



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

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Abstract. Aquatic habitats are severely threatened by human activities. For anadromous species, managing freshwater habitats to maximize production of more, larger juveniles could improve resilience to threats in marine habitats and enhance population viability. In some juvenile salmonid habitats, complexity created by large substrates provides resources and reduces competitive interactions, thereby promoting juvenile production. In lowland rivers, which lack large substrates, aquatic plants might provide similar complexity and enhance fish productivity. To test the influence of aquatic plants on juvenile Atlantic salmon and sympatric brown trout in a lowland river, we directly manipulated the cover of the dominant macrophyte, *Ranunculus*, in nine sites during summer and autumn for two years. We quantified the abundance, site retention and growth of salmon and trout under high, medium or low *Ranunculus* cover. To investigate the effects of *Ranunculus* cover on feeding opportunities and interspecific competition, we quantified available prey biomass and body size, fish diet composition and compared dietary niche overlap. Experimentally increased *Ranunculus* cover supported higher salmon abundance in summer and autumn, and higher site retention and growth of salmon in summer. Trout abundance and growth were not influenced by *Ranunculus* cover, but trout site retention doubled in high, relative to low, cover sites. Despite the weak effects of *Ranunculus* cover on prey availability, salmon and trout inhabiting high cover sites consumed larger prey and a higher biomass of prey. Furthermore, dietary niche overlap was lower in high, relative to low, cover sites, suggesting that abundant *Ranunculus* reduced interspecific competition. This field experiment shows that high *Ranunculus* cover can support more and better growing juvenile salmon, and facilitate foraging and co-existence of sympatric salmonid species. Maintaining or enhancing natural macrophyte cover can be achieved through sympathetic in-river and riparian vegetation management and mitigating pressures on them, such as sediment inputs and low flows, or through planting. Further research should test whether macrophyte cover benefits propagate to subsequent life stages, particularly juvenile overwintering associated with high mortality. This knowledge, in combination with our findings, would further clarify whether beneficial juvenile habitat can improve the viability of at-risk salmonid populations. Overall, our findings suggest that the aims of river restoration might be achieved through promotion of in-stream aquatic vegetation.

Key words: diet; fisheries management; habitat management; interspecific competition; niche overlap; restoration; *Salmo salar*; *Salmo trutta*.

INTRODUCTION

Natural habitats influence population and community dynamics by providing resources for growth and reproduction, refuge from predation, and protection from inclement environmental conditions (Morrison et al. 1998). Consequently, habitat degradation is one of the major causes of population declines and species

extirpation, especially in freshwater ecosystems (Butchart 2010, Reid 2019). Developing successful conservation strategies to improve population viability requires not only an understanding of how the species interacts with their habitat, but also how habitat management can be most effective, i.e., by targeting a critical life stage or a habitat where intervention is most feasible (Santini et al. 2019). For example, management actions to increase habitat complexity, including woody debris installations and channel braiding, have been linked to increased productivity in all ages of juvenile Chinook salmon *Oncorhynchus tshawytscha* in rivers discharging into Puget Sound in the northwestern United States (Hall et al.

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2018). Combinations of woody debris and boulder installations have led to increased densities in all ages of brown trout *Salmo trutta* in six forest streams in northern Finland that were detectable up to 12 years after their installation (Louhi et al. 2016). Similarly, river restoration actions, such as woody debris and boulder installations, have been shown to increase density and biomass of juvenile Atlantic salmon *S. salar* in a tributary of the Salmon River in Newfoundland, Canada (van Zyll de Jong and Cowx 2016). Such restoration actions aim to re-establish or improve degraded habitats by restoring fluvial processes, habitat connectivity and in-stream structures, and are increasingly common (Hendry et al. 2003, Foote and Biron 2020).

Multidecadal declines in wild populations of anadromous Atlantic salmon (from this point forwards salmon) are thought to result from reduced survival during the marine stage of their lifecycle and therefore fewer adults returning to rivers to reproduce (Friedland et al. 2009, Chaput 2012). Some causes of mortality can be targeted, such as reducing farmed salmon escapes and the attendant impacts on wild populations (Dempster et al. 2018), but the negative impacts of climate change on growth and survival at sea are more difficult to manage (Friedland et al. 2009, Russell 2012). There is recent evidence that larger juvenile salmon have a higher probability of surviving their post-smolt marine phase and returning as adults to spawn (Armstrong et al. 2018, Gregory and Armstrong 2018, Gregory et al. 2019). Yet, in multiple rivers, juvenile salmon have been getting smaller (Gregory et al. 2017). A better understanding of how freshwater habitats influence juvenile salmon could be used to design more tangible management and restoration actions (Russell et al. 2012) that promote more, larger juvenile salmon smolts (Gregory et al. 2019).

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

sedges (Cyperaceae) and pondweeds (Potamogetonaceae) (Beland and Triel 2004).

Yet, the mechanisms enhancing juvenile salmon densities in macrophyte-dominated habitats are unknown. Whereas macrophytes support abundant communities of macroinvertebrates (Harrison and Harris 2002, Lusardi and Jeffres 2018), it is unknown whether this enhances salmon feeding rates and improves their growth and survival (Keeley and Grant 1997, Armstrong et al. 2018). Manipulation of macrophyte cover during peaks of juvenile salmon growth, i.e., summer months, could therefore be a tangible management strategy to maximize their growth and subsequent survival. This could be particularly pertinent, considering the management of macrophyte cover, including *Ranunculus* spp., which is actively reduced to mitigate flood risk (Baatrup-Pedersen et al. 2018) and threatened by drought, abstraction, channel management and nutrient enrichment (Cranston and Darby 2004).

