The Response of River-resident Fish to Reservoir Freshet Releases of Varying Profiles Intended to Facilitate a Spawning Migration

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Key points:

- Artificial freshets from reservoirs are promoted in international guidance to stimulate spawning migrations of fish
- River-resident brown trout did not perform spawning migrations during freshets of differing timing, magnitude and duration
- These findings are important for water resource managers when designing ecologically appropriate flow regimes for regulated rivers

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Abstract

Natural hydrological regimes encompass varying seasonal flow characteristics that provide fish with cues and opportunities for upstream spawning migrations, but these flows are often modified/absent in regulated rivers. Compensatory artificial flows (freshets) can be released from reservoirs to replicate these characteristics, but studies testing their effectiveness are limited. To address this, river-resident brown trout, a species known to undertake spawning migrations, were manually tracked using radio telemetry in a regulated upland river in northern England in response to 11 freshet releases of differing timing, magnitude and duration. Spawning migrations were not observed because extent of movement during freshets was generally small and the pattern of movement (i.e. directionality and relocation indices) was comparable between impact/control reaches. Movements during freshets were comparable with those observed the days immediately before/after and were small relative to the entire tracking period. In conclusion, freshets characteristic of those recommended to produce "naturalized" autumn/winter flow elevations did not stimulate/facilitate spawning migrations of river-resident brown trout under the given seasonal conditions. Outside freshets, longer unidirectional movements occurred during low flow periods and elevated river level due to rainfall, including during periods of reservoir overtopping. Notwithstanding, fish in experimental reaches were significantly more active (total distance moved) and occupied a larger extent of river (range during freshet) than those in control reaches during short-duration freshets. Therefore, during dry years/when (autumn/winter) reservoir overtopping events are unlikely, small-magnitude freshets providing flows that allow fish short opportunities to search for/find superior local habitat whilst minimising total water released are recommended.

1 Introduction

River ecosystems are hydrological networks structured by the flow of water, sediment and nutrients, which may facilitate the movement and migration of inhabiting fauna (McCluney et al., 2014). All elements of the natural flow regime (Poff et al., 1997), including the quantity, timing and variability of flows, are considered ecologically important drivers for riverine ecosystem functioning (Enders et al., 2009; Nislow & Armstrong, 2012). Fish populations rely on a variety of flows to migrate between and exploit a diversity of habitats (feeding, spawning and refuge) and complete their life cycles (Cowx & Welcomme, 1998; Nislow & Armstrong, 2012). The majority of rivers in the developed world are impounded in some way, often by water-storage reservoirs for potable supply, flood control or hydropower (Gillespie et al., 2015; Vörösmarty et al., 2010). Impoundments alter the magnitude, timing and duration of ecologically important natural flood flow characteristics, which should typically facilitate spawning migrations (by providing the cue and opportunity) with subsequent impacts on the downstream fish communities (Nilson et al., 2005).

The European Union Water Framework Directive (WFD) states that all heavily modified water bodies, such as those impounded by dams, must reach Good Ecological Potential (GEP) by 2027 (WFD; 2000/60/EEC). GEP is the ecological quality that can be achieved in the affected water bodies without significant adverse impacts to the societal benefits provided. In an attempt to comply with this, the UK Technical Advisory Group (UKTAG, 2013) provided recommendations, using the concept of "environmental flows" or eflows, to identify a number of ecologically important components of river flows. The application of environmental flows is widely used (Acreman et al., 2014) as a mitigation measure in regulated rivers around the world and is defined as "the quantity, timing, duration, frequency and quality of water flows required to sustain freshwater, estuarine and near-shore ecosystems and the human livelihoods and well-being that depend on them" (Acreman and Ferguson, 2010). Regulated rivers receive these flows through artificial freshet releases of appropriate magnitude, duration, timing and frequency. These components are referred to as 'building blocks' (Figure 1) and provide guidance to identify which are likely to be ecologically beneficial in a particular river, at a particular time of year. This approach aims to find the most efficient flow regime that conserves ecosystem functioning whilst preserving water for potable supply.

Research into the impacts of reservoir releases on downstream biota and the importance of sustainable water management is increasing worldwide (Chen & Olden, 2017; Pahl-Wostl et al., 2013; Sabo et al., 2017; Vörösmarty et al., 2010). Research into fish migration during freshets has predominantly focused on anadromous salmonids, which move from the sea into fresh water to spawn (e.g. Aprahamian et al., 1998; Hawkins & Smith, 1986; Hawkins, 1989; Laughton, 1991; Smith et al., 1994; Solomon et al., 1999; Webb & Hawkins, 1989). Few studies have investigated the response of river-resident species, which perform spawning migrations entirely within fresh water, in response to artificial freshet releases from reservoirs. River-resident brown trout (*Salmo trutta* L.) are reported to undertake spawning migrations over many kilometres in unregulated rivers (Arnekleiv & Kraabøl, 1996; Ovidio et al., 1998). Further studies are hence required to develop evidence-based mitigation guidance to provide suitable freshet reservoir-release. Notwithstanding, there is currently a dearth of knowledge about the migration of brown trout to their spawning grounds during artificial freshets in regulated rivers, despite explicit recommendations for the timing, frequency, magnitude and duration of the autumn/winter flow elevation building block to reach GEP in UKTAG guidance (Table 1; UKTAG, 2013). Brown trout are often the dominant fish species in upland rivers where reservoirs are prevalent in many regions, making them a suitable study species.

During this empirical investigation, the influence of the timing, magnitude and duration of autumn/winter freshet releases from two impounding water-storage reservoirs on brown trout movements was assessed over multiple years. The UKTAG recommendations for the autumn/winter flow building block for dispersal and fish migration were used to guide freshet releases (Figure 1; Table 1). The freshet profiles were iteratively adapted based on findings and knowledge from the previous year(s). To provide control data, movements of fish during freshets were compared to movements of the same fish on days when freshets were not being released, and to fish in reaches not being impacted by the freshet release, i.e. to compare movements to those under 'normal' conditions. By using multiple years of research and a control reach, we uniquely attempted to robustly quantify the autumn/winter flow building block required to stimulate and facilitate river-resident brown trout spawning migrations. Fish movements during freshets, in comparison to the days before and after freshets and relative to the entire tracking period were analysed to identify whether a spawning migration occurred. Movement for reasons other than a spawning migration inevitably occurred and were also explored to establish if there were unintended benefits of the freshet releases and to help understand the general ecology of river-resident fish in regulated rivers. The findings will inform practical and evidence-based guidance on environmental flows for reservoirs operated by the water industry.

2 Materials and methods

2.1 Study area

The impact of reservoir freshet releases, intended to simulate natural high-flow events, on brown trout movements during the spawning migration season was assessed downstream of two potable water supply reservoirs in the River Holme catchment in northern England. The reservoirs and downstream river were deemed a typical heavily modified water body that must reach GEP according to WFD (2000/60/EEC). The aim was to find the most efficient flow regime that provides conditions required by inhabiting fish in order for them to complete their life cycles whilst conserving water for potable supply. Brownhill and Digley water storage reservoirs on Ramsden Clough and Marsden Clough, respectively, were located approx. 4km southwest of Holmfirth, West Yorkshire (Figure 2). The study was performed in three reaches in October and November 2012 (a, b and c; Figure 2) and two reaches further downstream were added to the investigation in October to February 2013/14 and 2014/15 (d and e; Figure 2). The experimental design allowed the movements of fish in response to freshets (in impact reaches) to be compared with those in a reach unaffected by the release (control reaches), as only one reservoir released water at any one time; i.e. when a freshet was released from Digley Reservoir, fish in Ramsden Clough were used as controls and Marsden Clough for Brownhill Reservoir (Figure 2). It was expected that if freshets resulted in upstream migrations and brown trout were seeking areas that are inaccessible due to impassable weirs (indicated in Figure 2), they would congregate downstream in weir pools. Reservoir overtopping was logged on approximately a weekly basis but was ungauged, and did not coincide with any freshet releases. The study reach was typical brown trout habitat and spawning habitat was identified throughout using qualitative walkover survey, Wolman pebble count (Wolman, 1954) and quantitative assessment of depth, flow and substrate size (Armstrong et al., 2003).

2.2 Freshet design

Eleven freshets (09:00 am release start) of contrasting timing, magnitude and duration were investigated during three study years, i.e. 2012, 2013 and 2014. These were employed using an iterative process based on direct observation of river flow and fish movements in previous years (Table 2; Figure 3) whilst complying with the licensing restrictions ad health and safety regulations of the water managers. Specifically, a single small-magnitude (peak = 17.3 × Qn95; 69.0 ML/d) and short-duration (10-hours) freshet was released in November 2012 (Figure 3).

The profile was comparable to freshets released for ecological reasons since 2004. In 2013, freshets of differing timing and magnitude were released: i.e. freshets were released in October, November and December, alternating between small- and large-magnitude (peak = 122.4 × Qn95; 465.0 ML/d) (Figure 3). In 2014, the magnitude and duration of freshets released were medium-magnitude (peak = 43.1 × Qn95; 163.9 Ml/d) and long-duration (28-hours) in October, November and December, but a small-magnitude and long-duration freshet was released in December (Figure 3). Small-magnitude and long-duration freshets scheduled for October and November 2014 were cancelled due to natural reservoir overtopping events presenting a downstream flood risk.

Brown trout spawning migrations in unregulated rivers occur in October, November and December (e.g. Ovidio et al., 1998; Armstrong et al., 2003). During the investigation, UKTAG guidance specifying that autumn and winter flow elevations should have a 6 × Qn95 magnitude, 12-hour duration and occur once per week at night in October, November and December "to support the migration… to their spawning grounds" (UKTAG, 2013). Operational constraints and reservoir licensing restrictions prevented a magnitude of exactly 6 × Qn95 being achieved at this site at night during small and medium magnitude, long duration releases in 2014, i.e. 5.0 (20.0 ML/d) and 8.4 (32.1 ML/d) × Qn95 were released, respectively.

