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RESEARCH ARTICLE

River connectivity restoration for upstream-migrating European river lamprey: The efficacy of two horizontally-mounted studded tile designs

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Abstract

Many rivers are heavily fragmented, resulting from anthropogenic cross-channel structures. Cost-effective solutions are needed to restore habitat connectivity for migratory fishes, including those of conservation concern, such as the European river lamprey (*Lampetra fluviatilis*). Studded material is becoming increasingly used as a low-cost retrofit solution for lamprey passage at sloping weirs, although little is known about the efficacy of the material or what stud arrangements may be most effective. This study tested whether expanding a single-density studded tile (SDT) lane from 1 to 2-m width increased passage success (n_{released} = 133), and also compared the passage performance between a SDT lane and a dual-density studded tile (DDT) lane (n_{released} = 115) at a sloping weir, using PIT telemetry. No passage was recorded ($n_{\text{attempted}}$ = 89) at the 2-m wide SDT lane, but 61.6% ($n_{\text{passed/attempted}}$ = 53/86) passed using DDT/SDT lane combination. However, increased passage efficiency was likely a result of high river flow (Q2.0-Q30.6) during DDT/SDT comparison versus low (Q8.3-Q88.5) while the 2-m wide SDT lane was employed. There was no evidence that passage occurred using solely one stud configuration. It is, therefore, hypothesised that passage of river lamprey at weirs is more dependent on flow regime than the provision of either stud configuration. However, with 46.1% ($n_{\text{passed/released}}$ = 53/115) of those released during DDT/SDT comparison passing on the instrumented section (10.5% of weir face), the provision of studded tiles may aid in lamprey passage at high flows, presumably as the tiles generate a low-velocity boundary layer that can be utilised as lamprey swim above the studs.

KEYWORDS

fish passage, *Lampetra fluviatilis*, longitudinal connectivity, migration, river restoration, telemetry

1 | INTRODUCTION

River fragmentation has led to large declines in the abundance of many aquatic species (Richter, Braun, Mendelson, & Master, 1997). A major contributor to fragmentation within riverine habitats is the construction of cross-channel structures, such as dams and weirs (Rosenberg, McCully, & Pringle, 2000). These have been largely installed and maintained for societal reasons, including for hydropower generation, gauging river height, for irrigation and the creation of reservoirs for water supply to urban areas. Their presence as cross-channel structures alters river morphology and hinders the natural movement of aquatic fauna (Radinger & Wolter, 2015; Reidy-Liermann, Nilsson, Robertson, & Ng, 2012).

To restore river longitudinal connectivity for migrating and dispersing fishes, the optimal approach is to remove the barrier altogether (Birnie-Gauvin, Aarestrup, Riis, Jepsen, & Koed, 2017). However, this is often not possible for societal reasons, and fishways are increasingly installed to enable fish movements whilst still maintaining the function of the structure (Silva et al., 2018). Many fishway designs are costly and vary in their effectiveness at both attracting and passing target and non-target fish species (Bunt, Castro-Santos, & Haro, 2012; Noonan, Grant, & Jackson, 2012). Therefore, more cost-effective solutions are being explored.

Research into the use of studded and bristle substrates as a low-cost solution for fish passage, to be retrofitted to sloping weirs or installed on ramps, has increased globally (Baker & Boubee, 2006; Kerr, Karageorgopoulous, & Kemp, 2015; Montali-Ashworth, Vowles, de Almeida, & Kemp, 2020; Rooney, Wightman, O'Conchuir, & King, 2015; Tummers, Kerr, O'Brien, Kemp, & Lucas, 2018; Vowles, Don, Karageorgopoulous, & Kemp, 2017). They are designed to disturb the flow of water and to provide a physical structure in the form of studs/bristles for fish, particularly those with anguilliform movement, to use as lateral body support and afford forward propulsion through pushing-off the studs/bristles (D'Aguiar, 2011; Rooney et al., 2015). As such, horizontally-mounted studded tiles (where tiles are mounted flat so that the studs point upwards) are being increasingly recommended as either a mitigation measure for Petromyzontiformes passage at weirs (Rooney et al., 2015; Tummers et al., 2018; Vowles et al., 2017) or for selective removal of invasive Great Lakes sea lamprey (*Petromyzon marinus*; Hume, Lucas, Reinhardt, Hrodey, & Wagner, 2020). Nevertheless there remains limited knowledge regarding the efficacy of studded media, including the optimal configuration, size and spacing of studs for target species. The utility of studded ramps to restore habitat connectivity for European river lamprey (*Lampetra fluviatilis*; hereafter referred to as river lamprey) has rarely been tested and remains poorly understood (Tummers et al., 2018; Vowles et al., 2017). River lamprey and sea lamprey are of conservation importance in several countries (Lucas et al., 2020). In Europe, under the EU Habitats and Species Directive, these species are designated conservation features for many Natura 2000 protected areas (Special Areas of Conservation [SACs] in the United Kingdom and Ireland). Provision of adequate migration passage solutions for native migratory lampreys is, therefore, a global priority in lamprey conservation (Lucas et al., 2020).

Field trials using single-density studded tiles (SDTs; Figure 1a) suggested they were moderately effective for passing sub-adult river lamprey at a sloping weir (passage efficiency, 25.6%; Tummers et al., 2018), when compared to an adjacent non-tiled control section of the weir and a Larinier fishway (passage efficiency of 8.6 and 1.5%, respectively). However, for a semelparous, migratory species, as all lampreys are, this is an inadequate passage efficiency (a passage efficiency target exceeding 90% has been recommended for native diadromous fishes including lampreys; Lucas & Baras, 2001; Lucas, Bubb, Jang, Ha, & Masters, 2009). As a result, Tummers et al. (2018) recommended increasing the contiguous area, and proportion, of weir face covered by studded tiles, with the expectation that overall passage rates would be increased through (a) greater access opportunity, and/or (b) greater lateral continuity of the passage route. In comparison, observations during laboratory trials of dual-density studded tiles (DDTs; Figure 1b), originally designed to facilitate upstream European eel (*Anguilla anguilla*) passage when vertically-mounted (where tiles are mounted on their side with the studded surface directed sideways, often towards and against another surface such as a wall), showed a 14.1–23.9% passage efficiency for river lamprey under varying flow conditions at a model sloping weir when horizontally-mounted (Vowles et al., 2017). Although this is lower than the passage efficiency observed by Tummers et al. (2018) for SDTs, DDTs have not been tested in the field. Along with this, recent research from Hume et al. (2020) using a similar quincunx "5-dice" stud configuration in a mesocosm experiment, but with greater stud spacing for larger Great Lakes sea lamprey, demonstrated approximately 98% passage efficiency. Therefore, field-based assessment of different stud configurations, including DDTs, is needed, as there may be potential for DDTs to provide a more effective passage option for river lamprey at sloping weirs under field conditions.

