Enhancing the upstream passage of river lamprey at a microhydropower installation using horizontally-mounted studded tiles

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Abstract

Passage performance of upstream-migrating lamprey (*Lampetra fluviatilis*) was compared between sections of a Crump flow-gauging weir with and without studded tiles, and at a bottom-baffle fishway, on the River Derwent, England. The effects of microhydropower operation on attraction to multiple routes were also studied. Studded tiles were fixed horizontally on the weir face near the right bank, forming a 1 m wide treatment route, neighboured by a tileless control route. A bottom-baffle fishway was present at the right bank, alongside the hydropower tailrace. Two further weir-face control routes at the left bank, in combination with those on the right side, enabled comparison of lamprey attraction relative to the weir flow. Downstream and upstream ends of the right-hand weir-face routes, and of the fishway, downstream ends of the left-hand weir face routes, and the entrance of the hydropower tailrace area were instrumented with PIT antennas (n = 9 total). Of 395 PIT-tagged lamprey, released 0.52 rkm downstream of the weir on 10 separate dates in early winter 2017 (turbine on for 21/43 days of study period), 363 (91.9%) were detected by at least one of the antennas (median [IQR] minimum delay at weir: 15.0 [7.4 - 21.4] days). All lamprey detected at the left-bank antennas (attraction efficiency AE: 255/395 [64.6%]) were also detected elsewhere. The fishway was ineffective (AE: 343/395 [86.8%]; passage efficiency PE: 5/343 [1.5%]). While lamprey were more attracted towards the control relative to the adjacent tiled route, a higher number of fish traversed the weir using the latter (AE tiled route: 172/395 [43.5%]; PE tiled route: 44/172 [25.6%]; AE control route: 257/395 [65.1%]; PE control route: 22/257 [8.6%]). Lamprey were attracted towards the right half of the channel when the turbine was running, as only n = 88/4190 (2.1% of total attempts) detections were made at the two left-bank control antennas in the turbine-on condition, compared to 2775/13029 (21.3%) at the same two antennas when the turbine was off. While improved passage efficiency was achieved using surface-mounted studded tiles, further *in situ* evaluations are needed to optimize their performance.

Keywords: *longitudinal connectivity, hydropower, migration, fish passage, attempt behaviour, PIT telemetry*.

Introduction

Given the linear profile of rivers, obstructions to movement, both physical and behavioural, can fragment previously continuous populations (Peter, 1998; Baras and Lucas, 2001; McLaughlin *et al*., 2006). While impacts may be especially apparent following construction of large obstructions (≥ 5 m head), such as dams (Jungwirth, 1996; World Commission on Dams (WCD), 2000; Bednarek, 2001; Quinn and Kwak, 2003), smaller, low-head structures such as weirs, culverts and sluices, can affect the ecological persistence of fish assemblages as well (Jungwirth *et al*., 2000; Birnie-Gauvin *et al*., 2017a). While not always a complete barrier, the abundance of small obstructions (typically two to four orders of magnitude more than large dams [Sheer and Steel, 2006; Lucas *et al*., 2009; Entec, 2010]) affects longitudinal connectivity, vital for the ecological integrity of rivers (Grill *et al*., 2015; Magilligan *et al*., 2016; Dodd *et al*., 2017; Rincón *et al*., 2017).

River lamprey (*Lampetra fluviatilis*) are obligatorily migratory, jawless fish with an anguilliform body morphology, typically exhibiting an anadromous life history (Moser *et al*., 2015). This species has been dramatically affected throughout its native European range by loss of river connectivity and habitat modification (Lucas *et al*., 2009; Mateus *et al*., 2012; Aronsuu *et al.*, 2015), and is currently widely regarded as endangered throughout large parts of Europe (Thiel *et al*., 2009), partly because of insufficient consideration in terms of its upstream passage requirements (Lucas *et al*., 2009). They are highly vulnerable to river fragmentation because they cannot leap to overcome obstacles, have limited burst swimming performance and, unlike some lampreys (e.g. Pacific lamprey [*Entosphenus tridentatus*]), are unable to climb steep slopes (Russon *et al*., 2011; Keefer *et al*., 2012). Instead they use a burst-attach-rest approach to overcome obstacles, whereby a short burst of swimming is followed by attachment to the substrate with the oral disc to aid recovery (Kemp *et al*., 2011; Kerr *et al*., 2015; Moser *et al*., 2015).

Longitudinal connectivity restoration is crucial for recovery and sustainability of lamprey populations and can be achieved by removal or modification of the obstruction (Birnie-Gauvin *et al.*, 2017b) and/or installation of effective fishways (Clay, 1995; Silva *et al*., 2018). However, common technical fishway designs tend to perform poorly for upstream -moving river lamprey. For example, *in situ* investigation of the upstream movement of lamprey at pool and weir, superactive baffle (SAB) and Denil fishways revealed very low passage efficiency of 5%, 0.3% and 0% respectively (Foulds and Lucas, 2013; Tummers *et al*., 2016). In many countries, sloping weirs such as Crump and Flat-V designs are constructed to gauge river discharge (WMA, 2010; Russon *et al*., 2011) and are known to severely impact upstream migration for weaker swimming species such as lamprey (Lucas *et al*., 2009; Kerr *et al*., 2015). Due to their requirement for gauging, modification rather than removal of these weirs to improve longitudinal connectivity is often favoured. A proposed new low cost solution to improve upstream passage of fishes with an anguilliform morphotype at sloping weirs is the placement of studded tiles on the downstream face, which presumably creates a heterogeneous micro-environment with increased roughness and bulk drag (Vowles *et al*., 2015; Tummers *et al*., 2016). Originally designed for upstream migrating juvenile eel (*Anguilla anguilla* and *A. rostrata*), studded substrates have proved effective for eel *in situ* in the UK (Solomon and Beach, 2004) and France (Porcher, 2002) and under controlled laboratory conditions (Vowles *et al*., 2015). At a 0.34 m high experimental weir in a laboratory setting, both horizontally and vertically oriented dual-density studded tiles (having adjacent sections of high and low densities of studs) were shown to improve adult river lamprey passage (Vowles *et al.*, 2017). However, tiles with more widely spaced studs at a single density (*Figure* **1**) have been designed for lamprey passage (Rooney *et al*., 2015; A. Don, Environment Agency, *pers*. *comm*.), on the basis that adult anadromous lamprey are larger than elvers (and also most yellow eel) and also have lower body curvature than eel. The addition of single-density studded tiles mounted *in situ* vertically (studs projecting laterally) within a 15% gradient SAB fishway improved adult river lamprey passage through the fishway. However, passage efficiency was lower than across the unmodified weir (Tummers *et al*., 2016). Further work is required to test the same type of studded tiles for passing adult river lamprey, but in horizontal alignment directly on the weir face, a configuration untested in the field.

The aim of this study was to measure the performance of horizontally oriented single-density studded tiles fixed *in situ* on a low-head Crump weir, for aiding upstream passage of adult river lamprey. A SAB fishway and a newly installed micro-hydroelectric power station using a Kaplan turbine at the weir provide multiple passage options and conflicting attraction flows for fish. Attempts by individual lamprey and their passage behaviour, under varying flow conditions and water temperature, were quantified on the weir face, in the fishway and in the turbine tailrace area when the turbine was both on and off. Additionally the study provided comparison of lamprey passage metrics with those measured prior to operation of the microhydropower station (Tummers *et al.*, 2016). It was hypothesized that river lamprey would ascend the low-head weir more efficiently under a variety of flow conditions using a horizontally mounted studded tile route compared to a bare weir face. Furthermore, we predicted that lamprey attempt rate would be most frequent in areas of highest attraction flow and during periods of highest river discharge.