2.3 Sampling, tagging and tracking procedure

The largest available brown trout, i.e. the adults in the population, were caught by electric fishing, anaesthetised using buffered tricaine methanesulphonate (MS-222, 0.08 g L^{-1}), weighed (g) and measured (fork length, mm) (Table 3). The size of tagged brown trout did not differ significantly between batches (permutation tests for independence on length; $Z = -0.3688$, $n = 145$, $P = 0.712$ and weight; $Z = -1.280$, $n = 145$, $P = 0.200$). Prior to surgery, the unique frequency (between 173.000 and 173.999 MHz, with a nominal spacing of 10 kHz) of each tag was verified and logged using a hand-operated receiver. Radio transmitters were sterilised with diluted iodine solution and rinsed with distilled water prior to use. An 8-10 mm long, ventro-lateral incision was made anterior to the muscle bed of the pelvic fins and the whip antenna was run via the incision in the body cavity to the exterior, posterior to the pelvic fins using a shielded needle. The transmitter was then inserted into the body cavity and the incision closed with an absorbable suture. Gills were irrigated with a diluted dose (0.04 g/L^{-1}) of anaesthetic throughout the tagging procedure, which lasted between 3-4 min. Each fish was released at the approximate site of capture when fully recovered from the anaesthetic. All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986 (Home Office licence number PPL 60/4400). The radio transmitters used in 2012 (type PIP, 20 × 10 × 5 mm, 15 cm × 0.1 mm whip antenna, potted in medical-grade silicone, 0.96 g weight in air; Biotrack, UK) had an expected life of 56 days. In the 2013/14 and 2014/15 study years, radio transmitters (type Crystal controlled 2-stage, 15 × 7 × 4 mm, 12 cm × 0.1 mm whip antenna, potted in medical-grade silicone, 0.90 g weight in air; Advanced Telemetry Systems, USA) with a longer life expectancy of 135 days were used.

Radio tagged brown trout were located manually using a hand-operated receiver (Sika model, Biotrack, Wareham, UK) and a three-element Yagi antenna daily in 2012 and weekly in 2013 and 2014 as the study period was longer and over a larger area. In 2013 and 2014, fish we also located daily for three days before and two days after freshet releases. During freshets in 2012, 2013 and 2014, fish were located every 30-minutes, 1-hour and 4-hours, respectively. When a fish changed location, the longitudinal distance moved was measured (to the nearest metre) using a tape measure in order to record short distances accurately. Temperature was recorded at 15-min intervals on a Tinytalk logger in each study year (Gemini Data Loggers; www.geminidataloggers.com).

2.4 Brown trout movement data analysis

Fish move for a large spectrum of fundamental behavioural and ecological reasons, including spawning migrations, habitat exploration, for feeding and/or predator avoidance. The intention of freshet releases during this investigation was to initiate and facilitate a spawning migration, therefore the analysis performed was tailored to identify whether such a migration occurred. In doing so, non-spawning migration movements were inevitably reported and hence explored, although this was not the primary focus of the investigation. There is no universally accepted definition of migration, but fish movement during a spawning migration is thought to be persistent, undistracted and straightened-out (Dingle, 1996; 2006), and between separate habitats (Northcote, 1984), discrete sites (Baras & Lucas, 2001) or localities (Shaw & Couzin, 2012). Migrations are also thought to involve a substantial proportion of the population (Northcote, 1984; Shaw & Couzin, 2012) moving with predictability or synchronicity in time (Baras & Lucas, 2001; Brönmark et al, 2013; Shaw & Couzin, 2012). Therefore, if a freshet release facilitated a spawning migration during this investigation it was anticipated that a large proportion of radio tagged brown trout would have performed a unidirectional movement to a new location, i.e. a discrete patch of spawning habitat.

The spawning location fish are migrating towards will, in theory, be a different finite distance from the starting point of each individual and thus migration distance will vary between individuals. Therefore, both the pattern and extent of movements were analysed to deduce whether a spawning migration occurred to avoid concluding fish that moved a relatively short, unidirectional distance during a freshet did not perform a spawning migration. It was assumed a fish would stop moving when it reached a spawning location, and thus be at the extremities of its range during the freshet when the freshet ended. Likewise, if a freshet ended prior to a fish completing a spawning migration it would also be at the extremities of its range during the freshet.

2.4.1 Movements during freshet releases, in comparison to control reaches

Three metrics were used to quantify the extent of fish movement during a freshet, namely range, total distance moved and beeline distance. The *range* during a freshet was calculated as the longitudinal distance between the furthest upstream and downstream position recorded for each individual. The *total distance moved* during a freshet was the sum of the longitudinal distance moved by an individual between each occasion it was located. The *beeline distance* was distance between locations occupied immediately before and after a freshet (Bovet & Benhamou, 1988).

Two indices were used to quantify if the pattern of fish movement during a freshet was characteristic of a spawning migration, namely *directionality* and *relocation*. The *directionality* index, also referred to as straightness or tortuosity by others (Fritz et al., 2002; Morales & Ellner, 2002), was the ratio between the *beeline distance* and the *total distance moved* (*beeline distance* / *total distance moved*) during the freshet, ranging between 0 and 1, with a higher value indicating fish performed more unidirectional movements during freshets, as expected during a spawning migration. The *relocation* index was the ratio between *beeline distance* and the *range* (*beeline distance* / *range*) during a freshet, ranging between 0 and 1, with a higher value indicating the fish relocated closer to the extremity of the range occupied during a freshet release, as expected during a spawning migration. *Total distance moved* was plotted with *directionality*, and *range* with *relocation*, including a key to aid interpretation of fish movements; data in the top right sector of both plots would be indicative of a spawning migration.

2.4.2 Movement before, during and after freshet releases

It was assumed that fish movements during days immediately before and after freshets were normal for that month and prevailing environmental conditions. Hence movements by the same individuals would be larger on the day of a freshet if it facilitated a spawning migration. *Daily distance moved* by individual fish were calculated as the longitudinal distance between locations occupied on consecutive days for fish in the impact reach in the three days before and two days after a freshet, thus enabling comparison to distance moved during the day a freshet was released. Box plots of daily distance moved in the impact reach before (days 1 – 3), during (day 4) and after (days 5 and 6) each freshet were plotted to enable extent and direction of movements to be visualised; a box in the upper half of the plot (i.e. upstream movement) on day 4 would be indicative of a spawning migration.

2.4.3 Movements during freshets relative to the entire tracking period

A fundamental assumption of performing a freshet release to facilitate a spawning migration is that river-resident fish do not/cannot perform long distance movements in their absence. If this was true, the distance moved by an individual during a freshet would represent a large proportion of the distance moved by that individual during autumn/winter. In an attempt to quantify this, the *range* during a freshet was calculated as a percentage of the home range occupied during the whole tracking period for each individual, and was referred to as *relative range* during freshet. *Home range* was determined by the longitudinal distance between the furthest upstream and downstream position recorded for each individual during the entire tracking period (Hojesjo et al., 2007). *Range per day tracked* was also calculated by dividing the *home range* by the number of days over which the individual was tracked, which describes the extent of river used, standardised for the period of tracking (Ovidio et al., 2002). In addition, the extent and timing of the largest unidirectional movements performed at times other than during a freshet were also reported.

2.5 Statistical analysis

As there were no pairwise significant differences in *home range* between sites, data for fish inhabiting all reaches impacted by a freshet release were pooled for analysis. Data were tested for normality of variance using Shapiro-Wilk Normality tests. Data were non- normally distributed during comparisons between two groups (between control and impact reaches for *range, total distance moved* and *beeline distance* as well as *directionality* and *relocation* indices, and relative range during each release) and there were many tied values in the data. Therefore, in order to obtain exact P-values, permutation tests for independence were conducted using the 'coin' r package (referred to as permutation-test) (Hothorn et al., 2006). Permutation tests were also used to compare *daily distance moved* between the three days before, day during and two days after each freshet release. A Wilcoxon Rank Sum test was performed on *daily distance moved* between these groups (before, during and after) where necessary to identify in which days the movement was significantly different to each other. For other comparisons between multiple groups for non-parametric data that were not tied (i.e. overall *range per day tracked* between all three study years), Kruskal- Wallis tests (referred to as KW-test) were used with a Dunn non-parametric pairwise multiple comparisons post- hoc test (referred to as post-hoc test) using the r package 'Dunn.test' (Dinno, 2017). Fish length and *total distance moved*, *beeline distance*, *range*, *directionality* and *relocation* during freshets and *range per day tracked* in each study year were tested for correlations using Pearson product-moment correlation (referred to as cor-test). Median and interquartile ranges were extracted from data in tables using the r package 'purrr' (Henry & Wickham, 2018). All statistics were carried out in R studio v 3.3.0.

3 Results

3.1 Movements during freshet releases, in comparison to control reaches

3.1.1 Extent of movement

The extent of movement during freshets was generally small for the majority of fish and thus was not considered representative of a spawning migration. *Total distance moved* was less than 20 m (impact = 68.1% and control = 86.8%), *beeline distance* was less than 10 m upstream or downstream (83.3% and 98.9%) and *range* was smaller than 20 m (84.3% and 90.1%) (Figure 4). The *total distance moved* and *range* were significantly larger in impact than control reaches during all but one short-duration freshet studied (see Table 4 for statistics). *Total distance moved* and *range* were all larger during/after long rather than short-duration freshet releases in impact reaches, but were always comparable to control reaches (Table 4). *Beeline distance* from the location occupied prior to the release was statistically comparable between impact and control reaches after all freshets. There was also no correlation between fish length and *total distance moved*, *beeline distance* or *range* in impact reaches during freshets (Pearson's product-moment correlation, $P > 0.05$).

3.1.2 Pattern of movement

The pattern of movement in impact reaches was not statistically larger than in control reaches during any freshets (see table 5 for metrics and statistics), and thus were not considered representative of a spawning migration. Indeed, only a small proportion of fish performed exclusively directional movements indicative of a spawning migration during freshets (impact = 7.1% and control = 25.3%) or relocated at the extremities of their range after freshets (31.0% and 47.3%), i.e. *directionality* / *relocation* index = 1 (Figure 4). Instead, a substantial proportion of the population performed highly tortuous movements during freshets or were located close to the location they occupied prior to the release after the freshet, as indicated by the large proportion of data in the lower half of plots in Figure 4.

