

1 **High summer macrophyte cover increases abundance, growth and feeding of**
2 **juvenile Atlantic salmon**

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12 **Running head:** Aquatic plants benefit juvenile salmon

13 **Open Research Statement**

14 Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.612jm643t> (Marsh
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16 **Abstract**

17 Aquatic habitats are severely threatened by human activities. For anadromous species, managing
18 freshwater habitats to maximise production of more, larger juveniles could improve resilience to
19 threats in marine habitats and enhance population viability. In some juvenile salmonid habitats,
20 complexity created by large substrates provides resources and reduces competitive interactions,
21 thereby promoting juvenile production. In lowland rivers, which lack large substrates, aquatic
22 plants might provide similar complexity and enhance fish productivity. To test the influence of
23 aquatic plants on juvenile Atlantic salmon and sympatric brown trout in a lowland river, we
24 directly manipulated cover of the dominant macrophyte, *Ranunculus*, in nine sites during
25 summer and autumn for two years. We quantified the abundance, site retention and growth of
26 salmon and trout under high, medium and low *Ranunculus* cover. To investigate the effects of
27 *Ranunculus* cover on feeding opportunities and interspecific competition, we quantified available
28 prey biomass and body size, fish diet composition, and compared dietary niche overlap.

29 Experimentally increased *Ranunculus* cover supported higher salmon abundance in summer and
30 autumn, and higher site retention and growth of salmon in summer. Trout abundance and growth
31 were not influenced by *Ranunculus* cover, but trout site retention doubled in high relative to low
32 cover sites. Despite weak effects of *Ranunculus* cover on prey availability, salmon and trout
33 inhabiting high cover sites consumed larger prey and a higher biomass of prey. Furthermore,
34 dietary niche overlap was lower in high relative to low cover sites, suggesting that abundant
35 *Ranunculus* reduced interspecific competition. This field experiment shows that high *Ranunculus*
36 cover can support more and better growing juvenile salmon, and facilitate foraging and co-
37 existence of sympatric salmonid species. Maintaining or enhancing natural macrophyte cover can
38 be achieved through sympathetic in-river and riparian vegetation management and mitigating

39 pressures on them, such as sediment inputs and low flows, or through planting. Further research
40 should test whether macrophyte cover benefits propagate to subsequent life-stages, particularly
41 juvenile overwintering associated with high mortality. This knowledge, in combination with our
42 findings, would further clarify whether beneficial juvenile habitat can improve the viability of at-
43 risk salmonid populations. Overall, our findings suggest that the aims of river restoration might
44 be achieved through promotion of instream aquatic vegetation.

45

46 **Keywords:** Diet, fisheries management, habitat management, interspecific competition, niche
47 overlap, restoration, *Salmo salar*, *Salmo trutta*

48 **Introduction**

49 Natural habitats influence population and community dynamics by providing resources for
50 growth and reproduction, refuge from predation, and protection from inclement environmental
51 conditions (Morrison *et al.*, 1988). Consequently, habitat degradation is one of the major causes
52 of population declines and species extirpation, especially in freshwater ecosystems (Butchart *et*
53 *al.*, 2010; Reid *et al.*, 2019). Developing successful conservation strategies to improve
54 population viability requires not only an understanding of how the species interacts with their
55 habitat, but also how habitat management can be most effective, i.e. by targeting a critical life
56 stage, or a habitat where intervention is most feasible (Santini *et al.*, 2019). For example,
57 management actions to increase habitat complexity, including woody debris installations and
58 channel braiding, have been linked to increased productivity in all ages of juvenile Chinook
59 salmon *Oncorhynchus tshawytscha* in rivers discharging into Puget Sound in north-western
60 United States (Hall *et al.*, 2018). Combinations of woody debris and boulder installations led to
61 increased densities in all ages of brown trout *Salmo trutta* in six forest streams in northern
62 Finland that were detectable up to 12 years after their installation (Louhi *et al.*, 2016). Similarly,
63 river restoration actions, such as woody debris and boulder installations, have been shown to
64 increase density and biomass of juvenile Atlantic salmon *S. salar* in a tributary of the Salmon
65 River in Newfoundland, Canada (van Zyll de Jong & Cowx, 2016). Such restoration actions aim
66 to re-establish or improve degraded habitats by restoring fluvial processes, habitat connectivity
67 and in-stream structures, and are increasingly common (Hendry *et al.*, 2003; Foote *et al.*, 2020).
68 Multi-decadal declines in wild populations of anadromous Atlantic salmon (hereafter salmon)
69 are thought to result from reduced survival during the marine stage of their lifecycle and thus
70 fewer adults returning to rivers to reproduce (Friedland *et al.*, 2009; Chaput, 2012). Some causes

71 of mortality can be targeted, such as reducing farmed salmon escapes and the attendant impacts
72 on wild populations (Dempster *et al.*, 2018), but the negative impacts of climate change on
73 growth and survival at sea are more difficult to manage (Friedland *et al.*, 2009; Russell *et al.*,
74 2012). There is recent evidence that larger juvenile salmon have a higher probability to survive
75 their post-smolt marine phase and return as adults to spawn (Armstrong *et al.*, 2018; Gregory *et*
76 *al.*, 2018, 2019). Yet, in multiple rivers, juvenile salmon have been getting smaller (Gregory *et*
77 *al.*, 2017). A better understanding of how freshwater habitats influence juvenile salmon could be
78 used to design more tangible management and restoration actions (Russell *et al.*, 2012) that
79 promote more, larger juvenile salmon smolts (Gregory *et al.*, 2019).

80 Habitat complexity has been shown to regulate juvenile salmon abundance and growth by a
81 variety of mechanisms in rain-fed rivers, whose water levels are recharged by variable rainfall.
82 For example, shelter availability reduces metabolic costs, and large substrates, such as boulders,
83 visually isolate individuals from their competitors (Millidine *et al.*, 2006; Venter *et al.*, 2008).
84 Habitats of lowland rivers, whose water levels respond less to rainfall events and are
85 predominately groundwater-fed, tend to lack large substrates and are instead dominated by
86 submerged macrophytes (Baattrup-Pedersen *et al.*, 2018). Although the influence of macrophytes
87 on juvenile salmon have been less studied than, for instance, impacts of woody debris and
88 boulders, there is recent evidence to suggest that macrophyte cover benefits juvenile salmon, For
89 example, higher cover of the dominant water crowfoots (*Ranunculus* spp.) in a southern England
90 chalk stream was related to higher autumn densities of juvenile salmon (Marsh *et al.*, 2020), and
91 salmon were observed using vegetated habitat in the absence of large cobble cover in the
92 lowland North American Narraguagus River, which is characterised by a variety of macrophytes

93 including rushes (Juncaceae), sedges (Cyperaceae) and pondweeds (Potamogetonaceae) (Beland
94 *et al.*, 2004).

95 Yet, the mechanisms enhancing juvenile salmon densities in macrophyte-dominated habitats are
96 unknown. Whereas macrophytes support abundant communities of macroinvertebrates (Harrison
97 & Harris, 2002; Lusardi *et al.*, 2018), it is unknown whether this enhances salmon feeding rates
98 and improves their growth and survival (Keeley & Grant, 1997; Armstrong *et al.*, 2018).

99 Manipulation of macrophyte cover during peaks of juvenile salmon growth, i.e. summer months,
100 could therefore be a tangible management strategy to maximise their growth and subsequent
101 survival. This could be particularly pertinent considering management of macrophyte cover,
102 including *Ranunculus* spp., which is actively reduced to mitigate flood risk (Baattrup-Pedersen *et*
103 *al.*, 2018) and threatened by drought, abstraction, channel management and nutrient enrichment
104 (Cranston & Derby, 2004).

105 Here, we aimed to quantify the influence of the lowland macrophytes, *Ranunculus*, on juvenile
106 salmon abundance, movements and growth in the presence of sympatric brown trout (hereafter
107 trout) by directly manipulating in-situ *Ranunculus* cover across two seasons and two years.

108 Whereas this study focuses on the responses of salmon to *Ranunculus* manipulation, the natural
109 range of trout overlaps widely with salmon in Europe and many studies have highlighted the
110 potential for them to compete for limited resources by exploitative and interference competition
111 (reviewed in Nevoux *et al.*, 2019). Consequently, we also considered the responses of juvenile
112 trout to *Ranunculus* manipulation. Specifically, we quantified the effects of high, medium and
113 low *Ranunculus* cover on, i) abundance, site retention and growth of salmon and trout
114 (collectively referred to as salmonids) during summer and autumn, and ii) availability of
115 macroinvertebrate prey biomass in the environment and in salmonid diets, and dietary niche

116 overlap between salmon and trout, during summer. We hypothesised that high *Ranunculus* cover
117 would support greater abundances of both juvenile salmonids, but especially salmon (Marsh *et*
118 *al.*, 2020), and that they would remain in these areas during summer when prey abundance and
119 size was highest and interspecific dietary overlap was lowest, thereby promoting greater feeding
120 and growth opportunities. If our hypotheses were correct, the promotion of instream macrophytes
121 could potentially provide the heterogeneity desired by river restoration, adding a more natural
122 method to those already available.

