The importance of seasonal macrophyte cover for the behaviour and performance of brown trout (*Salmo trutta*) in a groundwater-fed river

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SUMMARY

1. Groundwater-fed rivers, such as the chalk streams of southern England, exhibit high levels of stability (e.g. flow and temperature) and physical homogeneity (e.g. depth and substrate grain size). However, growth of instream macrophytes is highly variable depending on season, providing an important but ever changing source of cover for stream dwelling salmonids, such as brown trout (*Salmo trutta*).
2. In this study, the behavioural ecology of brown trout inhabiting a chalk stream was assessed during periods that included summer and winter. In a reach of the River Lambourn (Berkshire, UK), a combination of physical habitat mapping, electric-fishing, passive integrated transponder and radio telemetry was used to quantify trout: (1) density relative to physical and thermal characteristics, (2) movement patterns, and (3) performance, in terms of growth.
3. Trout density was positively related to depth during winter (Feb) and spring (May), but not at the end of summer (Sept). Despite no statistical relation between trout density and macrophytes, periods of strong and no association between density and depth coincided with sparse and extensive macrophyte cover throughout the study reach, respectively.
4. Despite being greater for some fish in winter compared to summer, the daily distance moved was generally low (<3.5 m day^{-1}). While growth was mostly positive, less mass was gained, and performance deviated farther from optimal levels predicted by a growth model, during periods that included winter.
5. A number of factors likely contributed to lower growth in winter, including costs of reproduction, temperatures which deviated farther from those optimal for growth, and/or an inability to maximise energy intake, e.g. due to time spent holding position in deeper areas as cover provided by macrophytes declined.

6. Despite the lack of extremes in chalk stream environments, the behavioural ecology of brown trout appears to be influenced by seasonal variation in instream cover provided by macrophytes. This emphasises the importance of balancing the management (e.g. cutting and removal) of macrophytes with the ecological benefits they provide.

Introduction

Groundwater-fed rivers which flow through catchments dominated by chalk (known as chalk streams) maintain relatively constant flow and temperature regimes and represent unique freshwater habitats (Berrie, 1992). Accordingly, some chalk streams in southern England have received environmental protection at national (Sites of Special Scientific Interest designated under the Wildlife and Countryside Act, 1981) and international (Special Areas of Conservation designated by the EC Habitats Directive [92/43/EEC]) levels. They have also been extensively modified by human activity for centuries. For example, the removal of riparian vegetation, modification of river channels and elevated levels of fine sediment have been associated with extensive development of mill systems, water meadows and agriculture (Westlake et al. 1972). Chalk streams are typically characterised by low spatial variability in depth driven by poorly defined pool-riffle sequences and substrates that tend to lack larger material in favour of gravel, sand and silt (Acornley & Sear, 1999). A reduction in natural shade, shallow water depths, high levels of nutrients, and low turbidity can also lead to high growth of instream macrophytes (e.g. *Ranunculus* spp.) (Old et al. 2014). Growth is often rapid in spring and early summer, reaching maximum coverage in August, before declining to a minimum in March (Ham et al. 1981; Scarlett et al. 2015). This seasonal growth pattern may provide an element of physical and hydraulic heterogeneity (Biggs et al. 2018; Sand-

Jensen & Pedersen, 1999) in an environment that otherwise exhibits a high level of stability (e.g. flow and temperature) and physical homogeneity (e.g. depth and substrate).

Seasonal environmental heterogeneity exerts a strong influence over the behaviour of stream dwelling salmonids, such as brown trout (*Salmo trutta*). However, our understanding of seasonal habitat use by brown trout is biased towards research conducted in northern boreal and temperate upland systems dominated by hard rock geology, surface drainage, and dynamic flow regimes that respond rapidly to precipitation and snow-melt (Mäki-Petäys et al. 1997; Heggenes et al. 1999; Huusko et al. 2007). In these systems, relatively warm water temperatures during summer typically promote strategies that maximise growth (Heggenes & Wollebæk, 2013), with spatial habitat use influenced by intraspecific competition between trout that are active both day and night (Heggenes et al. 1993). Variability in depth, driven by well-defined pool-riffle sequences, allows shallow, swift flowing waters and deeper pools to be occupied by smaller and larger fish, respectively (Mäki-Petäys et al. 1997). This pattern of habitat use likely relates to larger, dominant individuals excluding smaller conspecifics from areas where predation risk is low or that are most favourable (Mäki-Petäys et al. 1997). In contrast, during winter a risk minimising sheltering strategy may be adopted in response to challenging environmental conditions (Heggenes et al. 1993). For example, daytime activity is reduced with trout seeking refuge within the interstices of large substrates or aggregating within deeper pools (Heggenes et al. 1999). Feeding at night may be driven by the need to reduce predation risk as temperatures drop, favouring endothermic, predominantly visually feeding piscivores, including mammals such as mink (*Mustela vison*) and otter (*Lutra lutra*), and birds such as grey heron (*Ardea cinerea*) and goosander (*Mergus merganser*) (Heggenes et al. 1999). While there is typically no, marginal or negative growth in winter (Cunjak & Power, 1987; Egglishaw & Shackley, 1977), such switches in behavioural strategy with season appear ecologically adaptive, aimed at minimising fitness costs (Heggenes et al. 1993).