The aims of this study were to (a) quantify river lamprey passage after expanding a SDT lane at a sloping weir from 1 to 2-m wide as suggested by Tummers et al. (2018), and (b) compare the efficacy of two available studded tile designs (DDT and SDT) at enabling river lamprey to pass upstream of the weir by replacing a 1-m wide section of the SDT tile lane with a 1-m wide DDT lane at a sloping weir (thereby creating two adjacent lanes of different tile designs). Our hypotheses were that (a) more river lamprey would be detected succeeding in passage as a result of increasing the width of SDT substrate available, and (b) more river lamprey would succeed in passing the weir using the DDT lane rather than the SDT lane, reflecting differences in sensitivity to alternative stud configurations.

2 | METHODS

2.1 | Study site

The study, conducted between October 30, 2018 and January 24, 2019 (2018 study year) and October 30, 2019 and January 24, 2020 (2019 study year), was carried out at Buttercrambe gauging weir (Latitude: 54.018884, Longitude: −0.885329; Figure 2) on the

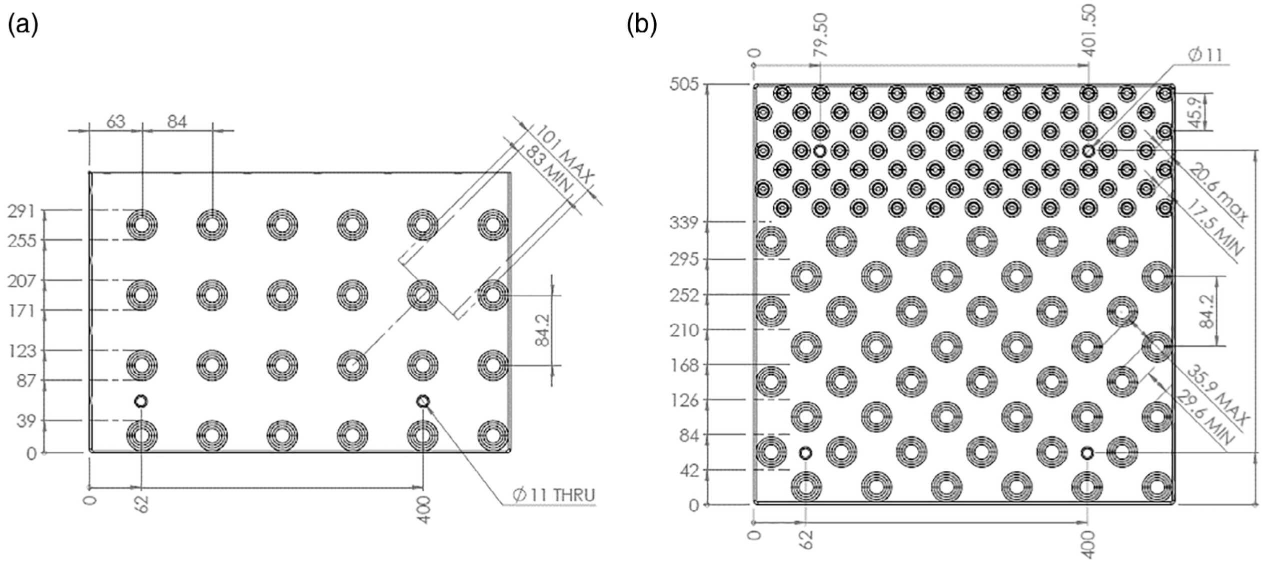

FIGURE 1 Top-view of the single-density studded tile (SDT; a) and the dual-density studded tile (DDT; b) designs (diagrams obtained from https://www.berryescott.co.uk/wp-content/uploads/2016/08/lamprey-tile-drawing.png and https://www.berryescott.co.uk/wp-content/uploads/2016/08/eel-tile-drawing1.png, respectively). Studs are represented by filled in circles. Values on figure are given in mm