Two fish that performed long-distance (>120 m) unidirectional movements (*directionality* = 0.95 and 0.93) to a new location (*relocation* = 0.97 and 0.96) during the medium-magnitude, long-duration freshet release in October 2014 (MLO14) were notable exceptions (Figure 4). In contrast, the largest *total distance moved* by an individual fish during a single release was 282 m in an impact reach during the small-magnitude, long-duration freshet in December 2014 (SLD14), but this individual had a 46 m *beeline distance* (*directionality* = 0.16; Figure 4) and 92 m *range* (*relocation* = 0.50; Figure 4), this movement was hence not considered a spawning migration. There was a positive correlation between fish length and *directionality* (t = 2.2645, df = 26, P = 0.032, cor = 0.41) and *relocation* (t = 2.3482, df = 26, P = 0.027, cor = 0.42) indices in impact reaches during the medium-magnitude, long-duration freshet in October 2014 but not during any other freshets.

3.2 Movement before, during and after freshet releases

There was no significant difference in the *daily distance moved* (longitudinal distance between the fish locations each day) in the impact reach before (days 1 – 3), during (day 4) and after (days 5 and 6) for any of the freshets (Permutation-tests; $P > 0.05$; Figure 5), these movements were hence not considered representative of a spawning migration. *Daily distance moved* was significantly different during the small-magnitude, short-duration freshet in December 2013 ($Z = 2.097$, $P = 0.036$*; Figure 5), but differences were between days before and after the freshet (Wilcox-test; $W = 3413.5$, $n = 196$, $P = 0.001$). The largest distance moved by an individual fish in a day did not coincide with a freshet release; this was 554 m upstream three days before the medium-magnitude, long-duration freshet release in November 2014 (Figure 5).

3.3 Movements during freshets relative to the entire study

The *home range* during the tracking period in 2012 was 67.3 ± 99.2 (5.8 – 525.3 m); in 2013 was 99.6 ± 77.2 (19.2 – 300.1 m), and in 2014 was 99.1 ± 128.2 (11.7 – 1090.5 m). *Range per day tracked* in 2012 (1.7 ± 2.5 (0.1 – 13.1 m)) and 2013 (1.8 ± 1.5 (0.3 – 8.3 m)) were significantly smaller than in 2014 (2.6 ± 6.7 (0.4 – 57.4 m)) (KW-tests; $X^2 = 7.8865$, df = 2, $P = 0.019$; 2012 post – hoc $P = 0.013$ and 2013 post – hoc $P = 0.012$). There was no significant correlation between brown trout length and *range per day tracked* in any of the three study years (cor-test, $P > 0.05$). The *relative range* during freshet releases was small in comparison to the entire tracking period, but it was always larger in impact than control reaches (Table 6) significantly so during small-magnitude, short-duration releases in October and December 2013 (Table 6).

The largest unidirectional movement during a freshet was 191 m. By contrast, there were six larger unidirectional movements at other times during the investigation in both directions. Specifically, these were 377 and 464 m downstream in 2012, 274 m upstream in 2013, and 194, 324 and 1065 m (the complete movement of the previously reported 554 m upstream movement two days before the medium-magnitude, long-duration freshet in November 2014) upstream in 2014 (Figure 6). These and other unidirectional movements (Figure 6) occurred during periods of low flow, elevated flow and reservoir overtopping but they rarely coincided with that of another fish and thus were not considered a spawning migration.

4 Discussion

Understanding the influence of flow on fish movement is invaluable when designing environmental flow regimes, also known as eflows, for efficient water resource management and to conserve inhabiting fauna (Acreman et al., 2014). This real-world and adaptive trial attempted to identify the capacity of artificial freshets to stimulate and facilitate river-resident brown trout spawning migrations using the building-block approach. Freshets of differing timing (October, November and December), magnitude (small, medium and large) and duration (short and long) over multiple years (2012, 2013 and 2014) did not result in brown trout performing movements that were characteristic of a spawning migration, i.e. unidirectional movements to a new location with high synchronicity in time, as indicated by *beeline distance*, *directionality* and *relocation* indices never being significantly greater in impact than control reaches.

In theory, reservoir releases should simulate the range of natural intra- and inter-annual variation of hydrological regimes to produce "naturalized" flows in regulated rivers (sensu Poff et al., 1997). Timing, frequency, magnitude and duration are key flow characteristics when designing an ecologically beneficial autumn flow building block (Acreman & Ferguson, 2010; UKTAG, 2013; Figure 1). Brown trout did not perform movements characteristic of a spawning migration during any combination of flow characteristics tested during this investigation. It is possible that the freshets trialled in this investigation did not provide the combination of flow characteristics required to stimulate (cue) and/or facilitate fish spawning migrations. Alternatively, fish may not have performed a spawning migration because areas of suitable spawning habitat were present throughout the reach studied. Solomon & Templeton (1976) found brown trout movements were more localised where spawning, nursery and adult habitat were in close proximity. Further, although not tested here, Heggenes et al. (1999) reported competition and trophic interactions (predation risk) affect habitat selection while Johnsson & Forser (2002) found increased residence duration with increased perceived territory value in brown trout, which may also help explain lack of movement in the present study. From an applied perspective, the current guidance (i.e. UKTAG, 2013) applies to all water storage reservoirs, regardless of distribution and quantity of spawning habitat in the downstream reach. That said, the downstream river and prevailing fish population were considered typical of a heavily modified water body thus raising doubts over the efficacy of artificial freshets for river-resident fish to perform a spawning migration.

In this study, brown were more active (i.e. *total distance moved*) and had a greater extent of movement (i.e. *range* during freshet) relative to fish in control reaches during short duration freshets and *relative range* was significantly larger for two short-duration freshets (both small-magnitude in October and December 2013). Brown trout are known to occupy flow refugia during severe spates and/or extreme floods to minimise energy expenditure and avoid displacement or mortality (Lobón-Cerviá, 1996), but the magnitude of freshets studied were relatively small and extent of movement was not indicative of fish occupying the least metabolically costly habitat. Instead, while not the objective of the freshets released, short duration freshets may have benefitted individual fish by providing a short opportunity to search to gain knowledge (Gowan & Fausch, 2002) or find superior habitat (Crook, 2004; Gowan et al., 1994; Smithson & Johnston, 1999). Some individuals homed to the location previously occupied, as reported for other freshwater fish after diel feeding (Clough & Ladle, 1997), spawning (Fredrich et al., 2003) and displacement by high flows (Lucas, 2000). Gillespie et al., (2015) performed a critical analysis of regulated river ecosystem responses to managed environmental flows from reservoirs and found only three of 76 studies investigated how freshet duration affected downstream biota and none specifically investigated fish. The majority focused on the influence of increased flow magnitude (69 out of 76 assessed) on ecological response, with 38% reporting an increase, 25% had no change and 21% had a decrease (Gillespie et al., 2015), with magnitude having little influence during this study.

The largest unidirectional movements in the present study occurred when a freshet was not being released from a reservoir, though such movements rarely coincided with that of another fish and thus were probably not a spawning migration. Movements also did not seem to be in response to a particular flow or temperature change, which is in contrast to studies from unregulated rivers with Ovidio et al., (1998) who found spawning migrations occur when water temperature was 10-12 °C and Jonsson and Jonsson (2002) who reported both rising temperature and increased flow were important in stimulating the upstream movement of brown trout. More importantly, in the context of freshet releases, some fish performed long-distance movements during periods of low flow, and thus were not reliant on freshets for the opportunity to perform a long-distance spawning migration. That said, long-distance movements mostly occurred during periods of elevated river level due to rainfall and reservoir overtopping events. Such observations have been found previously for brown trout (Bunnell et al., 1998; Heggenes et al, 2007; Ovidio et al., 2002). Ovidio et al., (1998) also reported large movements occurred in response to reservoir overtopping events rather than freshets of comparable timing. This could be related to the predictability of such events due to preceding rainfall (not present prior to freshet releases), difference in discharge profile and/ or water quality when compared to artificial freshet releases, and is something that could be investigated further. Based on these findings, measures to promote overtopping such as storing water during the spawning season for target species may be pursued by water companies.

Despite this study finding little evidence to support the use of freshets for river-resident fish to perform spawning migrations they may have had unquantified benefits, such as mobilising food items (Gibbins et al., 2007) and releasing and redistributing (also known as flushing) fine sediment from spawning gravels beds (Petticrew et al., 2007), as well as structuring invertebrate communities (Lagarrigue et al., 2002; McKinney et al., 2001). Further, it is widely accepted that understanding the natural flow regime has played a large part in the development of environmental flows science and application in the past two decades (Poff, 2017). Since the 2007 Brisbane Declaration which proposed the aforementioned definition of eflows, there was a call for global research to quantify ecological goods and services in rivers worldwide, through development and assessment of ecological models (Arthington et al., 2018). Research conducted therein (see Kennen, Stein, & Webb, 2018) has seen implementation of new frameworks that have advanced implementation of alternative environmental water hypotheses and management schemes (Arthington et al., 2018). Frameworks include the Ecological Limits of Hydrologic Alteration framework (ELOHA, Poff et al.,2010) which paves the way for holistic flow–ecological models to be developed for rivers of a particular hydrological nature through flow regime classification (Arthington et al., 2018). Arthington et al (2018) provide a review of how this along with associated derivative frameworks have been implemented in the U.S.A (Buchanan, et al., 2013; Kendy & Blan 2012; Reidy Liermann et al., 2012; Sanderson et al., 2012), Spain (Belmar, Velasco, & Martinez-Capel, 2011), China (Zhang et al., 2012), Australia (Arthington et al., 2012; James et al., 2016; Mackay, Arthington, & James, 2014) and Africa (O'Brien et al., 2017).