Comparatively less research on the seasonal habitat use by brown trout has been conducted on groundwater-fed rivers. In English chalk streams, trout are an important component of the community and are of high recreational angling value. Although information is limited, trout inhabiting chalk streams in winter appear to behave in a way that is similar to those occupying northern boreal and temperate systems. For example, fish aggregate in pools and maintain high levels of site fidelity, but with periodic movements at dawn and dusk (Kemp et al. 2017). In chalk stream habitats where the frequency of pools and riffles is low, fish may seek cover from predators where deeper areas occur in response to macrophyte dieback and a lack of alternative shelter (e.g. interstices of large substrates; Heggenes et al. 1999). High site fidelity might be expected as benefits of patch switching are low when growth remains positive (Kemp et al. 2017) and food availability is high (Wright, 1992), while periodic movements at dawn and dusk suggests nocturnal foraging may be adopted as a risk minimising strategy when instream macrophyte cover is reduced (Kemp et al. 2017). Such behaviours, therefore, may represent an optimal strategy to maximise fitness in chalk streams during winter.

Given the high levels of stability (flow and temperature) and physical homogeneity (depth and substrate) in chalk streams, trout behaviour and performance (in terms of growth) might be expected to vary little with season. However, direct seasonal comparisons are lacking (but see Riley et al. 2006), and it may be that temporal variability in macrophyte growth strongly influences behaviour. In this study, we compared the behaviour and performance of a population of brown trout in a chalk stream in southern England during periods that included summer and winter. We quantified: (1) density relative to physical (depth, velocity and macrophyte cover) and thermal characteristics, (2) movement patterns, and (3) performance, in terms of growth. As chalk streams are productive, stable and homogenous environments, but with seasonal growth of macrophytes providing an element of physical and hydraulic heterogeneity, we hypothesised that trout would: (1) select habitat based on availability of instream cover, (2) exhibit high levels of site fidelity as benefits of patch switching vary little spatially, and (3) maintain consistent growth performance independent of season due to high productivity and stability in the thermal regime.

Methods

Site description, and physical and thermal characteristics

The study was conducted along a 500 m section of the River Lambourn Observatory at Boxford, Berkshire, UK (Figure 1). The site, which is owned by the Centre for Ecology and Hydrology, is approximately 14 km from the ephemeral source of the River Lambourn and includes 600 m of river and 10 ha of wetlands (Old et al. 2014). At the site, the river channel is typically 9 m wide, 0.4 m deep and low gradient (0.05°) (Old et al. 2014). The river flows through a catchment (162 km^2) dominated by agricultural land prior to entering the River Kennet, a tributary of the River Thames (Evans et al. 2003). Discharge exhibits low seasonal variation as river base flow is dominated (typically > 95%) by groundwater from chalk aquifers (Evans et al. 2003). During the periods that included summer and part of autumn (May to October 2011, and subsequently referred to as summer for brevity), and winter and part of spring (November to April 2010-2011 and 2011-2012, and subsequently referred to as winter for brevity), river discharge (± SD and range) was 0.63 (± 0.18, 0.45 – 1.17) $m^3 s^{-1}$ and 0.71 (± 0.25, 0.36 – 1.33) $m^3 s^{-1}$, respectively (Rameshwaran et al. 2015).

The spatial variability of key physical habitat characteristics was quantified between 23 and 26 August 2011. Measurements were typically taken at four approximately equidistant points along transects that spanned the width of the river at 10 m longitudinal intervals. As few as two and as many as five points were taken along transects at narrow and wide river sections, respectively. In total, data were collected at 177 locations across 50 transects. Dominant substrate type was visually categorised as silt (< 0.0063 cm), sand (0.0063 – 0.2 cm), gravel (0.2 – 1.6 cm) or pebble (1.6 - 6.4 cm). Water depth (cm) and mean mid-column (60% depth) water velocity (cm s^{-1}) was measured using a metre rule and electromagnetic flow meter (Valeport Model 801, Totnes, UK), respectively. Percent instream macrophyte cover was estimated using a 0.5 x 0.5 m quadrat. Seasonal variability of physical habitat characteristics (depth, velocity and dominant substrate type) was quantified by conducting an additional survey of a 270 m section of the study reach on 22 February 2011 (Figure 1). Measurements were taken at six approximately equidistant points along transects that spanned the width of the river at 5 m longitudinal intervals using the same method outlined above. In total, data were collected at 330 locations across 55 transects. A final survey of the full study reach was conducted on 11 March 2019, where percent instream macrophyte cover was estimated, using the same method as in August 2011, to represent a time when seasonal coverage is low (Scarlett et al. 2015). Measurements were typically taken at five approximately equidistant points along transects that spanned the width of the river at *ca.* 10 m longitudinal intervals. In total, data were collected at 257 locations across 52 transects. The exact location of point measurements was recorded using a Leica Viva GS14 Global Navigation Satellite System in

August 2011 and March 2019. The location of point measurements was manually measured from the river bank in February 2011.