Here, we aimed to quantify the influence of the lowland macrophytes, *Ranunculus*, on juvenile salmon abundance, movements and growth in the presence of sympatric brown trout (from this point forwards trout) by directly manipulating *in situ* *Ranunculus* cover across two seasons and two years. Whereas this study focuses on the responses of salmon to *Ranunculus* manipulation, in Europe the natural range of trout overlaps widely with salmon and many studies have highlighted the potential for them to compete for limited resources by exploitative and interference competition (reviewed in Nevoux 2019). Consequently, we also considered the responses of juvenile trout to *Ranunculus* manipulation. Specifically, we quantified the effects of high, medium or low *Ranunculus* cover on: (1) abundance, site retention and growth of salmon and trout (collectively referred to as salmonids) during summer and autumn, and (2) availability of macroinvertebrate prey biomass in the environment and in salmonid diets, and dietary niche overlap between salmon and trout, during summer. We hypothesized that high *Ranunculus* cover would support greater abundances of both juvenile salmonids, but especially salmon (Marsh et al. 2020), and that they would remain in these areas during summer when prey abundance and size was highest and interspecific dietary overlap was lowest, thereby promoting greater feeding and growth opportunities. If our hypotheses were correct, the promotion of in-stream macrophytes could potentially provide the heterogeneity desired by river restoration, adding a more natural method to those already available.

METHODS

Study area and Ranunculus manipulation

We carried out a *Ranunculus* manipulation experiment over two years (2016–2017) in the North stream, a relatively homogenous carrier of the lowland River Frome in Dorset, UK (Fig. 1). We selected three blocks,

approximately 100 m in length and with a mean channel width of 7.1 m (± 1.0 m SD), in locations with similar in-river habitats and limited riparian vegetation. Within each block, we selected three sites that were each 20 m in length and had natural *Ranunculus* beds (mean spring cover ranged from 5% to 32%). To achieve an experimental gradient of *Ranunculus* cover, each of these sites was assigned one of three *Ranunculus* treatment levels – high (>60%), medium (30–40%) or low (<10%) – using a Latin square design. There was no difference in mean *Ranunculus* cover between treatment levels before the initial *Ranunculus* manipulation in 2016 (one-way ANOVA: $F_{2,6} = 0.174$, $P = 0.844$). At the beginning of spring (March/April) each year, we dug out and replanted *Ranunculus* plants between sites as required to achieve their targeted treatment level. Plants were replanted in random patches to emulate the mosaic of natural *Ranunculus* beds. Buffer strips of 5 m upstream and downstream of each site were created by cutting existing *Ranunculus* stands back, to minimize any edge effects (Fig. 1). *Ranunculus* treatment levels were maintained over the course of the experiment until natural plant senescence at the end of summer. At sites that did not require plant maintenance, we simulated maintenance disturbance by walking through the sites and disturbing sediment.

To determine whether we maintained effective *Ranunculus* treatment levels throughout the experiment, we

measured *Ranunculus* cover at 25 quadrats per site every six weeks from the initial manipulation in March 2016 until the end of the experiment in December 2017. Percentage cover of *Ranunculus* was estimated visually in quadrats (0.5×0.5 m) spaced evenly across five transects that spanned the channel wetted width and were spaced evenly over the length of the site. This manipulation effectively maintained a gradient in *Ranunculus* cover until natural senescence, although cover peaked in June/August and differences in percentage cover between treatment levels were greatest during this period (Fig. 2; Appendix S1: Table S1).

Sampling procedure and data preparation

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

Habitat characteristics.—Habitat characteristics considered to be particularly influential to juvenile salmonids (Armstrong et al. 2003) were surveyed in each quadrat

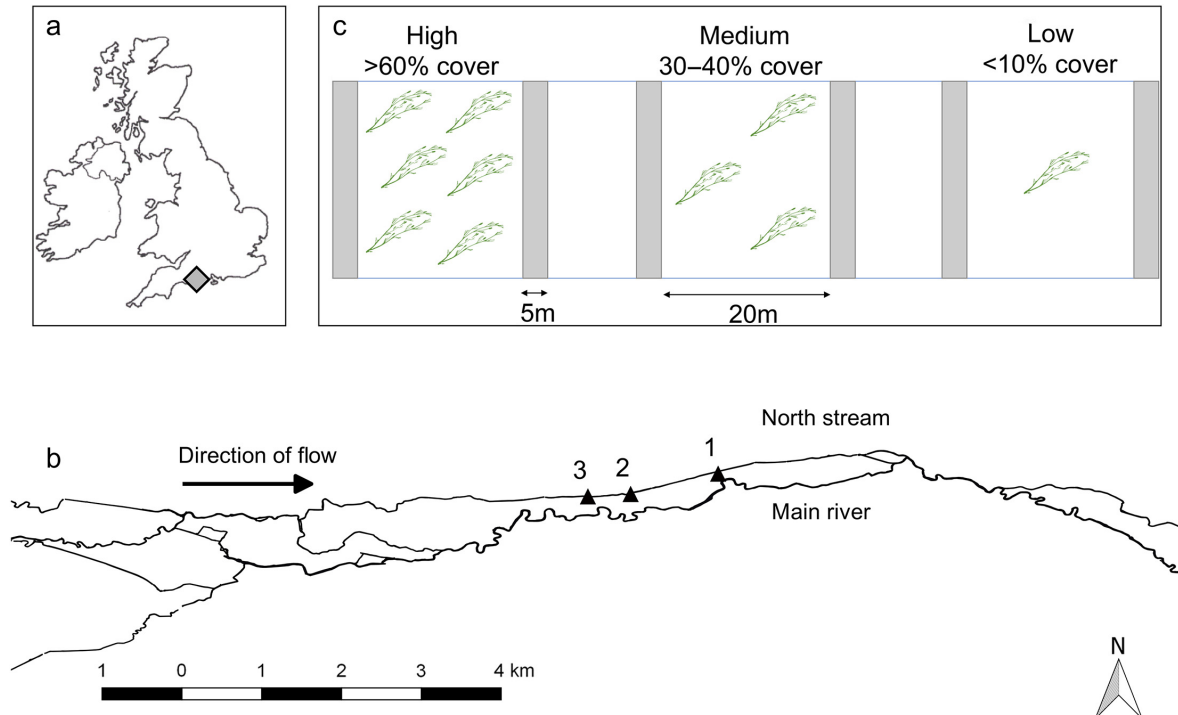


FIG. 1. Schematic illustration of the study locations and experimental manipulations: (a) location of the River Frome in Dorset, UK; (b) locations of the three experimental blocks on the North stream (black triangles); and (c) a schematic representation showing that each experimental block consisted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