123

124 **Materials and methods**

125 ***Study area and Ranunculus manipulation***

126 We carried out a *Ranunculus* manipulation experiment over two years (2016-17) in the North
127 stream, a relatively homogenous carrier of the lowland River Frome in Dorset, UK (Fig. 1). We
128 selected three blocks, approximately 100 m in length and with a mean channel width of 7.1 m (\pm
129 1.0 m SD), in locations with similar in-river habitat and limited riparian vegetation. Within each
130 block, we selected three sites that were each 20 m in length and had natural *Ranunculus* beds
131 (mean spring cover ranged from 5 to 32 %). To achieve an experimental gradient of *Ranunculus*
132 cover, each of these sites were assigned one of three *Ranunculus* treatment levels – high (>60
133 %), medium (30-40 %), and low (<10 %) – using a Latin square design. There was no difference
134 in mean *Ranunculus* cover between treatment levels prior to the initial *Ranunculus* manipulation
135 in 2016 (one-way ANOVA: $F_{2, 6} = 0.174, p = 0.844$). At the beginning of spring (March/April)
136 each year, we dug out and re-planted *Ranunculus* plants between sites as required to achieve
137 their targeted treatment level. Plants were replanted in random patches to emulate the mosaic of

138 natural *Ranunculus* beds. Buffer strips of 5 m upstream and downstream of each site were
139 created by cutting existing *Ranunculus* stands back, to minimise any edge effects (Fig. 1).
140 *Ranunculus* treatment levels were maintained over the course of the experiment until natural
141 plant senescence at the end of summer. At sites that did not require plant maintenance, we
142 simulated maintenance disturbance by walking through the sites and disturbing sediment.

143 To determine whether we maintained effective *Ranunculus* treatment levels throughout the
144 experiment, we measured *Ranunculus* cover at 25 quadrats per site every six weeks from the
145 initial manipulation in March 2016 until the end of the experiment in December 2017.

146 Percentage cover of *Ranunculus* was estimated visually in quadrats (0.5 x 0.5 m) spaced evenly
147 across five transects that spanned the channel wetted width and were spaced evenly over the
148 length of the site. This manipulation effectively maintained a gradient in *Ranunculus* cover until
149 natural senescence, although cover peaked in June/August and differences in percentage cover
150 between treatment levels were greatest during this period (Fig. 2, Appendix S1: Table S1).

151 ***Sampling procedure and data preparation***

152 In addition to measuring *Ranunculus* cover between June-October, we also monitored other
153 habitat characteristics, macroinvertebrate prey biomass and fish during this period, when the fish
154 were of a catchable size (hereafter referred to as the ‘fishing period’). Wetted channel width (m)
155 was measured at each transect, averaged for the site, and multiplied by site length (20 m) to
156 calculate site area (m²).

157 **Habitat characteristics**

158 Habitat characteristics considered to be particularly influential to juvenile salmonids (Armstrong
159 *et al.*, 2003) were surveyed in each quadrat on each sample occasion ($n = 1,800$) to allow us to

160 control for site- and time-specific influences in subsequent analyses. Water depth was measured
161 to the nearest cm, and the water surface velocity was estimated visually as one of five categories
162 [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 >100 cm s⁻¹] by
163 comparing the height and turbulence of surface water changes around a wooden metre stick. We
164 calculated the site-level proportion of fast velocities as the proportion of velocity categories 3, 4
165 and 5 recorded in quadrats at each site. The steepness in velocity gradients between a quadrat
166 and its neighbouring quadrats was calculated using the Terrain Ruggedness Index (TRI) and
167 absolute values of TRI were averaged to represent site-level velocity heterogeneity (Marsh *et al.*,
168 2020).

169 Macroinvertebrate biomass and size

170 To measure available prey in the environment, aquatic macroinvertebrates were sampled from
171 benthic substrates at three random locations within each site on each sample occasion ($n = 216$).
172 Samples were collected using a Surber sampler (0.25 m x 0.25 m, mesh aperture 250 μm), where
173 the substrate was disturbed by hand for 30 seconds. Samples were preserved in 70 % ethanol
174 solution and macroinvertebrates were identified and measured. To calculate the
175 macroinvertebrate measures for each sample, biomass of individual taxa was determined from
176 published length-mass relationships (Appendix S1: Table S2) and multiplied by their abundances
177 (Fig. 3a) in each sample. These biomasses were used to calculate macroinvertebrate biomass and
178 macroinvertebrate size as the sum and mean of biomasses at each site, respectively.

179 Macroinvertebrate biomass was used as an explanatory variable to account for differences in
180 available prey between sites in fish abundance and site retention analyses. Macroinvertebrate
181 biomass and size in June and August ($n = 108$) were used as response variables to characterise
182 the prey available in the environment as a function of *Ranunculus* cover during summer.

183 *Fish abundance, diet, site retention and growth*

184 To determine juvenile (0+) salmonid abundance and retention rate, we electrofished each site on
185 each sample occasion ($n = 72$). To maximise capture efficiency, stop nets were set in the
186 downstream and upstream buffer strips of the site. We electrofished in an upstream direction,
187 capturing and removing all individuals encountered, known as an electrofishing *pass*. Sites were
188 fished repeatedly until two consecutive passes yielded zero salmonid captures, indicating that all
189 salmonids present in the site had been removed. Each captured fish was identified to species,
190 sedated, measured (fork length, to nearest mm), weighed (to nearest 0.2 g) and marked with a
191 Passive Integrated Transponder (PIT) tag (12.5 mm length, 2.12 mm diameter; Biomark, Idaho,
192 USA). We inserted the PIT tag into the body cavity and clipped the adipose fin as an external
193 indicator for recapture. Fish smaller than 60 mm in length were not tagged to avoid detrimental
194 effects on their growth or survival (Richard *et al.*, 2013). To determine summer diet, 182 salmon
195 and 98 trout were randomly sampled across the sites during June and August. After weighing,
196 diet samples were collected by stomach flushing (Kamler & Pope, 2001) and preserved in 4%
197 formaldehyde. Diet composition was characterised as prey biomass and prey size following the
198 procedures used for macroinvertebrate biomass and macroinvertebrate size. After processing,
199 fish were released back into the site of capture once all fishing passes had been completed. All
200 procedures were carried out by licenced personnel under a UK Home Office A(SP)A licence
201 (PPL 30/3277). Observed abundance of salmon and trout caught in each site and sample
202 occasion are shown in Figs. 3b-c.

203 An unusually wet and warm 2015/16 spawning season resulted in poor recruitment of juvenile
204 salmonids on a national scale (Gregory *et al.*, 2020), including the River Frome (Marsh *et al.*,
205 2020). Indeed, fishing in June 2016 returned low numbers or no juveniles across all sites in

206 blocks 2 and 3 (Fig. 3b-c). To augment low captures of our focus species, in July 2016 we
207 transferred 50 juvenile salmon from the main river that runs parallel to the North stream (Fig. 1)
208 into each site in blocks 2 and 3. We did not tag these individuals prior to translocation because
209 we considered that the benefits would be outweighed by the added stress of anaesthetising and
210 PIT-tagging following capture by electrofishing and relocation could be detrimental to the
211 individual. Although it would have been desirable to identify whether these salmon remained in
212 the sites or were more likely to emigrate than resident salmon, the increase in salmon abundance
213 in blocks 2 and 3 in August relative to June (Fig. 3b-c) suggests that the translocation was
214 successful. We used June fish data in calculations of site retention rate and growth of recaptured
215 individuals but excluded these June abundance data from all other analyses.

216 PIT-tagged individuals caught in the same site on consecutive sampling occasions were
217 considered as recaptures and assumed to have been exposed to the site-specific *Ranunculus*
218 cover for the intervening period. In June, 28% of salmon, and 4% of trout caught were too small
219 to be tagged (fork length <60 mm) and we acknowledge the potential bias that fish tagged in
220 June and re-caught in August could represent larger individuals in the population. However,
221 there was no difference between treatments in the proportion of untagged (smaller fish) to tagged
222 (larger fish) individuals in June (one-way ANOVA, $F_{2, 11} = 0.39, p = 0.69$) and so any effect of
223 this bias should be consistent across all treatment levels.

224 Recaptured fish were used for growth analyses; as most fish were recaptured once, we consider
225 only fish measurements at their initial capture and their first recapture. Initial captures ($t-1$) could
226 include the sample occasions in June, August and September, and first recaptures (t) could
227 include the sample occasions in August, September or October. We calculated growth as the

228 change in weight of individuals, ($W_r - W_c$), where W_r and W_c represent the weight of an
229 individual at first recapture and initial capture, respectively.