Spatially, substrate was dominated by gravel, with smaller patches of sand/silt and pebble associated with deep/slow and shallow/fast flow, respectively (Figure 2a). Shallow stretches of moderate water velocity dominated the upper and middle sections of the study reach (Figure 2b, c). These sections were interspersed with deep slow flowing pools, and a long deep section towards the bottom of the reach (Figure 2b, c). Instream macrophyte cover was extensive in August (Figure 2d), but varied temporally (Figure 3). Growth was rapid in spring and coverage throughout the reach was greater in August (mean: 75.8%) compared to March (mean: 32.8%; Figure 2e). Although similar, water depth (August: 38.3 ± 15.4 cm; February: 31.9 ± 15.5 cm) and velocity (August: 21.2 ± 15.2 cm s^{-1}; February: 33.3 ± 22.7 cm s^{-1}) were higher and lower in summer compared to winter, respectively. Substrate was dominated by gravel independent of season. A footpath ran along the true left bank and there was near continuous riparian cover along the right.

Data loggers accurate to ± 0.47 ˚C (Hobo Temp/Light Pendant, Onset Computer Corporation, MA, USA) recorded river temperature hourly at 30 transects positioned on average every 17.5 m along the study reach. At each transect, a logger was deployed towards the left, right and centre of the channel and recorded temperature at the substrate. Additional loggers recorded ambient air temperature. During summer and winter, mean river water temperature (± SD) was 11.99 ± (1.49) °C and 8.92 ± (1.89) °C, respectively. During the same time periods, mean air temperature at the site was 13.53 ± (4.98) °C and 6.00 ± (5.58) °C, respectively.

Fish Capture and Tagging

Five electric fishing surveys were conducted between June 2010 and May 2012 during which trout were captured in 17.5 (± 1.2) m long reaches isolated by stop nets, throughout the entire 500 m study site using a single pass method (Table 1). Captured trout were anesthetised (0.3 ml L^{-1} 2-phenoxyethanol), measured (fork length mm), weighed (g), and scanned to identify individuals tagged in previous surveys. If sufficiently large, trout that had not previously been tagged were implanted with 12 mm full duplex Passive Integrated Transponder (PIT) (Wyre Micro Design Ltd, Lancashire, UK; > 100 mm fork length) and radio (24 mm length, 1.9 g mass in air, estimated battery life = 8.7 months; Biotrack, Wareham, UK; > greater than 150 g mass) tags (Table 1). A small sample were also implanted with micro archival data storage (DS) tags, data for which were used by Kemp et al. (2017). Prior to surgery, the functionality and frequency (between 173.199 and 173.994 MHz) of radio tags was verified using a hand-operated receiver. During surgery, fish were placed ventral side up in a v-shaped trough and the gills irrigated with a dilute dose of anaesthetic. All tags were inserted into the peritoneal cavity. PIT tags were implanted using an injector and tags pre-loaded in sterile hypodermic syringe needles. Radio tags were sterilised in ethanol, rinsed in purified water, and inserted through a 10 - 20 mm incision made immediately anterior to the pelvic girdle. The incision was closed with two separate dissolvable sutures (Vicryl Rapide^{R}; Ethicon Inc., Cornelia, GA, USA). The total tag burden did not exceed 2 % of the fish body mass. Fish were not tagged during the final survey. Fish recovered in tanks containing aerated river water before being returned to the electric fishing reach from where they were captured. Standard tagging protocols were conducted in compliance with the UK Animals (Scientific Procedures) Act 1986 under Home Office licence.

Density

The density of brown trout in each of the 29 (17.5 m long) electric-fishing reaches was calculated using data from the February 2011, May 2011, September 2011 and May 2012 electric-fishing surveys as the quotient of number of fish captured and surface area of the reach (quantified using a base map in ArcGIS, ESRI ArcMAP v10). A multiple regression model was fitted to determine whether habitat variables (depth, velocity and water temperature [all electric-fishing surveys], and macrophyte cover [February and September surveys only]) were significant predictors of density. Equal variance, distribution of residuals, collinearity between predictors, independence of errors and influential cases were assessed by examining plots of the residuals against fitted values, Q-Q plots, the Variance Inflation Factor, Durbin-Watson statistic, and standardised residuals, respectively.

Movement

Meso-scale movement was assessed using radio telemetry. Radio tagged trout were located up to three times per week from the bank using a hand-held receiver (Sika, Biotrack, Wareham, UK) connected to a three-element Yagi antenna. Fish were detected up to distances of approximately 250 m with the antenna held above head height. Once located, the position of individual fish was estimated by reducing the gain on the receiver and moving along the bank in the direction of increasing signal strength until the best fix was attained, with occasional validation through visual identification of some individuals. Fish positions were recorded relative to bankside features of known location, and were subsequently projected onto a base map in ArcGIS (ESRI ArcMAP v10). Patterns of individual movement were quantified for fish detected at least 3 times as: 1) distance moved (m day^{-1}), calculated as the distance between successive radio tracking fixes divided by number of days between fixes, and 2) longitudinal home range defined as the distance between the most up- and down-stream locations recorded (Khan et al. 2004; Ovidio et al. 2002). Longitudinal home ranges were calculated from 95% trimmed data.

As data violated the assumption of normality which could not be corrected through transformation, Wilcoxon rank-sum and Wilcoxon signed-rank tests was used to investigate whether patterns of individual movement differed for fish detected in winter or summer (independent samples) and in both seasons (repeat measures), respectively.