During this study, the reservoirs, downstream river and prevailing fish population were considered typical of a heavily modified water body that must reach GEP according to WFD (2000/60/EEC). The study reach was bounded by weirs in both the upstream and downstream direction but the extent and pattern of fish movement during freshet releases was not restricted by their presence given fish did not congregate downstream of weirs, movements were comparable in control reaches/days and far larger movements occurred on days without freshet releases. The principle aim of this study was to investigate the influence of autumn/winter freshet releases, the timing of which as recommended in UKTAG (2013) guidance (i.e. October, November and December), on brown trout movements and thus dictated the timing of the investigation. Brown trout movements are temporally variable, such as for foraging in summer (e.g. Gowan and Fausch, 2002; Ovidio et al., 2002), but movements performed during periods when freshets were not being released were not investigated during this study. Although temporally focused, the findings are considered transferable to other heavily modified water bodies in upland rivers, including those with differing seasonal flow regimes provided the timing of brown trout spawning migrations is known. However, further investigation into the spawning migration of river-resident brown trout should be performed in regulated rivers, especially if prevailing spawning habitat is limited or distant from foraging habitat and longitudinal connectivity is less restricted.

4.1 Recommendations

The impact that water resources management policy has on downstream biological and ecological processes is poorly understood. This investigation used telemetry techniques over multiple years to gain an understanding of how individual, river-resident, adult brown trout responded to anthropogenic alterations to river level downstream of potable water supply reservoirs during autumn/winter. Fish did not perform a spawning migration during freshets of differing timing, magnitude and duration, possibly due to the presence of spawning habitat in the study reach, thus raising doubts over the efficacy of artificial freshets as a mitigation measure in regulated rivers, to achieve, for example, GEP (WFD; 2000/60/EEC). That said, more research is needed to definitely constrain application of freshet flows, including by replicating this investigation in different regulated rivers, potentially over a greater spatial or temporal extent, and by further altering freshet timing, magnitude and/or duration, and would ideally incorporate fish in a local unregulated river to enable comparison. The majority of the longest unidirectional fish movements in this investigation occurred during periods of reservoir overtopping and thus measures to promote overtopping could be pursued by water companies. Notwithstanding this, brown trout in experimental reaches were more active and occupied a larger range than fish in control reaches during short-duration releases, regardless of timing and magnitude. During years when overtopping events are unlikely to occur, small-magnitude releases could be performed to maximise benefits to downstream fish communities while minimising the total amount of water released. This case-study demonstrates the importance of robustly quantifying flow characteristics for specific downstream biota at potable water supply reservoirs, and findings should inform evidence-based guidance on environmental flows for water resource managers globally.

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6 References

Acreman, M.C., I.C. Overton, J. King, P.J. Wood, I.G. Cowx, M.J. Dunbar, E. Kendy & W.J. Young, (2014), The changing role of ecohydrological science in guiding environmental flows, Hydrological Sciences Journal, 59(3-4), 433–450.

Acreman, M. C. & A. J. D Ferguson (2010), Environmental flows and the European Water Framework Directive, Freshwater Biology, 55, 32–48.

Aprahamian M.W., G.O. Jones & P.J. Gough (1998), Movement of adult Atlantic salmon in the Usk estuary, Wales, Journal of Fish Biology, 53, 221–225.

Armstrong, J.D., P.S. Kemp, G.J.A. Kennedy, M. Ladle & N.J., Milner, (2003), Habitat requirements of Atlantic salmon and brown trout in rivers and streams, Fisheries research, 62(2), 143–170.

Arnekleiv, J. V., & M. Kraabøl (1996), Migratory behaviour of adult fast-growing brown trout (Salmo trutta L.) In relation to water flow in a regulated Norwegian river, Regulated Rivers: Research and Management, 12, 39–49.

Arthington, A.H., S.J. Mackay, C.S. James, R.J. Rolls, D. Sternberg, A. Barnes & S.J. Capon (2012), Ecological-limits-of-hydrologic-alteration: a test of the ELOHA framework in south-east Queensland, Waterlines Report Series, (75).

Arthington, A.H., J.G. Kennen, E.D. Stein, & J.A. Webb (2018), Recent advances in environmental flows science and water management—Innovation in the Anthropocene, Freshwater Biology.

Baras, E. & M.C. Lucas (2001), Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. International Journal of Ecohydrology and Hydrobiology, 3(01).

Belmar, O., J. Velasco & F. Martinez-Capel, (2011), Hydrological classification of natural flow regimes to support environmental flow assessments in intensively regulated Mediterranean rivers, Segura River Basin (Spain), Environmental Management, 47, 992–1004.

Bovet, P. & S. Benhamou, (1988), Spatial analysis of animals' movements using a correlated random walk model, Journal of theoretical biology, 131(4), 419–433.

Brönmark, C., K. Hulthén, P.A Nilsson, C. Skov, L.A. Hansson, J. Brodersen & B.B. Chapman (2013), There and back again: migration in freshwater fishes. Canadian Journal of Zoology, 92(6), 467–479.

Buchanan, C., H.L.N. Moltz, H.C. Haywood, J.B. Palmer & A.N. Griggs, (2013), A test of the ecological limits of hydrologic alteration (ELOHA) method for determining environmental flows in the Poto-mac River basin, USA, Freshwater Biology, 58, 2632–2647.

Bunnell Jr, D.B., J.J. Isely, K.H. Burrell & D.H. Van Lear, (1998), Diel movement of brown trout in a southern Appalachian river. Transactions of the American Fisheries Society, 127(4), 630– 36.

Chen, W. & J.D. Olden (2017), Evaluating transferability of flow–ecology relationships across space, time and taxonomy. Freshwater Biology.

Clough, S. and M. Ladle (1997), Diel migration and site fidelity in a stream-dwelling cyprinid, Leuciscus leuciscus, Journal of Fish Biology, 50(5), 1117-1119.

Cowx, I.G. & R.L. Welcomme (1998), Rehabilitation of Rivers for Fish, Blackwell Science, Oxford.

Crook, D.A., (2004), Is the home range concept compatible with the movements of two species of lowland river fish?, Journal of Animal Ecology, 73(2), 353–366.

Declaration, B., (2007), September, The Brisbane Declaration: environmental flows are essential for freshwater ecosystem health and human well-being, In 10th International River Symposium, Brisbane, Australia, 3-6.

Dingle, H. (1996), Migration: The Biology of Life on the Move, New York Oxford University Press, USA.

Dingle, H. (2006), Animal migration: is there a common migratory syndrome? Journal of Ornithology, 147(2), 212 – 220.

Dinno, A. (2017). dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. https://CRAN.R-project.org/package=dunn.test

Enders, E. C., D. A. Scruton & K. D. Clarke (2009), The ‘natural flow paradigm’ and Atlantic salmon—moving from concept to practice. River Research and Applications, 25, 2 – 15.

Fredrich, F., S. Ohmann, B. Curio & F. Kirschbaum (2003), Spawning migrations of the chub in the River Spree, Germany. Journal of Fish Biology 63, 710 – 723.

Fritz, H., S. Said, & H. Weimerskirch (2003), Scale–dependent hierarchical adjustments of movement patterns in a long–range foraging seabird. Proceedings of the Royal Society of London B: Biological Sciences, 270(1520), 1143 – 1148.

Gibbins, C., D. Vericat & R.J. Batalla, (2007), When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events, Freshwater Biology, 52(12), 2369–2384.

Gillespie, B. R., S. Desmet, P. Kay, M. R. Tillotson & L. E. Brown (2015), A critical analysis of regulated river ecosystem responses to managed environmental flows from reservoirs. Freshwater Biology 60, 410–425.

Gowan, C. & K.D. Fausch (2002), Why do foraging stream salmonids move during summer? Environmental Biology of Fishes 64, 139–153.

Gowan, C., M.K. Young, K.D. Fausch & S.C. Riley (1994), Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences, 51(11), 2626–2637.

Hawkins, A. D., & G. W. Smith (1986), Radio-tracking observations on Atlantic salmon ascending the Aberdeenshire Dee. In Scottish fisheries research report (Vol. 36). Department of Agriculture and Fisheries for Scotland.

Hawkins, A.D. (1989), Factors affecting the timing of entry and upstream movement of Atlantic salmon in the Aberdeenshire Dee. In Salmonid Migration and Distribution Symp, 101–105.

Heggenes, J., P.K. Omholt, J.R. Kristiansen, J. Sageie, F. Økland, J.G. Dokk & M.C. Beere (2007), Movements by wild brown trout in a boreal river: response to habitat and flow contrasts. Fisheries Management and Ecology,14(5), 333-342.

Heggenes, J., J.L. Bagliniere & R.A. Cunjak,, (1999) Spatial niche variability for young Atlantic salmon (Salmo salar) and brown trout (S. trutta) in heterogeneous streams, Ecology of Freshwater Fish, 8(1), 1–21.

Henry, L. & Wickham, H., (2018). purrr: Functional Programming Tools. R package version 0.2.5, url = https://CRAN.R-project.org/package=purrr

Höjesjö, J., F. Økland, L.F. Sundström, J. Pettersson & J.I. Johnsson (2007), Movement and home range in relation to dominance; a telemetry study on brown trout Salmo trutta. Journal of Fish Biology, 70(1), 257–268.

Hothorn., T, Hornik., K, van de Wiel, M.A. & Zeileis, A (2008). Implementing a Class of Permutation Tests: The coin Package. *Journal of Statistical Software 28*(8), 1-23. URL http://www.jstatsoft.org/v28/i08/.

James, C., S.J. Mackay, A.H. Arthington & S. Capon (2016), Does flow structure woody riparian vegetation in subtropical south-east Queensland? Ecology and Evolution, 6, 5950–5963.

Johnsson, J.I. & A., Forser (2002), Residence duration influences the outcome of territorial conflicts in brown trout (Salmo trutta), Behavioral Ecology and Sociobiology, 51(3), 282–286.

Jonsson N. & Jonsson B. (2002) Migration of anadromous brown trout in a Norwegian river. Freshwater Biology 47, 1391-1401.

Kendy, E., Apse, C., & Blann, K., (2012), A practical guide to environmental flows for policy and planning. Arlington, VA: The Nature Conservancy.

Kennen, J.G., E.D. Stein & J.A. Webb, (2018). Evaluating and managing environmental water regimes in a water-scarce and uncertain future. Freshwater Biology (Special Edition).

