmonids in lowland rivers. PhD thesis. Queen Mary University of London, London, UK.

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Kratina, P., Scott, L. J., Cooling, D. & Jones, J. I. (2021a). High summer macrophyte cover increases abundance, growth and feeding of juvenile Atlantic salmon. *Ecological Applications* https://doi.org/10.1002/eap.2492

Marsh, J. E., Lauridsen, R.B., Riley, W. D., Simmons, O. M., Artero, C., Scott, L. J… & Gregory, S. D. (2021b). Warm winters and cool springs negatively influence recruitment of Atlantic salmon (*Salmo salar* L.) in a southern England chalk stream. *Journal of Fish Biology*, 99, 1125-1129.

Marsh, J. E., Lauridsen, R. B., Gregory, S. D., Beaumont, W. R. C., Scott, L. J., Kratina, P. & Jones, J. I. (2021c). Data from: High summer macrophyte cover increases abundance, growth and feeding of juvenile Atlantic salmon, *Dryad Digital Repository*, https://doi.org/10.5061/dryad.612jm643t.

McCormick, D. P., and Harrison, S. S. C. (2011). Direct and indirect effects of riparian canopy on juvenile Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in south-west Ireland. *Fisheries Management and Ecology* 18:444–455.

Millidine, K. J., Armstrong, J. D. & Metcalfe, N. B. (2006). Presence of shelter reduces maintenance metabolism of juvenile salmon. *Functional Ecology,* 20, 839-845.

Morantz, D. L., Sweeney, R. K., Shirvell, C. S. & Longard, D. A. (1987). Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 44, 120-129.

O'Hara, R. B. & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution,* 1, 118-122.

Piccolo, J. J., Hughes, N. F. & Bryant, M. D. (2007). The effects of water depth on prey detection and capture by juvenile coho salmon and steelhead. *Ecology of Freshwater Fish,* 16, 432-441.

Puckett, K. J. & Dill, L. M. (1984). Cost of sustained and burst swimming to juvenile Coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences,* 41, 1546-1551.

R Development Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riley, W. D., Ives, M. J., Pawson, M. G. & Maxwell, D. L. (2006). Seasonal variation in habitat use by salmon, *Salmo salar*, trout, *Salmo trutta* and grayling, *Thymallus thymallus,* in a chalk stream. *Fisheries Management and Ecology,* 13, 221-236.

Riley, W. D., Pawson, M. G., Quayle, V. & Ives, M. J. (2009). The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream. *Fisheries Management and Ecology,* 16, 100-111.

Sagnes, P., Mйrigoux, S. & Pйru, N. (2008). Hydraulic habitat use with respect to body size of aquatic insect larvae: Case of six species from a French Mediterranean type stream. *Limnologica*, 38, 23-33.

Scheffer, M., S. Szabo, A. Gragnani, E. H. Van Nes, S. Rinaldi, N. Kautsky, J. Norberg, R. M. M. Roijackers, and R. J. M. Franken. 2003. Floating plant dominance as a stable state. *Proceedings of the National Academy of Sciences USA*, 100, 4040–4045.

Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling: A Multidisciplinary Journal,* 7, 206-218.

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology,* 90, 363-368.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M. & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography,* 31, 79-92.

Teixeira de Mello, F., Meerhoff, M., González-Bergonzoni., Kristensen, E.A., Baattrup-Pedersen, A., Jeppesen, E. (2015). Inflence of riparian forests on fish assemblages in temperate lowland streams. *Environmental Biology of Fishes*, 99, 133–144.

Venables, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*. Fourth Edition, Springer, New York.

Venter, O., Grant, J. W. A., Noël, M. V. & Kim, J-W. (2008). Mechanisms underlying the increase in young-of-the-year Atlantic salmon (*Salmo salar*) density with habitat complexity. *Canadian Journal of Fisheries and Aquatic Sciences,* 65, 1956-1964.

Wankowski, J. W. J. & Thorpe, J. E. (1979). Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L. juveniles. *Journal of Fish Biology,* 14, 239-247.

Warfe, D. M. & Barmuta, L. A. (2004). Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia,* 141, 171-178.

Waters, T. F. (1972). The drift of stream insects. *Annual Review of Entomology,* 17, 253-272.

Wharton, G., Cotton, J. A., Wotton, R. S., Bass, J. A. B., Heppell, C. M., Trimmer, M., Sanders, I. A. & Warren, L. L. (2006). Macrophytes and suspension-feeding invertebrates modify flows and fine sediments in the Frome and Piddle catchments, Dorset (UK). *Journal of Hydrology,* 330, 171-184.

Wilkinson, C.L., Chua, K.W.J., Fiala, R., Liew, J.H., Kemp, V., Fikri, A.H., Ewers, R.M., Kratina, P. and Yeo, D.C.J. 2021. Forest conversion to oil palm compresses food chain length in tropical streams. Ecology, 102(1): e03199.

Zabel, R. W. & Achord, S. (2004). Relating size of juveniles to survival within and among populations of chinook salmon. *Ecology,* 85, 795-806.