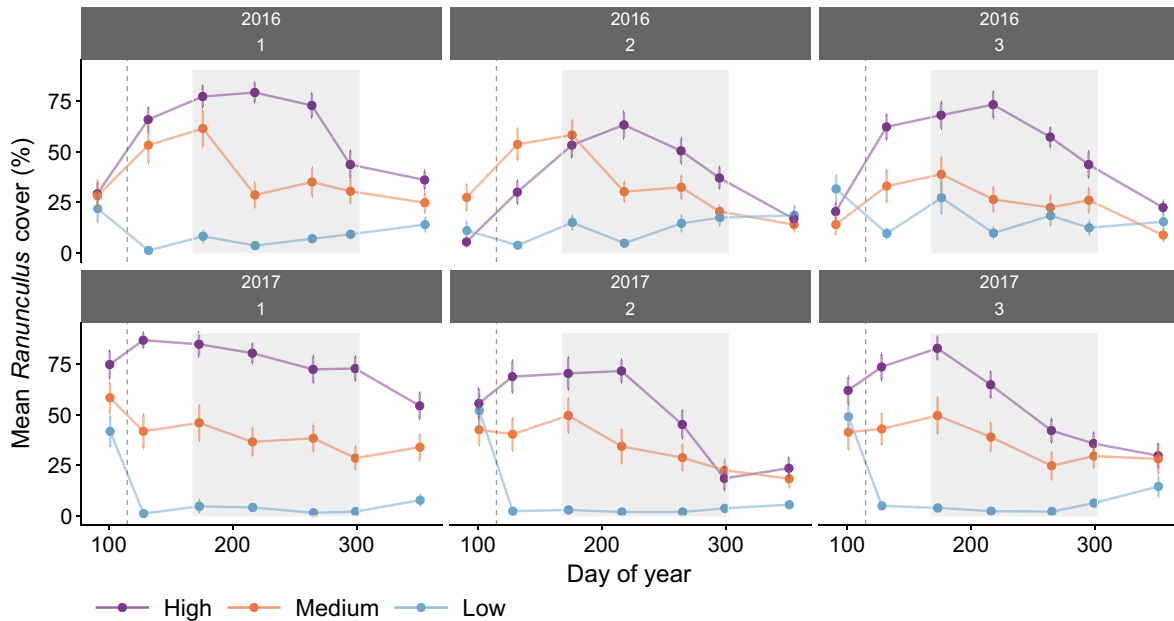


FIG. 2. Mean observed *Ranunculus* cover in each treatment level (vertical lines around the mean show the standard error) during all sample occasions ($n = 3,150$) including before manipulation (left of the dashed line) rows of plot indicate each year (2016 and 2017), columns illustrate experimental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

on each sample occasion ($n = 1,800$) to allow us to control for site-specific and time-specific influences in subsequent analyses. Water depth was measured to the nearest cm, and the water surface velocity was estimated visually as one of five categories [1 = 0–25 cm/s; 2 = 25–50 cm/s; 3 = 50–75 cm/s; 4 = 75–100 cm/s; 5 > 100 cm/s] by comparing the height and turbulence of surface water changes around a wooden meter stick. We calculated the site-level proportion of fast velocities as the proportion of velocity categories 3, 4 and 5 recorded in quadrats at each site. The steepness in velocity gradients between a quadrat and its neighboring quadrats was calculated using the Terrain Ruggedness Index (TRI) and absolute values of TRI were averaged to represent site-level velocity heterogeneity (Marsh et al. 2020).

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

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

Fish abundance, diet, site retention and growth.—To determine juvenile (0+) salmonid abundance and retention rate, we electrofished each site on each sample occasion ($n = 72$). To maximize capture efficiency, stop nets were set in the downstream and upstream buffer strips of the site. We electrofished in an upstream direction, capturing and removing all individuals encountered, known as an electrofishing *pass*. Sites were fished repeatedly until two consecutive passes yielded zero salmonid captures, indicating that all salmonids present in the site had been removed. Each captured fish was identified to species, sedated, measured (fork length, to nearest mm), weighed (to nearest 0.2 g) and marked with a Passive Integrated Transponder (PIT) tag (12.5 mm length, 2.12 mm diameter; Biomark, Idaho, USA). We inserted the PIT tag into the body cavity and clipped the adipose fin as an external indicator for recapture. Fish smaller than 60 mm in length were not tagged to avoid detrimental effects on their growth or survival (Richard et al. 2013). To determine summer diet, 182 salmon and 98 trout were sampled randomly across the sites during June and August. After weighing, diet samples were collected by stomach flushing (Kamler and Pope 2001) and preserved in 4% formaldehyde. Diet composition was

