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Challenging convention: the winter ecology of brown trout (*Salmo trutta*) in a productive and stable environment

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Running heading: The winter ecology of brown trout

SUMMARY

1. Understanding of the winter ecology of stream salmonids is biased by research conducted in northern temperate and boreal regions dominated by hard rock geology. Such systems are driven by highly dynamic surface flow regimes and tend to be physically diverse, nutrient poor, and influenced by ice. This study investigated how the behaviour of brown trout, *Salmo trutta*, inhabiting a stable groundwater-fed, productive, and comparatively warm southern English chalk stream differs from that described for other systems, and how this is translated to performance, measured as growth.

2. Physical characteristics were mapped, and high-resolution temperature data collected using a spatial array of data loggers installed throughout the study reach during the winter. A combination of passive integrated transponder and radio telemetry was used to monitor distribution, density, and movement of trout. Micro-archival data storage tags inserted in some individuals provided information on temperature regimes experienced. Growth performance was calculated for recaptured fish.

3. Trout density was positively related to depth and there was no evidence that temperature influenced microhabitat selection. Three patterns of movement were observed. Over three-quarters of tracked fish exhibited high site fidelity and tended to remain in a single focal position throughout the study. Fourteen percent of trout exploited more than one distinct location, while the remainder were detected at multiple locations and showed no preference for any one.

4. Trout exhibited regular daily activity patterns and highly periodic local movements at dusk and dawn and tended to experience positive growth performance during periods that included winter.

5. This study challenges the conventional view of salmonid winter ecology, which is biased towards populations that inhabit hard rock surface-flow dominated rivers that experience the influence of ice. Despite inhabiting a distinctly different winter habitat template than more commonly studied populations, trout occupying a hydrologically stable and productive chalk stream exhibited behaviours similar to those described for elsewhere, yet performed considerably better.

Introduction

Physical and chemical environments vary with time and space, and the rate and extent by which they change characterise degree of habitat heterogeneity. The unequal challenges and opportunities imposed by heterogeneous habitats influence ecological organisation; the habitat acts as a template (Southwood 1977) that defines characteristics operating at the population and community (e.g. species diversity and abundance, Tews et al. 2004) levels (Poff and Ward 1990). Spatial and temporal heterogeneity drives the individual adaptive response adopted to enable exploitation of opportunities encountered to maximise fitness. Thus, the relationship between behavioural traits and habitat heterogeneity should be predictable.

Stream-dwelling salmonids provide a particularly apt model to compare behaviour and performance among populations that experience differing degrees of habitat heterogeneity. Throughout their range, salmonids inhabit diverse river types where they may experience dynamic environments that impose severe ecological challenges, particularly during the winter bottleneck (Armstrong et al. 2003). Understanding of the winter ecology of salmonids is primarily based on research conducted in highly heterogeneous habitats, with little comparison made with populations that inhabit relatively stable environments. The current study focused on a population of brown trout, *Salmo trutta*, inhabiting a southern English chalk stream during the winter, which when compared with systems that have received most attention, tend to be both spatially and temporally more physically stable, and substantially more productive.

Based on current understanding, the conditions imposed by the winter template are among the most critically challenging during the life history of stream dwelling salmonids. Stressful temporal environmental change may limit abundance (Cunjak et al. 1998) and productivity (Armstrong et al. 2003) through a variety of mechanisms. These include limiting the availability of suitable habitat (Cunjak 1996) and creating adverse conditions that isolate and damage fish when ice forms (Huusko et al. 2007), or displace them during scour and flooding events with the thaw (Cunjak et al. 1998). Furthermore, declines in temperature not only regulates physiological (e.g. maintenance of energy reserves; Finstad et al. 2004) and locomotory (e.g. Webb 1978) performance during the winter, but also a range of other biotic relationships. For example, shifts in predator prey dynamics in favour of homeothermic mammalian and avian piscivores has been described (Fraser et al. 1993), while production and drift of invertebrate food is typically reduced as temperature declines (Simpkins and Hubert 2000, but see Cunjak and Power 1987).

In response to the wintertime challenges imposed, salmonids display a multitude of adaptive behaviours. The benefits to juveniles of maintaining territories, as during the summer, are lost as costs of maintenance increase relative to energetic gains when food becomes limited (Dill et al. 1981). Aggressive interactions become less common (Heggenes et al. 1993) as fish become more gregarious and form aggregations in pools (e.g. Heggenes et al. 1999). Further, stream salmonids become increasingly nocturnal (Heggenes et al. 1993) below some threshold temperature (Fraser et al. 1993), and commonly seek shelter during the day (Heggenes et al. 1999) to avoid visual predators (Orpwood et al. 2006, 2010).

At the onset of winter, salmonids commonly seek alternative microhabitat that provides refuge from both predators and unfavourable hydrodynamic and thermal conditions. Compared to the summer and autumn, winter microhabitat is associated with slower water velocities (Mäki-Petäys et al. 1997), greater depth (Heggenes et al. 1999), and access to shelter provided by larger non-compacted substrate (Stickler et al. 2008), submerged woody material (Swales et al. 1986), and overhead cover (Cunjak and Power 1986), including surface ice (Linnansaari et al. 2009). The availability of suitable microhabitats can dictate overwinter survival (e.g. Solazzi et al. 2000; Hedger et al. 2013), and thus influence population abundance and productivity (Cunjak et al. 1998).

The generalised perspective of the winter ecology of stream salmonids so far considered focuses predominantly on populations inhabiting systems that exhibit high physical and chemical heterogeneity over both spatial and temporal scales (Table 1). Past research has often focused on northern temperate and boreal rivers and streams based on a hard rock geology and driven by surface flow, such as those that occur in Canada (e.g. Catamaran Brook, Cunjak et al. 1998; Linnansaari and Cunjak 2010) and Scandinavia (e.g. Orkla River, Norway, Stickler et al. 2007; River Alta, Norway, Hedger et al. 2013). These rivers experience dynamic flow regimes as they rapidly respond to precipitation and snow melt events, have gravel beds with a wide range of substrate size classes, and well developed frequent riffle-pool sequences. Salmonid populations that inhabit them often are adapted to nutrient poor, low pH conditions, and, due to the wide fluctuations in temperatures experienced, may suffer extensive periods of freezing and the influence of ice dynamics. Conversely, salmonids that inhabit lowland groundwater-fed systems experience quite different environmental conditions. For example, in southern England, several lowland salmon and trout rivers flow through chalk catchments, and do not share the same heterogeneous physical, chemical, and ecological characteristics described for upland gravel-bed rivers (Table 1). Referred to as chalk streams, these rivers are predominantly aquifer fed and so maintain relatively constant annual flow and temperature regimes. Many chalk streams exhibit a gravel bed matrix with limited geomorphological diversity owing to their characteristically low stream power.

To improve understanding of how environmental variability influences behaviour, this study explored the winter ecology of a stream dwelling salmonid in a southern English chalk stream. We aimed to quantify: 1) trout behaviour as indicated by distribution relative to available habitat, patterns of movement, and levels of activity; and 2) trout performance, measured as growth. Compared with more dynamic systems, chalk streams during the winter are: a) spatially homogeneous, in terms of hydrodynamic and physical characteristics, b) warm and ice free, c) temporally constant in relation to flow and food abundance, and d) highly productive. Therefore, we predicted that under these less challenging conditions there would be: a) no need, and less opportunity, for fish to select refugia from adverse physical conditions (e.g. hydrodynamics and ice formation), and thus a lack of an association with deep, slow flowing areas; b) a positive relationship between fish density and areas of warm water, potentially associated with groundwater upwelling, to enhance growth; c) a high degree of site fidelity and limited movements of fish, including at night; and d) a high growth performance during the winter when compared with boreal systems.