Performance

Performance metrics were calculated for two growth periods in 2011 using data collected during electric fishing surveys. Period 1 (4 February to 5 May), included part of winter and most of spring and was cooler (9.9 ± 1.7 °C) than period 2 (5 May and 9 September) which spanned summer and some of autumn (12.6 ± 1.2 °C).

Performance was expressed as mean rate of increase (% day^{-1}) in specific mass (eq. 1) and length (eq. 2) for PIT tagged fish recaptured during electric fishing surveys:

$$G_w = 100 \cdot \left((\log_e W_2 - \log_e W_1)/t\right) \quad (1)$$

$$G_L = 100 \cdot \left((\log_e L_2 - \log_e L_1)/t\right) \quad (2)$$

where W_1 and W_2 are the initial and final fish mass (g), L_1 and L_2 are the initial and final fish fork length (mm) and t is the number of days between surveys (i.e. the growth period). Differences in performance between period 1 and 2 were compared using a Wilcoxon rank-sum test as data violated the assumption of normality which could not be corrected through transformation. For each fish, G_w was subtracted from an estimate of optimal growth (G_{op}) to determine deviation in observed performance compared to that expected assuming fish are fed to satiation under laboratory conditions. G_{op} was calculated using the model developed by Elliott et al. (1995):

$$G_{\mathrm{op}} = c \cdot W_1^{-b}(T - T_{\mathrm{lim}})/(T_{\mathrm{M}} - T_{\mathrm{lim}}) \quad (3)$$

where T is the mean water temperature during the growth period, and T_{M} and T_{lim} respectively represent the temperatures at which growth is maximised (13.11 ˚C) and ceases (limit). T_{lim} is the lower or upper value at which growth rate is zero (T_{L} [3.56 ˚C] or T_{U} [19.48 ˚C]) depending on whether T is higher or lower than T_{M} (i.e. $T_{\mathrm{lim}} = T_{\mathrm{L}}$ if $T < T_{\mathrm{M}}$ or $T_{\mathrm{lim}} = T_{\mathrm{U}}$ if $T > T_{\mathrm{M}}$). The mass exponent b is the power transformation that produces linear growth with time (0.308), and c is the growth rate of a 1 g trout at optimal temperature (2.803). All values were obtained from Table 1 in Elliott et al. (1995). As assumptions of normality and homogeneity of variance were met, an Independent samples T-test was used to determine whether the deviation in performance from that estimated under optimal conditions differed between growth periods.

Results

Density

Physical habitat was a strong predictor of brown trout density in the River Lambourn in February (2011), May (2011) and May (2012), explaining 73%, 49% and 37% of the variance, respectively (Table 2). In September (2011), physical habitat was not a good predictor of density (Table 2). Trout density was positively related to depth in February

(2011), and to a lesser degree in May (2011 and 2012) (Figure 4). In September (2011) the relationship between trout density and depth was not evident (Figure 4). There was no relationship between trout density and water temperature, velocity or macrophyte cover during any season (Table 2).

Movement

Of the 83 radio tagged fish, 55 (66%) were detected more than twice during the summer and/or winter and included in subsequent analysis. Of those detected, 13 (24%) and 18 (33%) were detected only during summer and winter, respectively, while 24 (44%) were present during both seasons. Twenty-eight (34%) were either detected two times or fewer, or not at all. The fate of these fish is unknown (the tag may have failed, the fish may have been predated, or they may have moved out of the study site). For those detected, median distance moved (Figure 5) and home range (Figure 6) were low. Fish that were detected during both seasons (within group comparison) moved greater distances per day during winter than summer (z = -2.21, r = -0.32, p <0.05; Figure 5). There was no difference in distance moved between the summer and winter for fish detected during one season only (between group comparison) (z = -0.48, r = -0.09, p =0.631; Figure 5) or for home range (independent samples: z = -1.50, r = -0.27, p =0.135; repeat measures: z = 0.69, r = -0.10, p =0.493; Figure 6).

Performance

Most trout exhibited positive year round growth in length (Figure 7a) and mass (Figure 7b). While mean growth in specific length did not differ between periods (z = -1.51, r = -0.13, p =

0.132), mean growth in specific mass was greater during period 2, which spanned summer and part of autumn, compared to period 1 which included winter and spring (z = -5.22, r = -0.44, p < 0.001; Figure 7b).

The deviation between estimated optimal and observed levels of growth (mass) was greater in period 1 (February to May) compared to period 2 (May to September) (t = 2.71, d.f. = 140, p < 0.01; Figure 8).