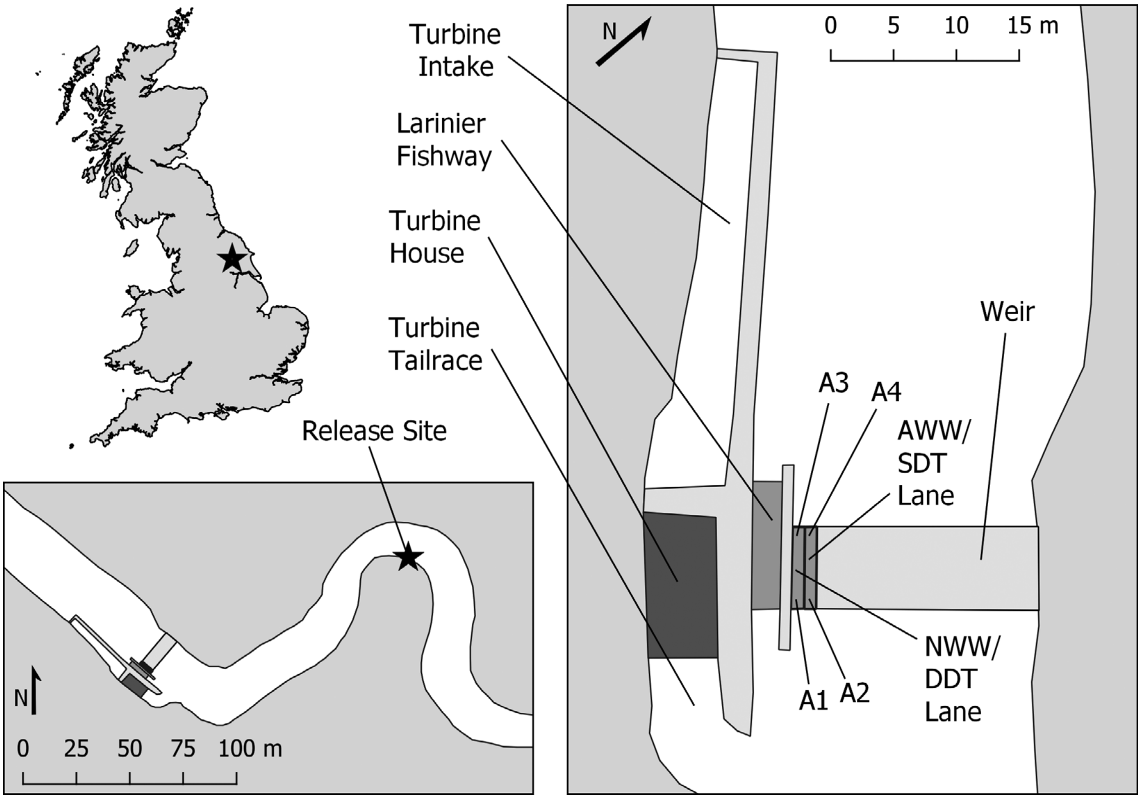

FIGURE 2 Map of the study site at Buttercrambe gauging weir. Antennas (A1-A4) are shown on the Near Wing-Wall (NWW)/dual-density studded tile (DDT) lane and the Away from Wing-Wall (AWW)/single-density studded tile (SDT) lane. The turbine intake is bounded by vertical screens to prevent entrainment of juvenile and adult river lamprey

River Derwent, a tributary of the Yorkshire Ouse, Humber River Basin, Northeast England. The autumn/winter season was chosen as it represents the main period of upstream migration by river lamprey in the Humber system (Foulds & Lucas, 2013; Lucas et al., 2009). River lamprey, and sea lamprey, are designated features of the Yorkshire Derwent SAC and the Humber SAC, but both areas are recorded as being in unfavourable condition for river and sea lamprey, largely due to barriers restricting their access to suitable habitat (Birnie-Gauvin et al., 2017).

Buttercrambe gauging weir is owned by the Environment Agency and was originally built for flow-gauging, but now provides a water head for Aldby Park hydropower plant which has been active since September 2017 (see Tummers et al., 2018). Over 98% of Derwent lamprey spawning habitat is upstream of Buttercrambe (Lucas et al., 2009). The weir design and use is typical of many of the sites where lamprey passage solutions are required, particularly in the United Kingdom. Buttercrambe gauging weir is a sloping weir (of Crump design) with a triangular profile. It is 19 m wide, and has a downstream weir face length of 6.0 m (gradient = 1:5) and an upstream weir face length of 1.8 m (gradient = 1:2). The downstream weir face is vertically truncated at its end. The weir has a mean daily flow of 16.9 m^3/s (Q34.6; over the period September 1973–January 2020), and drowns out (defined as the downstream gauged height exceeding that of the weir crest) at approximately 30.0 m^3/s (Q13.5).

Pre-existing fish passage infrastructure at Buttercrambe includes a Larinier fishway installed in May 2013 (Tummers et al., 2016) that is located between the weir and a turbine house (Figure 2), and a 1-m wide lane of SDTs installed in August 2017 that extended from 1 to 2 m from the wing-wall (Tummers et al., 2018).

2.2 | Tile lanes

Two studded tile designs were used in this study (Figure 1). The DDTs (identical to those described by Vowles et al., 2017; Berry and Escott Engineering, UK) measured 0.50 × 0.50 m and consisted of 48 large (spaced 55 mm on rows and 29 mm on diagonals at stud base) and 77 small (spaced 30 mm on rows and 17 mm on diagonals at stud base), 55 mm high, blunt-ended studs (Figure 1b). The small studs occupy approximately 33% of the tile, and the large studs approximately 67%. Each stud row is offset from the previous, resulting in a stud arrangement resembling a quincunx “5-dice” configuration. The size and spacing between the DDT studs was designed to fit the observed range of wavelengths from serpentine locomotion of juvenile European eel, and so modifications to the DDTs, suggested by the environmental regulator, were carried out to adapt the tiles for the larger river lamprey adults (Tummers et al., 2018). The SDTs (identical to those described by Tummers et al., 2018; Berry and Escott Engineering, UK) were created by removing the small studs and every second row of larger studs from the DDTs. As a results, the SDTs measured 0.50 × 0.34 m, with 24 large (spaced 68 mm on rows and 88 mm on diagonals at the stud base), 55 mm high, blunt ended studs (Figure 1a). This stud arrangement resembles a square “4-dice” configuration.

In summer 2018, a 1-m wide lane of SDTs was installed between the wing-wall adjacent to the Larinier fishway and the pre-existing, 1-m wide SDT lane (Figure 2). In doing so, a continuous lane of horizontally-mounted SDTs stretched for 2 m (10.5% of weir face width) from the right (when looking downstream) wing-wall and were available for use by river lamprey. The new 1-m wide SDT lane (0–1 m from the Larinier wing-wall) was designated the Near Wing-Wall (NWW) route, and the original SDT lane (1–2 m from the Larinier wing-wall) was designated the Away-from Wing-Wall (AWW) route (Figure 2). The tiles started 0.4 m upstream of the truncated downstream-edge of the weir face (the downstream water level is generally higher than the edge of the most downstream tile and so the start of the tile lanes would be submerged) and ended on the upstream-facing weir face to create a continuous lane across the weir crest that followed the change in angle either side of the weir crest.