Methods

Site description, and physical and thermal characteristics

The study was conducted at a 500 m long reach of the River Lambourn (owned by the Centre for Ecology & Hydrology [CEH]) at Boxford (51.445542,-1.382947), Berkshire, UK (Figure 1). The site is situated approximately two-thirds (14 km) of the river length from the ephemeral source near the village of Lambourn. The river flows through a catchment (upstream area: 162 km^2) dominated by arable and mixed farmland prior to entering the River Kennet, a tributary of the River Thames. The catchment, dominated by cretaceous chalk geology with deposits of clays and flints, lacks impermeable strata and overland flow resulting in a low drainage density (0.12 km km^{-2}) (Evans et al. 2003). The mean river discharge (± SD and range) at the site during the two study winters was 0.90 m^3 s^{-1} (winter 1: ± 0.23, 0.53-1.33) and 0.52 m^3 s^{-1} (winter 2: ± 0.06, 0.36-0.98) (Rameshwaran et al. 2015). Discharge exhibits low seasonal variation and is dominated by a stable groundwater-fed base-flow contribution, which typically exceeds 95% (Evans et al. 2003). The river water chemistry is driven by the calcium-bicarbonate component. The riverbed substrate comprises of gravel and coarse sub-angular flint and the channel gradient is 0.05° (Evans et al. 2003).

A baseline survey was conducted between 23 and 26 August 2011 to quantify the spatial variability of key physical habitat characteristics throughout the study reach. Key parameters were recorded at approximately five equidistant points along transects that spanned the width of the channel at 10 m longitudinal intervals. Temporal variability was quantified by conducting a survey of a 270 m section of the study reach on 22 February 2011. Dominant substrate type was visually classified using the Wentworth grain size scale and ranged from silt (< 0.0063 cm) to pebble (1.6-6.4 cm), but was dominated by gravel (0.2 – 1.6 cm) (Table 2, Figure 2a). Water depth and mean (± SD) mid-column (60% depth) water velocity was measured using a metre rule and electromagnetic flow meter (0.001 m s^{-1} resolution averaged over 10 seconds, Valeport Model 801, Totnes, UK), respectively. Shallow, moderate velocity reaches dominated the upper and middle sections interspersed with a few deep ($\geqslant$ 1 m) low velocity areas, and a deep reach at the downstream end of the site (Figure 2b, c). There was nearly continuous riparian cover along the true right bank, but scarce vegetation on the left.

Data loggers accurate to 0.47˚C (Hobo Temp/Light Pendant, Onset Computer Corporation, MA, USA) recorded river temperature hourly at transects positioned approximately every 20 m along the study reach. Three loggers were deployed at each transect; one each at the left and right bank, and one in the centre of the channel. Loggers recorded temperature at the substrate. Two additional loggers recorded ambient air temperature in the shade at hourly intervals. Missing data points (e.g. due to loss of loggers, delays in downloading, and equipment failure) were substituted with values (T_r) obtained by regressing mean daily water against air temperature for each position. Winter temperature regime obtained for the Svarttjønnbekken River (Norway) over the same period allowed comparison between the River Lambourn and a northern boreal system.

During Winter 1 the UK experienced heavy snowfalls and record low temperatures, with the coldest (mean air temperature: -1°C) December recorded since Met Office records began in 1910 (Met Office data). On the 20 December 2010 a minimum ambient air temperature of -13.72°C was recorded at the study site. Mean UK air temperatures for December and January were 5.0°C and 0.3°C below average. The mean temperatures in the UK were much milder during Winter 2, with December, January and February being 0.6°C, 1.3°C and 0.7°C above average (Met Office data). Despite this, a cold spell lasting 2 weeks in England started at the end of January. This resulted in a minimum winter ambient air temperature recorded at the study site of -12.81°C on 11 February 2012. River temperature varied temporally during the two winter periods (Figure 3). Average mean river temperatures during Winters 1 and 2 (recorded from start of December until end of February) were 7.55°C and 7.84°C, respectively. This is consistently higher than the northern boreal system (Svarttjønnbekken River, Norway), which remained close to zero (Figure 3). River Lambourn water temperatures showed high variability (average SD Winter 1: 0.38; Winter 2: 0.52), being closely correlated with ambient air temperature throughout the two periods (Winter 1: $\alpha = 6.5$, $\beta = 0.42$, $R^2 = 94.5\%$, $p < 0.001$; Winter 2: $\alpha = 6.3$, $\beta = 0.40$, $R^2 = 85.0\%$, $p < 0.001$). River temperatures varied spatially (Figure 2d). For example, on the coldest day in Winter 2 (11 February 2012, mean air temperature = -6.6°C) maximum and minimum river temperatures were recorded as 8.1 and 2.7°C at locations 52.7 and 81.3 cm deep, respectively.

Fish distribution, movement, and activity

The distribution, movement and activity of fish were recorded at coarse and meso-scale resolution using a combination of electric fishing, mark recapture, and telemetry surveys.

Trout were captured through the entire study site by electric fishing upstream through 20 m long reaches (confined by stop nets) using a single pass on five occasions (Table 3). Trout captured were anesthetised (0.3 ml L^{-1} 2-phenoxyethanol), measured (fork length mm), weighed (g), and scanned to identify recaptured individuals tagged in previous surveys. If sufficiently large, trout were implanted with 12 mm full duplex Passive Integrated Transponder (PIT) (Wyre Micro Design Ltd, Lancashire, UK; > 100 mm fork length), radio (24 mm length, 1.9 g mass in air, estimated battery life = 8.7 months; Biotrack, Wareham, UK; > greater than 150 g mass), and micro-archival data storage (DS) (25.4 mm length, 3.3 g mass in air, estimated battery life = 18 months; DST micro-T, Star Oddi, Reykjavik, Iceland; > 300 g) tags (Table 3). The total tag burden did not exceed 2 % of the fish body mass. Fish were not tagged during the final survey. Prior to surgery, the functionality and unique frequency (between 173.199 and 173.994 MHz) of all radio tags was verified using a hand-operated receiver, and DS tags were programmed to record fish body temperature every 15 minutes. Fish were allowed to recover (approx. 1 hour) in tanks containing aerated river water before being returned to the electric fishing reach from which they were captured. Standard tagging protocols were conducted in compliance with the UK Animals (Scientific Procedures) Act 1986 under Home Office licence.

<u>Distribution and density</u>: Trout density for each (20 m) electric-fishing reach was calculated using data from the winter electric-fishing survey (February 2011) as the quotient of number of fish captured and surface area (quantified using the GIS base map) of the reach. A linear regression model was fitted to determine whether habitat variables (depth, velocity and water temperature) were significant predictors of density during winter.

Coarse-scale site fidelity was described as the percentage of previously tagged fish recaptured within ± 1 electric fishing reach during subsequent surveys.

To investigate whether trout selected and tracked thermal microhabitat to maximise growth performance, i.e. areas exhibiting the highest temperatures (e.g. groundwater upwelling or a tributary confluence), the difference between mean daily body and maximum daily river temperatures (ΔT) was calculated for recaptured fish containing DS tags. To assess how this changed during low temperature periods when fish may experience highest thermal stress, ΔT was plotted against minimum daily river temperature. If trout exhibited behavioural thermoregulation they were expected to track patches that provided the greatest opportunity for growth, i.e. those areas where maximum water temperatures were recorded. In this case, no difference between maximum daily river and mean daily body temperature was expected, and this would remain the case independent of minimum daily river temperature. In the event that trout exhibit high site fidelity, a difference between maximum daily river and mean daily body temperature should be observed, and this would unlikely remain constant over time.