Discussion

For a population of brown trout occupying the River Lambourn, a groundwater-fed chalk stream in southern England, despite low levels of spatial variability, there was a positive relationship between depth and density in winter (February). This pattern of habitat use remained evident in spring (May), but not at the end of summer (September), providing support for our hypothesis that trout select habitat based on availability of instream cover. A similar pattern of habitat use in which trout typically seek shelter in deeper water in winter (e.g. Heggenes et al. 1999) has been observed in the more frequently studied northern boreal and temperate rivers, although the causal mechanisms likely differ. In northern boreal and temperate systems, the drive to seek deeper water is often considered part of a risk minimising strategy to avoid endothermic predators as water temperatures decrease (e.g. from 15 – 17 °C in summer to between 0 and 1 °C in winter; Mäki-Petäys et al. 1997). Given the high contribution of groundwater to the base-flow of the River Lambourn throughout the year, temperature remains relatively stable (e.g. decreasing from a mean of 12°C in summer to 9 °C in winter) and is unlikely to have caused the shift in habitat use observed in this study. Indeed, trout density was not correlated with water temperature during any season. In an environment exhibiting low variability in abiotic habitat parameters (flow, temperature, depth, velocity, substrate grain size), the highly seasonal growth of submerged macrophytes may explain variations in habitat use. Although there was no statistical relation between trout density and macrophyte cover, the strong relationship and lack of association between fish density and depth occurred in February and September, respectively, coinciding with periods of low and high macrophyte cover in the River Lambourn (Scarlett et al. 2015). In late summer/early autumn, trout likely remained in close proximity to cover because of the ubiquitous nature of macrophytes throughout the study reach. However, as instream cover is reduced during macrophyte dieback in winter, fish must seek shelter from predators (e.g. piscivorous birds such as the grey heron) in alternative (deeper) areas of refuge. Therefore, despite the drivers behind the shift in habitat use differing (reduction in instream cover provided by macrophytes rather than reduction in water temperature), movement to deeper areas likely reflects a predator avoidance (risk minimising) strategy in both stable groundwater-fed rivers as well as northern boreal / temperate systems.

Daily movements of radio tagged trout in this study was limited (<3.5 m), supporting our hypothesis of high levels of site fidelity. However, fish did move greater distances during winter compared to summer. This may reflect spawning movements (which typically occur between November and February) or greater propensity to switch between suitable instream cover (e.g. provided by pools and macrophytes), which are spaced farther apart during winter. However, the absolute difference in average distance moved between seasons was low (0.6 m) and not significant for fish monitored during only the summer or winter (rather than during both seasons). High site fidelity resulted in small home ranges (median 21.6 m – 50.6 m). This is likely because the potential to acquire food and grow varies little spatially in a system where productivity remains high year round. In such an environment, patch switching may be detrimental to fitness as it increases risk of predation (Höjesjö et al. 2015). The maximum home range in this study (470 m) was similar to those reported elsewhere for brown trout, e.g. in Belgium (480 m; Ovidio et al. 2002) and North Carolina (357 m ; Bunnel Jr et al. 1998). This suggests that although infrequent, longer distance movements are also made by a small proportion of trout occupying stable, groundwater-fed rivers where pressure from the environmental factors (temperature, flow, food availability) which typically influence movement are weak. If such movements are indeed associated with greater individual risk, then a greater understanding of factors causing some fish to have larger home ranges would be of interest from a management perspective.

Performance, in terms of growth, is found to be largely positive in salmonids inhabiting groundwater-fed rivers (French et al. 2016; Kemp et al. 2017). The lack of extremes in the abiotic environment (French et al. 2016) and high aquatic invertebrate abundance throughout the winter (Bouchard Jr & Ferrington Jr, 2009; Wright, 1992) likely mediates this. Despite being largely positive, performance varied seasonally during this study, contrary to our hypothesis. Growth in terms of mass was lower and deviation from the predictions of a growth model (developed by Elliott et al. 1995) greater during a growth period that included winter compared to one which spanned summer. During winter, a combination of factors, including costs of reproduction and lower temperatures that deviate farther from those that are optimal for growth, ensure trout likely experience greater energetic demands compared to the summer, and thus lower growth rates. Additionally, trout in the River Lambourn may have experienced lower food intake during the winter, e.g. as a result of a need to seek shelter from predators in deeper sections because instream cover provided by macrophytes diminished, or a reduction in habitat complexity resulted in greater intraspecific competition for feeding sites (Huntingford and Garcia De Leaniz, 1997). Further information is needed on how foraging behaviour and food intake varies seasonally in systems that remain productive year round.

Conclusion

As chalk streams remain relatively productive and stable environments throughout the year it is reasonable to assume that behavioural strategies adopted by trout may differ little with season. This was not the case in this study, conducted on the River Lambourn in southern England. Brown trout density was positively related to depth, distance moved was greater, and performance (growth) lower in a period which included winter compared to one which spanned summer. Trout may exhibit a risk minimising strategy, seeking refuge in deep pools during winter to reduce predation risk, while using abundant macrophyte cover at other times of the year. As cover becomes patchier, fish that switch patches may move over greater distances. However, further insight to explain lower growth in winter is needed. Of particular interest is the foraging behaviour and energy intake of stream dwelling salmonids that occupy pools and highly vegetated habitat. For management, there is a clear trade-off between macrophyte cutting practices (e.g. to reduce localised flood risk or impacts on recreational angling) and benefits to ecology, which include provision of cover for brown trout in systems with limited pool habitat. This study also emphasises the need to consider the effect of river restoration on the growth of macrophytes, which provide an ecologically important element of physical and hydraulic heterogeneity in an otherwise stable and homogenous environment.

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TABLES AND FIGURES

Table 1. Survey data for brown trout, *Salmo trutta*, caught on the River Lambourn by electric-fishing. Trout were tagged with a combination of Passive Integrated Transponder (PIT), radio, and data storage (DS) tags so behaviour and performance could be quantified (Kemp et al. 2017).