230 ***Statistical analyses***

231 *Fish abundance, site retention and growth*

232 Salmonid abundance, site retention rate and growth were each modelled assuming appropriate
233 and different error structures, and separate models were constructed for each fish species.
234 Salmonid abundances ($n = 54$) were described using a negative binomial model (log-link
235 function) to account for suspected overdispersion (O'Hara & Kotze, 2010). To account for
236 variation in their abundances due to differences in habitat size, log site area was included in the
237 model as an offset (O'Hara & Kotze, 2010). This effectively models abundance per unit area and
238 does not introduce any additional parameters (Kery & Royle, 2016). Site retention rate ($n = 54$)
239 was modelled as a rate based on the numbers of tagged individuals at time $t-1$ that were
240 recaptured in the same site at time t in a binomial model (logit-link) to ensure the expected rate
241 was bounded between 0-1. We weighted occasions by the number of fish caught in time $t-1$ to
242 account for our ability to estimate the site retention rate accurately. Growth of recaptured salmon
243 ($n = 173$) and trout ($n = 85$) were described using a Gaussian mixed-effects model (identity-link).
244 To account for the influence of initial weight on growth (i.e., lower growth potential with larger
245 initial weight, Appendix S1: Fig. S1), log initial weight was included in the model as an offset.
246 All saturated models included main effects of *Ranunculus cover*, *month* or *period*, *block* and *year*
247 and a *Ranunculus cover* x *month* or *period* interaction. Where response variables covered a
248 *period* (e.g. June to August), continuous explanatory variables were averaged across periods to
249 represent a mean site-level variable. We were able to include *Site* as a random effect in the

250 growth models because we had multiple measures of the response variable (i.e. multiple
251 individuals) at each sample occasion to estimate the *Site* random effect variance. We had only
252 one measure per sample occasion of abundance and site retention that prohibited estimation of a
253 *Site* random effect variance. Instead, we included the variables representing the site- and time-
254 specific habitat characteristics that might influence the fish response variables, specifically *water*
255 *depth*, *velocity heterogeneity*, *proportion of fast velocities* and *macroinvertebrate biomass*. We
256 included all site- and time-specific habitat variables in saturated abundance and site retention rate
257 models. To account for multicollinearity between these variables and *Ranunculus cover*, we
258 calculated the variance inflation factor (VIF) for saturated models (Appendix S1: Table S3).
259 *Water depth* was excluded from all saturated models as the VIF >10 (Graham, 2003). We then
260 simplified the saturated models using backward and forward stepwise AIC variable selection to
261 test for the effect of *Ranunculus cover* whilst controlling for any non-negligible site-specific
262 influences on each response variable, i.e. the main effect of *Ranunculus cover* and interactions
263 between *Ranunculus cover* and *month* or *period* were also subject to simplification. The
264 variables *block*, *month* or *period* and *year* were excluded from the stepwise selection because
265 they represented the experimental design. Note that the growth models were not simplified
266 because site-specific influences were controlled for with a *Site* random effect.

267 *Macroinvertebrate and prey biomass and size*

268 To test whether macroinvertebrate and prey biomass and size variables were influenced by
269 *Ranunculus cover* during summer, we fit Gaussian mixed-effects models with these responses as
270 a function of main effects of *Ranunculus cover*, *month*, *year* and *block*, and a *Ranunculus cover*
271 *x month* interaction. We included a main effect of *fish species* and a *Ranunculus cover x fish*
272 *species* interaction in the analyses of prey biomass and size to determine potential interspecific

273 differences in the response, and a main effect of *fork length* because larger fish can consume
274 larger prey (Keeley & Grant, 1997). All models included a random effect of *Site* to account for
275 the multiple measures taken at the same site. Response variables were natural log transformed if
276 necessary, to meet assumptions of normality and homoscedasticity.

277 Dietary niche overlap

278 The mean proportional abundance of prey taxa in gut contents of individual fish was used to
279 measure dietary niches of salmon and trout. Dietary niche overlap was calculated using the FT
280 index (Smith & Zaret, 1982):

$$281 \quad FT = \sum \sqrt{p_{s,i} \times p_{t,i}},$$

282 where $p_{s,i}$ and $p_{t,i}$ are the mean proportion of the i th prey taxa in salmon and trout, respectively.

283 The value of FT can range between 0 (no overlap) and 1 (complete overlap). In addition to being
284 among the least biased measures of overlap, the FT index is unaffected by unequal sample sizes
285 (Smith and Zaret, 1982) and was therefore appropriate for our data. To test the statistical
286 significance of dietary overlap between salmon and trout in the different *Ranunculus* cover levels
287 in June and August, we used bootstrap resamples of individual salmon and trout dietary niche
288 measures to calculate 1000 estimates of the FT index that captured variance in the FT index due
289 to individual dietary variation (Smith, 1985). We then compared the influence of *Ranunculus*
290 cover level on niche overlap using the empirical bootstrap 95% confidence intervals. This
291 procedure was repeated to compare salmon and trout niche overlap between *Ranunculus* cover
292 levels using mean proportional biomass of prey taxa in the gut contents of individual fish.

293 Model fitting and performance

294 To compare the effects of variables recorded on different measurement scales, all numerical
295 explanatory variables were standardised prior to analyses by subtracting their mean and dividing
296 by their standard deviation. All statistical analyses were performed in R version 3.4.4 (R
297 Development Core Team, 2018) using packages lmerTest (Kuznetsova, Brockhoff &
298 Christensen, 2017) and MASS (Venables & Ripley, 2002). Model performance and goodness of
299 fit was assessed using packages MuMin (Barton, 2009) and pscl (Jackman 2017). Model
300 residuals were inspected to check assumptions of homogeneity, normality and independence
301 (Appendix S1: Figs. S2-4).

302

303 **Results**

304 Salmon abundance was positively influenced by *Ranunculus cover* (Table 1a, Fig. 4a). Marginal
305 effects plots showed that salmon abundance was strongly positively related to *Ranunculus cover*
306 in August, reducing to a weaker and negligible effect by the end of the fishing period in October
307 (Fig. 4a). This corresponds with the seasonal decline in *Ranunculus cover* in high and medium
308 treatment levels, and concomitant declines in salmon and trout abundances (Fig. 4a & Appendix
309 S1: Fig. S5a). Trout abundance was not influenced by *Ranunculus cover* (Table 1a).

310 Salmon and trout abundances differed among blocks (Table 1a), with higher abundances of both
311 species observed in block 1 relative to blocks 2 and 3 (Fig. 3b-c, Appendix S1: Figs. S5b & S6a).
312 Trout abundance was higher in 2017 relative to 2016 (Fig. 3c, Appendix S1: Fig. S5c). None of
313 the variables controlling for site-specific influences were retained over the effects of *Ranunculus*
314 *cover* and the *Ranunculus cover* x *month* interaction for salmon, although a positive effect of
315 *macroinvertebrate biomass* was retained alongside them (Appendix S1: Fig. S6b). A positive

316 effect of *velocity heterogeneity* explained trout abundance better than any *Ranunculus cover*
317 effects (Appendix S1: Fig S5d).

318 After accounting for differences between blocks and years and controlling for site-specific
319 variables (Table 1b, Appendix S1: Figs S7-8), site retention rates of salmon and trout were
320 influenced by *Ranunculus cover* and the strength and direction of this effect changed over time
321 for each species (Table 1b, Fig. 4b). Between June-August, there was a positive effect of
322 *Ranunculus cover* on salmon and trout site retention rate. The estimated proportion of trout
323 remaining in high cover sites was double that of trout remaining in low cover sites between
324 August-September, but between September-October there was no effect of *Ranunculus cover*.
325 Between August-September and September-October, there was a negative effect of *Ranunculus*
326 *cover* on salmon site retention, suggesting that site retention was lower in high cover sites, where
327 cover declined more strongly in autumn than in low cover sites.

328 Salmon growth was significantly influenced by the interaction between *Ranunculus cover* and
329 *period* (Table 2). There was a positive effect of *Ranunculus cover* between June-August, which
330 reversed direction between August-September (Fig. 4c). Trout growth was not influenced by
331 *Ranunculus cover*, only by *period* (Table 2), with this effect driven by greater growth between
332 June-August relative to other periods.

333 Macroinvertebrate biomass was influenced by *Ranunculus cover* differently between months and
334 years (Fig. 5a). Macroinvertebrate size was greater in June relative to August (Fig. 5b). Prey
335 biomass was greater in higher *Ranunculus cover* (Fig. 5c), and the influence of cover did not
336 differ between *fish species* or between months. Prey size was greater in the diets of fish captured
337 in high cover (Fig. 5d). Trout fed on larger prey than salmon but the relationship between

338 *Ranunculus* cover and prey size did not differ between the *fish species* (Fig. 5d). There was no
339 influence of *fork length* on the prey biomass or prey size in the diets of the fish (Fig. 5c-d).

340 Dietary niche overlap between salmon and trout prey abundance was higher in low relative to
341 high *Ranunculus* cover (Fig. 6a). When based on prey biomass, niche overlap was on average
342 greater in low *Ranunculus* cover relative to medium and high *Ranunculus* cover, which had very
343 similar distributions of niche overlap (Fig. 6b).