Lagarrigue, T., R. Céréghino, P. Lim, P. Reyes-Marchant, R. Chappaz, P. Lavandier & A. Belaud (2002), Diel and seasonal variations in brown trout (Salmo trutta) feeding patterns and relationship with invertebrate drift under natural and hydropeaking conditions in a mountain stream, Aquatic Living Resources, 15, 129 – 137

Laughton, R., (1991), The movements of adult Atlantic salmon (Salmo salar L.) in the River Spey as determined by radio telemetry during 1988 and 1989, Great Britain, Agriculture and Fisheries Department.

Lobón-Cerviá, J. (1996). Response of a stream fish assemblage to a severe spate in northern Spain. Transactions of the American Fisheries Society 125, 913– 919.

Lucas, M.C., (2000), The influence of environmental factors on movements of lowland river fish in the Yorkshire Ouse system. The Science of the Total Environment 251/252, 223 – 232.

Mackay, S. J., Arthington, A. H., & James, C. S., (2014), Classification and comparison of natural and altered flow regimes to support an Australian trial of the Ecological Limits of Hydrologic Alteration framework. Ecohydrology, 7, 1485–1507.

McCluney, K. E., N. L. Poff, M. A. Palmer, J. H. Thorp, G. C. Poole, B. S. Williams & J. S. Baron (2014), Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations, Frontiers in Ecology and the Environment, 12, 48–58.

McKinney, T., D. Speas, R. Rogers & W. Persons (2001), Rainbow trout in a regulated river below Glen Canyon Dam, Arizona, following increased minimum flows and reduced discharge variability, Journal Articles, 21.

Morales, J.M. & S.P. Ellner (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behaviour, Ecology, 83(8), 2240–2247.

Nilsson, C., C. A. Reidy, M. Dynesius & C. Revenga (2005), Fragmentation and flow regulation of the world's large river systems, Science 308, 405–408.

Nislow, K. H. & J. D. Armstrong (2012), Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management Ecology 19, 451 – 463.

Northcote, T.G., (1984), Mechanisms of fish migration in rivers, In Mechanisms of migration in fishes, Springer US, 317 – 355.

O'Brien, G. C., C. Dickens, E. Hines, V. Wepener, R. Stassen, L. Quayle & W.G. Landis (2017), A regional-scale ecological risk framework for environmental flow evaluations, Hydrology and Earth Systems Science, 22, 957–975.

Ovidio, M. & J.C., Philippart (2002), The impact of small physical obstacles on upstream movements of six species of fish, In Aquatic Telemetry, Springer Netherlands, 55–69.

Ovidio, M., E. Baras, D. Goffaux, C. Birtles & J.C. Philippart (1998), Environmental unpredictability rules the autumn migration of brown trout (Salmo trutta L.) in the Belgian Ardennes, In Advances in Invertebrates and Fish Telemetry, Springer Netherlands, 263–274.

Pahl-Wostl, C., A. H. Arthington, J. Bogardi, S. E. Bunn, H. Hoff, L. Lebel, E. Nikitina, M. Palmer, L. N. Poff, K. Richards, M. Schlüter, R. Schulze, A. St-Hilaire, R. Tharme, K. Tockner and D. Tsegai (2013), Environmental flows and water governance: managing sustainable water uses. Current Opinion in Environmental Sustainability, 5, 341–351.

Petticrew, E.L., A. Krein and D.E. Walling (2007), Evaluating fine sediment mobilization and storage in a gravel-bed river using controlled reservoir releases. Hydrological Processes, 21(2), 198–210.

Poff L.N., D.J. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks and J.C. Stromberg (1997), The natural flow regime. A paradigm for river conservation and restoration, Bio Science, 47, 769–784.

Poff, N. L., B.D. Richter, A.H. Arthington, S.E. Bunn, R.J. Naiman, E. Kendy & A.T. Warner (2010), The Ecological Limits of Hydro-logic Alteration (ELOHA) : A new framework for developing regional environmental flow standards, Freshwater Biology.

Poff, N.L., (2017), Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world, Freshwater Biology, 55(1), 147-170.

Reidy Liermann, C. A., J.D. Olden, T.J. Beechie, M.J. Kennard, P.B. Skid-more, C.P. Konrad & H. Imaki, (2012). Hydrogeomorphic classification of Washington State rivers to support emerging environmental flow management strategies. River Research and Applications, 28(9), 1340–1358

Sabo, J.L., A. Ruhi, G.W. Holtgrieve, V. Elliott, M.E. Arias, P.B. Ngor, T.A. Räsänen & S. Nam, (2017), Designing river flows to improve food security futures in the Lower Mekong Basin, Science, 358(6368), 1053.

Sanderson, J. S., Rowan, N., Wilding, T., Bledsoe, B. P., Miller, W. J., & Poff, N. P. (2012). Getting to scale with environmental flow assessment: The watershed flow evaluation tool. River Research & Applications, 28, 1369–1377. https://doi.org/10.1002/rra.1542

Shaw, A.K. & I.D. Couzin (2012), Migration or residency? The evolution of movement behavior and information usage in seasonal environments. The American Naturalist, 181(1), 114 – 124.

Smith G.W., I.P. Smith & S.M. Armstrong (1994), The relationship between river flow and entry to the Aberdeenshire Dee by returning adult Atlantic salmon, Journal of Fish Biology, 45, 953 – 960.

Smithson, E.B. &C.E. Johnston (1999), Movement patterns of stream fishes in a Ouachita Highlands stream: an examination of the restricted movement paradigm. Transactions of the American fisheries Society, 128(5), 847–853.

Solomon D.J., H.T. Sambrook & K. Broad (1999), Salmon Migration and River Flow, Results of Tracking Radio Tagged Salmon in Six Rivers in South West England. Bristol: Environment Agency R&D Publication No. 4, 110 pp.

Solomon, D. J. & R. G. Templeton (1976), Movements of brown trout Salmo trutta L. in a chalk stream. Journal of Fish Biology, 9, 411 – 423.

UKTAG, (2013). River flow for good ecological potential; final recommendations. Water Framework Directive.

Vörösmarty C.J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies (2010), Global threats to human water security and river biodiversity, Nature, 467, 555 – 561.

Webb, J. & A. D. Hawkins (1989), Movements and spawning behaviour of adult salmon in the Girnock burn, a tributary of the Aberdeenshire Dee, 1986, In Scottish Fisheries Research Report (40), Department of Agriculture and Fisheries for Scotland.

WFD (2000)/60/EC, The Water Framework Directive, available online at http://ec.europa.eu/environment/water/water-framework/index_en.html

Wickham, H (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wolman, M.G., (1954), A method of sampling coarse river-bed material, EOS, Transactions American Geophysical Union, 35(6), 951 – 956.

Zhang, Y., A.H. Arthington, S.E. Bunn, S. Mackay, J. Xia, & M. Kennard (2012), Classification of flow regimes for environmental flow assessment in regulated rivers: The Huai River Basin, China, River Research and Applications, 28, 989–1005.

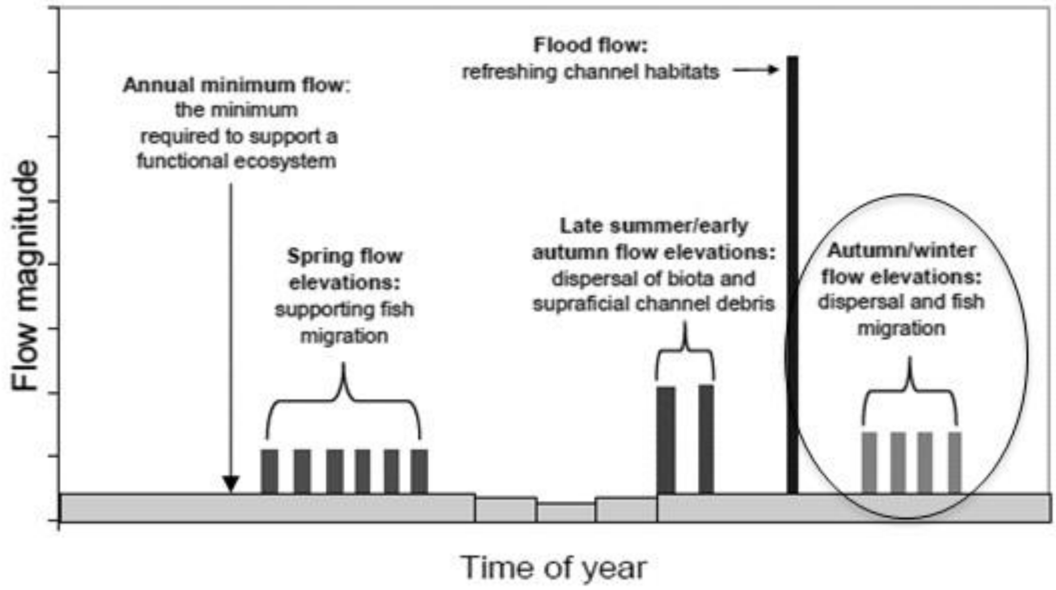


Figure 1. Schematic representation of a mitigation flow regime based on the recommended flow 'building blocks' (from UKTAG, 2013), including autumn/winter flow elevations for fish dispersal and migration (black circle).