**Table 1.** Summary of the variables used in path analysis of salmon abundance ($n$ = 36) and growth rates ($n$ = 71) with mean and standard error (prior to standardising).

| Model | Variable (unit) | Type | Error | Mean (± SE) |
|---|---|---|---|---|
| Abundance | Salmon abundance (N) | Response | Negative binomial | 14.47 (2.07) |
| | Proportion of fast velocities | Response/Explanatory | Gaussian | 0.62 (0.04) |
| | Velocity heterogeneity (Index) | Response/Explanatory | Gaussian | 0.80 (0.06) |
| | Water depth (cm) | Response/Explanatory | Gaussian | 31.58 (1.82) |
| | Total biomass of prey (mg) | Response/Explanatory | Gaussian | 221.27 (17.31) |
| | Basal resources (mg) | Response/Explanatory | Gaussian | 0.83 (0.07) |
| | *Ranunculus* cover (%) | Explanatory | - | 34.00 (4.28) |
| Growth | Salmon growth in weight (g) | Response | Gaussian | 4.55 (0.20) |
| | Average salmon abundance (N) | Response/Explanatory | Negative binomial | 33.97 (1.47) |
| | Average trout abundance (N) | Response/Explanatory | Negative binomial | 13.23 (1.06) |
| | Average proportion of fast velocities | Response/Explanatory | Gaussian | 0.72 (0.01) |
| | Average velocity heterogeneity (Index) | Response/Explanatory | Gaussian | 0.95 (0.05) |
| | Average total biomass of prey (mg) | Response/Explanatory | Gaussian | 191.62 (11.73) |

| | | | |
|---|---|---|---|
| Average size of prey (mg) | Response/Explanatory | Gaussian | 0.32 (0.01) |
| Average *Ranunculus* cover (%) | Explanatory | - | 53.50 (3.57) |

**Table 2.** Standardised effects of the paths retained in the best fitting model between *Ranunculus* cover (R) and salmon abundance (A) and growth in weight (G), shown in section (a) and (b), respectively. Variables represented as VH – velocity heterogeneity, FV – fast velocity, WD – water depth, P – total biomass of prey. Indirect effects are calculated by multiplying the partial path coefficients and represent the effect of *Ranunculus* on salmon abundance and growth directly and mediated by the physical habitat/food resource variables. The overall effect of *Ranunculus* on salmon abundance and growth is calculated by summing all direct and indirect effects.

| **Response variable** | **Pathways** | **Direct effects** | **Indirect effects** | **Overall effect** |
|---|---|---|---|---|
| **(a)** | | | | **0.35** |
| Salmon | R → A | 0.52 | - | |
| abundance | R → VH → FV → A | - | -0.05 | |
| | R → WD → A | - | -0.12 | |
| **(b)** | | | | **0.64** |
| Salmon growth | R → P → G | - | 0.68 | |
| in weight | R → VH → FV → P → G | - | -0.04 | |

Figure Captions

**Figure 1**. Partial effects showing the influence of *Ranunculus* through time on (a) juvenile (0+) salmon abundance during August and September, and on (b) 0+ salmon growth of marked individuals caught in June and recaptured in August. These partial effects were predicted from separate models including other explanatory variables that together described the effects of a *Ranunculus* manipulation experiment on salmon abundance and growth (for full details see Marsh et al. 2021a). The solid line and shaded area represent the mean estimate and 95% confidence interval of the marginal effect of *Ranunculus* cover and the solid circles show the raw data points. These data points form the response variables of this study.

**Figure 2**. Hypothesised relationships of the piecewise SEMs to describe variation in (a) 0+ salmon abundance, and (b) 0+ salmon growth. The path diagrams represent hypothesis of direct and indirect effects of *Ranunculus* cover on salmon abundance and growth, $\boldsymbol{\gamma}$ represents links between an exogenous and endogenous variable, $\boldsymbol{\beta}$ represents links between two endogenous variables, numbers correspond to the variable number, e.g. $x_1$, $y_2$, that are linked. Black arrows denote positive links and red arrows denote negative links, and the strength of effect is highlighted by arrow thickness.

**Figure 3**. Schematic illustration of the study locations and experimental manipulations: (a) location of the River Frome in Dorset, UK; (b) locations of the three experimental blocks on the North stream (black triangles); and (c) a schematic representation showing that each experimental block consisted of three sites (20 m in length), each manipulated to maintain contrasting *Ranunculus* cover (high / medium / low) and bounded by *Ranunculus* denuded buffer strips (5 m in length), from Marsh et al. 2021a.

**Figure 4.** Outcomes of the final piecewise SEMs testing direct and indirect effects of *Ranunculus* cover on (a) 0+ salmon abundance and (b) 0+ salmon growth. Non-significant pathways were omitted from the final model, and missing paths were identified using d-separation tests and incorporated. Coefficient estimates are shown for each pathway with significance levels are denoted as *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$, marginal $R^2$ values for each component response variable are shown under the response variable name. Black arrows denote positive links and red arrows denote negative links, and the strength of effect is highlighted by arrow thickness.