344

345 **Discussion**

346 Our in-situ manipulation experiment demonstrates that increased *Ranunculus* cover supports
347 larger populations of better growing juvenile (0+) salmon. We show that *Ranunculus* cover was
348 important for salmon abundance, site retention, and growth during summer, and that its positive
349 influence declined with its autumn senescence. The importance of *Ranunculus* cover for juvenile
350 trout was less clear, but site retention was substantially greater in high cover. Despite there being
351 few detectable effects on the prey availability, a higher biomass of prey and larger mean prey
352 were found in diets of salmon and trout inhabiting high *Ranunculus* cover sites. This suggests
353 that *Ranunculus* facilitates foraging and thus indirectly enhances salmonid growth. Moreover,
354 the dietary niche overlap between the two species was lowest in high cover sites, suggesting that
355 abundant *Ranunculus* might reduce interspecific competition. Together this evidence suggests
356 that managing freshwater habitats to promote or even enhance naturally occurring *Ranunculus*
357 beds could improve production of both salmon and trout juveniles.

358 Our results demonstrate that *Ranunculus* is important habitat for juvenile salmon in lowland
359 rivers. This is consistent with a catchment-wide study where high densities of juvenile salmon

360 were associated with high *Ranunculus* cover (Marsh *et al.*, 2020). This positive influence of
361 *Ranunculus* could act on salmon directly by providing shelter, or indirectly by promoting habitat
362 complexity. For example, the addition of boulders to increase complexity in rivers supports
363 higher densities of salmon, likely due to increased visual isolation between neighbours and
364 subsequent reduced territorial behaviour (Venter *et al.*, 2008). Individual salmon were more
365 likely to remain in sites with high *Ranunculus* cover during summer, possibly because this
366 habitat afforded better growth conditions. Floating canopy offers valuable overhead protection
367 from aerial predators, whereas the increased structural complexity within the water column
368 affords refuge from aquatic predators and competitors (Johnsson *et al.*, 2004; Venter *et al.*,
369 2008). This can reduce costly vigilance behaviour (Metcalf *et al.*, 1987), thus enhancing feeding
370 opportunities and ultimately, growth potential.

371 *Ranunculus* appeared to facilitate greater feeding opportunities for both salmon and trout and
372 reduce interspecific competition. While *Ranunculus* can support abundant macroinvertebrate
373 communities (Harrison & Harris, 2002), its influence on macroinvertebrate biomass in this study
374 differed between summer months, which could reflect seasonal fluctuations in abundance of
375 macroinvertebrates (Wright & Symes, 1999). Nevertheless, both prey biomass and prey size
376 consumed by salmon and trout were greater in high *Ranunculus* cover throughout summer,
377 suggesting that abundant *Ranunculus* enabled greater rates of prey encounter and capture,
378 including profitable larger prey items (Keeley & Grant, 1997). Moreover, dietary niche overlap
379 was greatest between salmonids occupying low *Ranunculus* cover, suggesting stronger
380 competition for limited and similar prey in these habitats. Complex macrophyte structures provide
381 more substrate for attachment and resource collection, supporting abundant and diverse
382 periphyton and macroinvertebrate communities (Sand-Jensen, 1998; Warfe & Barmuta, 2006).

383 Structures, such as *Ranunculus*, also create heterogenous water velocities which salmonids
384 utilise for energy-efficient foraging (Sand-Jensen, 1998; Riley *et al.*, 2009). Consequently,
385 *Ranunculus* could provide suitable foraging environments for salmonids to exploit.

386 Although we did not detect an effect of *Ranunculus* cover on trout abundance or growth,
387 individual trout were more likely to be recaptured in sites with high relative to low *Ranunculus*
388 cover throughout summer. This was perhaps caused by increased foraging opportunities and
389 reduced interspecific competition, suggesting that *Ranunculus* does convey some benefits for
390 trout. Juvenile trout use areas with high aquatic vegetation during summer (Maki-Petays *et al.*,
391 1997), but reported influences of riparian and in-river cover on trout growth are inconsistent
392 (Riley *et al.*, 2009; McCormick & Harrison, 2011). We found trout abundance was better
393 predicted by velocity heterogeneity, consistent with a correlative study of influences on trout
394 densities (Marsh *et al.*, 2020), which could suggest an indirect effect of *Ranunculus*. Together
395 with our results, these varied findings suggest that whilst macrophytes might afford benefits to
396 trout, the variables influencing their abundance and growth are complex, perhaps because trout
397 are more behaviourally plastic than salmon (Nevoux *et al.*, 2019).

398 By repeatedly sampling our experimental sites across multiple months and seasons, we were able
399 to identify important temporal distinctions in the estimated benefits of *Ranunculus* cover for
400 juvenile salmon and trout. However, this also potentially exposed individual fish to repeated
401 capture by electrofishing, which could have influenced the survival and movement of fish.

402 Although electrofishing can cause fish mortality, we used electrofishing settings known to return
403 high salmonid parr capture rates and cause <1% mortality rates on the River Frome (Marsh *et al.*,
404 2020). As such, we recorded only two dead individuals during post-tagging recovery (one
405 salmon and one trout) out of the 1,197 individuals that were sampled during this study.

406 Furthermore, it is generally accepted that any impact of electrofishing on fish mortality is
407 negligible in relation to population abundances (e.g., McMichael *et al.*, 1998). While sampling
408 could have affected fish movement, over a third of individuals captured throughout the study (n
409 = 401) were recaptured individuals, suggesting that individuals stayed in the experimental sites
410 and that any displacement could be temporary. Finally, the sampling protocol was consistent
411 across sites, thus any effects of sampling on fish abundance or site fidelity are unlikely to have
412 substantially affected our ability to test for an influence of *Ranunculus* cover on these response
413 variables.

414 Macrophytes in lowland rivers are typically managed by weed cutting to reduce the risk of
415 flooding, which takes place throughout the year and negatively impacts ecological status of
416 rivers (Baattrup-Pedersen *et al.*, 2018). Our findings can help prioritise the timing of weed cuts
417 to the mutual benefit of stakeholders and salmonids. For example, in the context of our findings,
418 cutting during spring would reduce plant biomass when flood risk is high, whilst stimulating
419 further plant regrowth (Baattrup-Pedersen *et al.*, 2018). This would enhance *Ranunculus* cover
420 during summer when its positive influence on salmonids was greatest. There are also
421 implications for the re-establishment of riparian canopy cover, which can mitigate against
422 bankside sediment loss and rising temperatures (Cole *et al.*, 2020), but limits macrophyte growth
423 (Riley *et al.*, 2009). We recommend maintaining a mosaic of bankside vegetation that would
424 supply shade to limit high temperatures that stress freshwater species, and direct sunlight to
425 promote in-river vegetation growth. Encouraging a mosaic of bankside vegetation and
426 modification of catchment land-use practices could also limit bank erosion and the input of fine
427 sediments into rivers (Cole *et al.*, 2020) that, along with low flows and nutrient enrichment, were

428 potential drivers of a widespread disappearance of *Ranunculus* in lowland rivers in southern
429 England during the early 1990's (Cranston & Darby, 2004).

430 Understanding the current threats to macrophytes, such as *Ranunculus*, and establishing cost-
431 effective measures to mitigate them could help safeguard at-risk salmonid populations in English
432 chalk streams and elsewhere. For example, studies have identified positive associations between
433 various species of macrophyte and salmonids, including brown trout in northern Finland (Maki-
434 Petays *et al.*, 1997) and Sweden (Eklov & Greenberg, 1998), Atlantic salmon in Ireland
435 (McCormick & Harrison, 2011) and northern USA (Beland *et al.*, 2004), and steelhead trout
436 *Oncorhynchus mykiss* in western USA (Lusardi *et al.*, 2018), suggesting that aquatic plants
437 constitute important habitats for salmonids across a wide range of regions and habitat types.

438 Artificial structures can improve habitat for wild salmonids, but are expensive, and can lose
439 effectiveness or be washed away downstream over time (Binns, 2004; Foote *et al.*, 2020). Such
440 structures may also be geared towards performing specific function, such as digging pools for
441 trout, or planting riparian canopy to provide terrestrial inputs and overhead cover (Binns, 2004;
442 McCormick & Harrison, 2011). Naturally occurring macrophytes, such as *Ranunculus*, can
443 create complex habitats to structure and support both biotic and abiotic components of salmonid
444 ecosystems, and could be cost-effective alternatives to artificial structures.

445 In response to three decades of declining Atlantic salmon populations throughout southern and
446 central Europe and North America, there have been calls to better understand how management
447 of juvenile rearing habitat could maximise the numbers and quality of seaward-migrating salmon
448 smolts to increase survival at sea and the number of returning spawners (Armstrong *et al.*, 2018;
449 Gregory *et al.*, 2019). Our findings suggest that maintaining naturally occurring or even
450 enhancing *Ranunculus* habitats in lowland rivers provides favourable conditions to support both

451 greater numbers of juveniles, and better feeding and growth opportunities during summer. Where
452 macrophytes are naturally present, augmenting their abundance and reducing their stressors
453 should be considered as river restoration management actions, alongside woody debris and
454 boulder installations, to ameliorate juvenile salmon abundance and growth. Further research
455 should investigate whether these benefits propagate to subsequent life stages, such as the
456 likelihood of surviving overwinter or growing into a large smolt. Together with our findings, this
457 knowledge would further elucidate the role of macrophytes in regulating juvenile salmon
458 production in lowland rivers. Improving juvenile freshwater habitat across river types could be
459 the key to unlocking improved sea survival and ultimately seeing more adult salmon returning to
460 our rivers.