Survey dates	Number caught	Number PIT tagged	Number radio tagged	Number DS tagged	Fork length [mean ± SD (range), mm]	Mass [mean ± SD (range), g]
15 to 16 July 2010	126	126	30	10	229.2 ± 53.1 (148-425)	161.3 ± 95.9 (44-418)
3 to 4 February 2011	318	203	10	0	204.5 ± 72.7 (85-387)	126.5 ± 111.1 (7-575)
5 May 2011	220	209	19	9	211.1 ± 63.7 (113-390)	124.9 ± 111.7 (12-654)
9 September 2011	347	278	24	11	197.1 ± 65.3 (83-392)	122.5 ± 112.2 (6-631)
31 May 2012	361	0	0	0	216.6 ± 66.9 (67-499)	170.0 ± 165.7 (2-1128)

Table 2. Regression statistics of physical habitat predictors of fish density in 29, 17.5 m long, stream sections of the River Lambourn (Berkshire, UK). Bootstrapping was used to generate 95% bias corrected and accelerated confidence intervals (reported in parentheses) and significance tests of model parameters.

Electric-fishing survey	**Predictor**	***b***	**SE *b***	**Standardised ß**	***p***
February 2011 (Model: $R^2 = .73$, $F_{4,24} = 16.58$, $p < 0.001$)	Depth	0.004 (0.002 - 0.005)	0.001	0.955	= 0.001
	Velocity	0.001 (-0.001 - 0.004)	0.001	0.157	= 0.232
	Temperature	-0.134 (-0.411 - 0.050)	0.142	-0.167	= 0.299
	Macrophyte cover	0.000 (0.000 – 0.001)	0.000	0.181	= 0.148
May 2011 (Model: $R^2 = .49$, $F_{3,23} = 7.49$, $p = 0.001$)	Depth	0.001 (0.001 - 0.002)	0.000	0.872	< 0.01
	Velocity	0.000 (-0.001 - 0.001)	0.001	0.094	= 0.569
	Temperature	0.015 (0.000 - 0.114)	0.01	0.295	= 0.112
September 2011 (Model: $R^2 = .07$, $F_{4,23} = 0.42$, $p = 0.791$)	Depth	0.000 (-0.001- 0.001)	0.001	-0.204	= 0.477
	Velocity	0.001 (-0.002 - 0.002)	0.001	0.156	= 0.485
	Temperature	-0.026 (-0.120- 0.070)	0.042	-0.237	= 0.481

	Macrophyte cover	0.000 (-0.001 – 0.001)	0.000	0.010	= 0.952
May 2012 (Model: R^2 = .37, $F_{3,25}$ = 4.87, p < 0.01)	Depth	0.002 (0.001 - 0.005)	0.001	0.598	< 0.05
	Velocity	0.000 (-0.002 - 0.005)	0.001	-0.065	= 0.648
	Temperature	0.016 (-0.142 - 0.387)	0.102	0.167	= 0.834

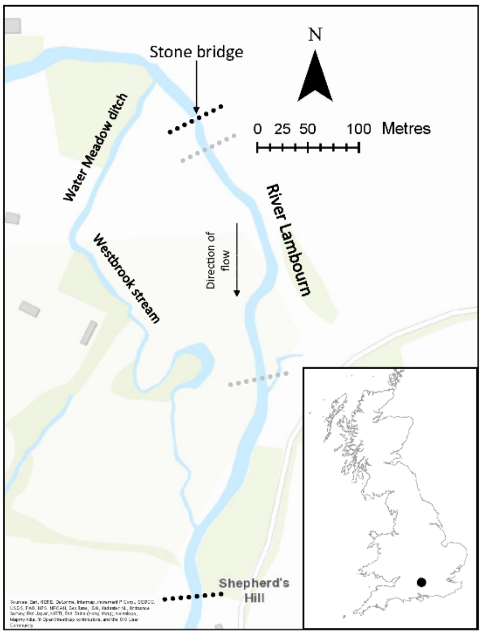

Figure 1. Study site on the River Lambourn (coordinates: 51.445542, -1.382947), a Chalk Stream in Berkshire (UK). The extent of a 500 m reach, where trout were monitored and physical / thermal characteristics were measured during the study, is denoted by the dashed black lines. The extent of the physical habitat survey conducted in February 2011 is denoted by dashed grey lines.