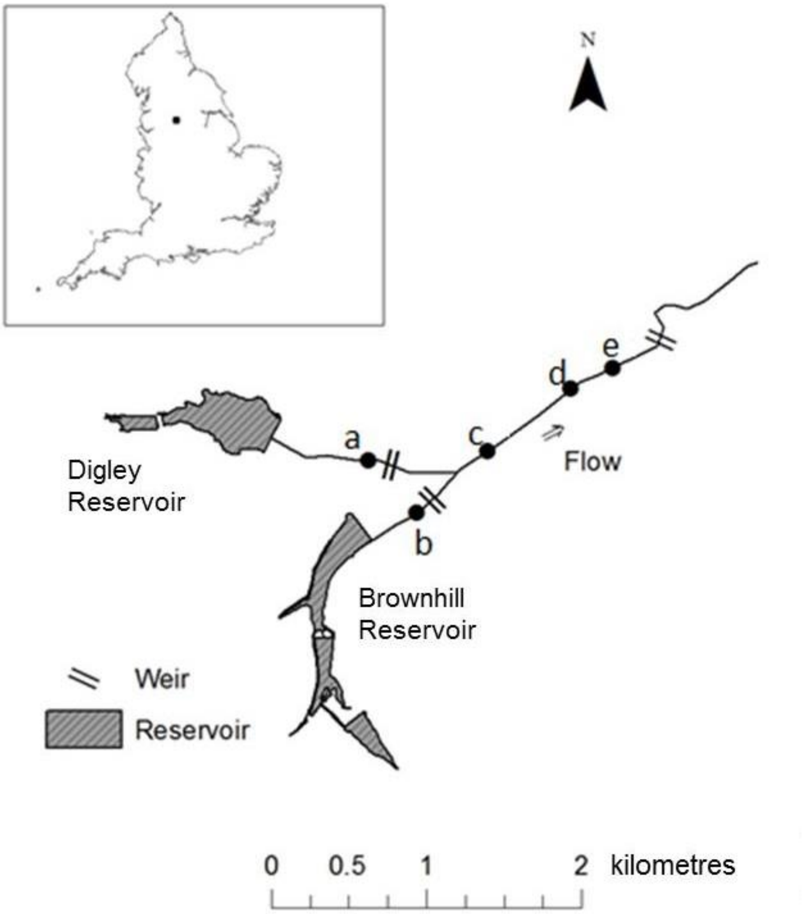


Figure 2. The release locations of radio tagged brown trout in (a) Marsden Clough (downstream of Digley Reservoir), (b) Ramsden Clough (downstream of Brownhill Reservoir), and the River Holme at (c) Co-op Lane, (d) Mill Pond and (e) Old Mill. Sites a – c studied in 2012 and sites a – e studied in 2013 and 2014. Three impassable weirs are displayed using parallel lines.

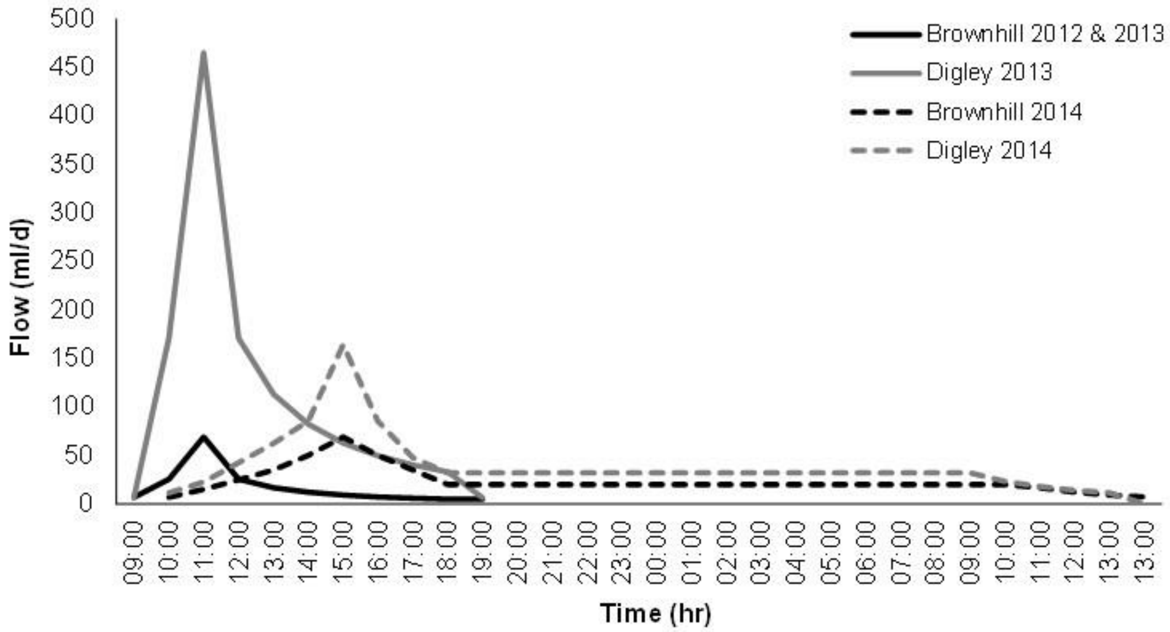
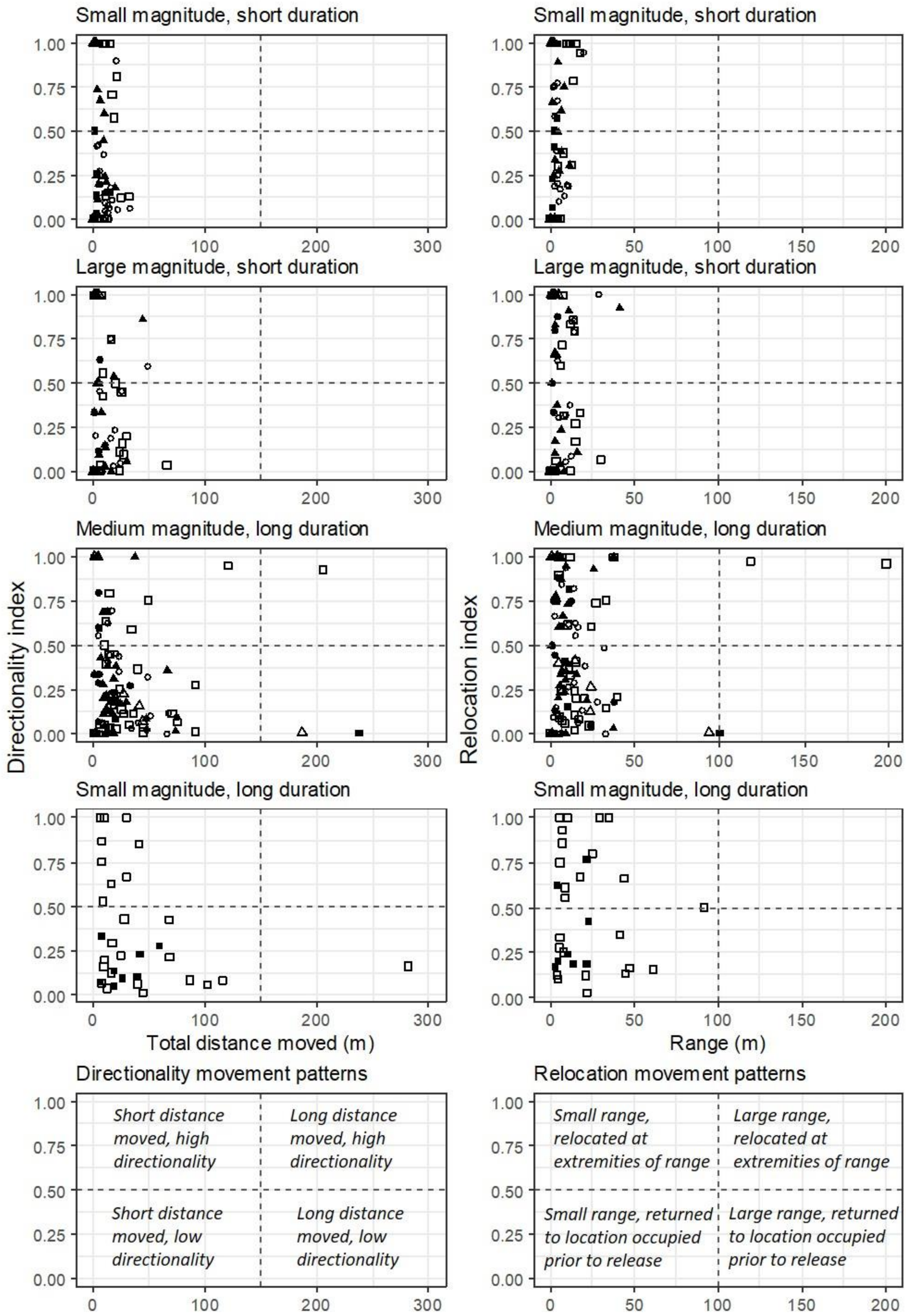


Figure 3. The magnitude (small, medium and large) and duration (short and long) of freshets released during the study from Digley (grey lines) and Brownhill (black lines) reservoirs. Solid lines indicate freshet profiles in 2012 and 2013 whilst dashed lines indicate modifications made in 2014.



Small magnitude, short duration
Large magnitude, short duration
Medium magnitude, long duration
Small magnitude, long duration
Directionality index
Relocation index
Total distance moved (m)
Range (m)
Directionality movement patterns
Short distance moved, high directionality
Long distance moved, high directionality
Short distance moved, low directionality
Long distance moved, low directionality
Relocation movement patterns
Small range, relocated at extremities of range
Large range, relocated at extremities of range
Small range, returned to location occupied prior to release
Large range, returned to location occupied prior to release

Figure 4. *Total distance moved* in relation to *directionality* index (left) and *range* in relation to *relocation* index (right) for brown trout in impact (solid symbol) and control (open symbol) reaches during freshets of differing magnitude, duration and timing (October = circle, November = triangle and December = square) (Table 2); including key to aid interpretation of fish movements.