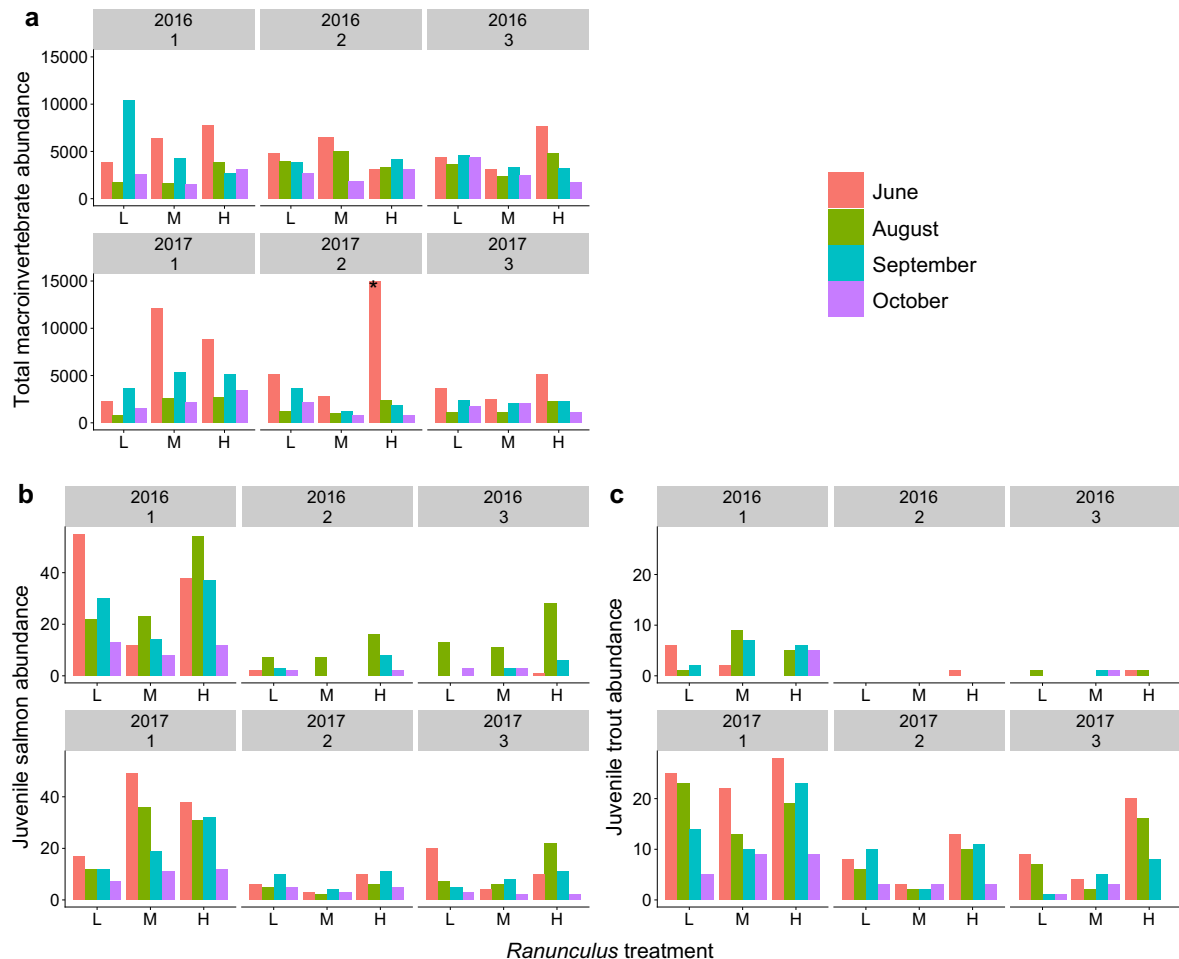


FIG. 3. Observed abundance of (a) total macroinvertebrates, (b) juvenile salmon, and (c) juvenile trout, in each year (row), block (column), *Ranunculus* treatment (L = low, M = medium, H = high), and sampling month (colored bars). In panel (a), the value of total macroinvertebrate abundance of bar *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

characterized as prey biomass and prey size following the procedures used for macroinvertebrate biomass and macroinvertebrate size. After processing, fish were released back into the site of capture once all fishing passes had been completed. All procedures were carried out by licensed personnel under a UK Home Office A (SP)A license (PPL 30/3277). Observed abundance of salmon and trout caught in each site and sample occasion are shown in Fig. 3b, c.

An unusually wet and warm 2015/2016 spawning season resulted in poor recruitment of juvenile salmonids on a national scale (Gregory et al. 2020), including the River Frome (Marsh et al. 2020). Indeed, fishing in June 2016 returned low numbers or no juveniles across all sites in blocks 2 and 3 (Fig. 3b, c). To augment low captures of our focus species, in July 2016 we transferred 50 juvenile salmon from the main river that runs parallel to the North stream (Fig. 1) into each site in blocks 2 and 3. We did not tag these individuals prior to translocation

because we considered that the benefits would be outweighed by the added stress of anesthetizing and PIT tagging following capture by electrofishing and that relocation could be detrimental to the individual. Although it would have been desirable to identify whether these salmon remained in the sites or were more likely to emigrate than resident salmon, the increase in salmon abundance in blocks 2 and 3 in August relative to June (Fig. 3b, c) suggested that the translocation was successful. We used June fish data in calculations of site retention rate and growth of recaptured individuals but excluded these June abundance data from all other analyses.

PIT-tagged individuals caught in the same site on consecutive sampling occasions were considered as recaptures and assumed to have been exposed to the site-specific *Ranunculus* cover for the intervening period. In June, 28% of salmon, and 4% of trout caught were too small to be tagged (fork length <60 mm) and we acknowledge the potential bias that fish tagged in June

and re-caught in August could represent larger individuals in the population. However, there was no difference between treatments in the proportion of untagged (smaller fish) to tagged (larger fish) individuals in June (one-way ANOVA, $F_{2,11} = 0.39$, $P = 0.69$) and so any effect of this bias should be consistent across all treatment levels.

Recaptured fish were used for growth analyses; as most fish were recaptured once, we consider only fish measurements at their initial capture and their first recapture. Initial captures ($t - 1$) could include the sample occasions in June, August and September, and first recaptures (t) could include the sample occasions in August, September or October. We calculated growth as the change in weight of individuals, ($W_r - W_c$), where W_r and W_c represent the weight of an individual at first recapture and initial capture, respectively.

Statistical analyses

Fish abundance, site retention and growth.—Salmonid abundance, site retention rate and growth were each modeled assuming appropriate and different error structures, and separate models were constructed for each fish species. Salmonid abundances ($n = 54$) were described using a negative binomial model (log-link function) to account for suspected overdispersion (O'Hara and Kotze 2010). To account for variation in their abundances due to differences in habitat size, log site area was included in the model as an offset (O'Hara and Kotze 2010). This effectively models abundance per unit area and does not introduce any additional parameters (Kery and Royle 2016). Site retention rate ($n = 54$) was modeled as a rate based on the numbers of tagged individuals at time $t - 1$ that were recaptured in the same site at time t in a binomial model (logit-link) to ensure that the expected rate was bounded between 0 and 1. We weighted occasions by the number of fish caught in time $t - 1$ to account for our ability to estimate the site retention rate accurately. Growth of recaptured salmon ($n = 173$) and trout ($n = 85$) were described using a Gaussian mixed-effects model (identity-link). To account for the influence of initial weight on growth (i.e., lower growth potential with larger initial weight; Appendix S1: Fig. S1), log initial weight was included in the model as an offset.