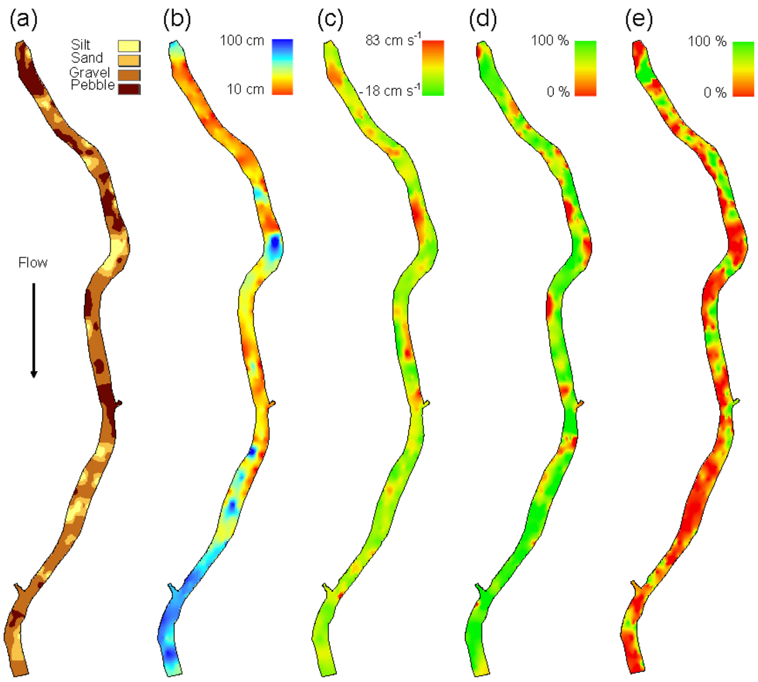

Figure 2. Spatial variability in (a) substrate type, (b) depth, (c) velocity, (d) and (e) instream macrophyte cover, along a 500 m reach of the River Lambourn (Berkshire, UK). Plots (a) – (d) represent data collected during the August 2011 habitat survey, and plot (e) represents data collected in March 2019.

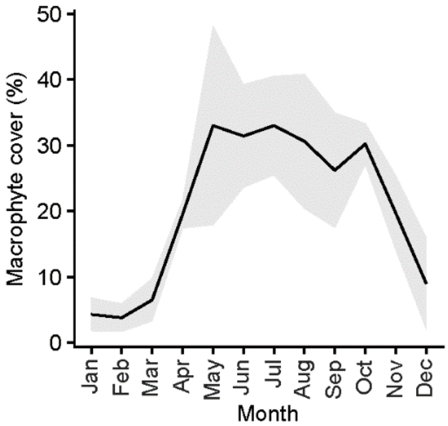

Figure 3. Median monthly macrophyte cover at the River Lambourn Observatory. The shading represents the median absolute deviation. Data were collected by CEH (Scarlett et al. 2016) between March 2009 and September 2014 at four locations representing areas (1) unshaded with average depth and velocity, (2) shaded with average depth and velocity, (3) limited shading, shallow and with high velocity, and (4) no shading, deep and low velocity. Data are available online at: https://doi.org/10.5285/37f0ab37-78f1-4ca6-b51f-950e43977b16

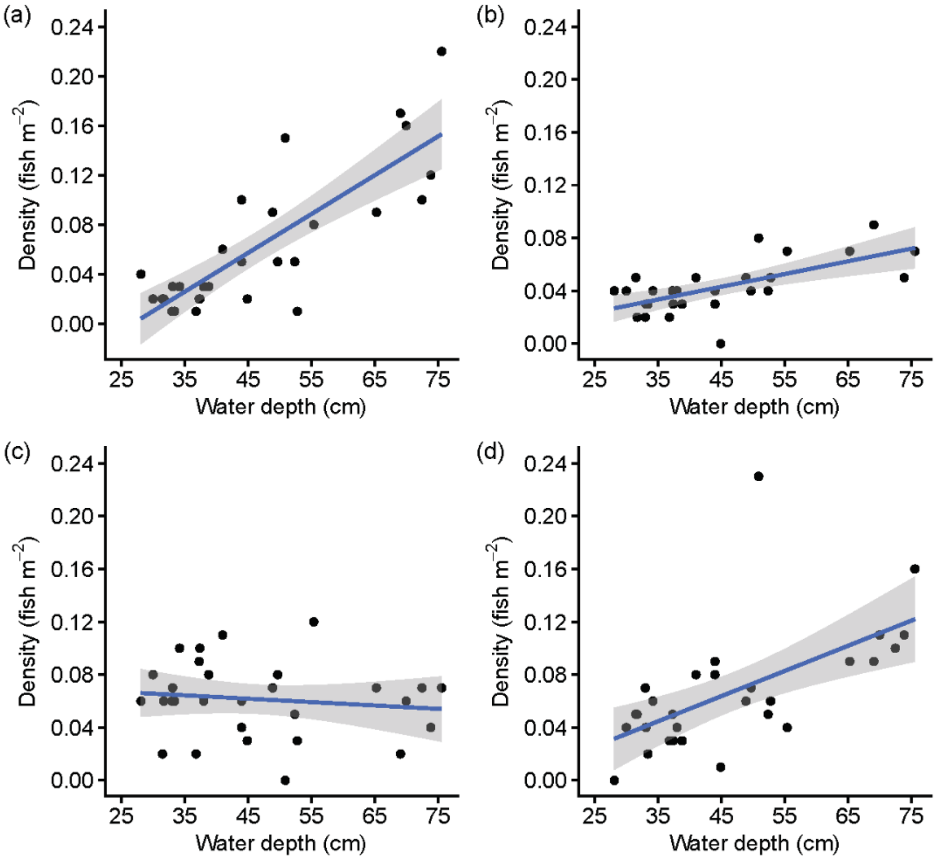

Figure 4. Density of fish (m^{-2}) in relation to mean water depth for the electric-fishing reaches surveyed in the River Lambourn (Berkshire, UK) in (a) February 2011, (b) May 2011, (c) September 2011, and (d) May 2012. Data are fitted with a linear regression line. The shading represents the 95% confidence intervals.