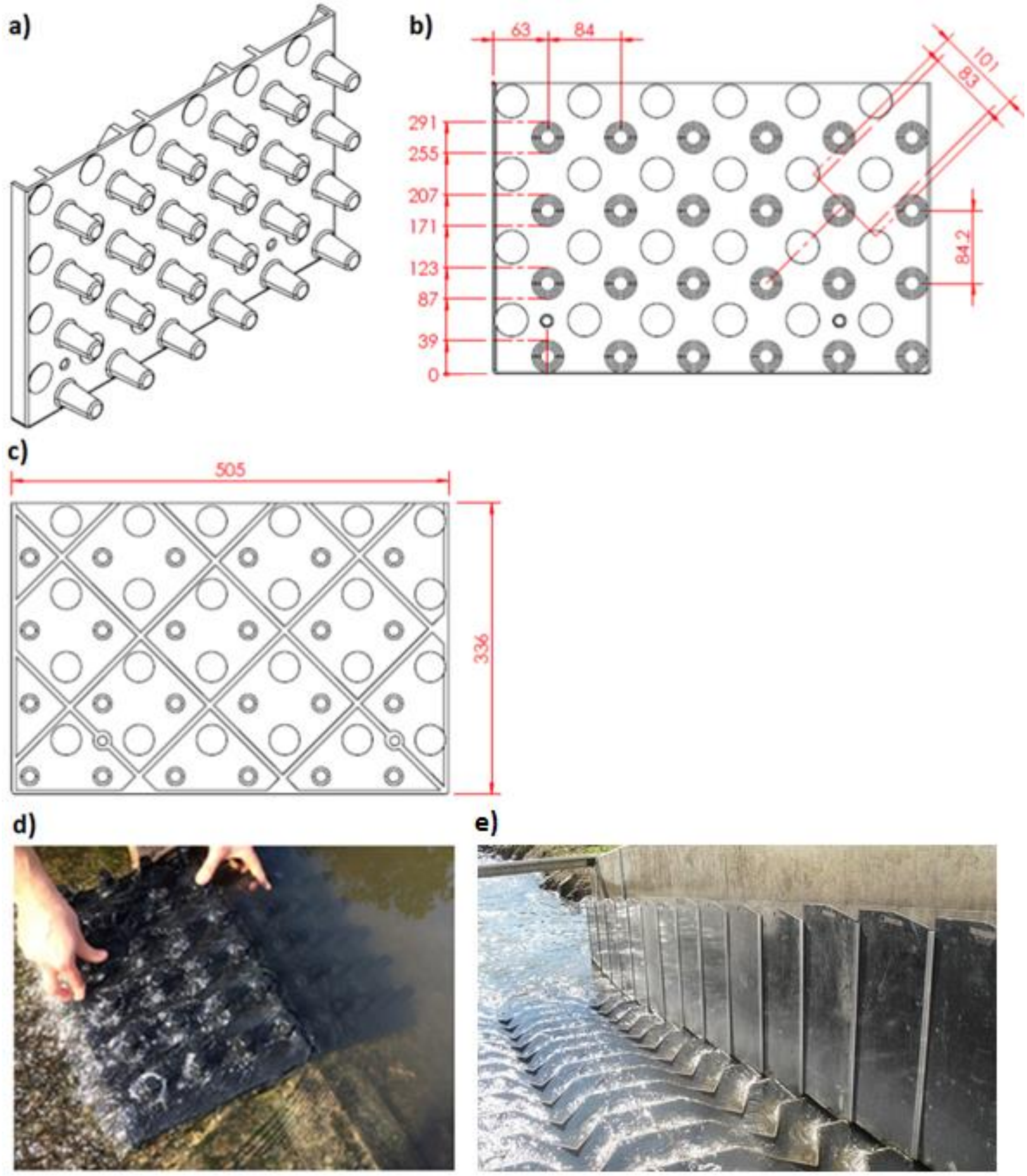

Figure **1**: **a**), **b**), **c**) Oblique, top-down and reverse view, respectively, of a studded tile as used in the current study, showing relevant dimensions (drawings obtained from http://www.berryescott.co.uk/wp-content/uploads/2016/08/lamprey-tile-drawing.png). Fully open circles represent studs cut off (presenting a flat surface for lamprey to attach to) during commercial production to provide Berry and Escott 'lamprey tile' specification; **d**) Initial placements of studded tiles on the weir face. Shown is the weir crest under very low flow (*ca*. Q_{95}) conditions, with one tile fixed on the upstream face and one on the downstream face. No further tiles were placed at the upstream side (extending over the weir crest by 0.5 m), while the tiles were fixed continuously on the downstream face up to 0.4 m from the downstream weir limit; **e**) Identical studded tiles but mounted vertically within the SAB fishway, with studs projecting laterally (continuously along right wing wall, shown is the mostly dewatered fishway while construction was ongoing), as evaluated in Tummers *et al*. (2016).

Material and Methods

Study site

The study was conducted in November and December 2017, for a total of 43 days, on the River Derwent, a tributary of the Yorkshire Ouse, Northeast England. The Derwent runs from its source in the North York Moors (lat.: 54.380583, long.: -0.623275) to eventually join the River Ouse at Barmby barrage (lat.: 53.749444, long.: -0.968889). It has a length of 115 river kilometres (rkm) and a catchment area of 2057 km^2. The study reach is located on the lower Derwent (gradient of *ca*. 0.3 m km^{-1}; 2 - 6 m mid-channel depths (Lucas *et al*., 2009); mean daily flow 17.8 $m^3 s^{-1}$ (National River Flow Archive [NRFA), 2018]), which is a Natura 2000 special area of conservation (SAC) for which river lamprey is a listed feature. Multiple anthropogenic structures (one tidal barrage, five weirs [all < 3 m]), which limit longitudinal connectivity, are located on the lower 60 km of the Derwent (Lucas *et al*., 1998), one of which is a Crump weir at Buttercrambe (lat.: 54.018884, long.: -0.88532951; 40.2 rkm upstream of Barmby barrage). The weir was constructed in 1973 for river discharge monitoring purposes (redundant now due to ultrasonic gauging) and has a standard triangular profile (1:2 upstream and 1:5 downstream slopes), a head loss of 1.31 m and discharge of 2.78 $m^3 s^{-1}$ at a flow-exceedance value of Q_{95}.

In September 2017 a microhydroelectric power station, consisting of two horizontally-placed Kaplan turbines (nominal power output 50 kW per turbine) became operational on the right bank of Buttercrambe weir. However, due to mechanical failure only one turbine was functional during the study period. No tailrace screens were in place. The turbine running regime at the site is flow-controlled (conditions set by the Environment Agency [EA]): a head difference over the weir outside the range of 0.390 - 0.750 m prevents turbine operation. Manual power-up and shutdown of the turbine was possible during the study, provided head difference was appropriate. Turbine-on and turbine-off conditions were maintained for 21/43 (48.8%) and 22/43 (51.2%) days of the study period, respectively, during which 395 lamprey were released (150 and 245 under turbine-on and -off conditions, respectively; *Figure* **2**).

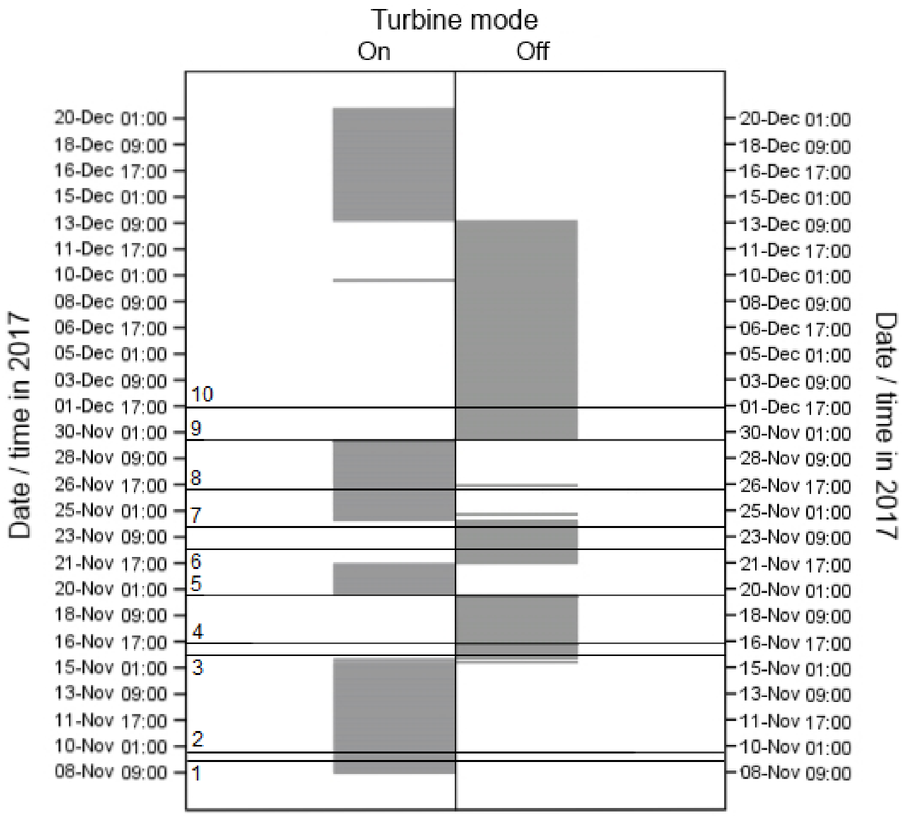

Figure **2**: Turbine operation during the study period. Date and time of river lamprey batch releases are presented as horizontal lines and batch numbers are indicated adjacent to each line.