461

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468 and J.I.J. carried out fieldwork and data collection; J.M. led the data analysis and writing with
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607 **Table 1.** Effects of *Ranunculus* manipulation on juvenile (age 0+) salmon and trout abundance and site retention rate. Parts (a) and (b)
 608 show analysis of deviance summaries for the negative binomial abundance models, and the binomial site retention rate model,
 609 respectively. Models tested for *Ranunculus cover* and *Ranunculus cover* x Month or Period effects while controlling for site- and time-
 610 specific habitat characteristics (that are shown in grey if retained) using model simplification.

		Salmon					Trout				
		<i>Df</i>	<i>Deviance</i>	<i>Residual Df</i>	<i>Residual deviance</i>	<i>Pr(>Chi)</i>	<i>Df</i>	<i>Deviance</i>	<i>Residual Df</i>	<i>Residual deviance</i>	<i>Pr(>Chi)</i>
(a)											
Abundance (<i>n</i> = 54)	<i>Ranunculus</i>	1	75.4	52	252.8	<0.01	-	-	-	-	-
	Month	2	55.1	50	197.7	<0.01	2	20.4	51	172.3	<0.01
	Block	2	104.8	48	92.9	<0.01	2	36.0	49	136.4	<0.01
	Year	1	0.4	47	92.5	0.55	1	75.9	48	60.5	<0.01
	Macroinvert. biomass	1	16.3	46	76.2	<0.01	-	-	-	-	-
	Velocity heterogeneity	-	-	-	-	-	1	5.6	47	54.9	0.02
	<i>Ranunculus</i> x Month	2	4.5	44	71.7	0.11	-	-	-	-	-
Total variance explained = 0.80						Total variance explained = 0.72					
(b)											
Site retention rate (<i>n</i> = 54)	<i>Ranunculus</i>	1	75.9	46	1986.9	<0.01	1	4.2	38	432.1	0.04
	Period	2	320.5	44	1666.5	<0.01	2	129.5	36	302.6	<0.01
	Block	2	333.6	42	1332.8	<0.01	2	12.5	34	290.1	<0.01
	Year	1	24.8	41	1308.0	<0.01	1	1.1	33	289.0	0.29
	Fast velocities	1	4.9	40	1303.2	0.03	-	-	-	-	-
	Macroinvert. biomass	1	93.6	39	1209.6	<0.01	1	27.4	32	261.6	<0.01
	Velocity heterogeneity	1	5.4	38	1204.2	0.02	1	17.3	31	244.3	<0.01
<i>Ranunculus</i> x Period	2	511.9	36	692.3	<0.01	2	32.4	29	211.9	<0.01	
Total deviance explained = 0.66						Total deviance explained = 0.51					

612 **Table 2.** Effects of *Ranunculus* manipulation on growth in weight of juvenile (age 0+) salmon and trout. Table shows the analysis of
 613 variance summary for the Gaussian mixed-effects model describing growth of recaptured individuals. Note: these models were not
 614 simplified.

		<i>Df</i>	<i>Sum sq</i>	<i>Mean sq</i>	<i>F value</i>	<i>Pr(>F)</i>	<i>Df</i>	<i>Sum sq</i>	<i>Mean sq</i>	<i>F value</i>	<i>Pr(>F)</i>
Growth (Salmon <i>n</i> = 173 Trout <i>n</i> = 85)	<i>Ranunculus</i>	1	4.8	4.8	1.8	0.22	1	0.1	0.1	0.0	0.88
	Period	2	319.0	159.5	60.0	<0.01	2	125.4	62.7	15.1	<0.01
	Block	2	2.8	1.4	0.5	0.62	2	14.4	7.2	1.7	0.24
	Year	1	1.3	1.3	0.5	0.49	1	4.1	4.1	1.0	0.32
	<i>Ranunculus</i> x Period	2	86.0	43.0	16.2	<0.01	2	9.9	5.0	1.2	0.31
Total variance explained = 0.62						Total variance explained = 0.37					

615

616 **Figure captions**

617 **Figure 1.** Schematic illustration of the study locations and experimental manipulations: (a)
618 location of the River Frome in Dorset, UK; (b) locations of the three experimental blocks on the
619 North stream (black triangles); and (c) a schematic representation showing that each
620 experimental block consisted of three sites (20 m in length), each manipulated to maintain
621 contrasting *Ranunculus* cover (high / medium / low) and bounded by *Ranunculus* denuded buffer
622 strips (5 m in length).

623 **Figure 2.** Mean observed *Ranunculus* cover in each treatment level (vertical lines around the
624 mean show the standard error) during all sample occasions ($n = 3,150$) including before
625 manipulation (left of the dashed line): rows of plot indicate each year (2016 and 2017), columns
626 illustrate experimental blocks (1-3), and the shaded grey area highlights the fishing period (June-
627 October).

628 **Figure 3.** Observed abundance of (a) total macroinvertebrates, (b) juvenile salmon, and (c)
629 juvenile trout, in each year (row), block (column), *Ranunculus* treatment (L = low, M = medium,
630 H = high), and sampling month (coloured bars). In panel (a), the value of total macroinvertebrate
631 abundance of bar * was far greater (30,535) than shown and was capped here for ease of viewing
632 the other panel values.

633 **Figure 4.** Influence of *Ranunculus* cover during different months or periods on juvenile
634 salmonid (a) abundance, (b) site retention rate (i.e. the weighted proportion of tagged individuals
635 that were recaptured in the same site in the following sample event) and (c) growth in weight. In
636 all plots, the solid line is the mean estimate, and the shaded area denotes the 95% confidence
637 bands, both of which are shown where the effect of *Ranunculus* cover is significant.

638 **Figure 5.** Coefficient estimates from Gaussian mixed-effects models describing variation in the
639 macroinvertebrate biomass and size (from Surber samples) and prey biomass and size (from
640 juvenile salmonid diet contents) during summer months. Four diet samples were empty and so
641 did not contribute to the prey size analysis. R^2_c is the conditional goodness of fit, i.e. the variance
642 explained by fixed and random effects. Points and values are the mean coefficient estimate, lines
643 are the 95% confidence bands, and significance levels are shown as * $p < 0.05$ and *** $p <$
644 0.001.

645 **Figure 6.** Mean (point) and 95% confidence intervals (vertical error bars) of the generated
646 bootstrap distribution of dietary niche overlap. Dietary niche overlap was calculated as the FT
647 index (Smith & Zaret, 1982) based on (a) proportional abundance, and (b) proportional biomass
648 of prey taxa observed in salmon and trout gut contents caught in low, medium and high
649 *Ranunculus* cover during summer months, with the mean (point) and 95% confidence intervals

650 (horizontal error bars) of the empirical *Ranunculus* cover at the site and time that those fish were
651 sampled.