In 2019, the 1-m wide lane of SDTs that comprised the NWW lane of the 2018 study period was replaced with DDTs (Figure 2), positioned so that the larger studs were adjacent to each other (i.e., small-large-large-small stud arrangement), thereby creating a continuous strip of the larger studs, and two strips of smaller studs either side of the DDT lane. The SDT lane which made-up the AWW lane in the 2018 study period was checked for damage, found to be undamaged and left in place, ensuring a continuous 2-m wide lane of horizontally-mounted studded tiles was maintained.

2.3 | Passive integrated transponder antenna array

Four flatbed, half-duplex (HDX) Passive Integrated Transponder (PIT) antennas (approximate dimensions of 0.35 × 0.97 m) constructed from two windings of 2.5 mm^2, 322 strand, braided, oxygen free, copper wire encased in an insulating PVC layer (FS Cables Ltd, England) were placed underneath the tiled lanes on the weir face to quantify passage performance. Two antennas were placed next to each other on adjacent tile lanes (A1: NWW/DDT; A2: AWW/SDT) approximately 0.7 m upstream from the foot of the weir face truncation, and two antennas on adjacent tile lanes (A3: NWW/DDT; A4: AWW/SDT) approximately 0.2 m downstream from the weir crest (Figure 2). Antennas were all connected to a single reader box (Oregon RFID, Oregon) with a four-port multiplexer which was synchronised to interrogate each antenna alternately to reduce interference due to their close proximity to one another (approximately 4 reads per second per antenna). The PIT antenna array was powered by a 110 Ah 12 V leisure battery that was trickle charged from 240 V mains power via a linear supply battery charger.

The PIT antennas were tested prior to river lamprey release, as well as during each site visit, by manually passing a PIT tag over the PIT antennas. The detection range was found to be approximately 0.3 m horizontal to the antenna plane (the normal orientation for tagged river lamprey swimming over the weir). Three of the four PIT antennas were operational throughout the 2018 study period. A1 suffered damage on December 19, 2018 and was subsequently not operational for the remainder of the 2018 study period (operational for 57.9% of the study period; A1 was repaired for the 2019 study period). However, the last time a river lamprey was detected on any antenna in the 2018 study period was January 2, 2019, suggesting that A1 was operational for 77.6% of the period with river lamprey movement, although there is a chance that river lamprey could have attempted passage again on A1 after this period and consequently not been detected. All PIT antennas were operational throughout the 2019 study period.

2.4 | River lamprey capture, transport and tagging

River lamprey were captured using a combination of Netlon and Apollo II type lamprey traps in the tidal Yorkshire Ouse, as a result of low catch per unit effort for river lamprey in the River Derwent (Jang & Lucas, 2005). This methodology has previously been shown not to affect subsequent post-release behaviour (Lucas et al., 2009) and Ouse/Derwent river lamprey are from the same population (Bracken, Hoelzel, Hume, & Lucas, 2015). Traps were checked weekly, and all river lamprey removed on a given day were placed in a sealed transport container (85 L bucket with clip-on lid, filled to approximately 50–60 L) with continuously aerated river water gathered from the Ouse. River lamprey were then transported to Buttercrambe (approximately 26 km by road; travel time approximately 30 min), for tagging and release. River lamprey were sedated in a solution of river water and buffered tricaine methanesulphonate (MS-222; 0.1 g/L) before being measured in length (mm) and weight (g). Individuals longer than 300 mm were selected for tagging. A HDX PIT tag (Oregon RFID, 3.65 × 32 mm, 0.8 g in air) was inserted into the body cavity via a 3–4 mm incision made on the ventral side of each river lamprey. Incisions were not closed using either sutures or glue. Previous laboratory studies by one of the authors adopting the tagging method described above found no PIT tag loss in a sample of 60 tagged lamprey over a period of 5 months (M. Lucas, unpublished). River lamprey were then placed in a container with aerated river water until they recovered from anaesthesia (approximately 1 hr) before being released approximately 150 m downstream of the weir (Figure 2). All procedures were conducted in accordance with the UK Scientific Procedures Act 2003 under a Home Office issued licence.

2.5 | Environmental data collection

Data for river discharge (m^3/s) and river height (m) from downstream of the weir were obtained directly from Buttercrambe gauging weir. Discharge was gauged every 15 min from an ultrasonic flow meter, and river height from an ultrasonic gauge approximately 2 m downstream from the weir. Historic daily mean discharge data were downloaded from the National River Flow Archive for Buttercrambe gauging weir for the period September 1973 to January 2020 in order to generate flow exceedance values (Q_x).

2.6 | Statistical analyses

The proportion of river lamprey attempting to pass the weir via the tiled lanes was calculated as the number of river lamprey detected on any PIT antenna divided by the total number of river lamprey released. Passage efficiency for each study year at the NWW or DDT route (2018/2019, respectively) and the AWW or SDT route (2018/2019, respectively) was calculated as the number of river lamprey that were detected on A3 or A4 divided by the number of attempting river lamprey detected on A1 or A2, respectively. For those which had completed passage of the weir and that were detected on A1/A2 before being detected on A3/A4, the time from first detection to passage (the time difference between the first detection on A1/A2 and the first detection on A3/A4) and the passage duration (the time difference between the last detection on A1/A2 and the first on A3/A4) was calculated.

The number of attempts made by a river lamprey, that was detected on A1/A2, until its first successful passage (first detection on A3/A4) was calculated. New attempts were considered to have been made if the time difference between two subsequent detections on A1/A2 was equal to or greater than 240 s. This was determined by calculating the time interval between all detections and identifying

TABLE 1 The number, length (mm) and weight (g) of river lamprey tagged per date, and the number of those tagged that were also detected attempting passage at the studded tile sections of Buttercrambe weir

Date	Number tagged	Length (mm; range)	Weight (g; range)	Number attempting passage
October 30, 2018	17	304–396	-	8
November 8, 2018	22	318–418	51–119	13
November 13, 2018	27	319–424	53–139	18
November 20, 2018	29	319–417	53–125	22
November 29, 2018	38	315–400	40–112	28
October 30, 2019	4	340–377	65–82	4
November 5, 2019	8	329–399	59–92	0
November 11, 2019	29	326–414	57–118	20
November 21, 2019	40	344–406	63–118	35
November 26, 2019	22	327–394	53–103	19
December 2, 2019	8	327–409	56–120	5
December 16, 2019	4	387–391	91–104	3
Total	248	304–424	40–125	175

the first interval where no detections occurred which was greater than 20 s (Castro-Santos & Perry, 2012). River lamprey that had been detected on A3/A4 before being detected on A1/A2 were not included as they had already succeeded in passing the weir.