Neighbouring the turbine house and parallel to the main river flow is a 15% gradient SAB technical fishway. Constructed from concrete, the fishway is 11.2 m long and has an internal width of 2.75 m (head loss of 1.31 m at Q_{95}), wherein 24 rows of super active stainless steel baffles (three per row, 12 mm thick,150 mm high, equally spaced [0.40 m]) dissipate the kinetic energy in the water column (Armstrong *et al*., 2010). The studded tiles (Berry and Escott Engineering, UK) consisted of 0.02 m thick polypropylene black boards (0.34 m long, 0.50 m wide) each covered with 24 blunt-ended studs (50 mm high, 30 mm base diameter and separated by 68 mm along rows and 88 mm at diagonals of the stud bases; *Figure* **1**). These single-density studded tiles differ from dual-density ones in that the latter is composed of thinner studs for 33% of the width, placed more compactly at a spacing of 30 - 35 mm along rows and 17 - 20 mm on the diagonal (see also Vowles *et al*., 2017). The remaining 67% part-width of the dual-density tile is identical to the single-density tile described above.

Identical single-density tiles were also used in the current study, but fixed horizontally directly on the weir face (*Figure* **1d**), near the right bank in the manner indicated in Vowles *et al*. (2017). A 1 m wide continuous route of tiles was installed, starting 1 m away from the right wing wall of the weir. This route was on the same side of the weir as the fishway and the turbine tailrace, as attraction was expected to be higher on that side due to the greater bulk flow). The tiles extended from 0.4 m upstream of the truncated end of the downstream weir face (downstream weir face length of 6.0 m, tile route length of 5.6 m) to 1.14 m from the end of the upstream weir face (upstream weir face length of 1.8 m, tile route length of 0.66 m). No cover was placed over the tiles and they were accessible laterally from the open weir apron as well as from downstream by river lamprey. Between the fishway wall and the treatment tile route, a 1 m wide control route was retained. The rationale for having the control route adjacent to the fishway wall was that, based on laboratory studies (Kemp *et al*., 2011; Russon *et al*., 2011) and observations on site (Tummers *et al*., 2016; J. Tummers, *pers. obs*.), lamprey activity was expected to be greatest at the side-walls as the water velocities are lower (boundary effects), it is nearest to the fishway attraction flow, and lamprey are edge- and bed-orientated. Positioning the treatment route 1 m from the edge, with no 'retaining wall', therefore, provided a conservative test of treatment effect compared to the 'best case' weir face environment for attraction and passage.

Capture and tagging procedure

Because of a low catch efficiency of river lamprey in the Derwent tributary of the River Ouse (Jang and Lucas, 2005), river lamprey were trapped near the tidal limit of the Ouse (lat.: 53.880002, long.: -1.1001047, and at 53.885945, -1.0959495) using double-compartment (two-funnel) eel pots (Masters *et al*., 2006) fishing on the river bed. Trapped lampreys were checked for any signs of tissue damage and undamaged lamprey transported to Buttercrambe in aerated holding tanks for tagging and release. Previous research demonstrated no difference in migration behaviour of lamprey caught in the Derwent and the Ouse and subsequently released in the Derwent (Lucas *et al*., 2009). Natal homing behaviour is absent for the strongly positively rheotactic river lamprey (Tuunainen *et al*., 1980). Furthermore, Bracken *et al*. (2015) showed that river lamprey in Ouse tributaries, including the Derwent, originate from the same genetic population.

On arrival at the tagging site, lamprey were sedated (stage IV on six-stage scale) using a buffered 0.1 g L^{-1} solution of tricaine methanesulphonate (MS-222). Total body length (mm) was measured and lamprey $\geq$ 310 mm were tagged intracoelomically with a 3.65 mm diameter x 32 mm long HDX passive integrated transponder (PIT) tag (Texas Instruments model RI-TRP-RRHP, 134.2 kHz, weight 0.8 g in air). A sub-sample was also (double) tagged with a coded 69 KHz acoustic transmitter (HTISonar Model 795-LD, 6.8 mm diameter x 20 mm long, 1.05 g in air) for a related study (Kerr *et al*., *in prep*.). PIT tags and acoustic transmitters were disinfected with ethanol and rinsed with distilled water before insertion. Three separate sutures (coated Vicryl, 4/0) were used to close the incision for lamprey double-tagged with a PIT tag and an acoustic transmitter. Following surgery, fish were checked continuously in a well-aerated tank of fresh river water. When fully recovered (after *ca*. 60 min), individuals were released 0.515 rkm downstream of the weir. Over 10 sessions from 08 November 2017 - 01 December 2017, *n* = 395 lamprey were tagged and released, of which 34 were double-tagged with an acoustic transmitter. All fish handling and tagging was conducted in compliance with UK Home Office Licence number PPL 70/8720 following the Animals (Scientific Procedures) Act 1986.

Telemetry

The tile route, on the weir face, was instrumented with two flatbed PIT antennas (formed from insulated multiwire copper cables), placed underneath the tiles, one antenna 0.3 m upstream of the downstream tile-limit and one 0.2 m from the weir crest (on the downstream slope). The right bank control route was also instrumented with two flatbed PIT antennas (*Figure* **3**) at identical positions and orientation as for the tiled route. At the left bank wing wall to the weir, two further 1 m wide antennas were placed at the mirror positions (*Figure* **3**) as the bottom ones of the right-bank tile and control routes, to serve as further controls. This enabled investigation of the degree to which discharge (majority near right bank, at exit of fishway and turbine tailrace) influenced attraction towards the weir and which routes were chosen to attempt to ascend it. Cables forming each of these weir face PIT flatbed antennas (*n* = 6) were installed in 1 cm deep recesses in the weir face. Detection range (0.15 m) was deliberately down-tuned so that only tagged lamprey located directly above these flatbed antennas were logged. While during elevated flows lamprey high in the water column would not be detected, lamprey activity at such tiles or on sloping weir faces is invariably close to the bed (Vowles *et al*., 2017). Each of these six antennas on the weir face had identical dimensions: 0.35 m long, 0.97 m wide.

At the fishway, PIT antennas were constructed at the downstream entrance and upstream exit (0.3 and 0.5 m from ends, respectively; downstream antenna: 2.75 m wide, 1.62 m high; upstream antenna: 2.75 m wide, 2.32 m high), and another at the turbine tailrace entrance (6.45 m wide, 1.25 m high; *Figure* **3**). These three antennas, all of the pass-through type, were connected to a single multiplexer PIT detection reader box (Oregon RFID, USA). Similarly, the four weir face antennas near the right bank were connected to an identical reader box. Because of their close proximity (< 10 m), reader boxes (1 x 4 antennas, 1 x 3 antennas) were synchronised for antennas connected to each. A 240 V AC mains supply powered these two PIT systems on the right bank, but because of mains noise a 12 V leisure battery trickle charged by a noise-filtering linear mode battery charger was used. The two control antennas near the left bank were connected to a synchronised master-slave reader pair (Wyre Microdesign, UK), and powered by a deep-cycle, 110 Ah 12V leisure battery trickle charged by a linear mode battery charger from a 240 V AC mains supply. On every instance of tag detection by a PIT antenna, the unique tag ID number, antenna number, date, time and detection period were recorded and stored, and data was downloaded weekly. Each antenna was tested for tag detection and range directly following construction and every 2 - 3 days over the study period using pole-mounted tags and by operation of automated marker tags. All antennas were interrogated at a read-write frequency of at least 4 times s^{-1}. The weir antennas interrogated the lowermost 0.15 m of water (full depth at low to moderate flows) and the fishway antennas interrogated the full depth and width of the fishway. The rectangular tailrace antenna had a detection gap underneath part of it due to the V-shaped (cross-section) tailrace channel and, at high river discharge, above it also. The tailrace antenna interrogated *ca*. 70% of cross sectional area at low river discharge, and *ca*. 45% of the area at high discharge conditions. Each of the nine fixed location PIT antennas ran continuously for > 99.9% of the time from 13 Nov to 20 Dec 2017 (38/43 days [88.4%] of study period). Prior to this, while weir antennas were operating normally, the fishway and tailrace antennas (n = 3) were running at reduced, but still adequate (based on extensive, repeated detection range tests), detection ranges due to technical, noise-related difficulties (08 Nov - 12 Nov, 5/43 days [11.6%]).