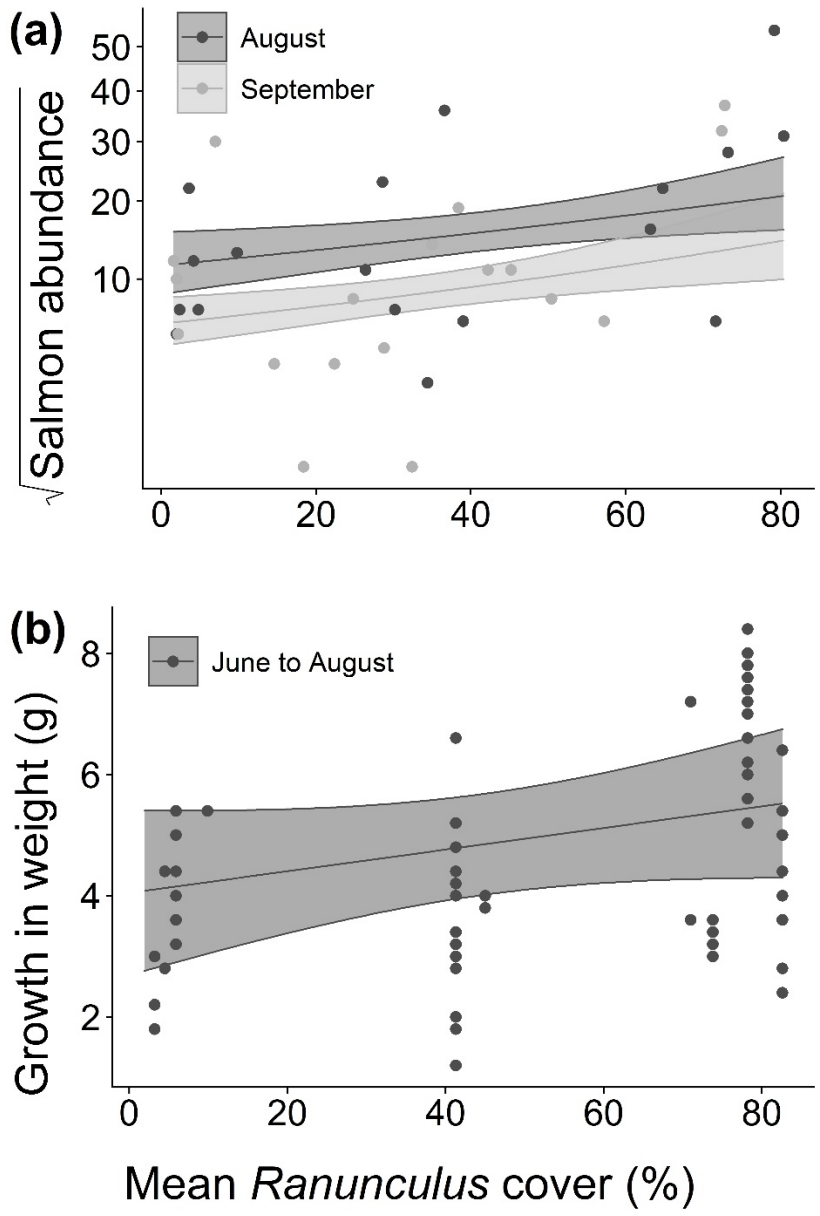
(a)
August
September
√Salmon abundance
50
40
30
20
10
0
20
40
60
80
(b)
June to August
Growth in weight (g)
8
6
4
2
0
20
40
60
80
Mean Ranunculus cover (%)

Figure 1.