Movement: Meso-scale movements were assessed using telemetry during two study periods: November to April in 2010-2011 (Winter 1) and 2011–2012 (Winter 2). Radio tagged trout were located from the bank using a hand-held receiver (Sika, Biotrack, Wareham, UK) connected to a three-element Yagi antenna during systematic surveys of the entire site up to 3 times per week. Tagged fish were detected up to distances of approximately 250 m. Once located, the position of individual fish was estimated by reducing the gain on the receiver and moving longitudinally 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 landmarks of known location.

Fish positions derived from mobile radio tracking were imported into ArcGIS, plotted on the base map of the river and underlying water depth data extracted. The relationship between fork length and average depth occupied during mobile radio tracking surveys was expressed using Pearson’s correlation.

Using fish positions derived from mobile radio tracking, patterns of individual movement were quantified using two metrics: 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. For each fish, the number of days between first and last detection (detection period) and number of radio fixes was also recorded.

To identify factors influencing variability in patterns of individual movement, linear regression models were applied to determine whether the independent variables (fish length, mass, detection period and/or number of radio fixes) were significant predictors of either movement metric. Due to multicollinearity between fish length and mass (r = 0.92), these predictors were combined and replaced in the models by condition factor (K), calculated as:

$$K = 100 \cdot \frac{W}{L^3}$$

where W is fish mass (g) and L is fork length (cm). Number of radio fixes was also removed from the model due to multicollinearity with detection period (r = 0.92).

To investigate whether patterns of individual movement differed between the two winter periods Mann-Whitney U tests were used as data violated the assumption of normality, and could not be successfully corrected through transformation. Comparisons between the two winter periods were deemed valid as number of radio fixes and detection period (measures of sampling frequency) were not significant predictors of either movement metric.

Activity: Four automated fixed radio receivers (SRX-DL Data loggers, Biotrack, Wareham, UK), installed during Winter 2 at the upper and lower ends of the site, and at two locations previously identified to contain a high number of tagged fish (Figure 2a), continually scanned for up to 20 frequencies. An autocorrelation function (ACF) was performed on mean signal strength per hour for individual fish using the ‘correl’ command in Microsoft Office Excel (Microsoft Corporation, Redmond, USA), with a one-hour time lag, for 336 hours (14 days) after detection for fish detected during ≥ 20% of those hours. Autocorrelation was deemed to have occurred for fish with ACF peaks outside the limits of 95% confidence.

Fish performance

Performance metrics were based on data collected during electric fishing surveys in July 2010 and February 2011 (which included Winter 1), and September 2011 and May 2012 (Winter 2).

Mean specific growth rate (% day^{-1}) for PIT tagged fish recaptured during electric fishing surveys was calculated as:

$$G = 100 \cdot \left((\log_e W_2 - \log_e W_1)/t \right)$$

where W_1 and W_2 are the initial and final fish mass (g), and t is the number of days between surveys (i.e. the growth period). For each fish, G was compared to an estimate of optimal growth (G_{op}) using the model developed by Elliott et al. (1995):

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

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 optimal (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. $T_{\text{lim}} = T_{\text{L}}$ if $T < T_{\text{M}}$ or $T_{\text{lim}} = T_{\text{U}}$ if $T > T_{\text{M}}$). 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). The growth model assumes fish fed to satiation under laboratory conditions.

Results

Fish distribution, movement, and activity

<u>Distribution and density</u>: Trout density was positively related to depth; there was no relationship with water temperature or velocity (Table 4; Figure 4).

Coarse resolution assessment of site fidelity indicated that 26% (*n* = 5) and 71% (*n* = 32) of trout that were recaptured were within ± 1 electric fishing reach during periods that included Winter 1 (July 2010 – February 2011) and 2 (September 2011 – May 2012), respectively.

For the five recaptured fish that contained DS tags the relationship between ΔT and minimum daily river temperature was positive (Figure 5). These fish did not utilise and track microhabitat based on selecting high temperature areas that may have maximised growth during winter. Instead, they remained site attached at mean water depths that ranged from 41.7 cm to 79.8 cm with body temperature conforming to river temperatures at those locations.

<u>Movement</u>: Of the 83 trout implanted with radio tags, 65 were detected during subsequent tracking. Of these, eight were excluded from further analysis due to low levels of certainty of their position or because they were detected once only. Of the remaining 57, 43 (75.4%) were detected within the study site more than once during the winter periods.

There was no relationship between fork length and the average water depth occupied during mobile radio tracking surveys ($r = 0.11$, $p = 0.493$).

Differences in distance moved (median [IQR] = 2.92 [4.07] m day^{-1}) and longitudinal home range (median [IQR] = 21.20 [45.20] m) among individual fish was not predicted by either condition factor or detection period (distance moved: Multiple regression $R^2 = 0.06$, $F_{2,40} = 1.30$, $p = 0.285$; home range: Multiple regression $R^2 = 0.05$, $F_{2,40} = 1.03$, $p = 0.365$). Median distance moved and home range was low and did not differ between the two winter periods (Mann-Whitney U: distance moved $U = 220$, z = -0.24, $p = 0.808$; home range $U = 228$, z = -0.06, $p = 0.951$). However, variability in behaviour among individual fish was evident with patterns of movement categorised into three groups based on levels of site attachment: 1) occupancy of a single position within the study reach (expressed by 76.7% of tracked fish, $n = 33$; e.g. Figure 6a); 2) utilisation of more than one distinct location (14.0% of fish, $n = 6$; e.g. Figure 6b); or 3) multiple detections throughout the study site with no clear single location for which fish exhibited high site fidelity (9.3% of fish, $n = 4$; e.g. Figure 6c). Larger home ranges (> 65 m) generally indicated occupancy of more than one distinct location within the study site (movement pattern 2 described above) rather than low site fidelity.

Activity: All nine fish detected in the vicinity of the continually logging fixed radio receivers during Winter 2 exhibited autocorrelated activity. Four fish displayed autocorrelation patterns with lags roughly every 24 hours, suggesting that they displayed regular daily activity patterns (e.g. Figure 7a). Two fish, both detected in the vicinity of deep low velocity areas, displayed particularly high levels of autocorrelation with a consistent 24 hour lag and no decay (Figure 7b). This is indicative of highly periodic behavioural rhythms. These fish moved in and out of the detection range of the receiver at dusk (17:00 h) and dawn (07:00 h), respectively (Figure 7c).

Fish performance

On average trout growth during the periods that included winter was positive (Winter 1 mean ± SD = 0.08 ± 0.09 % day^{-1}; Winter 2 = 0.22 ± 0.10 % day^{-1}), but differed among years (independent samples *t*-test: $t = 5.97$, d.f. = 90, $p < 0.001$), with higher rates in year 2. For some fish, growth approached that predicted by the optimum growth model that assumes fish are fed to satiation. Although rates were suboptimal during both years (Winter 1: $U = 2.00$, $n = 38$, $z = -5.21$, $p < 0.001$; Winter 2: $U = 216.50$, $n = 145$, $z = -9.54$, $p < 0.001$; Figure 8), there was a positive relationship between observed and predicted growth (for Winter 1: $r = 0.66$, $p < 0.01$; for Winter 2: $r = 0.81$, $p < 0.001$; Figure 8). Trout density and growth rates (% increase in g day^{-1}) were unrelated (Pearson's correlation: $r = -0.38$, $p = 0.055$) during mid-winter (February 2011).