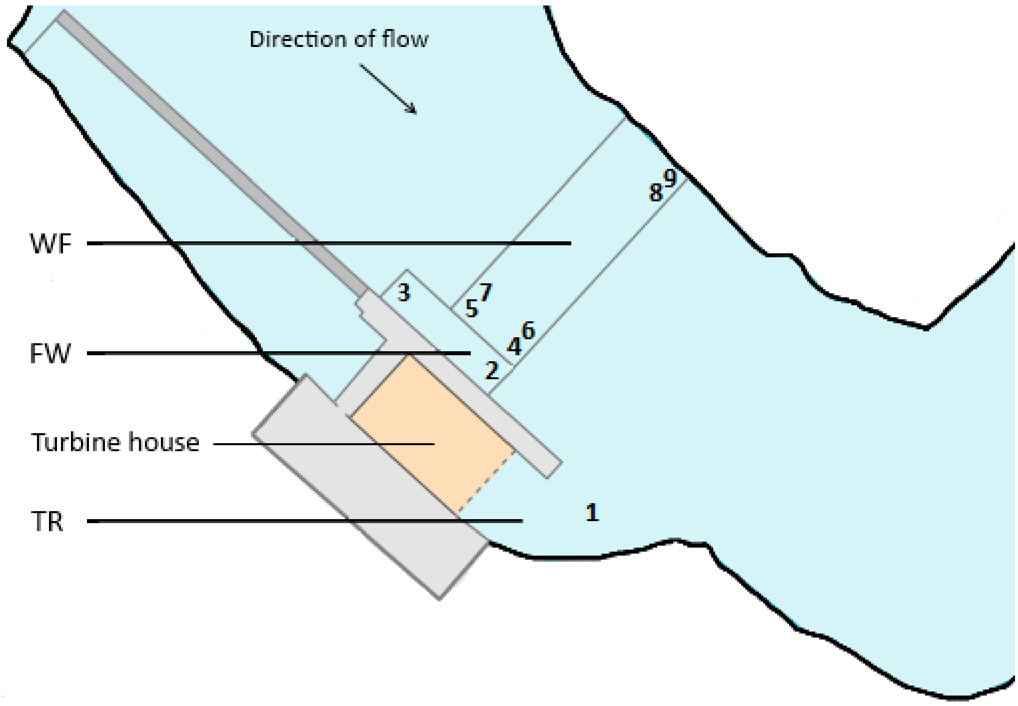

Figure **3**: Study site showing the turbine tailrace (TR, with antenna 1), bottom-baffle fishway (FW, antennas 2 and 3) and the Crump weir (WF, weir face; antennas 4 and 5 [controls right bank], 6 and 7 [tiled route] and 8 and 9 [controls left bank]).

Data analysis and environmental data

To enable direct comparison of the results from this study to Tummers *et al*. (2016) at the same site, attraction efficiency (AE) was defined as the percentage of tagged lamprey detected at a given downstream antenna. Passage efficiency (PE) was defined as the percentage of tagged lamprey detected at a route-specific upstream antenna of those that were detected at the corresponding downstream antenna. Consecutive detections by the same individual at one antenna were distinguished as separate attempts if the time interval between each detection was at least 30 s.

Following tests for deviation of normality (Kolmogorov-Smirnov) and unsuccessful attempts to transform data (log- and square root-transformation), nonparametric statistics were used for data analyses. Kruskal Wallis H tests were performed to determine if body length of lamprey detected and time taken to locate each route differed between the nine antennas and, if a difference was found, Mann-Whitney U tests (with post-hoc Benjamini-Hochberg procedure) were used to identify which combinations differed significantly. A Spearman rank-order correlation test was used to identify whether body length was correlated with total number of detections per lamprey at any antenna. Related samples Wilcoxon signed rank tests, corrected for false discovery rate with post-hoc Benjamini-Hochberg procedure, were used to test for differences between number of lamprey and attempts recorded at each of the nine PIT antennas under both the turbine off and on condition. A multivariate generalized linear mixed model was run to investigate whether river flow and water temperature had a significant effect on daily number of detections totalled for all antennas, excluding release days.

An ultrasonic flow meter, located *ca.* 100 m upstream from the weir, and the gauged stage recorders at the weir provided total discharge and upstream and downstream water level data at 15-minute intervals (D. Lindsay - Environment Agency, *pers*. *comm*.). Discharge over the weir and through the fishway were calculated based on structure dimensions and upstream water level. Discharge through the hydroelectric power station was estimated as total discharge at site (ultrasonic flow meter) minus the discharge through the fishway and over the weir (D. Lindsay - Environment Agency, *pers*. *comm*.). Flow annual exceedance values (Q_x) for the Derwent were derived from Buttercrambe gauged daily river flow time series data, for the period 1973 - 2011 (NRFA, 2018).

Water temperature was recorded at 1 h intervals on an automatic logger (HOBO Pendant UA-02-008; range -20 °C to +70 °C ± 0.53 °C; ONSET HOBO data logger; http://www.onsetcomp.com/products/data-loggers/ua-002-08) deployed 10 m downstream of the weir. Civil twilight times at Buttercrambe were derived from https://www.timeanddate.com/astronomy/@11126167. A circular event by time of day (24 h clock) plot was created to visualize total number of attempts (stacked) for all detected lamprey at each of the PIT antennas in relation to time of day. Statistical analyses were carried out in the R environment (R version 3.4.3.; R Core Team, 2012) and in SPSS 22.0 (IBM, 2013), whereby the significance threshold was set at $\alpha = 0.05$.

Results

Route-specific detections and attraction/passage efficiencies

Out of a total of 395 river lamprey tagged and released, 363 (91.9%) were detected by at least one antenna. While the turbine tailrace proved most effective in attracting lamprey (344/395, attraction efficiency AE: 87.1%), the tiled route was visited least frequently (172/395, AE: 43.5%; *Table* **1**). No lamprey were solely detected at the left-bank antennas (AE control left bank - channel-side route [#8]: 248/395 [62.8%]; AE control left bank - bankside route [#9]: 229/395 [58.0%]). Total number of attempts made at the tiled route was relatively low (n = 473) but high at the turbine tailrace (n = 2486) and especially high at the SAB fishway (n = 9852; *Table* **1**). Out of 363 lamprey recorded, 156 were first detected at the turbine tailrace, followed by 91 at the fishway (*Table* **1**). First-time detections of tagged lamprey were lowest at both the left-bank control antennas and the upstream exit of the tiled route (n = 29, n = 15 and n = 2, respectively. The latter may represent fish that entered the tiled route part way up the weir apron, and so were not detected at the route entrance (which generates a conservative detection efficiency for the tiled route lower antenna of 42/44 [95.5%]). At the remaining two upstream antennas for particular routes [fishway upstream and right-bank control], no fish were detected without being first detected at the respective downstream antenna - 100% detection efficiency for each). Comparing the number of distinct attempts between the right (antennas #4 and #6) and left (antennas #8 and #9) bank weir face antennas, more lamprey attempts were recorded at the latter group (n = 1905 against n = 2863 attempts), but in both cases more detections occurred at the bank-side antennas, adjacent to the wing walls, than at the channel-side antennas (*Table* **1**). With the turbine tailrace and the fishway included, n = 14243 attempts were made at the right bank downstream antennas (four in all, *Figure* **3**), although detection rates varied markedly between them. Forty-four lamprey that entered the tiled route exited it at the upstream end (passage efficiency PE: 44/172 [25.6%]). By contrast, half that number successfully ascended the adjacent control route (PE: 22/257 [8.6%]; *Table* **1**), while the number of attempting individuals was higher. The PE for lamprey ascending the SAB fishway was just 1.5% (5/343, *Table* **1**).