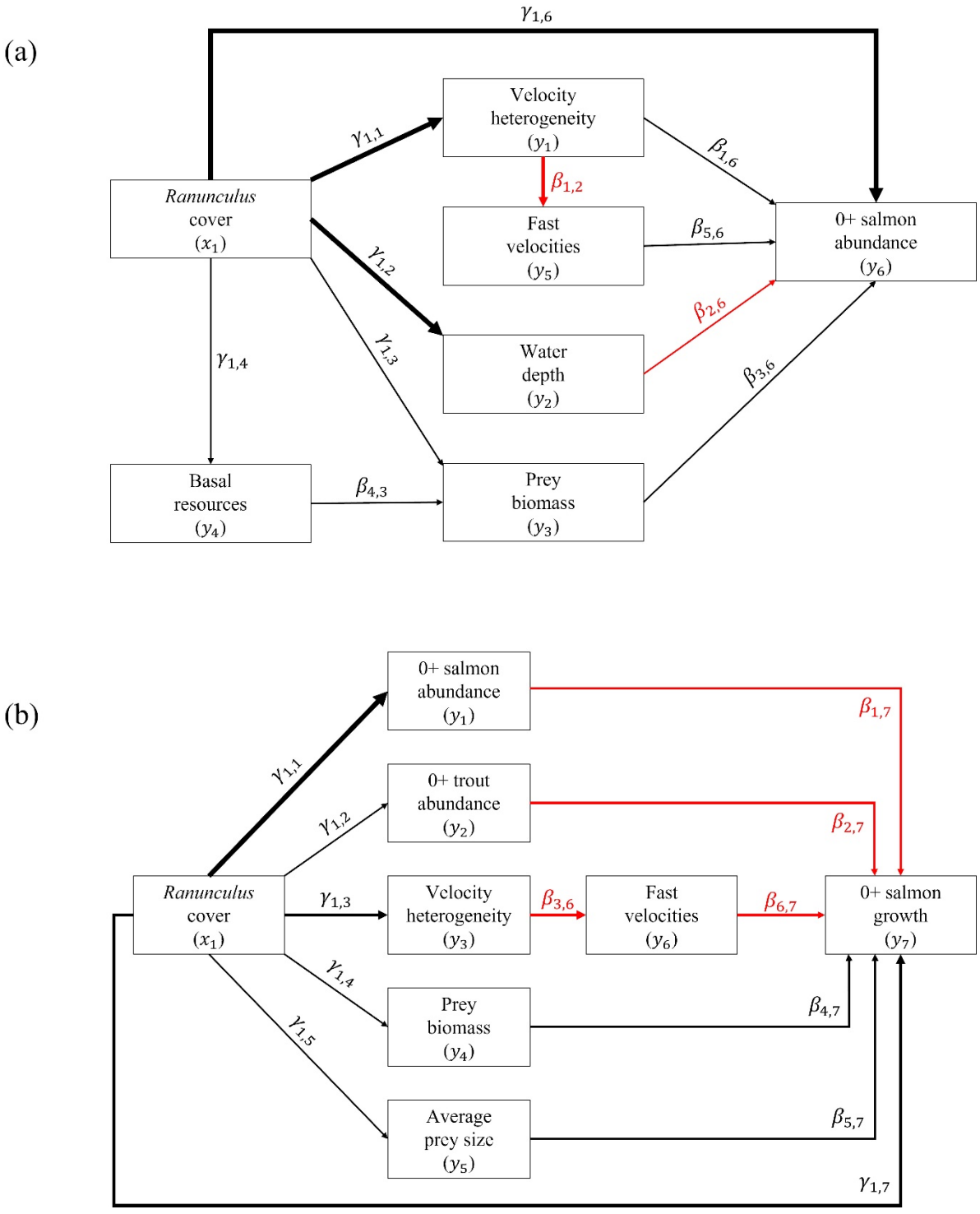
(a)
$\gamma_{1,6}$
Velocity heterogeneity ($y_1$)
$\gamma_{1,1}$
$\beta_{1,6}$
$\beta_{1,2}$
*Ranunculus* cover ($x_1$)
Fast velocities ($y_5$)
$\beta_{5,6}$
0+ salmon abundance ($y_6$)
$\gamma_{1,2}$
$\beta_{2,6}$
$\gamma_{1,3}$
Water depth ($y_2$)
$\gamma_{1,4}$
$\beta_{3,6}$
Basal resources ($y_4$)
$\beta_{4,3}$
Prey biomass ($y_3$)
(b)
0+ salmon abundance ($y_1$)
$\beta_{1,7}$
$\gamma_{1,1}$
0+ trout abundance ($y_2$)
$\gamma_{1,2}$
$\beta_{2,7}$
*Ranunculus* cover ($x_1$)
$\gamma_{1,3}$
Velocity heterogeneity ($y_3$)
$\beta_{3,6}$
Fast velocities ($y_6$)
$\beta_{6,7}$
0+ salmon growth ($y_7$)
$\gamma_{1,4}$
Prey biomass ($y_4$)
$\beta_{4,7}$
$\gamma_{1,5}$
Average prey size ($y_5$)
$\beta_{5,7}$
$\gamma_{1,7}$

Figure 2.

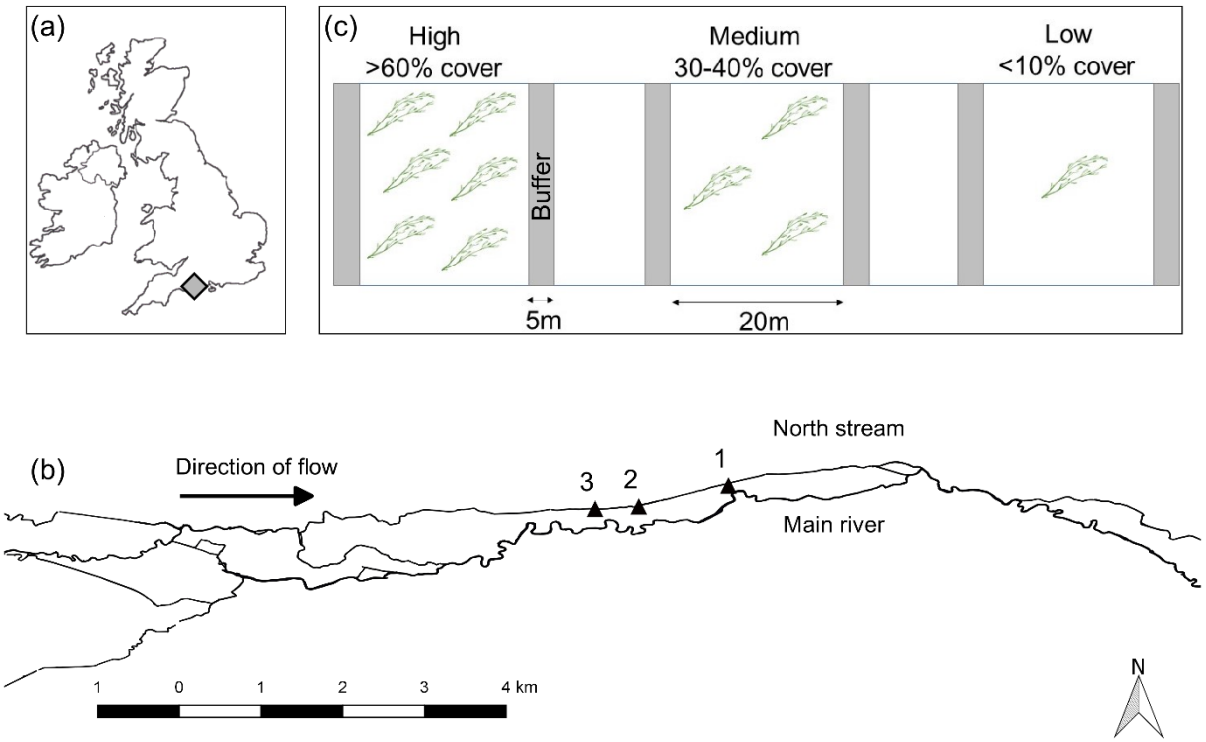
(a)
(c)
High
>60% cover
Medium
30-40% cover
Low
<10% cover
Buffer
5m
20m
(b)
Direction of flow
North stream
Main river
1
2
3
1 0 1 2 3 4 km
N