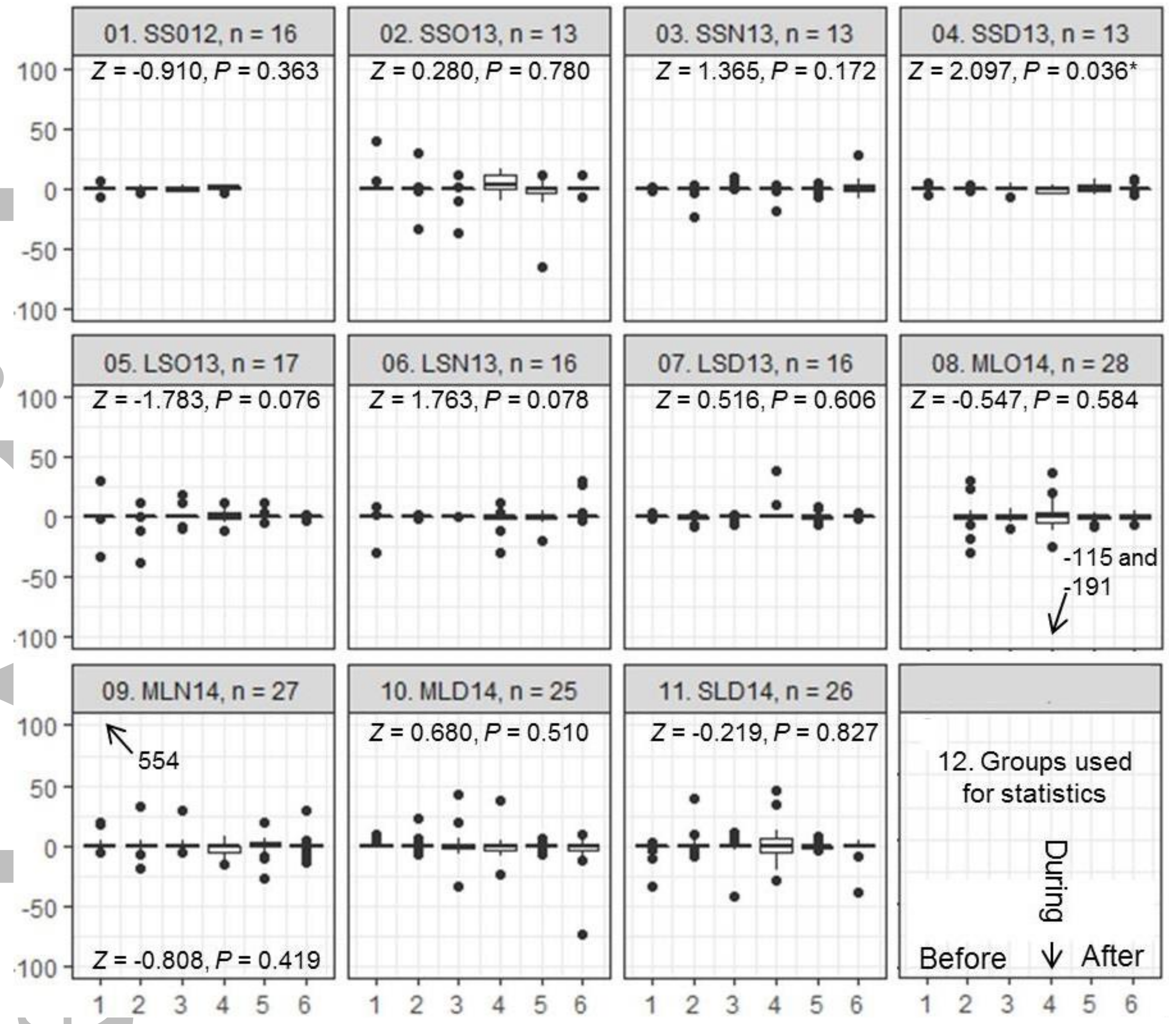


Figure 5. *Daily distance moved* in impact reach before (days 1 – 3), during (day 4) and after (days 5 and 6) freshets, with results of permutation-tests (grouping method for statistics demonstrated in plot 12). Freshet code (Table 2) = 1st letter: magnitude (S=small, M=medium, L=large), 2nd letter: duration (S=short, L=long), 3rd letter = month (O=October, N=November, D=December) and number = year (12=2012, 13=2013, 14=2014).

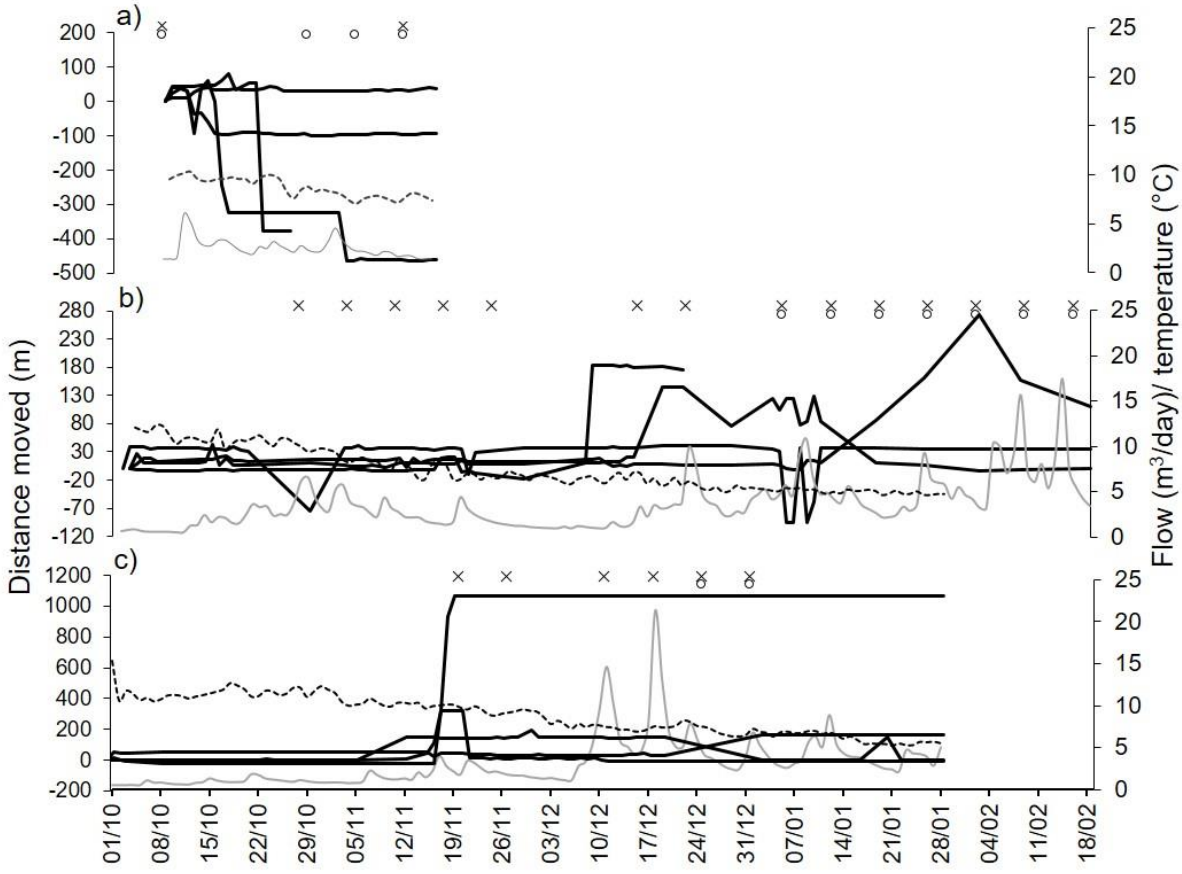


Figure 6. Flow in catchment (m^3/day, grey line), temperature (°C, black dotted line) and largest unidirectional movements (black solid lines) in a) 2012, b) 2013/14 and c) 2014/15, including reservoir overtopping (crosses = Brownhill and circles = Digley reservoir overtopping).

Table 1. UKTAG recommendations for autumn and winter flow elevations to support brown trout in rivers to their spawning grounds and the migration of adult salmon, sea trout, river and sea lamprey, in order to reach good ecological potential (UKTAG, 2013).

Building block	Description
Timing	October, November, December and, where possible, synchronised with catchment rainfall events.
Frequency	Once per week at night.
Magnitude	6x Qn95 (six times 95% of the daily naturalised flow). Ascending and descending limbs of flow rise to mimic those of comparable natural flow rises.
Duration	12 hours if no obstacles to migration are present. If a number of obstacles are present, two to three days.

Table 2. Freshet number, date, discharge prior to freshet (monthly mean; m^3/s), magnitude, duration, timing and year trialled.

Freshet	Date	Discharge prior to freshet (monthly mean; m^3/s)	Magnitude	Duration	Timing	Year	Code
1	15/11/2012	1.3 (3.9)	Small	Short	November	2012	SSN12
2	16/10/2013	1.4 (2.1)	Small	Short	October	2013	SS013
3	11/11/2013	3.0 (2.6)	Small	Short	November	2013	SSN13
4	11/12/2013	0.9 (2.6)	Small	Short	December	2013	SSD13
5	17/10/2013	2.0 (2.1)	Large	Short	October	2013	LSO13
6	19/11/2013	1.3 (2.6)	Large	Short	November	2013	LSN13
7	12/12/2013	0.9 (2.6)	Large	Short	December	2013	LSD13
8	22-23/10/2014	1.3 (0.9)	Medium	Long	October	2014	MLO14
9	25-26/11/2014	1.9 (1.8)	Medium	Long	November	2014	MLN14
10	9-10/12/2014	2.7 (5.4)	Medium	Long	December	2014	MLD14
11	3-4/12/2014	1.2 (5.4)	Small	Long	December	2014	SLD14

Table 3. Number (n), tagging date, fork length, mass, tag-body mass ratio and release location of brown trout in the River Holme catchment, northern England.