Temporal variety in passage behaviour

A conservative estimate of migration delay, calculated as the duration from time of release of each lamprey to last detection at any antenna, amounted to (median [IQR]) 15.0 [7.4 - 21.4] days. Time taken to locate each route (n = 9) differed significantly between them (Kruskal Wallis H: $\chi^2(8)$ = 414.927, p < 0.001; *Table* **1**). Lamprey took longer to locate the treatment (tiled) route than to locate any of the other instrumented areas (*Table* **1,** Mann-Whitney U tests). Duration of ascent was different between the three routes where successful passage was recorded (fishway: mean [range] 24.3 [5.6 -

362.4] min; tiled route: 8.6 [2.1 - 55.8] min; right bank control route: 14.6 [9.3 - 48.5] min; Kruskal Wallis H: $\chi^2(2) = 274.152$, $p = 0.032$). While lamprey were able to find the fishway and tailrace entrances faster than the other instrumented areas, no difference in time taken to locate the fishway versus the tailrace was found (*Table* **1**). Time to first detection for each antenna was variable, with the lowest median time taken of 0.76 h for the turbine tailrace and highest median of 2.75 h for the antenna at the bottom of the tiled route. Of all lamprey detected at any antenna ($n = 363$), 322 (88.7%) were recorded within 24 h post-release (median [IQR] of time between release and first detection on any antenna for all lamprey detected: 2.09 [0.07 - 578.93] h).

Table **1**: Numbers of individual lamprey detected per route (and resultant attraction and passage efficiencies), number of first detections, total numbers of detections, body length (mm) of those detected and time taken (h) to locate downstream end of alternative routes (*n* = 6). Mann-Whitney U tests corrected for false discovery rate with post-hoc Benjamini-Hochberg procedure (significant differences [$\alpha = 0.05$]) were undertaken for time taken to locate route (last column) and are shown as superscript, whereby different letters indicate significant differences between the antennas.

Passage route and antenna identities (1-9)	No. of lamprey (efficiencies, AE and PE)		No. of first detections		Total no. of detections (standardised per m antenna width)		Body length of lamprey detected (mm; mean ± SD)		Time taken to locate specific route (h; median [range])
	attraction (AE)	passage (PE)	downstream	upstream	downstream	upstream	downstream	upstream	downstream
Tailrace (**1**)	344 (87.1%)	n/a	156 (43.0%)	n/a	2486 (385 m^{-1})	n/a	369.2 ± 21.4	n/a	0.76 [0.07 - 571.43][a]
Fishway (**2,3**)	343 (86.8%)	5 (1.5%)	91 (25.1%)	0 (0.0%)	9852 (3583 m^{-1})	6 (2 m^{-1})	369.1 ± 21.6	360.6 ± 13.2	0.86 [0.08 - 561.72][a]
Weir face - control (right bank) route (**4,5**)	257 (65.1%)	22 (8.6%)	41 (11.3%)	0 (0.0%)	1432 (1476 m^{-1})	48 (49 m^{-1})	369.4 ± 22.1	371.0 ± 21.2	1.92 [0.77 - 564.35][b]
Weir face - treatment (tiled) route (**6,7**)	172 (43.5%)	44 (25.6%)	29 (8.0%)	2 (0.6%)	473 (488 m^{-1})	59 (61 m^{-1})	370.7 ± 20.4	372.5 ± 24.2	2.75 [1.03 - 577.20][c]
Weir face - control (left bank - channel-side) route (**8**)	229 (58.0%)	n/a	15 (4.1%)	n/a	1208 (1245 m^{-1})	n/a	369.4 ± 21.7	n/a	2.33 [1.10 - 546.11][d]
Weir face - control (left bank - bankside) route (**9**)	248 (62.8%)	n/a	29 (8.0%)	n/a	1655 (1706 m^{-1})	n/a	370.1 ± 21.7	n/a	2.38 [1.08 - 558.93][d]

Body length effect

There was no difference in body length between river lamprey released among the 10 batches (Kruskal Wallis H: $\chi^2(9) = 8.435$, $p = 0.491$). Lamprey detected at each of the nine PIT antennas were similar in length, except for those at the upstream exit of the SAB fishway, which were slightly smaller (Kruskal Wallis H: $\chi^2(8) = 15.174$, $p = 0.041$; *Table* **1**). Lamprey that successfully ascended the tiled ($n = 44$) or the right-bank control route ($n = 22$) were of similar body length to all lamprey released (Mann-Whitney U: $U = 7581$, $p = 0.165$; $U = 4041$, $p = 0.581$, respectively). However, the total number of detections at all antennas per lamprey (including lamprey which were never detected at any antenna, $n = 32$) was positively but weakly correlated with body length (Spearman's rho: $\rho_s(395) = 0.101$, $p = 0.049$). Only counting those lamprey which were detected at least once on any antenna ($n = 363$), no significant correlation was found ($\rho_s(363) = 0.078$, $p = 0.141$). Undetected lamprey were not significantly different in length from those detected (Independent samples t-test: $t(393) = -1.376$, $p = 0.176$).

Turbine operation effect

When the turbine was operating, most detections were logged at the downstream entrance of the fishway (2976/4190 [71.0% of total attempts under turbine-on condition]), while, under the same turbine condition, only 82 attempts (2.0%) were logged at the tiled route downstream entrance (*Figure* **4**). A higher number of detections were recorded at the downstream end of the neighbouring control route during turbine-on ($n = 259$ [6.2%]). Lamprey were attracted towards the right half of the channel when the turbine was running, as only $n = 88/4190$ (2.1% of total attempts when turbine on) detections were made at the two left-bank control antennas in the turbine-on condition, compared to 2775/13029 (21.3%) at the same two antennas when the turbine was off. The number of lamprey detected at each antenna and attempts per lamprey was higher in the turbine-off condition (*Table* **2**; Wilcoxon signed rank test: $Z = -2.407$, $p = 0.016$ and $Z = -2.240$, $p = 0.025$, respectively. Detection range efficiency tests showed no difference between the turbine on/off condition). Fewer PIT detections were logged at the turbine tailrace and fishway entrance, respectively, when the turbine was on ($n = 770$ and $n = 2976$; median [range] river flow turbine-on: 18.7 [10.5 - 36.3] $m^3\,s^{-1}$) compared to off ($n = 1716$ and $n = 6876$; flow: 36.2 [10.4 - 52.3] $m^3\,s^{-1}$; *Table* **2**). While water temperature was not different between the turbine operating conditions (on/off; $Z = -0.330$, $p = 0.741$), river flow was lower when the turbine was running than when it was not (median [range] river flow turbine-on: 18.7 [10.5 - 36.3] $m^3\,s^{-1}$, turbine-off flow: 36.2 [10.4 - 52.3] $m^3\,s^{-1}$, $Z = -28.678$, $p < 0.001$).