Figure 3.

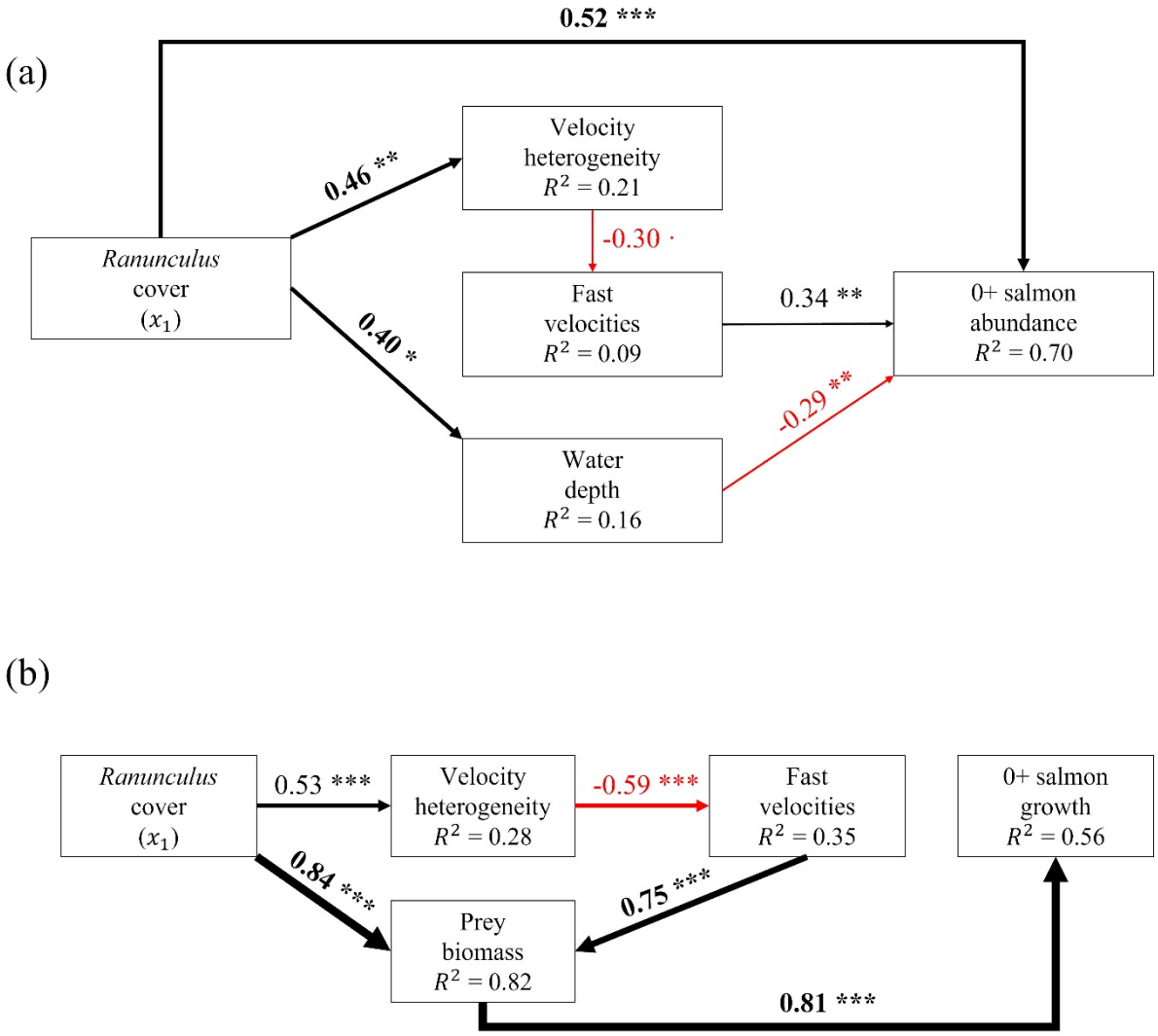
(a)
0.52 ***
Velocity heterogeneity $R^2 = 0.21$
0.46 **
-0.30 ·
*Ranunculus* cover ($x_1$)
Fast velocities $R^2 = 0.09$
0.34 **
0+ salmon abundance $R^2 = 0.70$
0.40 *
-0.29 **
Water depth $R^2 = 0.16$
(b)
*Ranunculus* cover ($x_1$)
0.53 ***
Velocity heterogeneity $R^2 = 0.28$
-0.59 ***
Fast velocities $R^2 = 0.35$
0+ salmon growth $R^2 = 0.56$
0.84 ***
0.75 ***
Prey biomass $R^2 = 0.82$
0.81 ***