All saturated models included main effects of *Ranunculus cover*, *month* or *period*, *block* and *year* and a *Ranunculus cover* \times *month* or *period* interaction. When response variables covered a *period* (e.g., June to August), continuous explanatory variables were averaged across periods to represent a mean site-level variable. We were able to include *Site* as a random effect in the growth models because we had multiple measurements of the response variable (i.e., multiple individuals) at each sample occasion to estimate the *Site* random effect variance. We had only one measurement per sample occasion of abundance and site retention that prohibited estimation of a *Site* random effect variance. Instead, we

included the variables representing the site-specific and time-specific habitat characteristics that might influence the fish response variables, specifically *water depth*, *velocity heterogeneity*, *proportion of fast velocities* and *macroinvertebrate biomass*. We included all site-specific and time-specific habitat variables in saturated abundance and site retention rate models. To account for multicollinearity between these variables and *Ranunculus cover*, we calculated the variance inflation factor (VIF) for saturated models (Appendix S1: Table S3). *Water depth* was excluded from all saturated models as the $VIF > 10$ (Graham 2003). We then simplified the saturated models using backward and forward stepwise Akaike Information Criterion (AIC) variable selection to test for the effect of *Ranunculus cover*, while controlling for any non-negligible site-specific influences on each response variable, i.e., the main effect of *Ranunculus cover* and interactions between *Ranunculus cover* and *month* or *period* were also subject to simplification. The variables *block*, *month* or *period* and *year* were excluded from the stepwise selection because they represented the experimental design. Note that the growth models were not simplified because site-specific influences were controlled for with a *Site* random effect.

Macroinvertebrate and prey biomass and size.—To test whether macroinvertebrate and prey biomass and size variables were influenced by *Ranunculus cover* during summer, we fitted Gaussian mixed-effects models with these responses as a function of main effects of *Ranunculus cover*, *month*, *year* and *block*, and a *Ranunculus cover* \times *month* interaction. We included a main effect of *fish species* and a *Ranunculus cover* \times *fish species* interaction in the analyses of prey biomass and size to determine potential interspecific differences in the response, and a main effect of *fork length* because larger fish can consume larger prey (Keeley and Grant 1997). All models included a random effect of *Site* to account for the multiple measures taken at the same site. Response variables were natural log transformed if necessary, to meet assumptions of normality and homoscedasticity.

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

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

where $p_{s,i}$ and $p_{t,i}$ are the mean proportion of the i th prey taxa in salmon and trout, respectively. The value of FT can range between 0 (no overlap) and 1 (complete overlap). In addition to being among the least biased measures of overlap, the FT index is unaffected by unequal sample sizes (Smith and Zaret 1982) and was therefore appropriate for our data. To test the statistical significance of dietary overlap between salmon and trout in

the different *Ranunculus* cover levels in June and August, we used bootstrap resamples of individual salmon and trout dietary niche measures to calculate 1,000 estimates of the FT index that captured variance in the FT index due to individual dietary variation (Smith 1985). We then compared the influence of *Ranunculus* cover level on niche overlap using the empirical bootstrap 95% confidence intervals. This procedure was repeated to compare salmon and trout niche overlap between *Ranunculus* cover levels using mean proportional biomass of prey taxa in the gut contents of individual fish.

Model fitting and performance.—To compare the effects of variables recorded on different measurement scales, all numerical explanatory variables were standardized before analysis by subtracting their mean and dividing by their standard deviation. All statistical analyses were performed in R version 3.4.4 (R Development Core Team 2018) using packages *lmerTest* (Kuznetsova and Brockhoff 2017) and *MASS* (Venables and Ripley 2002). Model performance and goodness of fit was assessed using packages *MuMin* (Barton 2009) and *pscl* (Jackman 2017). Model residuals were inspected to check assumptions of homogeneity, normality and independence (Appendix S1: Figs. S2–S4).

RESULTS

Salmon abundance was positively influenced by *Ranunculus* cover (Table 1a, Fig. 4a). Marginal effects

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

Salmon and trout abundances differed among blocks (Table 1a), with higher abundances of both species observed in block 1 relative to blocks 2 and 3 (Fig. 3b, c; Appendix S1: Figs. S5b and S6a). Trout abundance was higher in 2017 relative to 2016 (Fig. 3c; Appendix S1: Fig. S5c). None of the variables controlling for site-specific influences were retained over the effects of *Ranunculus* cover and the *Ranunculus* cover \times month interaction for salmon, although a positive effect of macroinvertebrate biomass was retained alongside them (Appendix S1: Fig. S6b). A positive effect of velocity heterogeneity explained trout abundance better than any *Ranunculus* cover effects (Appendix S1: Fig S5d).

After accounting for differences between blocks and years and controlling for site-specific variables (Table 1b; Appendix S1: Figs. S7 and S8), site retention rates of salmon and trout were influenced by *Ranunculus* cover and the strength and direction of this effect changed over time for each species (Table 1b, Fig. 4b). Between June and August, there was a positive effect of *Ranunculus* cover on salmon and trout site retention rate. The

TABLE 1. Effects of *Ranunculus* manipulation on juvenile (age 0+) salmon and trout abundance and site retention rate.

	Salmon					Trout				
	df	Deviance	Residual df	Residual deviance	Pr (>Chi)	df	Deviance	Residual df	Residual deviance	Pr (>Chi)
(a) Abundance†										
<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
Macroinvertebrate biomass	1	16.3	46	76.2	<0.01	–	–	–	–	–
Velocity heterogeneity	–	–	–	–	–	1	5.6	47	54.9	0.02
<i>Ranunculus</i> \times Month	2	4.5	44	71.7	0.11	–	–	–	–	–
(b) Site retention rate‡										
<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	–	–	–	–	–
Macroinvertebrate 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> \times Period	2	511.9	36	692.3	<0.01	2	32.4	29	211.9	<0.01

Notes: Parts (a) and (b) show analysis of deviance summaries for the negative binomial abundance models, and the binomial site retention rate model, respectively. Models tested for *Ranunculus* cover and *Ranunculus* cover \times month or period effects while controlling for site- and time-specific habitat characteristics (that are shown in gray if retained) using model simplification.

†n = 54; salmon total variance explained = 0.80; trout total variance explained = 0.72.

‡n = 54; salmon total deviance explained = 0.66; trout total deviance explained = 0.51.