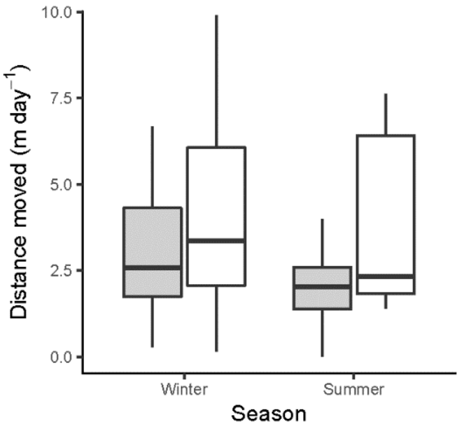

Figure 5. Distance moved (m day^{-1}) by brown trout in a 500 m reach of the River Lambourn (UK) during summer and winter. Fish analysed using repeated measures (fish detected during both periods) and independent samples (fish detected during one period) methods are represented by solid and clear boxes, respectively. The horizontal lines represent the median value, and boxes define the 25th and 75th percentile. The whiskers represent maximum and minimum values (excluding outliers). There were one and three outliers (> 1.5 x the interquartile range) in the repeated measures data during summer and winter, respectively, and one and two outliers in the independent samples data during summer and winter, respectively. Outliers are not show to aid interpretation of the data.

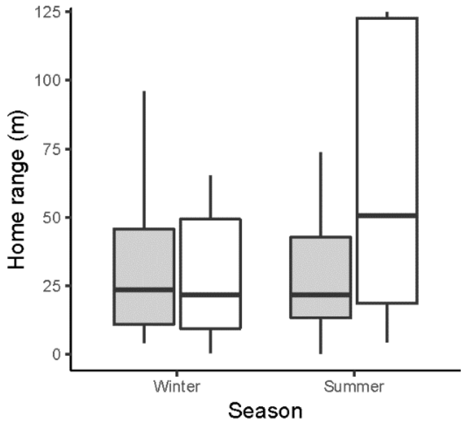

Figure 6. Home range (m) for brown trout in a 500 m reach of the River Lambourn (UK) during summer and winter. Fish analysed using repeated measures (fish detected during both periods) and independent samples (fish detected during one period) methods are represented by solid and clear boxes, respectively. The horizontal lines represent the median value, and boxes define the 25th and 75th percentile. The whiskers represent maximum and minimum values (excluding outliers). There were three and four outliers (> 1.5 x the interquartile range) in the repeated measures data during summer and winter, respectively, and two outliers in the independent samples data during both seasons. Outliers are not show to aid interpretation of the data.

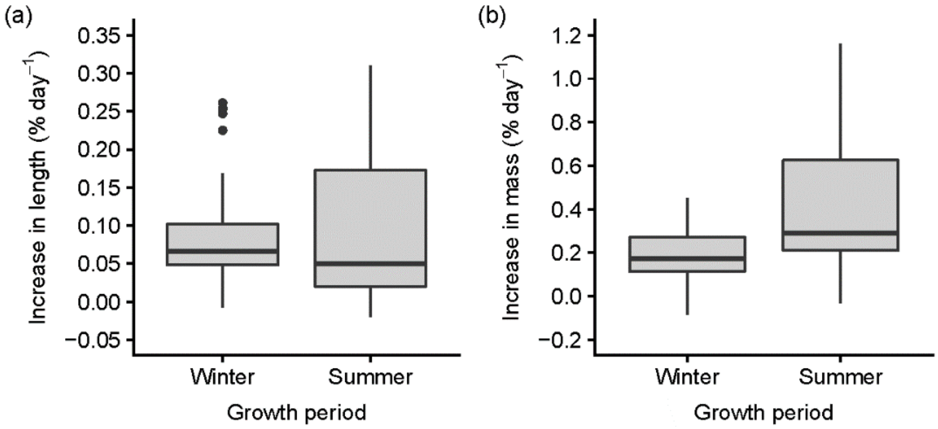

Figure 7. Mean growth in (a) fork length and (b) mass for brown trout occupying a stable and productive river system in Southern England during a period which included winter (Feb – May 2011) and spanned summer (May – Sept 2011). The horizontal lines contained within boxes represent the median value. Boxes show the 25th and 75th percentile. Vertical whiskers at the top and bottom of the boxes represent maximum and minimum values (excluding outliers), respectively. Outliers (> 1.5 x the interquartile range) are shown as circles.

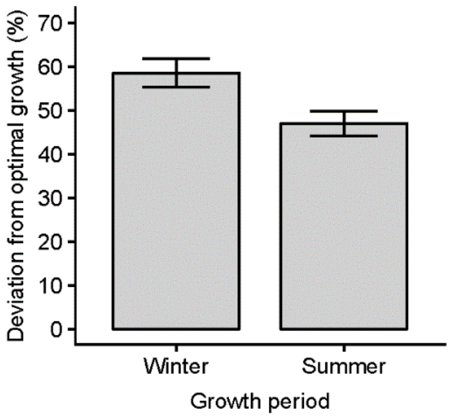

Figure 8. Deviation in growth in mass (% day^{-1}) from optimal growth estimated using a model by Elliott et al. (1995) which assumes fish are fed to satiation, during a period which contained winter (Feb – May 2011) and spanned summer (May – Sept 2011). Error bars are ± 1 SE.