Figure 4.

**Supplementary information in support of: Marsh, J. E., Jones, J. I., Lauridsen, R. B., Grace, J. B & Kratina, P. Direct and indirect influences of macrophyte cover on abundance and growth of juvenile Atlantic salmon. Submission to Freshwater Biology**

## Supplementary Tables

**Table S1**. Mass-length relationships used to calculate macroinvertebrate biomass. All macroinvertebrate specimens were identified to species, except Oligochaeta (sub-class), Hydrachnidae (family), Simuliidae (family) and Chironomidae (tribe), and counted to determine total abundances per sample. Measures of parasitic Nematoda and Nematomorpha were omitted from these calculations, as these were not considered to represent prey for salmon. We recorded body-size measurements of up to 30 randomly selected specimens of each taxon in each sample and used published length-mass relationships to estimate the mean biomass of each taxon. We then multiplied the mean biomass by the abundance of each taxa to estimate a total biomass of each taxon per sample.

| Taxa (Class/Sub-Class) | Reference |
|---|---|
| Hydrozoa, Insecta, Turbellaria | Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, 18, 308-343. |
| Insecta | Burgherr, P. & Meyer, E.I. (1997). Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv fur Hydrobiologie*, 139, 101-112. |
| Copepoda | Dumont, H.J., Van de Velde, I. & Dumont, S. (1975). The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, 19, 75-97. |
| Hirudinea | Edwards, F.K., Lauridsen, R.B., Armand, L., Vincent, H.M. & Jones, J.I. (2009). The relationship between length, mass and preservation time for three species of freshwater leeches (Hirudinea). *Fundamental and Applied Limnology*, 173, 321-327. |
| Gastropoda | Hawkins, J.W., Lankester, M.W., Lautenschlager, R.A. & Bell, F.W. (1997). Length-biomass and energy relationships of terrestrial gastopods in northern forest ecosystems. *Canadian Journal of Zoology*, 75, 501-505. |
| Branchiopods | Herzig, A. (1974). Some population characteristics of planktonic crustaceans in Neusiedlersee. *Oecologia*, 15, 127-141. |
| Insecta | Hildrew, A.G. & Townsend, C.R. (1982). Predators and prey in a patchy environment: A freshwater study. *Journal of Animal Ecology*, 51, 797-815. |
| Insecta | Johnston, T.A. & Cunjak, R.A. (2001). Dry mass-length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. *Freshwater Biology*, 41, 653-674. |
| Malacostraca, Hirudinea, Gastropoda, Oligochaeta | Mason, C.F. 1977. Populations and production of benthic animals in two contrasting shallow lakes in Norfolk. *Journal of Animal Ecology*, 46, 147-172. |
| Gastropoda, Insecta, Turbellaria | Meyer, E. (1989). The relationship between body length parameters and dry mass in running water invertebrates. *Archiv fur Hydrobiologie*, 117, 191-203. |

| | |
|---|---|
| Arachnida, Insecta | Sabo, J.L., Bastow, J.L. & Power, M.E. (2002). Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, 21, 336-343. |
| Insecta | Smock, L.A. (1980). Relationships between body size and biomass of aquatic insects. *Freshwater Biology*, 10, 375-383. |
| Gastropoda | Vincent, H.M. (2010). Algal resource depression by macro-invertebrate herbivory in a chalk stream: An empirical approach. *Unpublished PhD thesis*. Available online at http://etheses.bham.ac.uk/550/. |

**Table S2**. Model fitting procedure undertaken to identify the final model fit to describe salmon abundance. Non-significant pathways were removed iteratively, and model adequacy was assessed after each removal by calculating Fisher's C test. A – Abundance, R – Ranunculus, FV – Fast velocities, D – water depth, VH – velocity heterogeneity, P – biomass of prey, BR – basal resources.