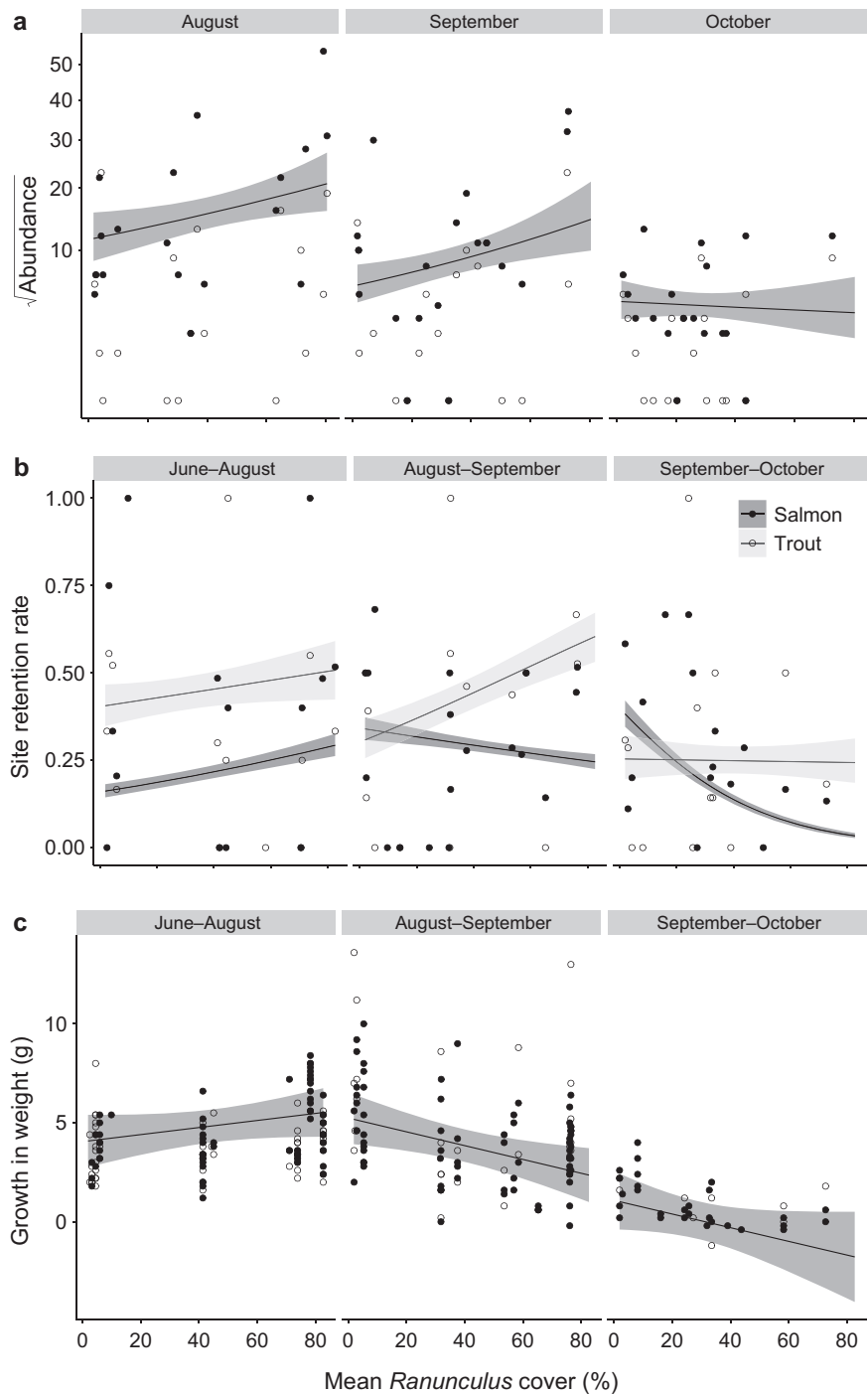


FIG. 4. Influence of *Ranunculus* cover during different months or periods on juvenile salmonid (a) abundance, (b) site retention rate (i.e., the weighted proportion of tagged individuals that were recaptured in the same site in the following sample event) and (c) growth in weight. In all plots, the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

estimated proportion of trout remaining in high cover sites was double that of trout remaining in low cover sites between August and September, but between September and October there was no effect of

Ranunculus cover. Between August and September, and September and October, there was a negative effect of *Ranunculus* cover on salmon site retention, suggesting that site retention was lower in high cover sites, where

TABLE 2. Effects of *Ranunculus* manipulation on growth in weight of juvenile (age 0+) salmon and trout.

	Salmon					Trout				
	df	Sum sq	Mean sq	F value	Pr (>F)	df	Sum sq	Mean sq	F value	Pr (>F)
Growth†										
<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> × Period	2	86.0	43.0	16.2	<0.01	2	9.9	5.0	1.2	0.31

Notes: Table shows the analysis of variance summary for the Gaussian mixed-effects model describing growth of recaptured individuals. Note: these models were not simplified.

†Salmon, $n = 173$; trout, $n = 85$. Salmon total variance explained = 0.62; trout total variance explained = 0.37.