The same criterion that a river lamprey had to have been detected on A1/A2 before A3/A4 was used to compare lane fidelity (i.e., detection only at antennas within one lane, suggesting a lamprey remained within a single lane, rather than switched between lanes) during passage. Lane fidelity identified whether a river lamprey had completed passage (first detection on A3/A4) on the same lane as it had begun its passage attempt on (last detection on A1/A2), or if it completed on the other lane. This provided an indication of lamprey preference for tile location (near to wing wall or further from wing wall) and design (SDT or DDT).

A Welch two sample *t* test was carried out to compare the lengths of river lamprey that had and had not attempted passage, and for those that had attempted and succeeded in passage. Chi-squared tests were carried out to compare: location of first detection; location of last detection for successful attempts; and the proportions of river lamprey attempting passage when the weir was and was not drowned out. Analysis of Variance (ANOVA) was carried out to compare river flows between the two study years. Wilcoxon rank sum test was used to compare the flows experienced at time of first attempt and time of passage success. All data investigation and analyses were performed in RStudio using R (v3.5.1; R Core Team, 2014).

3 | RESULTS

A total of 248 river lamprey (n_{2018} = 133; n_{2019} = 115) were tagged and released downstream of Buttercrambe weir (Table 1). The mean (±*SD*) length and weight of those released were 362 (±23) mm and

TABLE 2 The number of river lamprey that remained in or changed between tiled lanes during the first complete successful passage attempt during the 2019 study period. There were no successful passages during the 2018 study period

Lane at start of attempt	Lane at end of attempt	Number of lamprey
DDT	DDT	13
SDT	SDT	3
DDT	SDT	12
SDT	DDT	10

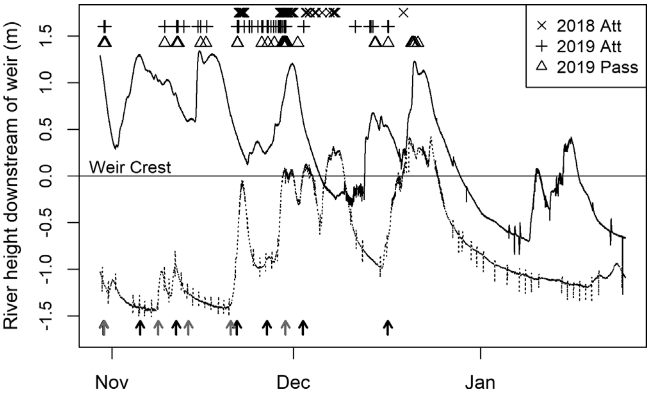

FIGURE 4 River lamprey passage attempts and successes in relation to the river height downstream of Buttercrambe weir, relative to the weir crest, during the 2018 study period (October 30, 2018 to January 24, 2019; dashed line) and the 2019 study period (October 30, 2019 to January 24, 2020; solid line). Crosses and pluses indicate first passage attempts by river lamprey released downstream in 2018 and 2019, respectively, and triangles indicate first successful passage in 2019. Grey and black arrows indicate times of river lamprey release in 2018 and 2019, respectively

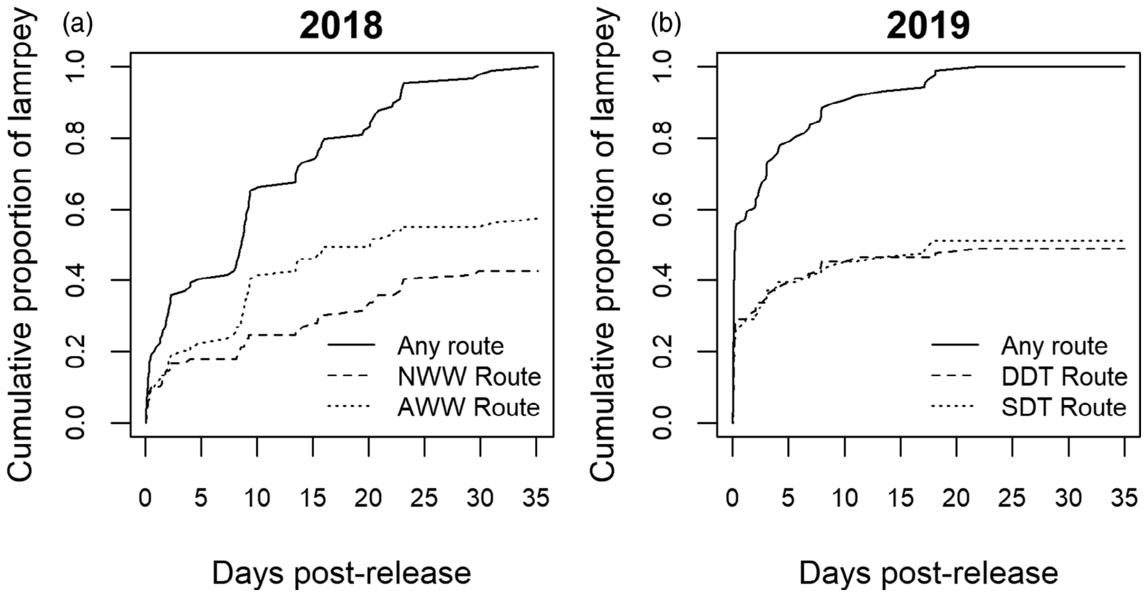

FIGURE 3 The cumulative proportion of the first detection of river lamprey that attempted passage of the weir via either studded tile route (solid line), and the cumulative proportion of river lamprey attempting passage that were first detected on either the Near Wing-Wall (NWW SDT, dashed line) route or Away-from Wing-Wall (AWW SDT, dotted line) route in 2018 (a), and on either the dual-density studded tile (NWW DDT, dashed line) route or the single-density studded tile (AWW SDT, dotted line) route in 2019 (b)