| Model | Model terms | Model term change | Fisher's C | df | *P* value |
|---|---|---|---|---|---|
| 1 | A ~ R + FV + D + VH + P<br>D ~ R<br>FV ~ R + VH<br>VH ~ R<br>P ~ R + BR<br>BR ~ R | Full model | 28.11 | 18 | 0.06 |
| 2 | A ~ R + FV + D + P<br>D ~ R<br>FV ~ R + VH<br>VH ~ R<br>P ~ R + BR<br>BR ~ R | Removed velocity heterogeneity (VH) from abundance (A) model | 28.26 | 20 | 0.10 |
| 3 | A ~ R + FV + D + P<br>D ~ R<br>FV ~ VH<br>VH ~ R<br>P ~ R + BR<br>BR ~ R | Removed Ranunculus (R) from fast velocities (FV) model | 28.55 | 22 | 0.16 |
| 4 | A ~ R + FV + D + P<br>D ~ R<br>FV ~ VH<br>VH ~ R<br>P ~ R | Removed basal resources (BR) model and BR term in prey (P) model | 22.60 | 14 | 0.07 |
| 5 | A ~ R + FV + D<br>D ~ R<br>FV ~ VH<br>VH ~ R | Removed prey (P) model and P term in abundance (A) model | 6.97 | 8 | 0.54 |

**Table S3**. Model fitting procedure undertaken to identify the final model fit to describe growth in weight of salmon individuals. Non-significant pathways, and important missing pathways were identified using Shipley's d-sep test and were removed/added iteratively. Model adequacy was assessed after each removal/addition by calculating Fisher's C test.

| Model | Model terms | Model term change | Fisher's C | df | *P* value |
|---|---|---|---|---|---|
| 1 | G ~ R + VH + FV + PS + P + SA + TA<br>PS ~ R + P<br>P ~ R<br>FV ~ VH<br>VH ~ R<br>SA ~ R<br>TA ~ R | Full model | 558.51 | 28 | 0 |
| 2 | G ~ R + VH + FV + PS + P + TA<br>PS ~ R + P<br>P ~ R<br>FV ~ VH<br>VH ~ R<br>TA ~ R | Removed salmon abundance (SA) model, and SA term in growth (G) model | 455.04 | 18 | 0 |
| 3 | G ~ VH + FV + PS + P + TA<br>PS ~ R + P<br>P ~ R<br>FV ~ VH<br>VH ~ R<br>TA ~ R | Removed Ranunculus (R) from growth (G) model | 455.01 | 20 | 0 |
| 4 | G ~ VH + FV + PS + P<br>PS ~ R + P<br>P ~ R<br>FV ~ VH<br>VH ~ R | Removed trout abundance (TA) model, and TA term in growth (G) model | 254.59 | 12 | 0 |
| 5 | G ~ FV + PS + P<br>PS ~ R + P<br>P ~ R<br>FV ~ VH<br>VH ~ R | Removed velocity heterogeneity (VH) from growth (G) model | 256.2 | 14 | 0 |
| 6 | G ~ FV + P<br>P ~ R<br>FV ~ VH<br>VH ~ R | Removed prey size (PS) from growth (G) model | 101.19 | 10 | 0 |
| 7 | G ~ P<br>P ~ R<br>FV ~ VH<br>VH ~ R | Removed fast velocity (FV) from growth (G) model | 102.40 | 12 | 0 |
| 8 | G ~ P<br>P ~ R + FV<br>FV ~ VH<br>VH ~ R | Included fast velocity (FV) in prey biomass (P) model after identified as an important missing pathway | 10.27 | 10 | 0.42 |