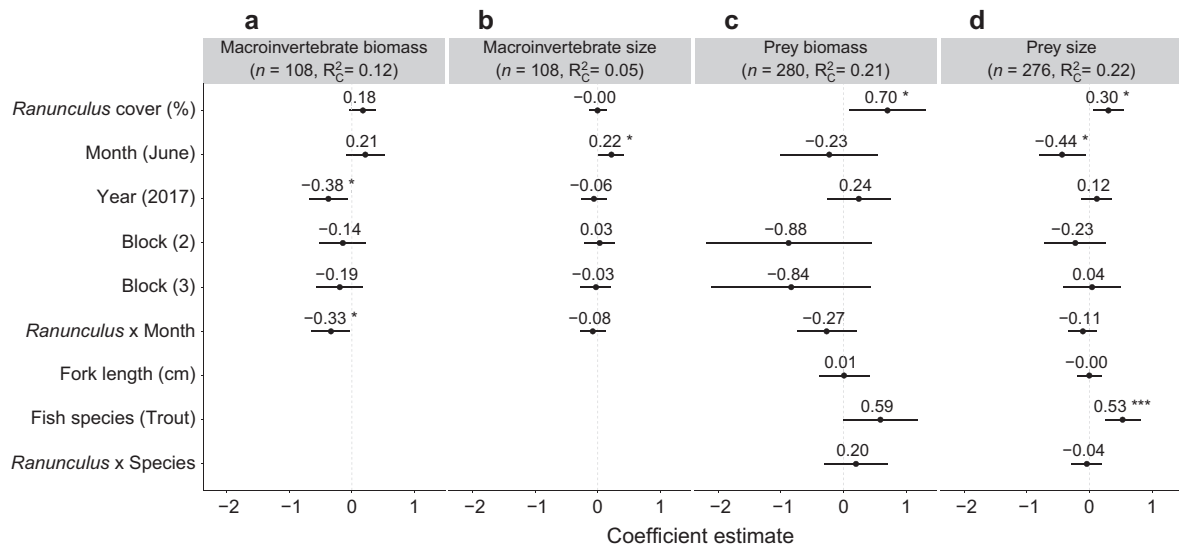


FIG. 5. (a–d) Coefficient estimates from Gaussian mixed-effects models describing variation in the macroinvertebrate biomass and size (from Surber samples) and prey biomass and size (from juvenile salmonid diet contents) during summer months. Four diet samples were empty and so did not contribute to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

cover declined more strongly in autumn than in low cover sites.

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

Macroinvertebrate biomass was influenced by *Ranunculus* cover differently between months and years (Fig. 5a). Macroinvertebrate size was greater in June relative to August (Fig. 5b). Prey biomass was greater in higher *Ranunculus* cover (Fig. 5c), and the influence of cover did not differ between fish species or between months. Prey size was greater in the diets of fish captured in high

cover (Fig. 5d). Trout fed on larger prey than salmon but the relationship between *Ranunculus* cover and prey size did not differ between the fish species (Fig. 5d). There was no influence of fork length on the prey biomass or prey size in the diets of the fish (Fig. 5c, d).

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

DISCUSSION

Our *in situ* manipulation experiment demonstrated that increased *Ranunculus* cover supports larger populations of better growing juvenile (0+) salmon. We showed

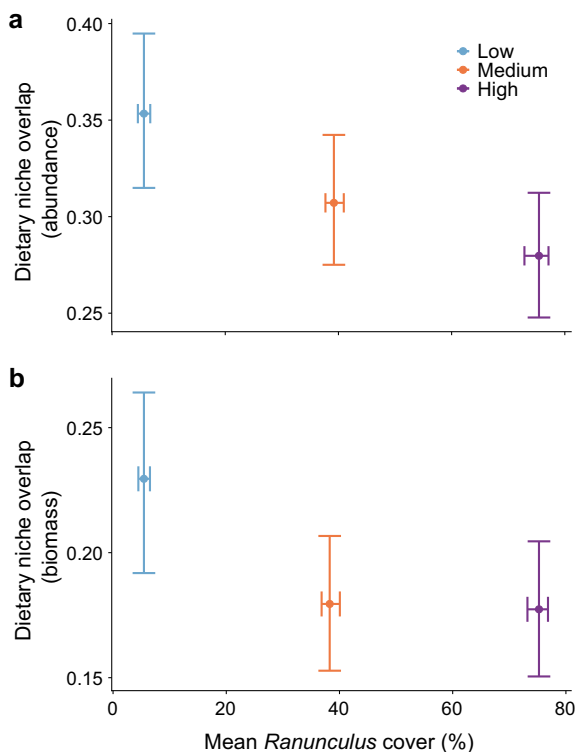


FIG. 6. Mean (point) and 95% confidence intervals (vertical error bars) of the generated bootstrap distribution of dietary niche overlap. Dietary niche overlap was calculated as the FT index (Smith and Zaret 1982) based on (a) proportional abundance, and (b) proportional biomass of prey taxa observed in salmon and trout gut contents caught in low, medium or high *Ranunculus* cover during summer months, with the mean (point) and 95% confidence intervals (horizontal error bars) of the empirical *Ranunculus* cover at the site and time that those fish were sampled.

that *Ranunculus* cover was important for salmon abundance, site retention, and growth during summer, and that its positive influence declined with its autumn senescence. The importance of *Ranunculus* cover for juvenile trout was less clear, but site retention was substantially greater in high cover. Despite there being few detectable effects on the prey availability, a higher biomass of prey and larger mean prey were found in diets of salmon and trout inhabiting high *Ranunculus* cover sites. This suggests that *Ranunculus* facilitates foraging and, therefore, indirectly enhances salmonid growth. Moreover, the dietary niche overlap between the two species was lowest in high cover sites, suggesting that abundant *Ranunculus* might reduce interspecific competition. Together this evidence suggests that managing freshwater habitats to promote or even enhance naturally occurring *Ranunculus* beds could improve the production of both salmon and trout juveniles.

Our results demonstrated that *Ranunculus* is an important habitat for juvenile salmon in lowland rivers. This finding is consistent with a catchment-wide study in which high densities of juvenile salmon were

associated with high *Ranunculus* cover (Marsh et al. 2020). This positive influence of *Ranunculus* could act on salmon directly by providing shelter or indirectly by promoting habitat complexity. For example, the addition of boulders to increase complexity in rivers supported higher densities of salmon, probably due to increased visual isolation between neighbors and subsequent reduced territorial behavior (Venter et al. 2008). Individual salmon were more likely to remain in sites with high *Ranunculus* cover during summer, possibly because this habitat produced better growth conditions. Floating canopy offered valuable overhead protection from aerial predators, whereas the increased structural complexity within the water column affords refuge from aquatic predators and competitors (Johnsson and Rydeberg 2004, Venter et al. 2008). This can reduce costly vigilance behavior (Metcalf and Huntingford 1987), therefore enhancing feeding opportunities and ultimately, growth potential.

Ranunculus appeared to facilitate greater feeding opportunities for both salmon and trout and reduce interspecific competition. While *Ranunculus* can support abundant macroinvertebrate communities (Harrison and Harris 2002), its influence on macroinvertebrate biomass in this study differed between summer months, which could reflect seasonal fluctuations in abundance of macroinvertebrates (Wright and Symes 1999). Nevertheless, both prey biomass and prey size consumed by salmon and trout were greater in high *Ranunculus* cover throughout summer, suggesting that abundant *Ranunculus* enabled greater rates of prey encounter and capture, including profitable larger prey items (Keeley and Grant 1997). Moreover, dietary niche overlap was greatest between salmonids occupying low *Ranunculus* cover, suggesting stronger competition for limited and similar prey in these habitats. Complex macrophyte structures provide more substrate for attachment and resource collection, supporting abundant and diverse periphyton and macroinvertebrate communities (Sand-Jensen 1998, Warfe and Barmuta 2006). Structures, such as *Ranunculus*, also create heterogeneous water velocities that salmonids utilize for energy-efficient foraging (Sand-Jensen 1998, Riley et al. 2009). Consequently, *Ranunculus* could provide suitable foraging environments for salmonids to exploit.