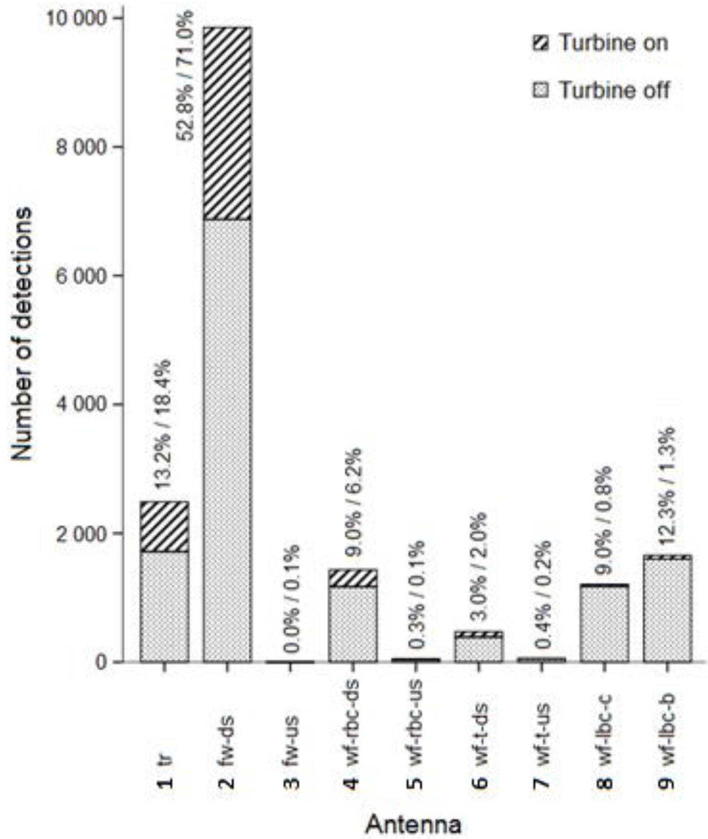

Figure **4**: Total number of detections logged at each of the PIT antennas (*n* = 9) under 'turbine off ' (shaded columns) and 'turbine on' (striped diagonal columns) conditions. Proportion of total attempts under turbine off / on conditions is shown on top / under the stacked column. tr: tailrace; fw-us/ds: fishway upstream/downstream; wf-lbc-b: weir face left-bank control bank-side; wf-lbc-c: weir face left-bank control channel-side; wf-t-us/ds: weir face tiled upstream/downstream; wf-rbc-us/ds: weir face right-bank control upstream/downstream. Numbers below antennas correspond to antenna locations as shown in *Figure* **3**.

Table **2**: Number of lamprey and attempts detected at each antenna (*n* = 9), separated for when the turbine was on / off. Abbreviations, wf-rbc-us/ds: weir face right-bank control upstream/downstream ; wf-t-us/ds: weir face tiled upstream/downstream; wf-lbc-c: weir face left-bank control channel-side; wf-lbc-b: weir face left-bank control bank-side; fw-ds: fishway downstream.

	No. of different lamprey detected, first time of detection on any antenna		Total no. of attempts		No. of lamprey detected		Mean no. of attempts per lamprey	
	turbine on	turbine off	turbine on	turbine off	turbine on	turbine off	turbine on	turbine off
wf-rbc-ds	9	32	259	1173	85	232	3.0	5.1
wf-rbc-us	0	0	3	45	3	22	1.0	2.0
wf-t-ds	11	18	82	391	50	150	1.6	2.6
wf-t-us	2	0	9	50	9	39	1.0	1.3
wf-lbc-c	1	14	32	1176	21	225	1.5	5.2
wf-lbc-b	8	21	56	1599	26	240	2.2	6.7
fw-ds	19	72	2976	6876	137	322	21.7	21.4
fw-us	0	0	3	3	3	3	1.0	1.0
tr	73	83	770	1716	156	300	4.9	5.7

Effects of environmental conditions

Lamprey were logged as having ascended the tiled route under high flow conditions only (median [range] Q values: Q_7 [Q_4 - Q_{17}], flow mean ± SD: 44.43 ± 8.85 $m^3 s^{-1}$; over the whole study period: Q_{23} [Q_4 - Q_{55}], 26.02 ± 13.25 $m^3 s^{-1}$). Of all the individuals that passed the weir using the tile route (*n* = 44), 29 (65.9%) did so on 22 November 2017, which coincides with the first high flow event recorded during the study period (*Figure* **5**). Lamprey were detected at the tailrace and fishway entrances under a wide variety of flow conditions (median [range] Q values: Q_8 [Q_4 - Q_{55}], flow mean ± SD: 36.13 ± 11.85 $m^3 s^{-1}$ for the tailrace and Q_8 [Q_4 - Q_{55}], 37.11 ± 10.65 $m^3 s^{-1}$ for the fishway, respectively). Out of all release days, lowest mean daily flow ($m^3 s^{-1}$) was recorded for batch #5 (19 Nov; 11.3 $m^3 s^{-1}$, Q_{55}), while highest mean release day flow was on 01 Dec (batch #10; 49.8 $m^3 s^{-1}$, Q_4; *Figure* **5**). Tested separately, there was an effect of river flow but not water temperature (mean ± SD over the whole study period: 5.61 ± 1.66 °C) on daily number of detections totalled for all antennas, excluding release days (ANOVA: $F_{1,43}$ = 13.706, p = 0.001 and $F_{1,43}$ = 2.448, p = 0.125, respectively). Considered together, river flow and water temperature had a positive effect on number of detections (multivariate mixed models: $F_{2,43}$ = 18.169, p = 0.008). Nearly all (321/363 - 88.4%) first detections of tagged lamprey were made from the start of the study until 2 days after the last release (08 Nov until 03 Dec - 60.5% of the study period), after which (04 Dec - 20 Dec - 39.5% of the study period) few new lamprey (*n* = 42/363 - 11.6%) were detected at any antenna (*Figure* **5**).

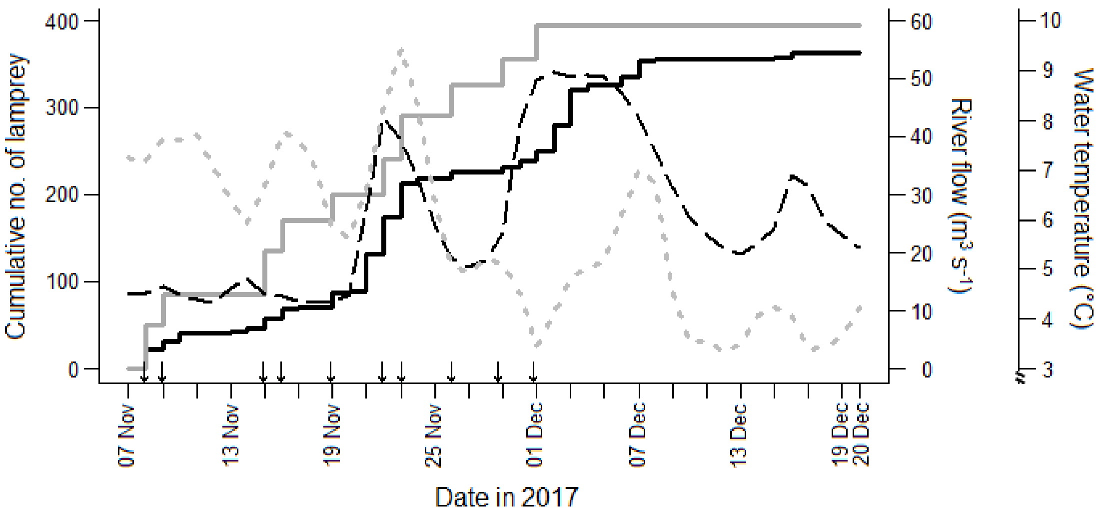

Figure **5**: Cumulative number of lamprey released (solid grey) and detected (solid black, both left-side y-axis) at any antenna, river flow ($m^3 s^{-1}$; dashed black; inner right y-axis) and water temperature (°C; dotted grey; outer right y-axis). Arrows indicate time of release on respective dates.

Diel activity

The greatest number of passage attempts in one hour of the daily cycle totalled for all antennas (*n* = 1101/17219 - 6.3%), were recorded just after dusk (18:00 - 19:00), while the least number of visits to the antennas in one hour (*n* = 361 - 2.1%) occurred in the early morning (06:00 - 07:00; *Figure* **6**). Between 16:00 and 20:00 (16.7% of diel time period) was the most active time for lamprey with 22.4% of all attempts (*n* = 3863/17219) recorded during this period. Calculated for the longest duration of daytime during the study (06:40, 16:53 [10 h 12 min daylight]), *n* = 9196 (53.4%) recordings were made during night time. As is also evident from *Figure* **4** and *Table* **1**, lamprey most frequently visited the fishway and tailrace (*Figure* **6**).