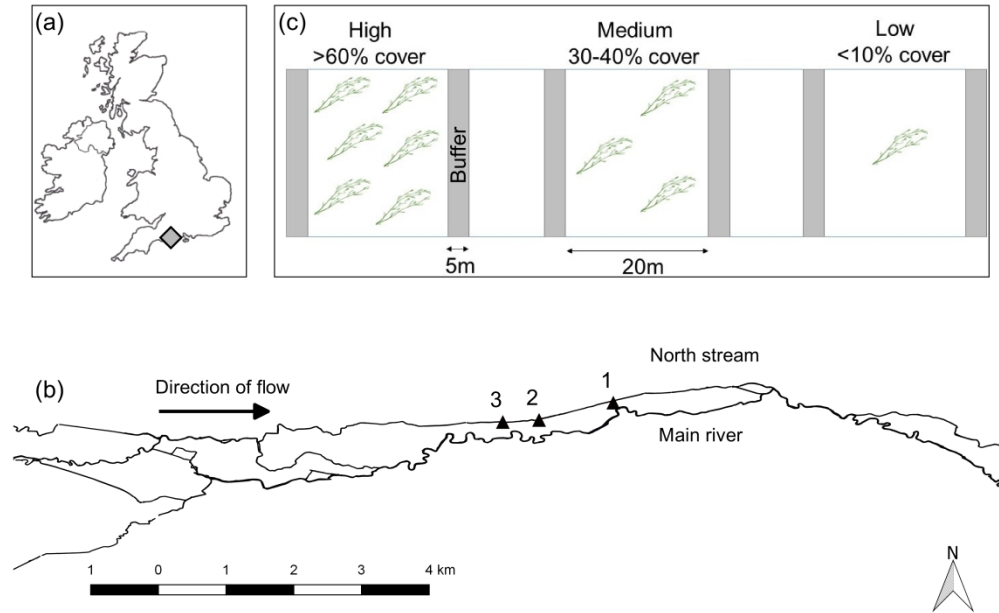
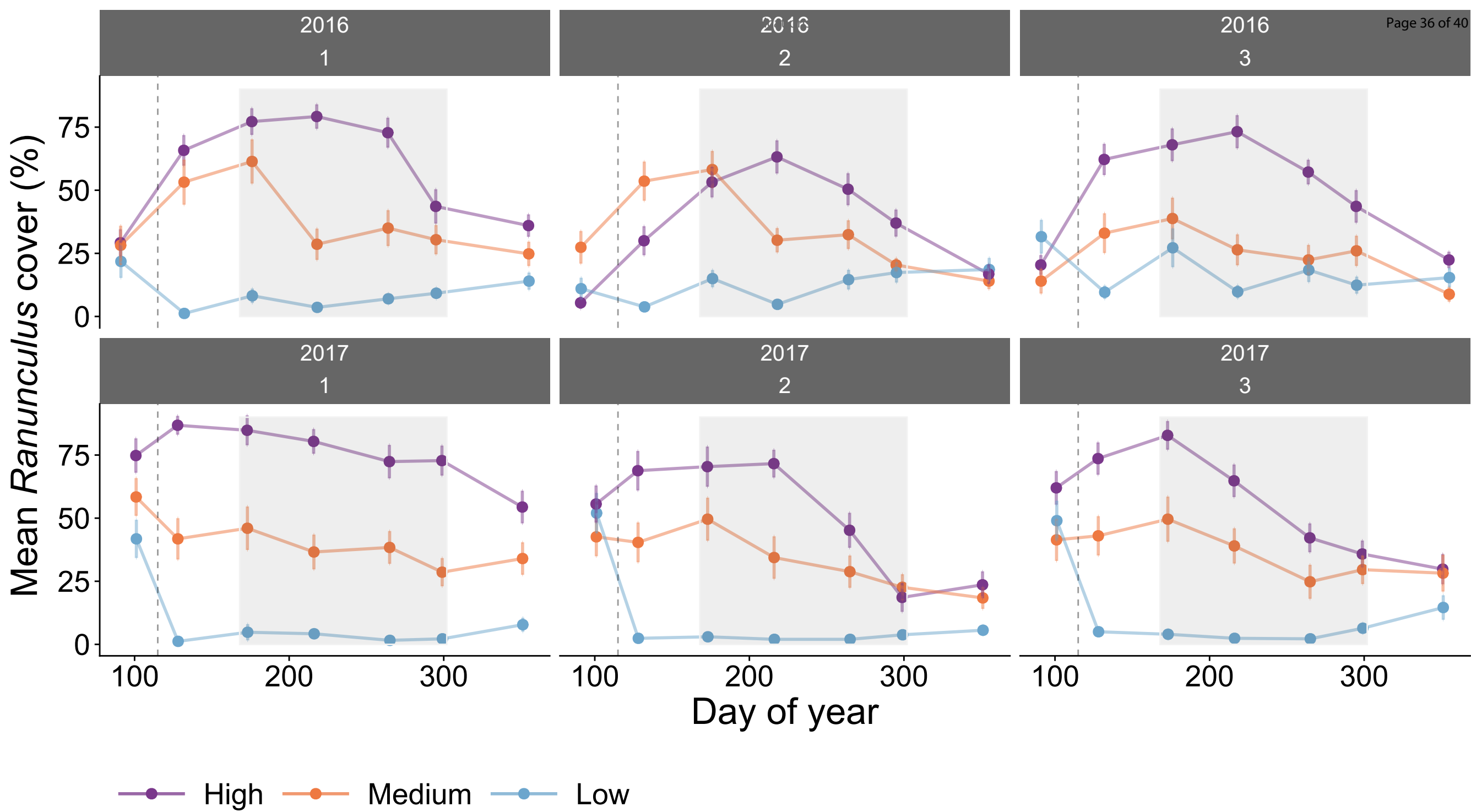
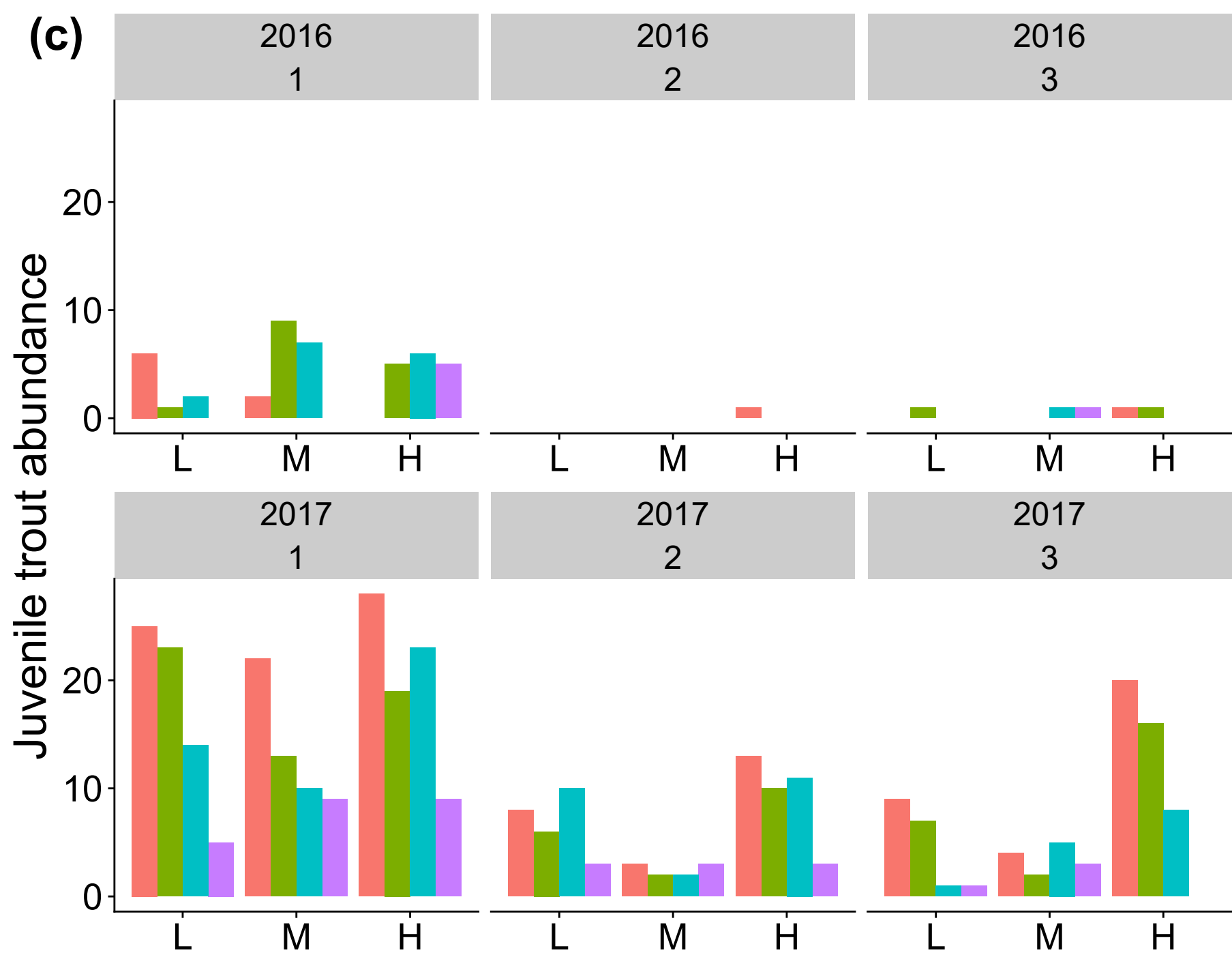
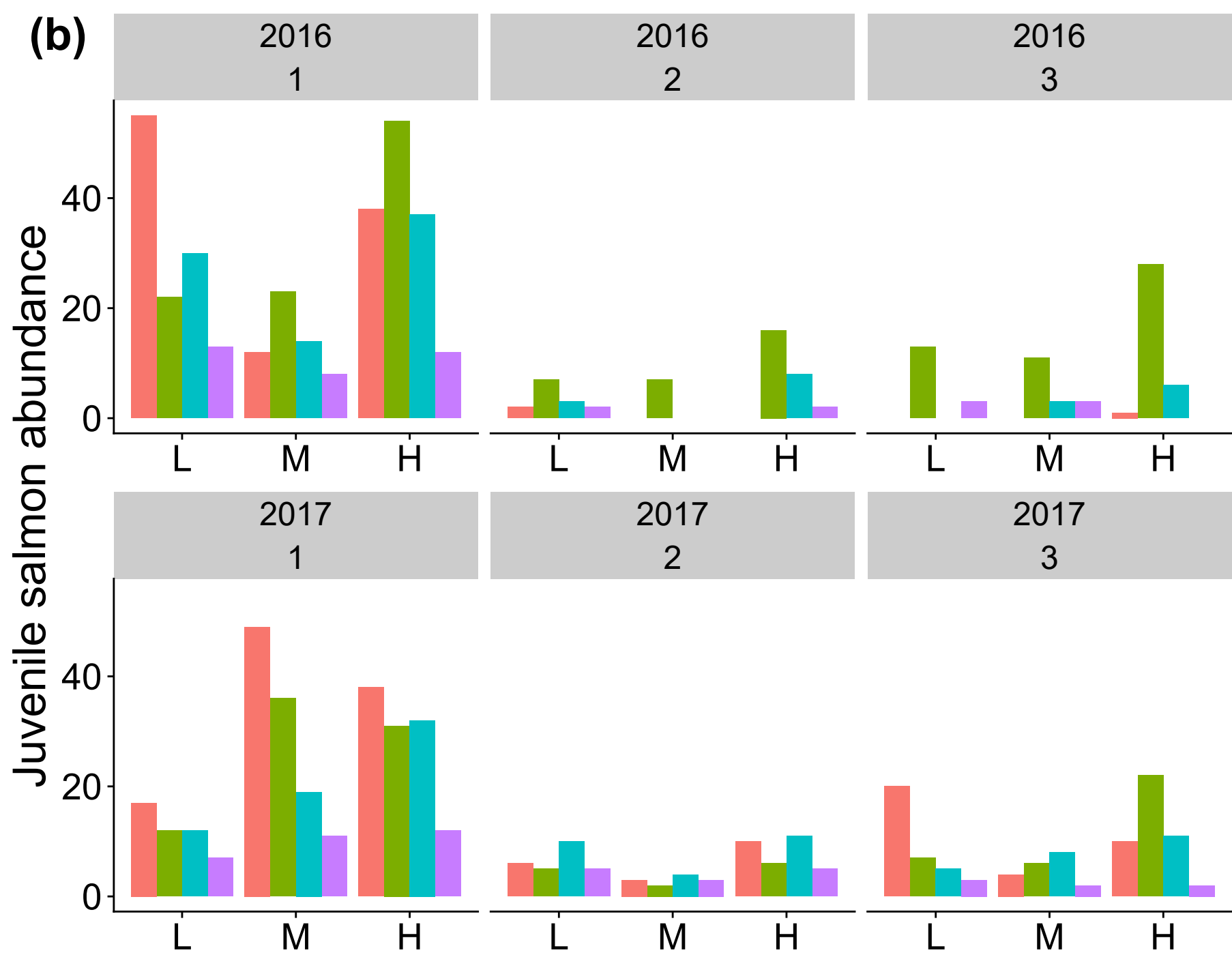