Supplementary Figures

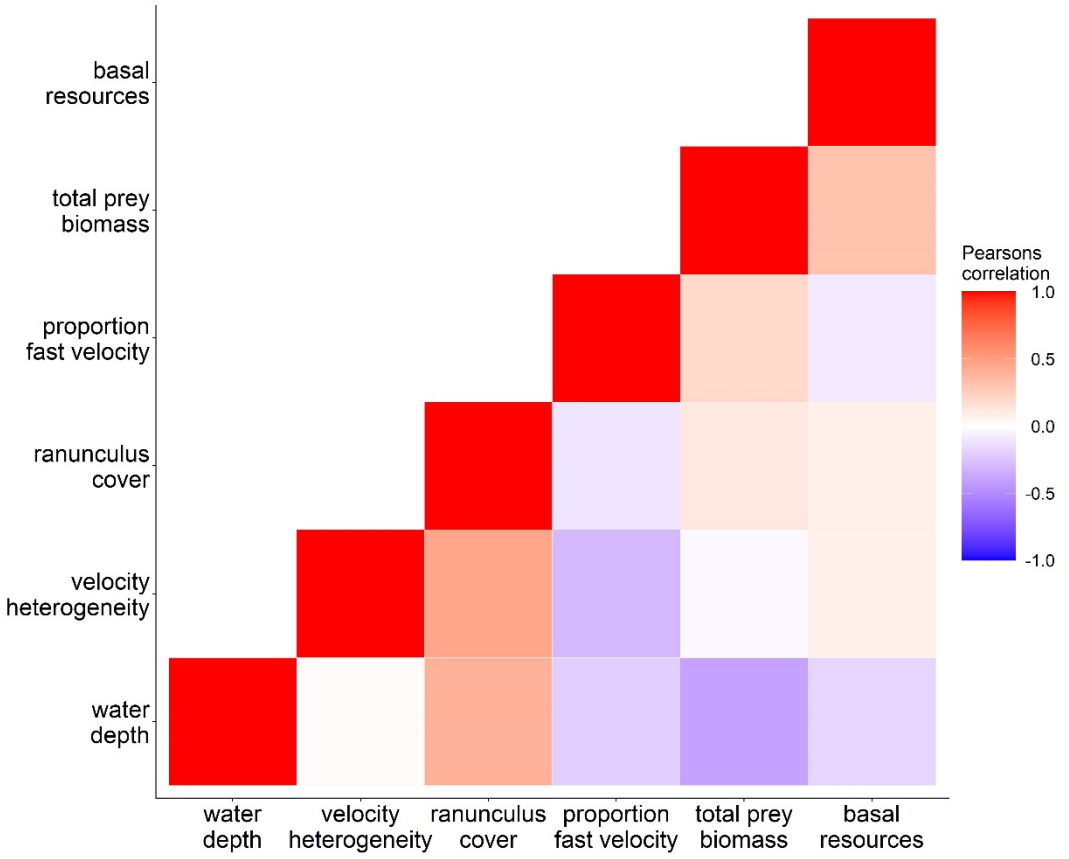


**Figure S1**. Correlation matrix for explanatory variables included in salmon abundance SEM.

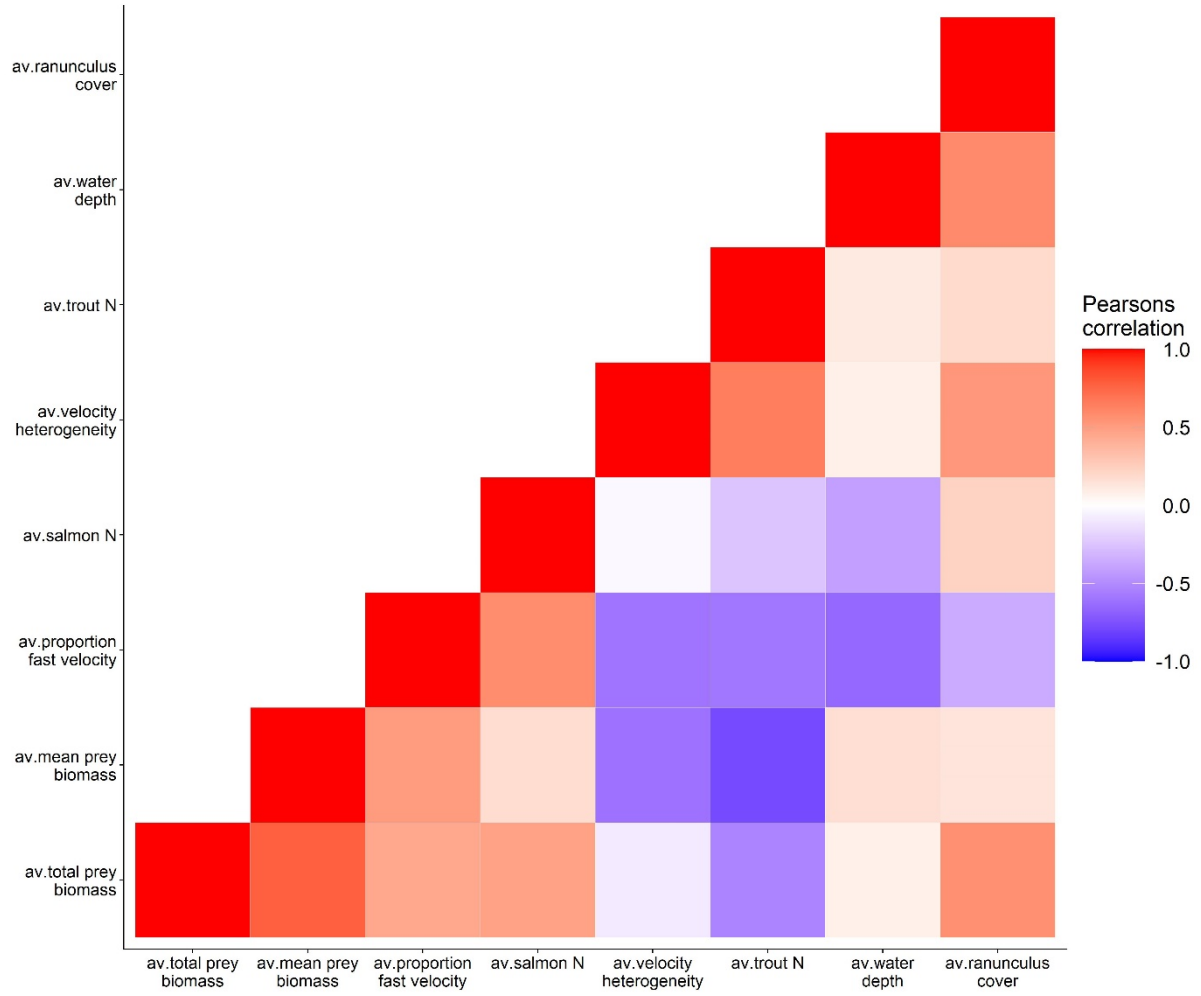


**Figure S2.** Correlation matrix for explanatory variables included in salmon growth SEM.