Although we did not detect an effect of *Ranunculus* cover on trout abundance or growth, individual trout were more likely to be recaptured in sites with high, relative to low, *Ranunculus* cover throughout summer. This was perhaps caused by increased foraging opportunities and reduced interspecific competition, suggesting that *Ranunculus* does convey some benefits for trout. Juvenile trout use areas with high aquatic vegetation during summer (Maki-Petäys et al. 1997), but reported influences of riparian and in-river cover on trout growth are inconsistent (Riley et al. 2009, McCormick and Harrison 2011). We found trout abundance was better predicted by velocity heterogeneity, consistent with a correlative study of influences on trout densities (Marsh et al. 2020), which could suggest an indirect effect of *Ranunculus*.

Together with our results, these varied findings suggest that, while macrophytes might afford benefits to trout, the variables influencing their abundance and growth are complex, perhaps because trout are more behaviorally plastic than salmon (Nevoux et al. 2019).

By repeatedly sampling our experimental sites across multiple months and seasons, we were able to identify important temporal distinctions in the estimated benefits of *Ranunculus* cover for juvenile salmon and trout. However, this also potentially exposed individual fish to repeated capture by electrofishing, which could have influenced the survival and movement of fish. Although electrofishing can cause fish mortality, we used electrofishing settings known to return high salmonid parr capture rates and cause <1% mortality rates on the River Frome (Marsh et al. 2020). As such, we recorded only two dead individuals during post-tagging recovery (one salmon and one trout) out of the 1,197 individuals that were sampled during this study. Furthermore, it is generally accepted that any impact of electrofishing on fish mortality is negligible in relation to population abundances (e.g., McMichael and Fritts 1998). While sampling could have affected fish movement, over a third of individuals captured throughout the study ($n = 401$) were recaptured individuals, suggesting that individuals stayed in the experimental sites and that any displacement could be temporary. Finally, the sampling protocol was consistent across sites, therefore any effects of sampling on fish abundance or site fidelity are unlikely to have substantially affected our ability to test for an influence of *Ranunculus* cover on these response variables.

Macrophytes in lowland rivers are typically managed by weed cutting to reduce the risk of flooding, which takes place throughout the year and negatively impacts the ecological status of rivers (Baatrup-Pedersen et al. 2018). Our findings can help to prioritize the timing of weed cuts to the mutual benefit of stakeholders and salmonids. For example, in the context of our findings, cutting during spring would reduce plant biomass when flood risk is high, while stimulating further plant regrowth (Baatrup-Pedersen et al. 2018). This would enhance *Ranunculus* cover during summer when its positive influence on salmonids was greatest. There are also implications for the re-establishment of riparian canopy cover, which can mitigate against bankside sediment loss and rising temperatures (Cole and Stockan 2020), but limits macrophyte growth (Riley et al. 2009). We recommend maintaining a mosaic of bankside vegetation that would supply shade to limit high temperatures that stress freshwater species, and direct sunlight to promote in-river vegetation growth. Encouraging a mosaic of bankside vegetation and modification of catchment land-use practices could also limit bank erosion and the input of fine sediments into rivers (Cole et al. 2020) that, along with low flows and nutrient enrichment, were potential drivers of a widespread disappearance of *Ranunculus* in lowland rivers in southern England during the early 1990s (Cranston and Darby 2004).

Understanding the current threats to macrophytes, such as *Ranunculus*, and establishing cost-effective measures to mitigate them could help safeguard at-risk salmonid populations in English chalk streams and elsewhere. For example, studies have identified positive associations between various species of macrophyte and salmonids, including brown trout in northern Finland (Maki-Petäys et al. 1997) and Sweden (Eklov and Greenberg 1998), Atlantic salmon in Ireland (McCormick and Harrison 2011) and northern USA (Beland et al. 2004), and steelhead trout *Oncorhynchus mykiss* in western USA (Lusardi et al. 2018), suggesting that aquatic plants constitute important habitats for salmonids across a wide range of regions and habitat types. Artificial structures can improve habitats for wild salmonids, but are expensive and can lose effectiveness or be washed away downstream over time (Binns 2004, Foote et al. 2020). Such structures may also be geared toward performing specific function, such as digging pools for trout or planting riparian canopy to provide terrestrial inputs and overhead cover (Binns 2004, McCormick and Harrison 2011). Naturally occurring macrophytes, such as *Ranunculus*, can create complex habitats to structure and support both biotic and abiotic components of salmonid ecosystems and could be cost-effective alternatives to artificial structures.

In response to three decades of declining Atlantic salmon populations throughout southern and central Europe and North America, there have been calls to better understand how the management of juvenile rearing habitat could maximize the numbers and quality of seaward-migrating salmon smolts to increase survival at sea and the number of returning spawners (Armstrong et al. 2018, Gregory et al. 2019). Our findings suggest that maintaining naturally occurring or even enhancing *Ranunculus* habitats in lowland rivers provides favorable conditions to support both greater numbers of juveniles, and better feeding and growth opportunities during summer. Where macrophytes are naturally present, augmenting their abundance and reducing their stressors should be considered as river restoration management actions, alongside woody debris and boulder installations, to ameliorate juvenile salmon abundance and growth. Further research should investigate whether these benefits propagate to subsequent life stages, such as the likelihood of surviving overwinter or growing into a large smolt. Together with our findings, this knowledge would further elucidate the role of macrophytes in regulating juvenile salmon production in lowland rivers. Improving juvenile freshwater habitat across river types could be the key to unlocking improved sea survival and ultimately seeing more adult salmon returning to our rivers.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2492/full>

OPEN RESEARCH

Data (Marsh et al. 2021) are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.612jm643t>