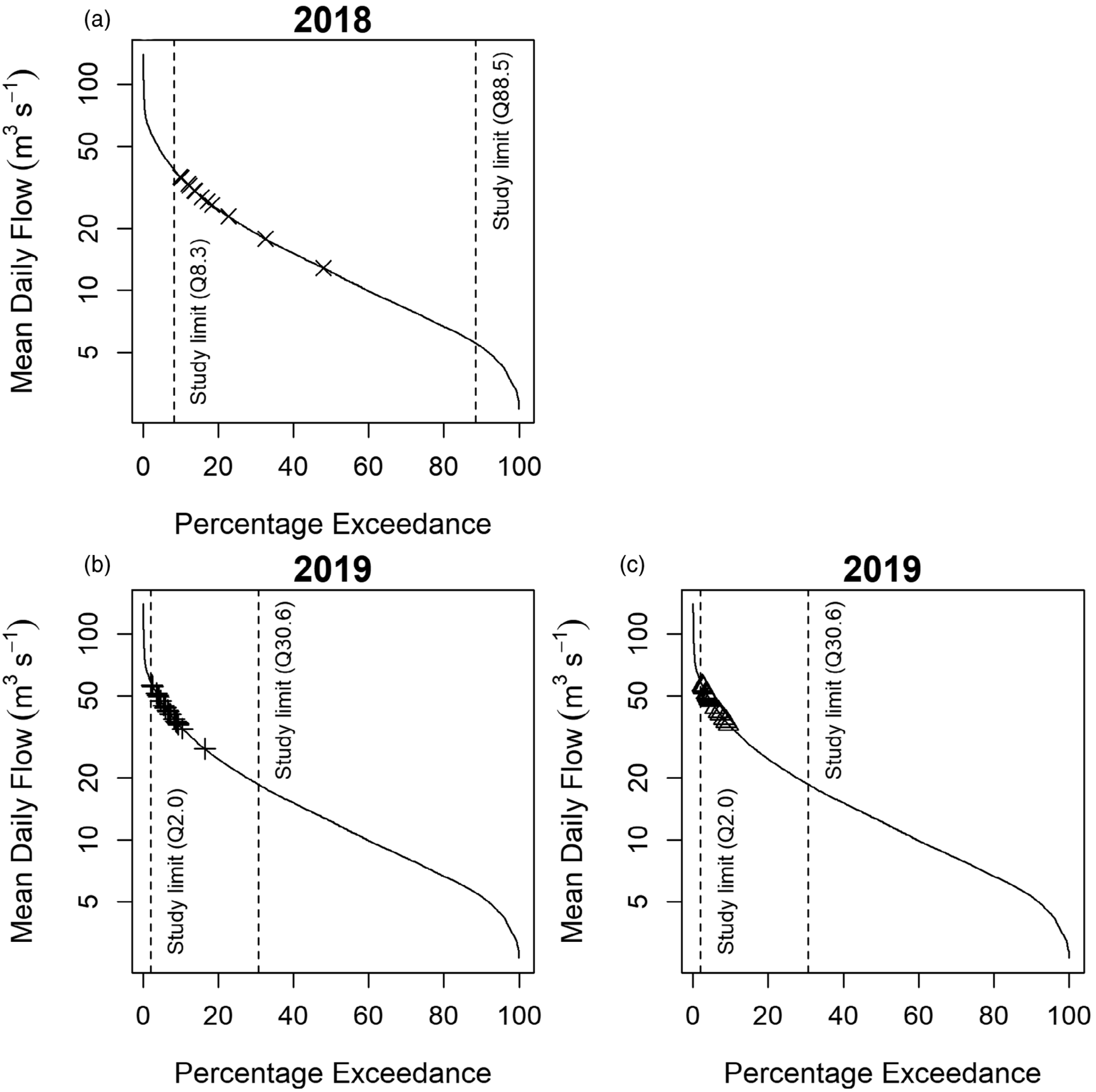

FIGURE 5 Percentage flow exceedance curves with first passage attempts indicated (2018 attempts [a]: crosses; 2019 attempts [b]: pluses), and 2019 successful passages (c): triangles

80 (±17) g, respectively. Of the 248 river lamprey released, 175 (70.6%; n_{2018} = 89/133 [66.9%]; n_{2019} = 86/115 [74.8%]) were detected attempting passage via the tiled lanes. There was no significant difference in the length (mean ± *SD*) of river lamprey that did attempt (360 ± 23 mm) and those that did not attempt (363 ± 23 mm; Welch two sample *t* test: $t_{135.4} = -0.7$, $p = .43$). Of the river lamprey that attempted passage in 2018, 21.3% (n = 19/89) attempted within 24 hr after release, and 65.2% (n = 58/89) made their first attempt within 10 days after release (Figure 3). In 2019, 55.8% (n = 48/86) attempted within 24 hr after release, and 89.5% (n = 77/86) made their first attempt within 10 days after release (Figure 3).

In total across the two experiments, 722 passage attempts were made (n_{2018} = 411; n_{2019} = 311; fifteen river lamprey had first been detected on A3 or A4, and so were not included in this analysis). The median (25th percentile, 75th percentile) number of attempts per river lamprey was 3 (2, 6) before a river lamprey succeeded in passing and continued upstream, moved downstream out of the study area, died, or passed on a non-instrumented route. The number of attempts made by individual river lamprey that visited the tiled routes ranged from 1 to 19 attempts. Similar proportions of attempting river lamprey were first detected on the NWW (n = 38, 42.7%) and AWW (n = 51, 57.3%; Chi-Squared test: $\chi^2_1 = 1.9$, $p = .17$) lanes in 2018, and likewise in 2019 (DDT: $n = 42$ [$n_{A1} = 34$, $n_{A3} = 8$], 48.8%; SDT: $n = 44$ [$n_{A2} = 37$, $n_{A4} = 7$], 51.2%; Chi-square test: $\chi^2_1 = 0.05$, $p = .83$).