Discussion

Understanding of the winter ecology of stream salmonids is largely based on populations that inhabit northern temperate and boreal surface flow dominated rivers with coarse-grained bed substrate situated on hard rock geology. Within this context, Cunjak (1996) provides a definition of winter that focuses on ecological and physical parameters, i.e. the period immediately following egg deposition, which coincides with a decline in water temperature, and that extends until the loss of all surface ice and the accompanying spate and snowmelt. This definition is inappropriate, however, for different hydromorphological systems, such as those fed by groundwater and that do not experience ice dynamics. In this study we considered a groundwater fed chalk stream and defined winter simply as being the coldest season of the year, which in the northern hemisphere extends from December to February. Chalk streams in southern England generally experience a relatively mild climate and consistently high mean annual groundwater temperatures (approximately 11°C), with little variance, and no freeze-up and thaw events. Focusing on the relatively stable and physically and chemically homogenous River Lambourn, this study investigated the behaviour (distribution, movement and activity patterns) and performance (growth) of a local brown trout population occupying an alternative habitat template (Southwood 1977) to those commonly considered. The findings discussed relative to a suite of predictions that are based on prevailing views provide further insight into the winter ecology of salmonids.

Salmonids in chalk streams do not face the adverse conditions imposed by freeze-up and thaw and the associated hydrodynamic challenges experienced by fish inhabiting many surface-flow dominated boreal rivers. For example, in the high energy dynamic systems that respond rapidly to precipitation and snowmelt, water velocities exceeding 5 m s^{-1} may be observed e.g. during surges of water and ice as ice dams rupture (Cunjak et al. 1998). Under such conditions, salmonids must attempt to escape the negative effects of high shear stresses and high-velocity scour. Perhaps as a consequence of adaptation to such pressures, stream-dwelling salmonids typically move to slower flowing (Mäki-Petäys et al. 1997), deeper areas (Heggenes et al. 1999), with access to large non-compacted substrate (Stickler et al. 2008), and woody structure (Swales et al. 1986) during the winter. Partly due to a more benign environment and the lack of structural complexity we did not expect brown trout to associate strongly with microhabitat based on either depth or velocity in this study. However, although trout distribution was not influenced by velocity, density was positively related to depth, an association that more likely reflected sheltering from predation than from adverse hydrodynamics. The value of deeper areas as refuge is apparent when the availability of alternative forms of shelter is considered. In many chalk streams sufficiently large particles and woody structure is limited, and the highly compacted and weathered nature of chalk bed materials means that the availability of interstitial space is low. Similarly, longitudinal pool and riffle frequency tends to be low in chalk streams, and thus where deeper areas do occur, they likely provide important and much sought after refugia in the absence of macrophyte cover during the winter.

As temperature is the most pervasive environmental factor influencing the life history of fishes (Wootton 1998) we predicted that should the study site exhibit thermal heterogeneity, e.g. due to the presence of upwelling ground water or other inputs, then trout would select areas of high temperature in an attempt to maximise fitness. Further, trout were expected to enhance opportunities for growth by tracking favourable temperature habitat patches should they change over time. Although chalk streams are considered homeothermous in character, exhibiting relatively limited variability in water temperature over the annual cycle (Edwards 1979), during the winter much higher temporal variability is observed than for boreal surface flow rivers that experience freeze-up. For example, the Svarttjønnbekken River (Norway) remained close to 0°C throughout the two study winters; and even in the event of supercooling, water temperatures would have declined by only a few hundredths to a tenth of a degree below zero Celsius (Brown et al. 2011). In comparison, the mean daily temperatures recorded for the River Lambourn during the two study winters (December to February) were much higher, ranging between 7.5°C and 8°C, and more variable, being closely correlated with ambient air temperature. Even during unusually cold periods for the UK for both winters, and especially December of winter 1, mean temperatures rarely dropped below 5°C. Further, the study site exhibited spatial variability in local temperatures, which was likely the result of warmer upwelling subsurface flow, the dominant direction of hyporheic exchange at the study site (Pretty et al. 2006), and the contribution of a tributary (Fig. 2d). Nevertheless, trout distribution was not influenced by either temporal or spatial variation in water temperature, and there was no evidence, based on a small sample of recaptured fish holding temperature sensitive data storage tags, that trout selected and then tracked warmer areas of microhabitat that would have enhanced growth potential.

In a stable and productive chalk stream, in which energy intake (high) and shelter opportunities (low) are predictable, we expected high site fidelity and low levels of patch switching because the drive to explore new areas was likely to be weak. It is suggested that high site fidelity represents an optimal foraging strategy in stable environments in which resource availability is high and predictable (Arthur et al. 2015). This is contrary to the situation that occurs in heterogeneous "patchy" environments, such as that described for surface-flow dominated river systems in which the spatial distribution of drifting invertebrate food is limited and temporally unpredictable. In such cases, stream-dwelling salmonids may be predicted to switch patches as profitability of the foraging position declines and they search for higher quality microhabitat. This assumption is supported conceptually (Marginal Value Theorem; Charnov 1976) and through observation (for juvenile Atlantic salmon in Scottish streams: Martin-Smith and Armstrong 2002). In line with our prediction, a large majority of tracked trout exhibited high site fidelity and limited movement, with over three-quarters occupying a single location. Alternative strategies were demonstrated, but were rarer. Less than 10% of trout tracked throughout the study area did not favour any distinct locations. However, nearly 28% of the radio-tagged trout were recorded either only once or never again.

The fate of these fish remain unclear. They may have emigrated out of the study site and travelled an undetermined distance, were predated, or suffered tag failure. Similarly high levels of site fidelity have been previously described for salmonids in other systems and at other times of the year, including for a proportion of those populations in which patch shifting was commonly observed (e.g. Martin-Smith and Armstrong, 2002), possibly reflecting a strategy by some individuals to limit detection by predators. Thus, site fidelity is not necessarily limited to spatially and temporally homogenous habitat templates during the winter.

Where food is abundant and lower temperatures favour homeothermic mammalian and avian visual predators in attacks against ectothermic prey during the winter (Fraser et al. 1993; Orpwood et al. 2006, 2010), maximisation of energy intake during the night is likely to represent an advantageous strategy. In other systems, stream-dwelling salmonids become increasingly nocturnal with reductions in temperature during the winter and generally less active during the day when they commonly seek shelter (Cunjak 1988; Heggenes et al. 1993; Heggenes et al. 1999). For juvenile Atlantic salmon the shift to increasingly nocturnal foraging appears to occur at some threshold temperature between 8-10°C (Fraser et al. 1993; Rimmer et al. 1983). Although fish in this study tended to exhibit high site fidelity, there was also evidence of high periodicity of movement exhibited by some fish, with changes in position at dawn and dusk, which may suggest nocturnal foraging. This may not reflect a strategy unique to the winter, however, as radio-tagged trout on the River Aisne were most active at dusk in all seasons (Ovidio et al. 2002). Further research is needed to clarify how salmonid foraging behaviour and anti-predator response varies with season and river type.