Study year	Site code	n	Date	Length (mean ± SD (range), mm)	Mass (mean ± SD (range), g)	Tag-body mass ratio (mean (range), %)
2012	a	15	7/10/12	185.8 ± 19.8 (164 – 238)	76.9 ± 29.0 (51 – 162)	1.4 (0.6 – 1.9)
	b	15	7/10/12	198.5 ± 27.9 (163 – 256)	92.0 ± 41.4 (51 – 190)	1.2 (0.5 – 1.9)
	c	15	8/10/12	199.5 ± 21.5 (163 – 240)	96.3 ± 32.9 (53 – 167)	1.1 (0.6 – 1.8)
2013	a	10	2/10/13	179.2 ± 7.7 (169 – 196)	64.3 ± 8.2 (55 – 81.2)	1.5 (1.2 – 1.8)
	b	10	2/10/13	189.4 ± 14.5 (171 – 222)	76.7 ± 21.7 (54 – 129)	1.3 (0.7 – 1.8)
	c	10	3/10/13	208.7 ± 16.7 (191 – 241)	102.3 ± 22.3 (76 – 150)	1.0 (0.6 – 1.3)
	d	10	3/10/13	202.4 ± 29.9 (164 – 241)	99.6 ± 40.3 (49 – 148)	1.1 (0.6 – 2.0)
	e	10	3/10/13	203.3 ± 23.0 (168 – 239)	93.4 ± 27.6 (52 – 141)	1.1 (0.7 – 1.9)
2014	a	10	1/10/14	176.0 ± 10.3 (166 – 197)	65.0 ± 10.2 (54 – 84)	1.5 (1.1 – 1.8)
	b	10	1/10/14	214.1 ± 20.3 (184 – 247)	117.9 ± 32.3 (65 – 175)	0.9 (0.5 – 1.5)
	c	10	30/9/14	192.6 ± 30.6 (166 – 269)	94.2 ± 43.3 (59 – 205)	1.1 (0.5 – 1.6)
	d	10	30/9/14	198.5 ± 33.5 (170 – 282)	88.1 ± 25.5 (61 – 147)	1.2 (0.7 – 1.6)
	e	10	30/9/14	219.1 ± 23.4 (182 – 258)	130.8 ± 40.7 (77 – 203)	0.8 (0.5 – 1.2)

Table 4. *Total distance moved*, *beeline distance* and *range* (all median, interquartile range) of brown trout in control and impact reaches during freshets of differing magnitude (M), duration (D), timing (T), year (Y). Permutation test significance indicated by * = $P < 0.05$, ** = $P < 0.02$ and *** = $P < 0.01$.

Freshet features				Total distance moved			Beeline distance			Range		
M	D	T	Y	Control	Impact	Statistics	Control	Impact	Statistics	Control	Impact	Statistics
Small	Short	Nov	2012	2.7, 2.9	11, 8.7	$Z = -2.401$, $n = 26$, $P = 0.016$**	0.05, 1.5	0.5, 1	$Z = 0.126$, $n = 26$, $P = 0.900$	1.5, 1.1	4, 2.9	$Z = -2.387$, $n = 26$, $P = 0.017$**
Small	Short	Oct	2013	0.2, 1.1	12, 9	$Z = -3.451$, $n = 23$, $P = <0.001$***	0, 0.6	3, 11	$Z = -1.673$, $n = 23$, $P = 0.094$	0.2, 1.1	9.5, 8	$Z = -3.456$, $n = 23$, $P = <0.001$***
Small	Short	Nov	2013	0, 1	2, 4.5	$Z = -1.668$, $n = 22$, $P = 0.095$	0, 0	0, 0	$Z = 0.516$, $n = 22$, $P = 0.606$	0, 1	1, 3	$Z = -1.266$, $n = 22$, $P = 0.206$
Small	Short	Dec	2013	0, 1	6.2, 6.7	$Z = -3.046$, $n = 22$, $P = 0.002$**	0, 0	-1.5, 4	$Z = 1.627$, $n = 22$, $P = 0.104$	0, 1	4.7, 3.7	$Z = -2.955$, $n = 22$, $P = 0.003$***
Large	Short	Oct	2013	2.5, 2.5	16, 18.9	$Z = -2.067$, $n = 23$, $P = 0.039$*	0.5, 3.3	0, 7.5	$Z = -0.471$, $n = 23$, $P = 0.638$	2.5, 1.8	8, 11.1	$Z = -2.149$, $n = 23$, $P = 0.032$*
Large	Short	Nov	2013	0, 0	9.3, 14	$Z = -2.122$, $n = 22$, $P = 0.039$*	0, 0	0, 1	$Z = 0.566$, $n = 22$, $P = 0.572$	0, 0	4.5, 9.5	$Z = -2.039$, $n = 22$, $P = 0.042$*
Large	Short	Dec	2013	4, 1.9	8.9, 10.8	$Z = -1.405$, $n = 22$, $P = 0.16$	-0.5, 3	0.2, 1.6	$Z = -0.935$, $n = 22$, $P = 0.35$	2.3, 1.3	3, 5.9	$Z = -1.001$, $n = 22$, $P = 0.317$
Med	Long	Oct	2014	11.5, 37.4	29.8, 31.5	$Z = -0.331$, $n = 37$	-0.2, 3.4	-0.5, 8.3	$Z = 0.575$, $n = 37$,	6.5, 19.5	14.5, 16.3	$Z = -0.485$, $n = 37$

						, *P* = 0.741			*P* = 0.566			, *P* = 0.628
Med	Long	Nov	2014	5, 16.5	13.5, 15.5	*Z* = 0.851, n = 36, *P* = 0.395	-0.5, 3	-0.2, 6.3	*Z* = 0.618, n = 36, *P* = 0.537	4, 7.6	9, 11.6	*Z* = 0.694, n = 36, *P* = 0.488
Med	Long	Dec	2014	5, 28.7	14, 10.3	*Z* = 0.134, n = 34, *P* = 0.894	1, 1.2	-0.5, -2	*Z* = 0.251, n = 34, *P* = 0.80	4.5, 9.7	7.5, 4.5	*Z* = -0.109, n = 34, *P* = 0.913
Small	Long	Dec	2014	22.8, 23.9	20.8, 34	*Z* = -0.712, n = 34, *P* = 0.477	-2.5, 5.3	0, 12.3	*Z* = -0.800, n = 34, *P* = 0.423	12, 16.8	10, 27.4	*Z* = -1.202, n = 34, *P* = 0.230

Table 5. *Directionality* and *relocation* index (median, interquartile range) in control and impact reaches during freshets of differing magnitude (M), duration (D), timing (T), year (Y). Permutation test significance indicated by indicated by * = $P < 0.05$, ** = $P < 0.02$ and *** = $P < 0.01$.

Freshet features				Directionality index			Relocation index		
M	D	T	Y	Control	Impact	Stats	Control	Impact	Stats
Small	Short	Nov	2012	0.2, 0.4	0.1, 0.1	*Z* = 1.389, n = 26, *P* = 0.165	0.5, 0.8	0.2, 0.2	*Z* = 1.436, n = 26, *P* = 0.151
Small	Short	Oct	2013	0, 1	0.1, 0.8	*Z* = -0.107, n = 23, *P* = 0.914	0, 1	0.4, 1	*Z* = -0.590, n = 23, *P* = 0.556
Small	Short	Nov	2013	0, 1	0, 0.4	*Z* = 0.607, n = 22, *P* = 0.544	0, 1	0, 0.7	*Z* = 0.147, n = 22, *P* = 0.883
Small	Short	Dec	2013	0, 1	0, 0.4	*Z* = -0.211, n = 22, *P* = 0.833	0, 1	0.5, 0.5	*Z* = -1.158, n = 22, *P* = 0.247
Large	Short	Oct	2013	1, 0.4	0.2, 0.5	*Z* = 1.931, n = 23, *P* = 0.054	1, 0.3	0.3, 0.8	*Z* = 1.576, n = 23, *P* = 0.115
Large	Short	Nov	2013	0, 0	0.1, 0.3	*Z* = -0.187, n = 22, *P* = 0.8514	0, 0	0.2, 0.4	*Z* = -0.750, n = 22, *P* = 0.453
Large	Short	Dec	2013	0.5, 0.2	0, 0.2	*Z* = 2.460, n = 22, *P* = 0.014*	0.7, 0.3	0.1, 0.4	*Z* = 2.436, n = 22, *P* = 0.015 **
Medium	Long	Oct	2014	0.2, 0.2	0.1, 0.4	*Z* = 0.161, n = 37, *P* = 0.872	0.3, 0.3	0.3, 0.7	*Z* = -0.41378, n = 37, *P* = 0.679
Medium	Long	Nov	2014	0.6, 0.9	0.2, 0.4	*Z* = 1.918, n = 36, *P* = 0.055	0.8, 0.8	0.3, 0.6	*Z* = 1.2355, n = 36, *P* = 0.217
Medium	Long	Dec	2014	0.3, 0.2	0.2, 0.2	*Z* = 0.144, n = 34, *P* = 0.886	0.5, 0.6	0.3, 0.5	*Z* = 0.25988, n = 34, *P* = 0.795
Small	Long	Dec	2014	0.1, 0.2	0.3, 0.6	*Z* = -1.898, n = 34, *P* = 0.058	0.2, 0.3	0.6, 0.7	*Z* = -1.480, n = 34, *P* = 0.139

Table 6. Difference in *relative range* (median, interquartile range) of brown trout between control and impact reaches during freshets of differing magnitude (M), duration (D), timing (T) and year (Y). Permutation test significance indicated by * = P < 0.05, ** = P < 0.02 and *** = P < 0.01.

Freshet features				Relative range		Statistics
M	D	T	Y	Control	Impact	
Small	Short	Nov	2012	3.5, 16.9	9.7, 5.5	Z = 0.304, n = 16, P = 0.761
Small	Short	Oct	2013	0.2, 1.1	15.9, 20.3	Z = -3.377, n = 13, P = 0.0007***
Small	Short	Nov	2013	0.0, 0.5	0.9, 10.5	Z = -1.774, n = 13, P = 0.076
Small	Short	Dec	2013	0.0, 0.7	10.4, 8.2	Z = -2.399, n = 13, P = 0.016**
Large	Short	Oct	2013	5.4, 4.8	6.3, 16.3	Z = -1.338, n = 17, P = 0.181
Large	Short	Nov	2013	0.0, 0.0	5.7, 8.2	Z = -1.613, n = 16, P = 0.107
Large	Short	Dec	2013	4.4, 4.0	4.0, 8.9	Z = -0.722, n = 16, P = 0.470
Med	Long	Oct	2014	10.6, 19.2	20.2, 25.3	Z = -0.563, n = 28, P = 0.574
Med	Long	Nov	2014	6.7, 9.6	11.3, 19.1	Z = -0.593, n = 27, P = 0.553
Med	Long	Dec	2014	8.1, 16.9	9.4, 23.2	Z = -1.179, n = 26, P = 0.239
Small	Long	Dec	2014	9.1, 12.6	20.1, 38.0	Z = -1.827, n = 27, P = 0.068