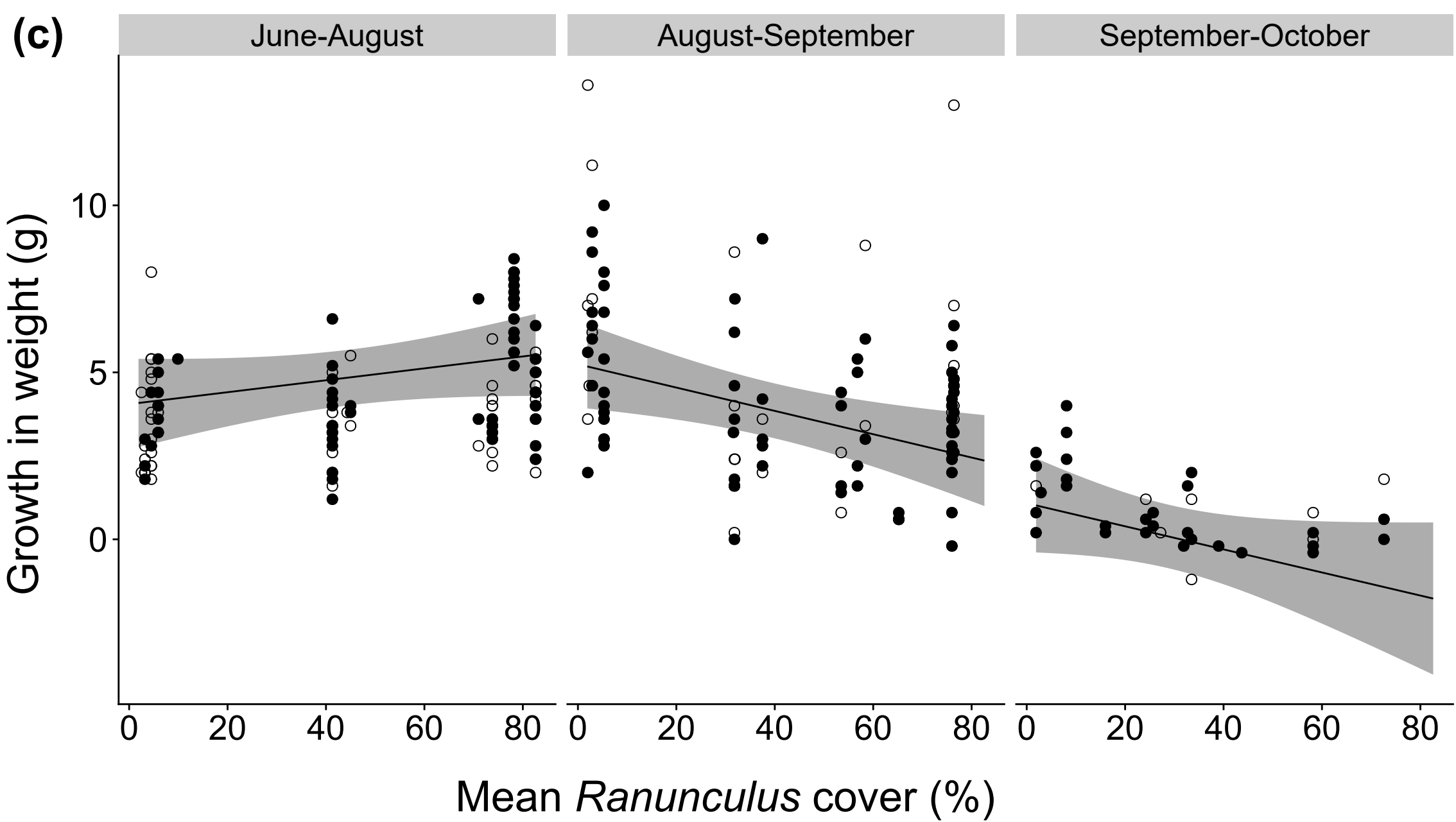
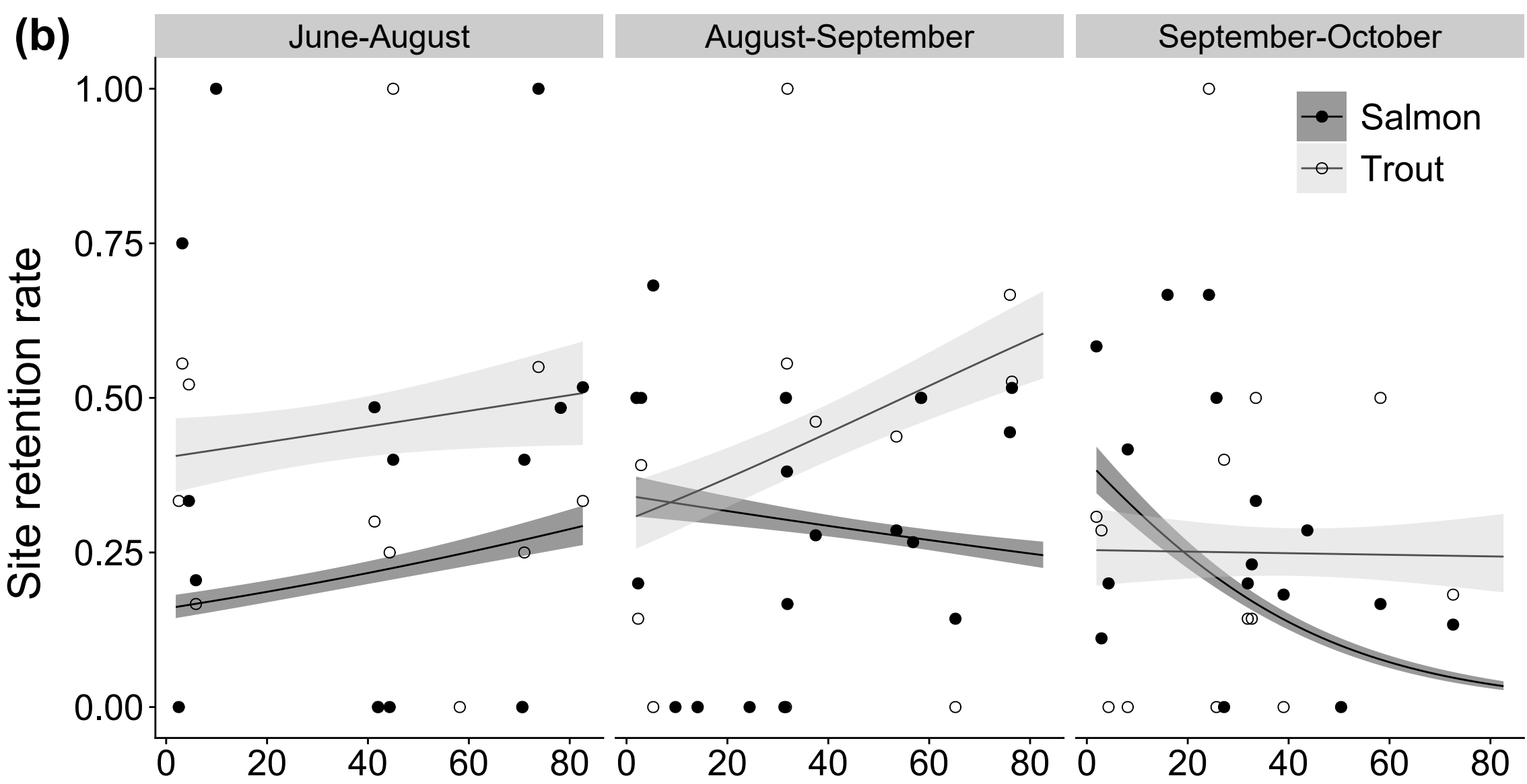
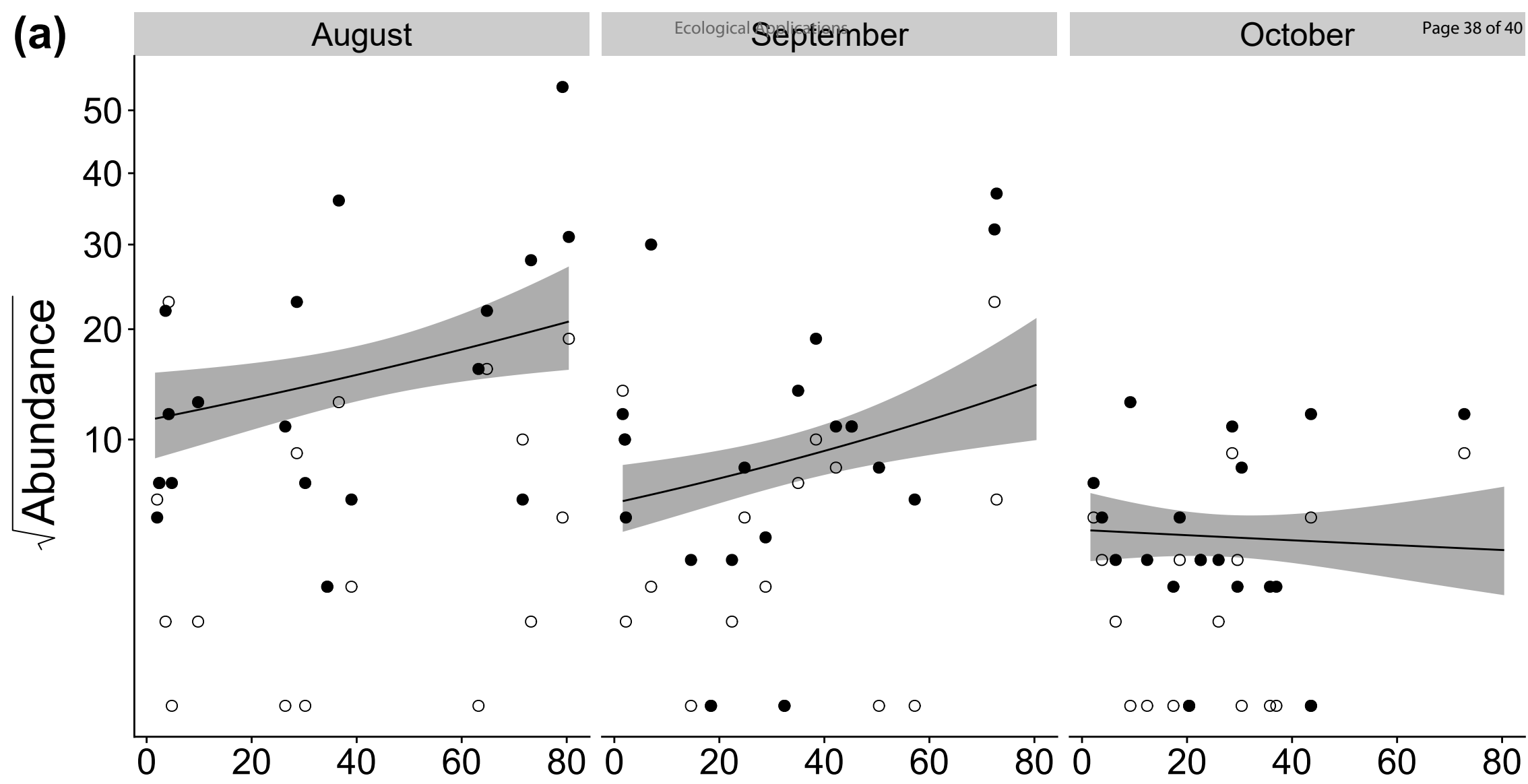