As chalk streams are highly productive aquatic environments it was predicted that trout would exhibit high growth during the winter in this study. Indeed, the River Lambourn supports elevated primary and secondary production, and exceptional invertebrate biomass

(Pretty et al. 2006). At Bagnor, approximately 3 km downstream of the study site, invertebrate biomass tends to peak in December with total density found to range from approximately 15,000 to 70,000 macroinvertebrates m^{-1} (data collected between 1971-1978, Wright 1992). This high density of invertebrates during the winter reflects the energy provided by abundant decaying macrophytes that act as a nucleus for the deposition of allochthonous tree leaves in the autumn (Westlake et al. 1972). In contrast, boreal and northern temperate surface-flow systems tend to be oligotrophic, and during the winter low temperatures create a stressful period during which growth of salmonids is sufficiently low as to be considered negligible (Cunjak and Power 1987), ceases altogether, or in some cases is negative as indicated by a loss in mass (Egglishaw and Shackley 1977). The River Lambourn trout exhibited positive growth during periods that included winters 1 and 2. It is unsurprising that mean growth rates were below those predicted by the Elliott et al. (1995) growth model that is more applicable to summer growth situations (Jensen et al. 2000) for trout fed on maximum ration. Unfortunately, these results were influenced by growth periods during autumn (year 1) and spring (year 2). Nevertheless, it is likely that the higher mean ambient temperature regimes and high biomass of invertebrates resulted in elevated growth rates when compared with other systems. This suggestion is supported by earlier studies that quantified the annual instantaneous brown trout growth in which the River Lambourn yielded the highest values of nine examples of UK rivers studied (Edwards et al. 1979).

Conclusions

Using passive integrated transponder and radio telemetry combined with information obtained from data storage tags this study sheds light on the behaviour and performance of brown trout inhabiting a comparatively stable, warm and productive habitat template provided by a chalk stream during the winter. In this often ignored system, the hydrodynamic, physical and thermal environment was mapped at a fine-resolution scale appropriate to study the distribution and movement patterns of the target species. Interestingly, several behaviours exhibited by trout were similar to those observed for other systems and seasons. Distribution was strongly correlated with depth, but not velocity or temperature, and the majority of radio-tracked fish exhibited high site fidelity and limited movement. There was evidence for high periodicity of movement with changes in position at dawn and dusk for some fish, potentially suggesting nocturnal foraging. Trout growth was positive during the periods that included winter in both years, indicating higher performance than for populations that suffer an intensely challenging winter bottleneck. Recognition of regional variation in winter ecology of salmonids is important in developing appropriate management strategies to preserve or rehabilitate winter habitat in the face of increasing urbanisation, altered land use, and climate change.

Acknowledgments

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TABLES AND FIGURES

Table 1. Comparison of generalised physical and chemical habitat templates for boreal surface flow rivers on hard rock catchments and temperate ground water dominated chalk streams during the winter.

Characteristics	Boreal surface flow hard rock rivers	Temperate ground water fed chalk streams
Physical		
- Hydrological regime	Moderate – high temporal variability. Dynamic and "flashy" – responsive to precipitation and snow-melt events.	Low temporal variability, relatively stable regime sustained for long periods by high baseflow component.
- Depth	Moderate to high spatial variability. Well defined riffle-pool sequences.	Low spatial variability. Lack of well-defined and low longitudinal frequency of riffle-pool sequences. Frequently shallow cross sectional area in unmodified reaches.
- Hydrodynamics (velocity, turbulence etc.)	Moderate to high spatial and temporal heterogeneity dictated by flow and substrate complexity.	Low meso-scale hydrodynamic heterogeneity. Fine scale complexity associated with aquatic plants.
- Substrate and structure	Potential for high spatial variability ranging from fine sediments to large boulders and large woody debris. Considerable potential for refuge sites including interstitial space.	Generally low variability and predominantly sands and flint gravels with a lack of large clasts. Fine sediment component is often high. The riverbed may be highly compacted and weathered with limited interstitial space. Infrequent gravel shoals and exposed river bed substrate.
- Channel planform and drainage	High variability, ranging from natural channels with high sinuosity to those influenced by anthropogenic modification. Moderate to high drainage density and dendritic drainage patterns are common.	Often influenced by long history of anthropogenic modification and management. Channel frequently diverted along alternative paths running in parallel (e.g. mill lades). Low drainage density and limited tributary network. Headwaters may be ephemeral.
Chemical		
- pH	High acidity. pH ranges from 4.5 – 7.0.	High alkalinity. pH typically 7.4 – 8.0.
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- Temperature	High variability of river temperatures during the year, but low temperatures (0°C) for long periods during the winter months, especially in systems that experience freeze-up.	In southern England spring water temperature is typically 11°C. Temperatures remain relatively warm throughout the winter.

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Table 2. Physical habitat variables quantified through a 270 m section of the study reach on the River Lambourn during two surveys (February 2011 and August 2011).

Habitat variable	Measure	Values	Survey date
Substrate	Dominate size	Gravel (35%)	Feb 2011
		Gravel (57%)	Aug 2011
Depth	Mean	31.9 cm	Feb 2011
		38.3 cm	Aug 2011
	Range	2-115 cm	Feb 2011
		13-98 cm	Aug 2011
Velocity (cm s^{-1})	Mean	31.7 cm/s	Feb 2011
		21.0 cm/s	Aug 2011
	Range	-4-89 cm/s	Feb 2011
		1-54 cm/s	Aug 2011

Table 3. Telemetry survey data for brown trout, *Salmo trutta*, caught on the River Lambourn by electric fishing.

Survey dates	Number caught	Number PIT tagged	Number radio tagged	Number DS tagged	Fork length [mean ± SD (range), mm]	Weight [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 4. Regression statistics of physical habitat predictors of fish density at a coarse scale in a 500 m reach of the River Lambourn (Berkshire, UK). 95% bias corrected and accelerated confidence intervals are reported in parentheses. CIs, SEs and significance values for all predictors are based on 1000 bootstrap samples.

Electric-fishing survey	**Predictor**	***b***	**SE *b***	**ß**	***p***
Feburary 2011 (Model: R^2 = .71, $F_{3,25}$ = 20.10, $p < 0.001$)	Depth	0.004 (0.002 - 0.005)	0.001	0.918	= 0.001
	Velocity	0.002 (-0.001 - 0.004)	0.001	0.207	= 0.141
	Temperature	-0.158 (-0.475 - 0.069)	0.136	-0.197	= 0.193

Figure 1. Site of a study conducted on the River Lambourn, a chalk stream in Southern England (United Kingdom), to quantify habitat use by brown trout, *Salmo trutta*, during the winters of 2010/11 and 2011/12. The 500 m reach of river is owned by the Centre for Ecology and Hydrology.

Figure 2. Physical characteristics of a 500 m reach of the River Lambourn (Berkshire, UK) based on a topographic survey conducted in May 2012: a. dominant substrate, b. depth, c. velocity, and d. temperature (data for 11 February 2012, the coldest day during Winter 2 based on air temperature records [mean = -6.6°C]). Plots a – c represent data collected during a habitat survey conducted in August 2011. Stars represent the locations of the fixed radio receivers. Physical habitat and temperature contour plots were constructed using a spline interpolation within the boundaries of an ArcGIS base map.

Figure 3. River Lambourn temperatures recorded at Boxford during years 1 (a) and 2 (b). Solid green, red and blue lines represent mean, maximum and minimum temperatures measured at the river bed, while the dashed line denotes the ambient air temperature. For comparison, the dotted line represents mean instream temperatures recorded at the Svarttjønnbekken River, a northern boreal system in Norway.

Figure 4. Relationship between density of fish (per m^2) and mean water depth for the electric fishing reaches surveyed.

Figure 5. Relationship between Δ*T* (the difference between mean daily fish and maximum daily river temperatures) and minimum daily river temperature for brown trout occupying a reach of the River Lambourn during winter.

Figure 6. The majority of radio tagged brown trout were observed clustered around a single position within the study site on the River Lambourn, UK (a). Occupancy of 2 distinct locations (b) or observation at multiple sites to which fidelity was low (c) were less common.