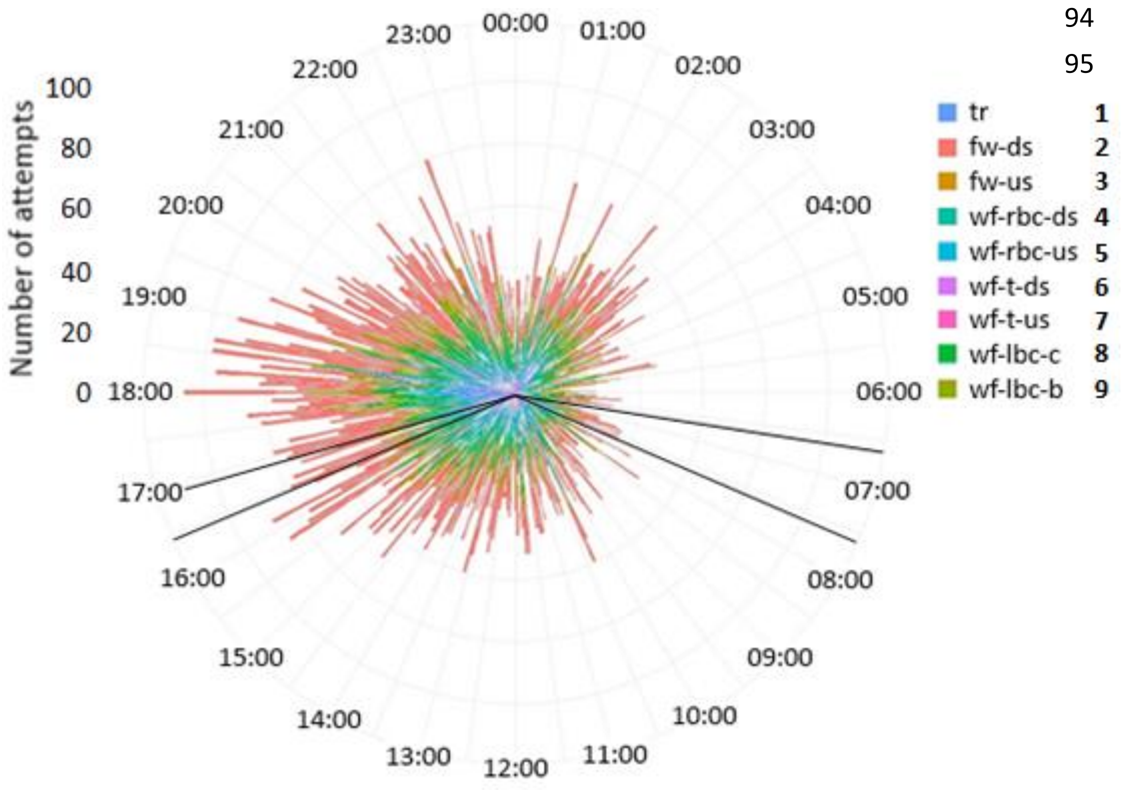

Figure **6**: Total number of attempts (stacked) for all detected lamprey at each of the PIT antennas (*n* = 9) in relation to time of day. Morning and evening civil twilight times (06:40 to 16:53 at study start, 07:36 to 16:26 at study end) at Buttercrambe are indicated by black lines. fw-ds/us: fishway downstream/upstream; wf-lbc-b: weir face left-bank control bank-side; wf-lbc-c: weir face left-bank control channel-side; wf-rbc-ds/us: weir face right-bank control downstream/upstream; tr: tailrace; wf-t-ds/us: weir face tiled downstream/upstream. Numbers next to antennas correspond to antenna locations as shown in *Figure* **3**.

Discussion

This study found that the studded tile route exhibited a threefold increase in lamprey passage efficiency when compared with a neighbouring bare weir face route of equal dimensions and gradient (25.6% against 8.6%). This was hypothesized, although passage over the weir using the studded tiled route occurred predominantly at high river discharge. Comparing the efficiency of horizontally versus vertically aligned tiles, the former arrangement was more effective (PE: 25.6% against 7.1%) in passing lamprey, although vertical tiles were situated in the SAB fishway in Tummers *et al.* (2016) while the horizontal alignment was employed on the weir face in the current study. The tiles in the fishway were attached to the inner right wing-wall, had studs facing horizontally towards the wall, and were identical single-density modular plastic tiles (Tummers *et al*., 2016). Under the conditions of the current study the studded tile media was easier to pass at high discharge, possibly due to greater water depth over the medium.

This study highlights the effect of attraction flow and discharge on lamprey behaviour. Tile passage efficiency was marginally higher than recorded in the study of a *ca*. 0.3 m head experimental Crump weir under laboratory conditions for dual-density, horizontally mounted, tiles (25.6% against 22.0% passage efficiency [Vowles *et al*., 2017]). It is probable that moving the studded tiles to a position directly adjacent to the wing wall, and increasing the width of cover would increase overall attempt rates and passage efficiency, and this needs to be tested in the field. It should be noted that the passage efficiency achieved in this study (25.6%) is still inadequate in the context of the recommended 90-100% passage efficiency target per barrier to maintain viable diadromous populations as suggested by Lucas and Baras (2001). Wilkes *et al.* (2018) have pointed out that passage targets need to consider several measures, including habitat availability above and below barriers, as well as demographic modelling. Lamprey are semelparous, so that lifetime fitness is zero for any that fail to reach spawning habitat and reproduce, and in the Derwent over 99% of lamprey spawning habitat occurs upstream of the study site and over 98% of spawning habitat occurs beyond a further two barriers upstream of the study site (Lucas *et al*., 2009). Thus, in this instance, upstream passage targets exceeding 90% per barrier are appropriate. The consistently low PE of the unmodified SAB fishway before (0.3%, Tummers *et al*., 2016) and after (1.5%, this study) operation of an adjacent microhydropower plant supports the view that SABs are inappropriate for achieving upstream river lamprey passage and should not be adopted as passage solutions for river lamprey. By contrast, Pereira *et al*. (2017) found a vertical slot fishway to be moderately efficient (31% overall passage efficiency) for sea lamprey (*Petromyzon marinus*) adult ascent and facilitated rapid repopulation of the upstream reach which had plentiful spawning and larval habitat. It remains our view (see Foulds and Lucas, 2013) that appropriately designed nature-like and deep vertical slot fishways remain the best options, resources dependent, for efficient river lamprey passage at low-head freshwater obstacles that cannot be removed. Because SABs are cheaper, more easily retrofitted and take up less space than vertical slot and nature-like fishways, the current ‘design standard’ trend in the UK to facilitate lamprey passage at barriers that cannot be removed or lowered involves modification with studded tiles. These tiles can be installed horizontally or obliquely mounted within an SAB fishway; in a separate, walled eel-lamprey channel; or on a sloping weir face (where these exist). Yet no studies have been carried out to determine whether horizontally/obliquely mounted tiles within such eel-lamprey channels, or in SAB fishways, can provide an effective passage solution for lampreys. Such tests are needed urgently.

Despite relatively high attraction efficiency (86.8%, measured as in Tummers *et al.* [2016] or 343/363 = 94.5% if the sum of all fish detected on downstream antennas is used to determine ‘available’ fish instead of from the number of lamprey released [*n* = 395]), the SAB fishway in this study passed river lamprey extremely poorly, as only 1.5% of lamprey that attempted to ascend it successfully did so. To develop effective fishways, it is important to understand fish responses to environmental cues, of which current velocity and direction are often major factors (Castro-Santos *et al*., 2009). Lamprey exhibit strong thigmotactic behaviour (Keefer *et al*., 2011; Kemp *et al*., 2011) with a preferred position in the water column near the bed (Silva *et al*., 2017) and edge, and are effective in utilising areas with lower flow velocity (Moser *et al.*, 2015). Indeed, individual lamprey were, over the course of the whole study period, most often attracted towards the fishway and the turbine tailrace (near right bank), and least towards the tiled route (positioned more mid-channel) and the channel-orientated left hand control. When considering initial detections only, fewer lamprey were recorded at both the left-bank control antennas. In addition to thigmotaxis, river lamprey are strongly positively rheotactic (Kemp *et al*., 2011; Tummers *et al*., 2016) and attracted towards local areas of high current velocity (Tuunainen *et al*., 1980; Foulds and Lucas, 2013). These conditions occurred predominantly near the right bank, below the turbine tailrace and fishway entrances (J. Kerr and J. Tummers, *unpubl. data* from Acoustic Doppler Current Profiler). This flow effect was also evident when the turbine was running compared to when not, since lamprey activity was clearly biased towards the right bank (turbine outflow) on those days compared to a somewhat more equitable distribution when the flow was spread more evenly across the channel. This finding is in agreement with our hypothesis that a higher lamprey attempt rate was expected at the antennas closer to the turbine house when the turbine was in operation. Such effects of turbine management at low-head dams on fish behaviour approaching obstacles are important and require consideration in terms of fish passage management (Piper *et al*., 2018; Silva *et al*., 2018). Generally it is considered normal to locate a fishway entrance adjacent to a turbine tailrace or other bulk water source to enhance attraction for rheotactic fish such as salmon (Dodd *et al*., 2018). While this worked for lamprey, it resulted in them spending most time in localities where they had no passage option (tailrace) or where passage was extremely poor (SAB fishway), rather than locating the tiled passage route (albeit a route of smaller dimensions).