Figure 1. Schematic illustration of the study locations and experimental manipulations: (a) location of the River Frome in Dorset, UK; (b) locations of the three experimental blocks on the North stream (black triangles); and (c) a schematic representation showing that each experimental block consisted 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).





Ranunculus treatment



(a)

(b)

(c)

(d)

Macroinvertebrate biomass
(n = 108, R_C² = 0.12)

Macroinvertebrate size
(n = 108, R_C² = 0.05)

Prey biomass
(n = 280, R_C² = 0.21)

Prey size
(n = 276, R_C² = 0.22)

Ranunculus cover (%)

Month (June)

Year (2017)

Block (2)

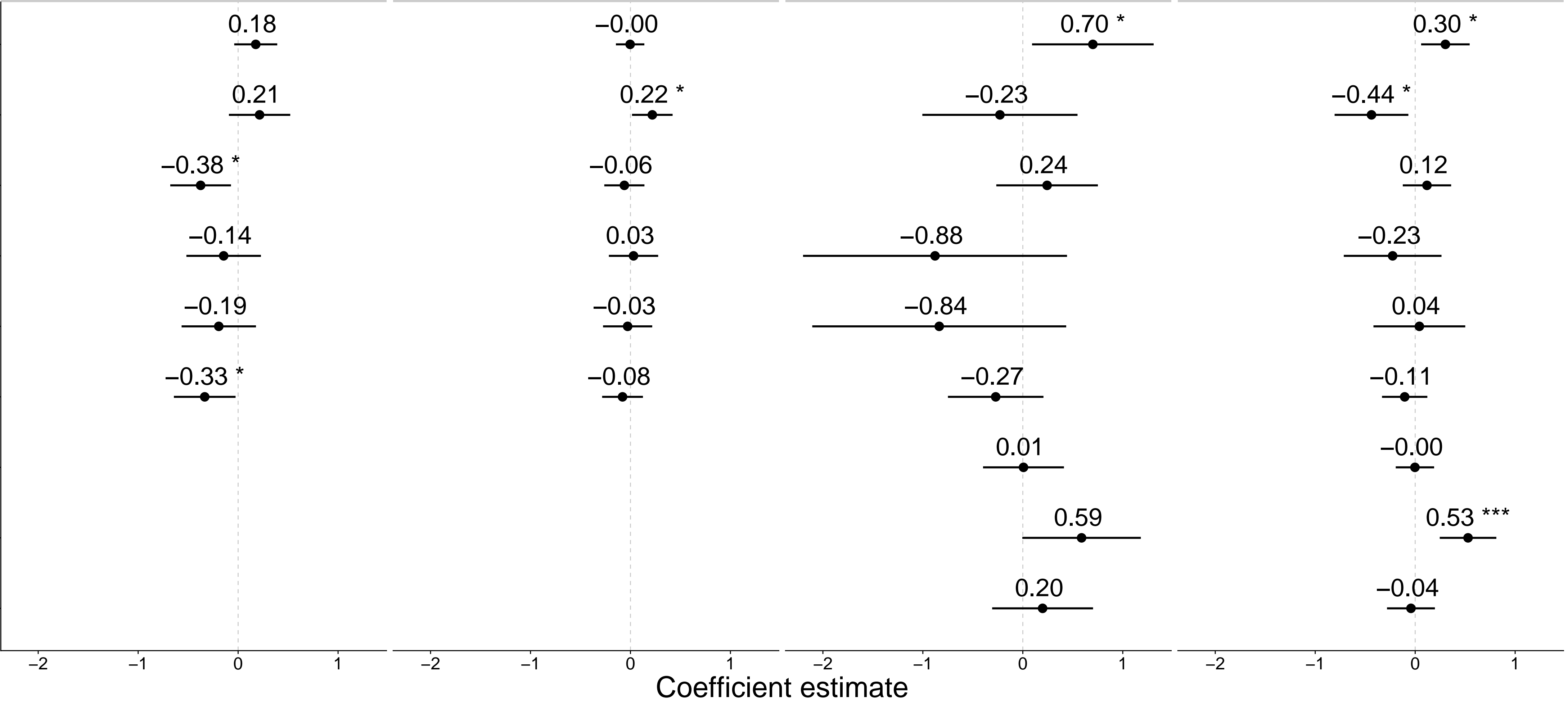
Block (3)

Ranunculus x Month

Fork length (cm)

Fish species (Trout)

Ranunculus x Species



Coefficient estimate