Figure 7. (a) Autocorrelation function (ACF) of mean signal strength with a one hour time lag; the plots represent 2 fish exhibiting a daily activity pattern. (b) two different fish exhibited extremely high levels of periodicity in activity as indicated by peaks in correlation every 24 hours with no decay. (c) the mean signal strength per hour (date plotted is 00:00 on 1st Nov 2011 – 23:00 on 7th Nov 2011, shaded area = night) for the two fish represented in (b).

Figure 8. The relationship between observed winter growth of brown trout and that predicted by an optimal growth model that assumes fish are fed to satiation under

laboratory conditions (Elliott et al. 1995). Solid and clear circles denote data for Winter 1 and 2, respectively. Points below the dashed line indicate suboptimal growth.

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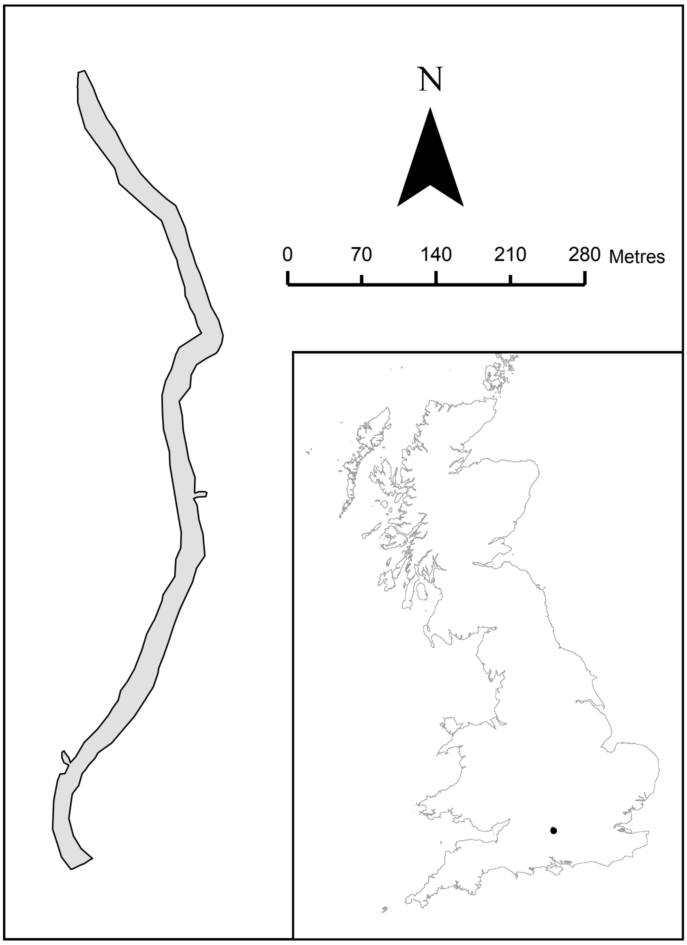