Lamprey might not be able to remain within narrow (*ca*. 1 m) strips of studded tile medium during ascent as forward movement by fish, including lamprey, is rarely a direct, straight-line phenomenon. Breakage in the longitudinal continuity of studded media is also likely to increase the probability of passage failure, so retrofitting of weir surfaces needs to account for possible loss of, tiles by introducing redundancy in the coverage with tiles across the weir. In this study all tiles remained in place and functional for the study duration. To maximize attraction and passage of river lamprey at small sloping weirs, the entire surface should be tiled, but for large weirs this may not be economically or logistically practicable. This study shows that the zones adjacent to the wing walls are preferred by lamprey, and so should be prioritised for modification with studded tiles, provided alternative passage routes (e.g. technical fishway) are available for fusiform fish. It would be preferable to modify areas several metres wide adjacent to each bank. If flow dominates on one side of the channel, that is the priority side for modification with studded tiles, to facilitate lamprey attraction and passage. However, if the relative proportion of flow across the channel alters periodically at a given site, for example due to periodic hydropower operation, then modification on both sides of the weir is likely to be more effective, and offers redundancy.

Higher detection rates of PIT tagged lamprey occurred at high flows. River flow was moderate (Q_{55} - Q_{45}) for parts of the study period (for example, from 08 Nov to 12 Nov (5/43 days [11.6%]). Under these conditions it is possible lamprey may not have been motivated to migrate upstream post-release and attempt to traverse the weir (Kemp *et al*., 2011; Foulds and Lucas, 2013; Tummers *et al*., 2016). From an evolutionary perspective, migrating under predominantly high flow and/or night time conditions (as found in the current study, which is consistent with results of diel activity in Tummers *et al*., 2016) may increase chances of survival and thus of successful spawning as risk of predation is lower (Álvarez and Nicieza, 2003; Furey *et al*. 2016). Under low to moderate flow conditions, lamprey may have had difficulties getting onto the weir face, and / or moving over or between the studs of the tiles. While no lamprey were first detected at the upstream exit of the right-bank control route nor at the fishway exit, there were two first-time detections at the tiled route weir-crest. These occurred on 22 and 23 Nov, at river flows of 43.2 and 39.1 $m^3 s^{-1}$ (Q_7 and Q_8 annual exceedance, respectively), when the weir was nearly submerged (head of *ca.* 0.10 m; J. Tummers, *pers*. *obs*.). Under flooded conditions in a flume, Kerr *et al*. (2015) reported high passage efficiency (PE: 100.0%), short delay, and low number of attempts before successful passage of adult river lamprey over an unmodified experimental Crump weir. When head difference was at its highest (0.23 m), high flow velocity (2.4 m s^{-1}) and downstream turbulence completely impeded lamprey from passing the experimental Crump weir. In the current study, flow velocities over the weir during high head (low water levels) were comparable to this experimental high head scenario (J. Tummers, *pers. obv*.) and likely prevented lamprey from passing the weir outside of the tiled route.

While Russon and Kemp (2011) recorded river lamprey achieving short burst swimming speeds of between 1.75 and 2.12 m s^{-1}, these lasted only a few seconds and were under relatively high water temperature conditions (mean ± SE: 15.10 ± 0.32 °C). Since maximum attainable swimming speeds are generally positively correlated with water temperature within the thermal tolerance range of a fish (Wardle, 1980; Videler and Wardle, 1991), maximum swimming speeds in the current study, at much lower water temperature (for whole study period: 5.6 ± 1.7 °C), are likely to have been considerably lower.

Within the studded tiled route, the formation of regions of reduced flow velocity by the studded tiles may have facilitated passage in the current study. Furthermore, altered micro-hydraulic conditions between the studs may have facilitated river lamprey resting opportunities in between burst swimming. When attached onto the tiled substrate with their oral disc (Quintella *et al*., 2004; Vowles *et al*., 2017), keeping the body mostly in between the studs, less drag is likely to be created on the lamprey body compared to attaching onto bare concrete, which may have allowed exhibition of repeat burst-attach-rest behaviour that enables lamprey to more effectively ascend the weir. Duration of ascent was different between the three routes where successful passage occurred, with a lower mean duration recorded for the tiled route than the right-hand bare weir face route and fishway. The change from vertically to horizontally oriented tiles (*cf.* Tummers *et al*., 2016) may have facilitated lamprey ascent by reducing drag on the lamprey body and assisting energy efficient and supported (as direction of locomotion is parallel to tile orientation for horizontally mounted tiles) attachment to the tiled substrate, enabling more effective recovery.

Although an increase in passage efficiency was achieved due to installation of horizontally-mounted studded tiles, PE remained low and might have been a result of the size, spacing and relative positioning of the studs on the tiles. This is not least because mesocosm studies with a studded tile ramp at a similar head to that encountered in this study have recorded close to 100% passage of Great Lakes sea lamprey attempting ascent (J. Hume, Michigan State University, *pers. comm.*). In the present study flow velocity may have been reduced by the studded tiles in the treatment route, thereby dissipating energy in the water column (as demonstrated for the bottom baffles in a SAB fishway [Larinier *et al*., 2002]); turbulence on top of and in between the studs may be higher as a result, but will be influenced by stud spacing, size and water flow. It has been shown that for Pacific lamprey, the transition from attachment to resuming upstream swimming proves difficult under turbulent conditions; lamprey were often unable to re-attach and were swept downstream (Keefer *et al*., 2010).

For river lamprey, similar fallback was observed within a Denil baffle fishway (W. Foulds, Durham University, *pers*. *comm*.). In a flume study, no effect of local turbulence on passage success of river lamprey was found (Vowles, 2012), although simplified, single-source localised turbulence was used. Those conditions are not comparable to the ones around studded tiles or in a baffle fishway as observed in the current study (J. Tummers, *pers*. *obs*.). In a flume study, only *ca*. 50% of the river lamprey adopted a burst-attach-rest behaviour when ascending a downstream Crump weir face (although shorter than the length of the weir face in the current study) modified with studded tiles (Vowles *et al*., 2017). Unlike eel, river lamprey burst swam over the horizontally installed tiles more often than weaving between the studs, attaching on to the tiles when fatigue set in. The cumulative effect of the length of the weir face in the current study, with multiple consecutive tiles present, is likely to hinder upstream traversal for anguilliform morphotype fish like river lamprey, which lack stabilizing paired fins (Liao, 2007).

Conclusions

Reduced longitudinal connectivity is likely to have played a major role in the decades-long decline of populations of anguilliform morphotypes like river lamprey (Lucas *et al*., 2009; Mateus *et al*., 2012; Aronsuu *et al.*, 2015). Although barrier removal is likely to be most effective in reconnecting impounded rivers (Kemp and O'Hanley, 2010), and is gaining popularity rapidly in river restoration programmes (Bednarek, 2001; Hart *et al*., 2002; Bernhardt *et al*., 2005), this approach is often difficult to realise, especially in urban areas, because of economic, historical, societal or political constraints (O'Hanley and Tomberlin, 2005). Despite a growing use of studded tiles (fixed either horizontally on the weir face with upward facing studs, vertically with studs protruding towards the channel wall, or set within a specific eel-lamprey channel; Armstrong *et al*., 2010; Vowles *et al*., 2015) and construction of fishways (Prato *et al*., 2011) to improve passage for anguilliform morphotypes (Nunn and Cowx, 2012), quantitative evidence on their performance is rare. While this study provides evidence that studded tiles mounted horizontally on a common sloping weir design had a higher passage efficiency compared to an adjacent control route (25.6% against 8.6%, respectively), further research on lampreys with different life histories and body sizes, and under a greater variety of environmental conditions, is needed to determine the degree to which this approach can provide sufficient passage to reverse the historic population declines of these species. Further research is also needed to determine optimal stud size and spacing, and flow provision to tiled substrates, to determine optimal arrangements for lamprey passage.

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