Passage success differed greatly across the two experiments. In 2018, no river lamprey were detected at the top of the studded sections, indicating 0% passage efficiency of the studded tile route over the study period. In contrast, in 2019, of the 86 river lamprey detected attempting passage of the weir via the studded tiles, 53 lamprey were detected at the top (A3/A4), indicating 61.6% passage efficiency of the studded tile routes over the study period. There was no difference in the length (mean ± *SD*) of river lamprey that were detected attempting and failed (372 ± 17 mm) or succeeded (368 ± 21 mm) in passage via the tiled route in 2019 (Welch two sample *t* test: $t_{78.2} = 0.9$, $p = .40$). For those 38 attempting lamprey that were successful and not previously detected on A3/A4, the median time (25th percentile, 75th percentile) from first detection to passage was 72.3 hr (0.7, 185.6 hr), and the median passage duration was 0.8 hr (0.1, 11.0 hr).

There was little evidence of lane fidelity (remaining solely in DDT lane or SDT lane) during passage in 2019 (42.1% remained in lane, 57.9% switched lane; Table 2) for the first complete passage success per river lamprey ($n = 38$; 15 river lamprey removed from analysis for being detected on A3/A4 before A1/A2). Lane fidelity could not be calculated for 2018 due to no river lamprey being detected on A3/A4. In 2019, the passage efficiency for those that remained in the DDT and SDT lanes were 52.0% ($n_{A1} = 25$, $n_{A3} = 13$) and 23.1% ($n_{A2} = 13$, $n_{A4} = 3$), respectively, suggesting that passage at DDT tiles and/or near to the wing-wall might be more efficient. Overall, 31 river lamprey (36.0% of the 86 that attempted) were first detected succeeding in passage on A3, and 22 (25.6% of the 86 that attempted) on A4, and these were not significantly different (Chi-square test, $\chi^2_1 = 1.53$, $p = .22$).

In both 2018 and 2019, significantly more passage attempts were made when the weir was drowned out ($n_{2018} = 260$; $n_{2019} = 305$) than when it was not ($n_{2018} = 151$; Chi-Squared test: $\chi^2_1 = 28.9$, $p < .001$; $n_{2019} = 6$; Chi-Squared test: $\chi^2_1 = 287.4$, $p < .001$; Figure 4). Eighty-five of the 86 river lamprey that were recorded attempting passage in 2019 were first detected when the weir was drowned out, and all 53 successful passages occurred when the weir was drowned out. The weir was drowned out for 14.0 and 64.0% of the study periods in 2018 and 2019, respectively (Figure 4).

The range of flows experienced during the study periods were 3.02–40.7 m^3/s (Q88.5-Q8.3) and 13.9–59.2 m^3/s (Q30.6-Q2.0) in 2018 and 2019, respectively, and differed significantly between the 2 years, and so also between the two experiments (ANOVA, $F_{1, 16,670} = 16,678$, $p < .001$; Figure 5). Passage attempts in both years were carried out across a range of flows, but predominantly during the higher flows (median [25th percentile, 75th percentile]; 2018:30.8 [28.0, 32.6] m^3/s; 2019:42.2 [38.1, 45.1] m^3/s; Figure 5). Successful passages in 2019 were completed at higher flows (36.8–57.5 m^3/s; median [25th percentile, 75th percentile]: 49.0 [46.8, 51.2] m^3/s) than the flows experienced during the first attempt, but not significantly so (Wilcoxon rank sum test with continuity correction, $W = 198$, $p = .11$). Under low flow conditions (<7 m^3/s; Q77.3; −1.3 m from weir crest; as experienced for parts of the Experiment 1 study period in 2018, especially during the first 3 weeks), not only was the downstream weir edge completely exposed generating a vertical step up to 0.2 m high that river lamprey would have to overcome, but there was also little water flowing over the tiles themselves.

4 | DISCUSSION

Restoring habitat connectivity for migratory fishes is important for allowing lifecycle completion, dispersal, gene flow and contribution to natural ecosystem processes (Lucas & Baras, 2001; Reidy-Liermann et al., 2012). Extensive research and development has been carried out on the design and installation of effective fish passage solutions for economically important species, such as salmonids (Bunt et al., 2012; Noonan et al., 2012). However, management practices for those species that have been less valued (e.g., lampreys) often incorporate less costly solutions, frequently because existing conventional fishway designs are often found to be ineffective for non-target species such as lampreys (Foulds & Lucas, 2013). As shown by Tummers et al. (2018) and the present study (a combined 3 years of research), the use of the relatively cheaper horizontally-mounted studded tiles (less than 10% of the cost of a conventional engineered fishway) for attempting to re-establish river connectivity for river lamprey has, to date, been rather ineffective, with passage efficiency in both studies of much less than the 90% target for a diadromous migratory fish (Lucas & Baras, 2001). However, this does not indicate that a studded ramp passage solution for river lamprey need be ineffective if researched from a "first principles" perspective of what makes a passage route attractive and effective. Hume et al. (2020) have demonstrated that a 45° studded ramp exceeding 1 m in height could deliver a passage efficiency of ~98% for Great lakes sea lamprey, suggesting that studded ramps with the right design can be effective for upstream lamprey passage.