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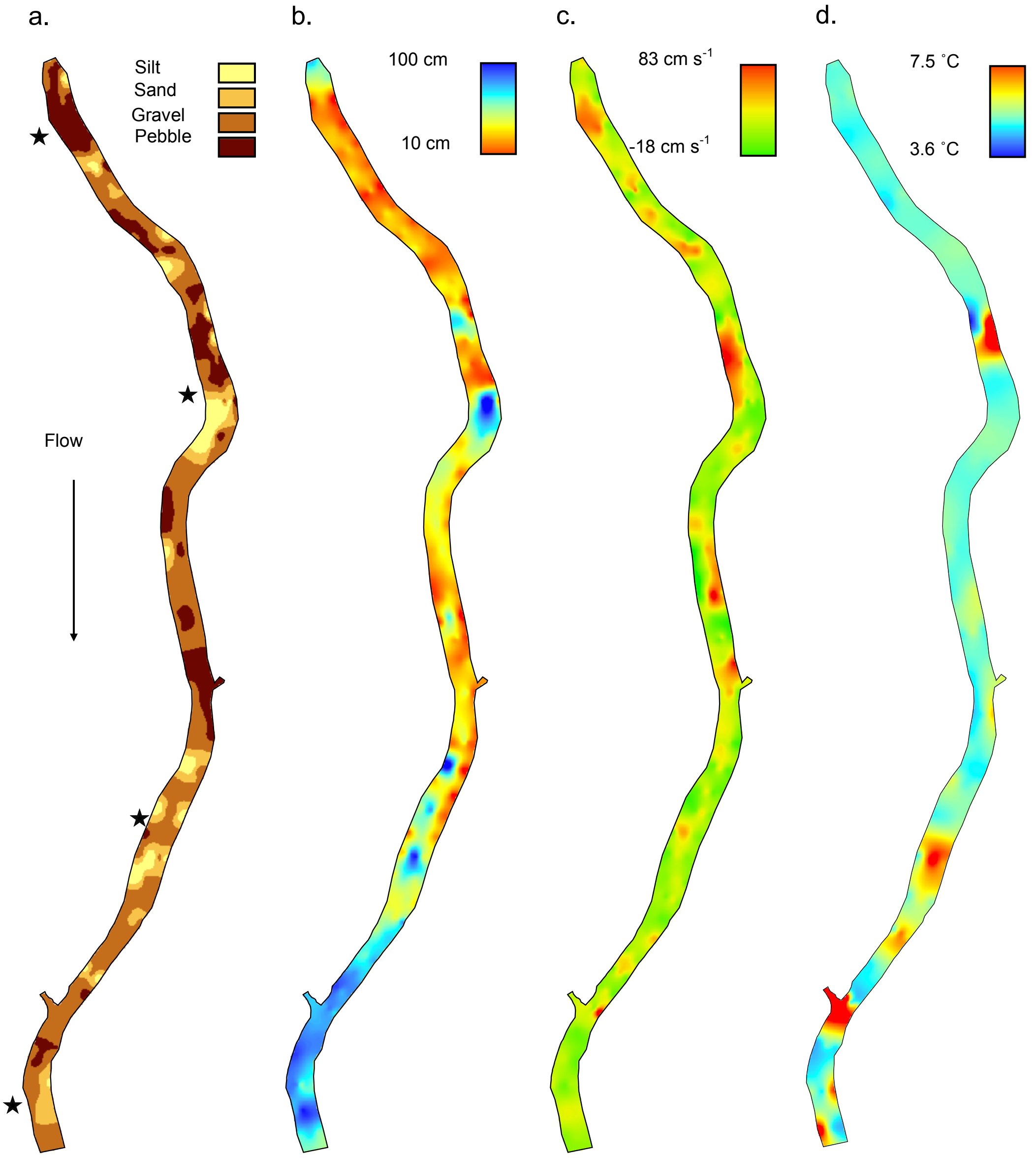
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d.
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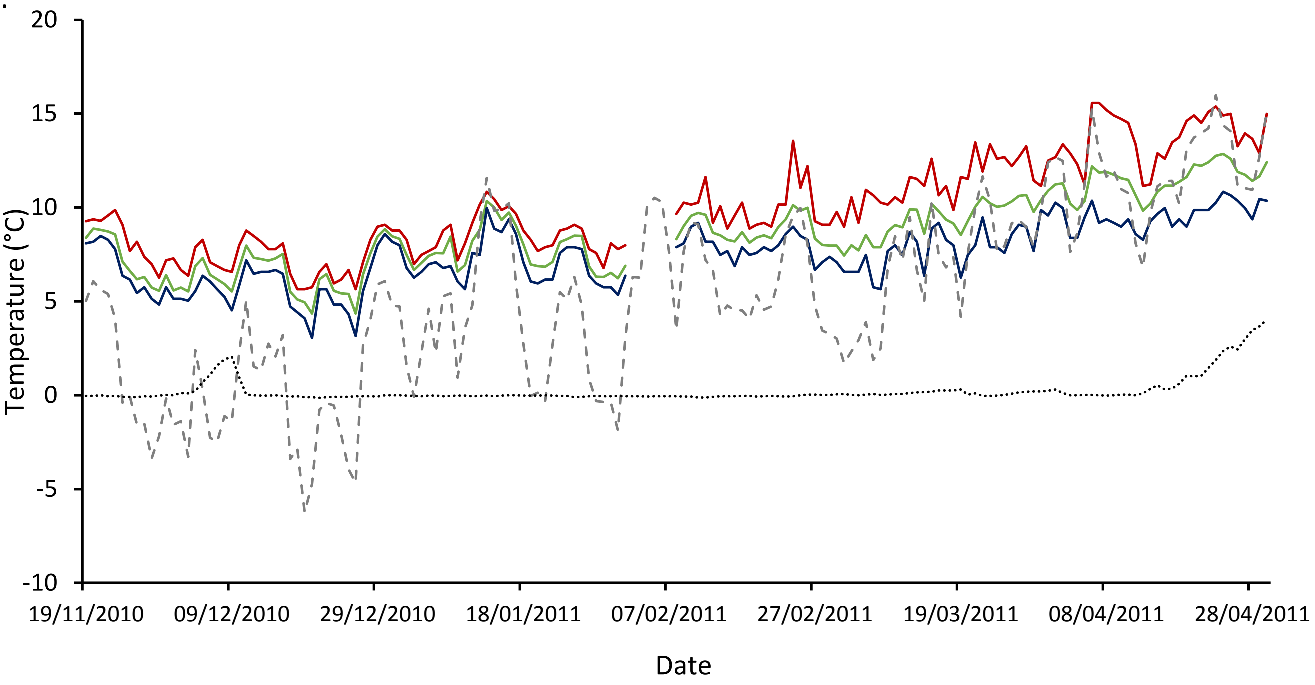
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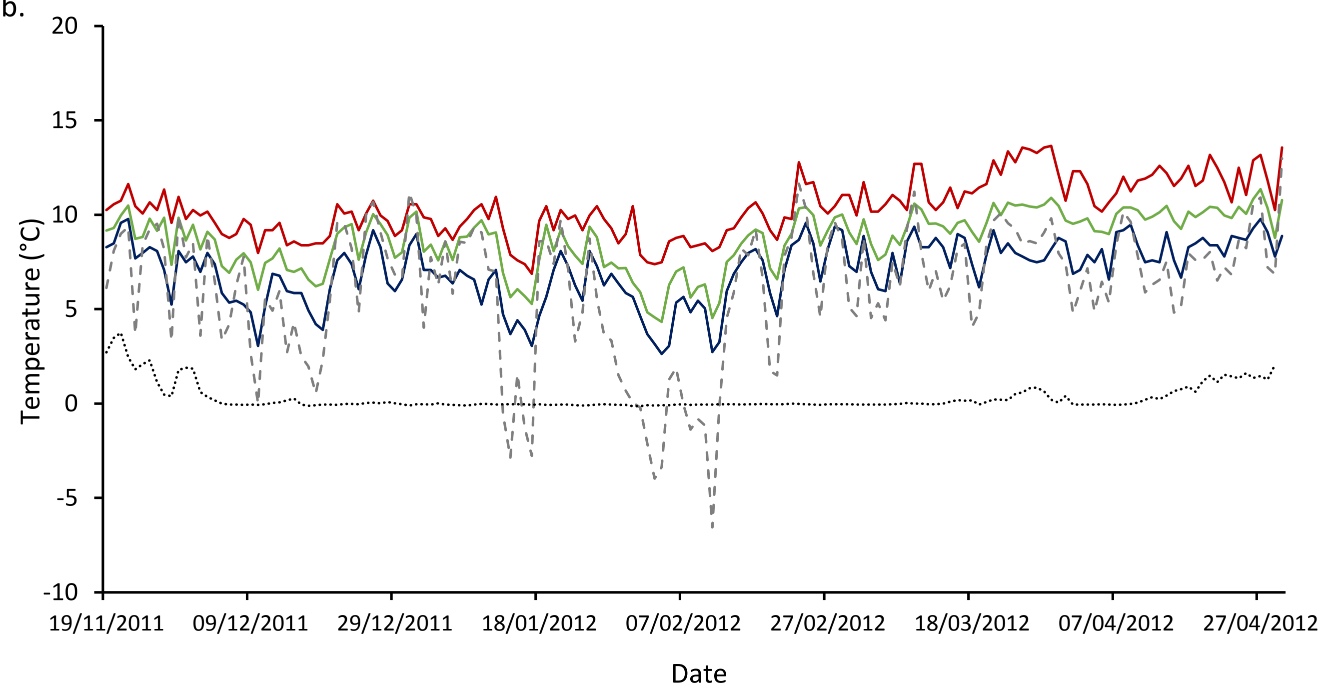
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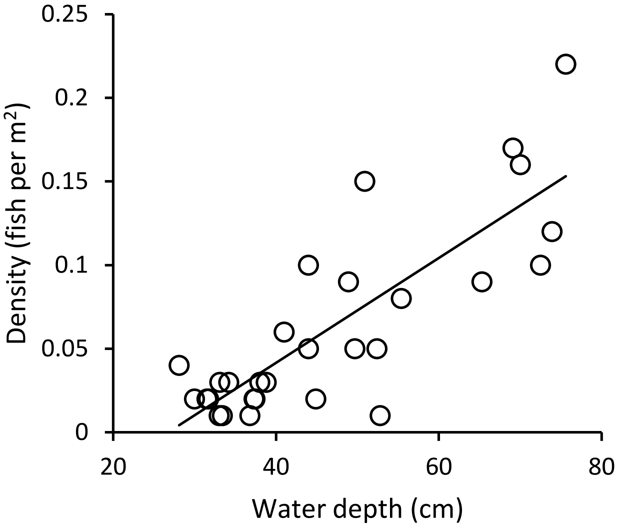
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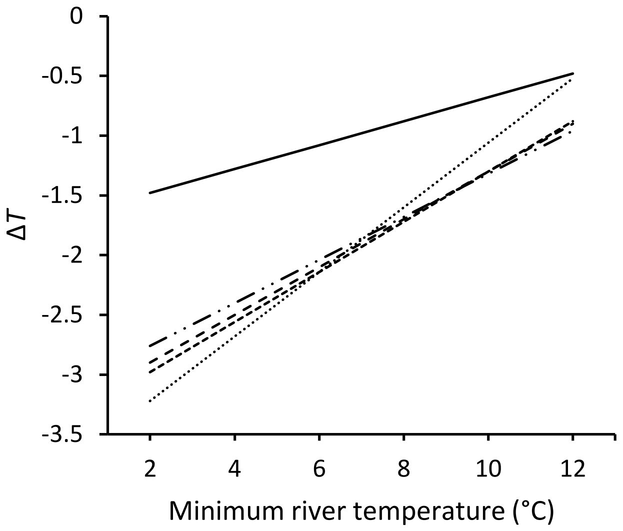
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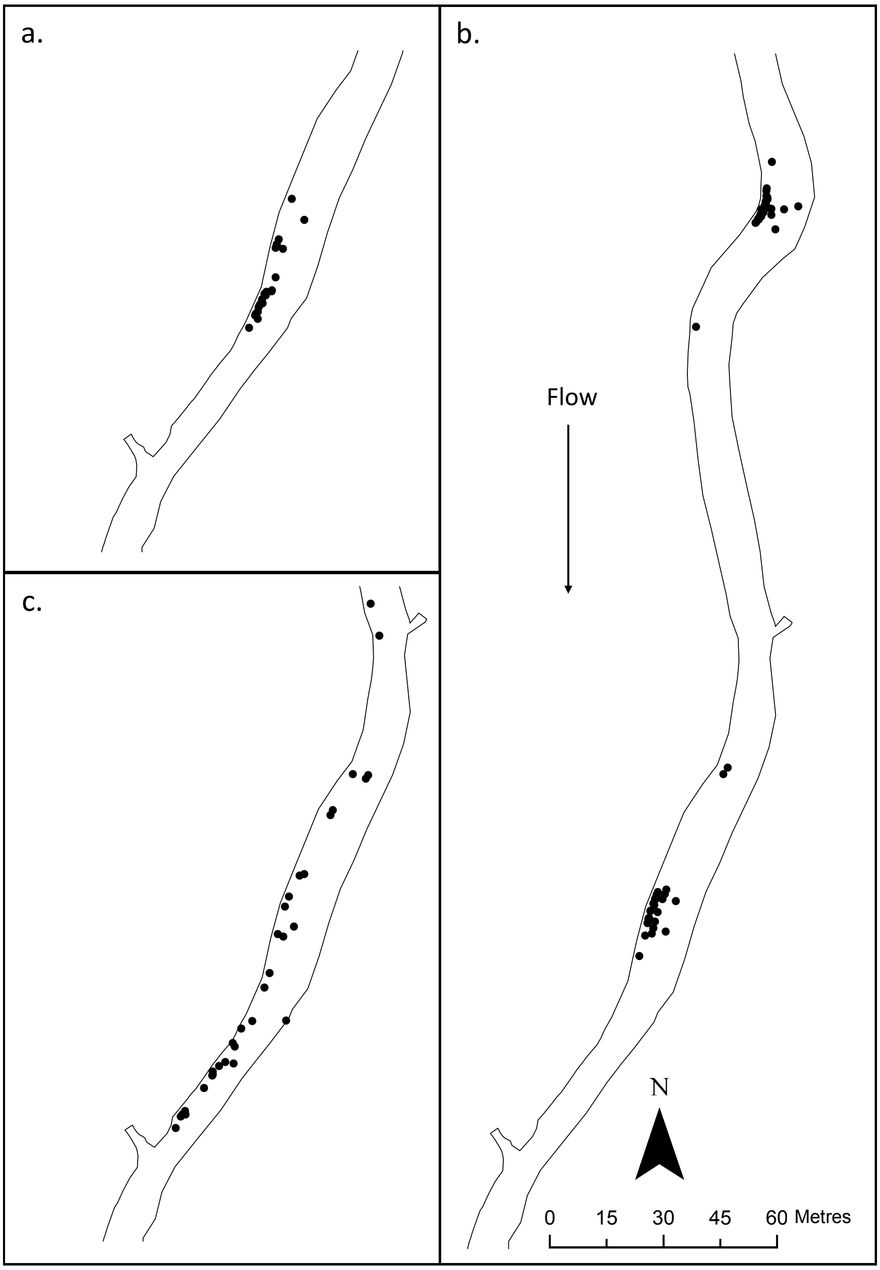
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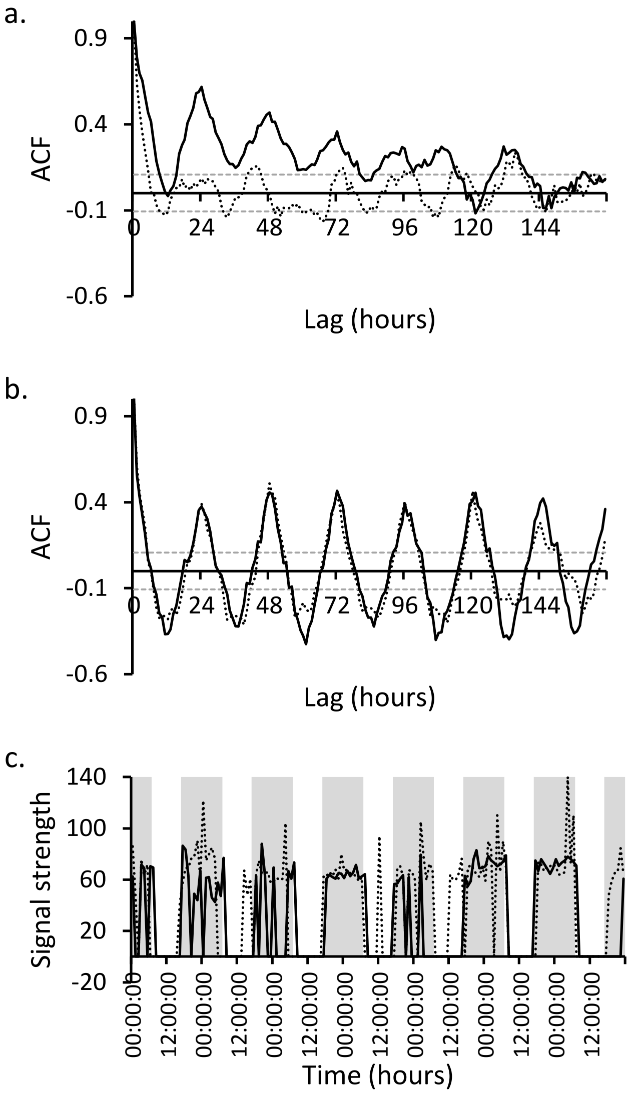
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ACF
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Lag (hours)