The proportion of river lamprey released that were recorded attempting passage during this study was slightly lower than in the previous years of study at the same weir (2019:74.8%; 2018:66.9%; 2017:91.9% [Tummers et al., 2018]; 2014:85.8%; 2013:90.1% [Tummers et al., 2016]). This reduction may in part be due to some river lamprey moving downstream post-release instead of continuing their upstream migration (Foulds & Lucas, 2013), but may also be due to the reduced and different areas of the weir-fishway infrastructure instrumented with PIT antennas across all studies. River lamprey, like many fish that migrate upstream, are attracted to areas of greater flow, and so are more likely to be detected attempting passage at a co-located fishway and turbine tailrace (Dodd et al., 2018; Tummers et al., 2018). In the previous studies at the same site, the Larinier fishway (Figure 2) was instrumented with PIT antennas, which may have attracted a greater proportion of river lamprey than only 2 m of the weir face, but was not instrumented in the present study due to its poor passage efficiency (0.3–7.1%; Tummers et al., 2016, 2018). It is, therefore, likely that more lamprey than were detected in this study attempted passage via the Larinier fishway route, but their success would have been limited. However, as there were similar proportions of first detections of river lamprey on both the NWW/DDT and AWW/SDT lanes, it is unlikely that the greater attraction flow from the Larinier fishway and turbine tailrace played a role in the decision of which lane to use.

The passage efficiency across the two experiments contrasted drastically. Where no river lamprey were recorded passing the weir during 2018 (although it may be that lamprey passed the weir via a non-instrumented route), 61.6% of river lamprey attempting passage in 2019 succeeded in passing the weir. This is the highest reported passage efficiency for river lamprey using horizontally-mounted studded tiles in the field (e.g., 25.6% in Tummers et al., 2018), and suggests that the expansion of the studded tile lane from 1 to 2 m enabled a greater passage efficiency, as predicted by Tummers et al. (2018). It is highly likely that the lower flow conditions of 2018 (Q8.3-Q88.5) hindered river lamprey attempting passage. This was especially so for the first 3 weeks of the 2018 study period, when the downstream edge of the weir was perched approximately 0.2 m above the downstream water surface and very low levels of water flowing over the tiles prevented river lamprey from mounting the weir face. But with the flow conditions in 2019 (Q2.0-Q30.6) being more comparable to that of Tummers et al. (2018; Q4-Q55), a 2.4-fold increase in passage success was observed. This is likely just a result of the increased area covered by studded tiles, and not due to the provision of DDTs, nor the placement of DDTs and SDTs adjacent to each other, as the majority of river lamprey recorded succeeding in passage did so on the opposite tile lane to which it begun its attempt. Although a greater lane fidelity was observed for the DDT lane than the SDT lane, it cannot be ruled out that the river lamprey remained within this lane simply due to its proximity to the wing-wall (Kemp, Russon, Vowles, & Lucas, 2011; Russon, Kemp, & Lucas, 2011; Tummers et al., 2016). Despite the greater passage efficiency, tiles in the current designs still do not provide adequate passage for river lamprey, as with over 98% of Derwent river lamprey spawning habitat located upstream of Buttercrambe weir (Lucas et al., 2009), a passage success (of those attempting) of at least 90% is a necessary target (Lucas & Baras, 2001). In conjunction with the lower than ideal passage success that the tiles provide, the tiles did not appear to alleviate delays to migration, with median delays (from first detection on A1/A2 to first detection on A3/A4) of 3 days being observed. Delays to migration may increase predation pressures on migratory fish populations (Schwinn, Baktoft, Aarestrup, Lucas, & Koed, 2018), and evidence of river lamprey predation at this site in terms of river lamprey remains adjacent to PIT tags found on the river banks have been observed throughout the study periods (A Lothian, *pers. obs.*)

Although neither SDTs nor DDTs appear to function adequately as retroactively-fitted passage solutions for river lamprey, the provisions of such engineered solutions, like studded tiles, enables some passage facility during periods of high flows. Despite only approximately 10.5% of the weir width (2 m of the 19 m wide Buttercrambe weir) being instrumented with PIT antennas, 46.1% of the released river lamprey in 2019 were detected succeeding in passing via that route, suggesting that the studded tiles might provide additional aid. We hypothesise that this is through surface roughening which produces a low-velocity layer above the tile that river lamprey can utilise while burst-swimming over the tiles (Kerr et al., 2015; Vowles et al., 2017; Watson, Goodrich, Cramp, Gordos, & Franklin, 2018). This requires a flow over the tiles deep enough to enable this behaviour, and would explain why the tiles were ineffective during the lower flow conditions of 2018. Further to this, river lamprey may be able to attach directly to the tile between the studs (if stud spacing allows) and utilise areas of further reduced velocity to rest during passage attempts (Kerr et al., 2015; Vowles et al., 2017).

It may be that the stud arrangements in the current study are limiting river lamprey to passing over the tiles and not travelling within the stud spacing. Hume et al. (2020), showed that plastic substrate with taller and wider studs, and a greater stud spacing in a quincunx "5-dice" arrangement, were highly effective (approximately 98% passage efficiency) at enabling ascent of Great Lakes sea lamprey (more similar in size to European river lamprey than European sea lamprey) when a low flow was passed over the studded material (depth of water between studs approximately 69.2 mm at a velocity approximately 0.2 m/s) which were also set at a steep angle (45° from horizontal). In the Hume et al. (2020) study, the Great Lakes sea lamprey were observed swimming within the studded matrix, potentially made possible by the wider stud spacing and alternating stud positions. Therefore, studded tiles may prove to be an effective solution for restoring habitat connectivity for river lamprey, but further research into the optimal stud arrangement and size which enables river lamprey to either swim through them or above them in a variety of flow conditions is needed. We recommend that the next avenue for research on studded tile design for river lamprey should incorporate a wider stud spacing in a quincunx "5-dice" arrangement, similar to that used by Hume et al. (2020).

In conclusion, although neither the SDT nor the DDT designs appear to be adequate for facilitating the necessary passage efficiency target (90%) for upstream migrating river lamprey, horizontally-studded tiles show promise if designed correctly, and thus more research is required to produce an optimal design considering stud size, spacing and arrangement. Currently, the SDT and DDT designs do not enable passage under low flow conditions, and therefore fail to meet legislative standards for providing adequate fish passage across a range of environmental conditions (Armstrong et al., 2010). However, in their current form, these horizontally-mounted studded tile designs may provide sufficient surface roughening when fully submerged to establish an effective, low-velocity boundary layer which river lamprey could utilise while burst swimming.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that data supporting the findings of this study are available from the corresponding author, AJL, upon reasonable request.

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