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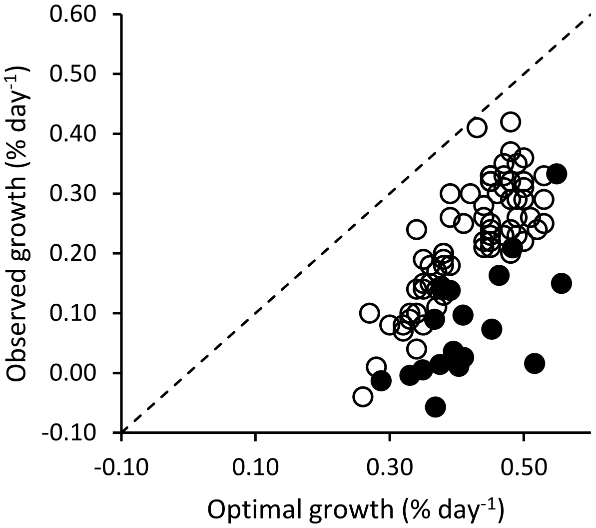
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-0.10
Observed growth (% day-1)
-0.10
0.10
0.30
0.50
Optimal growth (% day-1)

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	Range	2-115 cm	Feb 2011
		13-98 cm	Aug 2011
Velocity (cm s^{-1})	Mean	31.7 cm/s	Feb 2011
		21.0 cm/s	Aug 2011
	Range	-4-89 cm/s	Feb 2011
		1-54 cm/s	Aug 2011

Survey dates	Number caught	Number PIT tagged	Number radio tagged	Number DS tagged	Fork length [mean ± SD (range), mm]	Weight [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)

Electric-fishing survey	**Predictor**	***b***	**SE *b***	**ß**	***p***
Feburary 2011 (Model: $R^2 = .71$, $F_{3,25} = 20.10$, $p < 0.001$)	Depth	0.004 (0.002 - 0.005)	0.001	0.918	= 0.001
	Velocity	0.002 (-0.001 - 0.004)	0.001	0.207	= 0.141
	Temperature	-0.158 (-0.475 - 0.069)	0.136	-0.197	= 0.193