**Passage of European eel and river lamprey at a model weir provisioned with studded tiles**

Andrew S. Vowlesa\*, Andrew M. Donb, Perikles Karageorgopoulosc, Paul S. Kempa

a *International Centre for Ecohydraulics Research, Faculty of Engineering and the Environment, University of Southampton, Highfield, Southampton, SO17 1BJ, UK*

b *National Fisheries Services, Environment Agency, Bridgwater, TA6 4YS, UK*

c *National Fisheries Services, Environment Agency, South East, Worthing, BN11 1LD, UK*

\* Author to whom correspondence should be addressed: Tel: +44 02380 592700. Fax: +44 2380 593166. E-mail address: asv104@soton.ac.uk

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Using an open channel flume, this study quantified upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at a model Crump weir provisioned with vertically- or horizontally-oriented studded tiles, under high and low velocity. Tiles stopped short of the weir crest, as often required at gauging weirs. For eel, when velocity was high, passage efficiency improved from 47% during the control (tiles absent) to 67% and 93% under the vertical and horizontal treatment, respectively. Under the same velocity, passage efficiency was lower for lamprey (0%, 20% and 22% for the control, vertical and horizontal treatments, respectively). Number of passage attempts and delay were lowest for eel during the horizontal treatment, while for lamprey were lower compared to the control during both vertical and horizontal treatments. Although ≥50% of initial attempts made by eel to ascent the weir were through the tiles, the fish did not necessarily continue to use them to pass upstream. Weir passage having used the tiles to ascend was higher for lamprey and often provided the only route they were capable of passing. Thirty-three and 80% of eel and lamprey that reached the top of the vertical treatment, were washed downstream on exiting the tiles or turned around within the tiles and moved back to below the weir. Extending tiles to the crest of a weir will help improve passage performance. Despite difficulty manoeuvring between the smaller stud spacing, indicating further design optimisation is required, the tiles did improve upstream passage for both species.

Key words: Anguilliform, Behaviour, Eel tile, Fishway, Low-head barrier, Migration,

**Introduction**

Engineered fishways have been used for over 300 years with the intention to reconnect river habitat fragmented by man-made infrastructure (Clay 1995). The few studies conducted around the world on the performance of fishways for anguilliform species, such as eel (*Anguilla* spp.) and lamprey (*Petromyzon* spp. and *Lampetra* spp.), illustrate a common problem: conventional designs often function poorly. For example, on the Burnett River (Australia), juvenile long-fin (*Anguilla reinhardtii*) and short-fin (*A. australis*) eel were reported abundant at the bottom and absent at the top of a vertical slot fishway, suggesting a low passage efficiency (Stuart & Berghuis 2002). Similarly, on the Columbia River (USA), fishways designed for Pacific salmon (*Oncorhynchus* spp.) were inefficient (38 – 47 %) for Pacific lamprey (*Entosphenus tridentatus*) (Moser et al.2002), while on the River Derwent (UK), extreme inefficiencies of Denil (0%), Larinier super active baffle (0.3%) and pool-and-weir (5%) passes for river lamprey (*Lampetra fluviatilis*) were demonstrated (Foulds & Lucas 2013; Tummers et al. 2016). Therefore, structures continue to impede upstream movement despite the provision of fishways, restricting access to essential life-stage specific habitat.

Historically, anguilliform fishes have been seldom considered in the design of traditional fishways. Eel undertake their upstream migration as juveniles, initially as glass eels and elvers, and subsequently during the yellow phase when most colonisation occurs (White & Knights 1997; Briand et al. 2005). In contrast to adult salmon, on which most fish passage research has been focused (Noonan et al. 2012), juvenile European eel (*A. anguilla*) burst swimming capability is relatively low. Swim chamber tests indicate the elver (72 mm body length) and yellow phase eels (approx. 120 – 300 mm body length) can attain burst speeds in the region of 50 (McCleave 1980) and 100 – 150 cm s-1 (Clough et al. 2004), respectively. In an open channel flume, upstream moving European eel (661 mm mean body length) and river lamprey (359 mm mean body length) can achieve short (a few second) bursts of between 175 – 212 cm s-1 (Russon & Kemp 2011). When considering fishway design the burst swimming values of many anguilliforms may be inadequate, suggesting the need to design fishways that provide lower velocity routes.

Anguilliform fishes adopt a variety of behavioural strategies to aid their upstream migration. Juvenile eels are capable of climbing, with individuals (10 - 12 cm body length) able to use friction and surface tension to ascend wetted vertical surfaces (Jellyman 1977; Legault 1988). Some lamprey species also climb. Adult Pacific lamprey were observed to attach to the smooth vertical surfaces of an experimental weir with their oral disc, and ascend using powerful cycles of axial undulation interspersed with periods of stationary attachment (Kemp et al. 2009). Other anadromous lamprey (e.g. sea [*Petromyzon marinus*] and river lamprey) appear incapable of such climbing behaviour. Instead, they frequently adopt intermittent locomotion when occupying high velocity flow; rapid bursts of swimming are interspersed with periods of rest by attaching to structures using the oral disc (Quintella et al. 2004; Kemp et al. 2011).

Species specific fishways have been designed and constructed to take advantage of the climbing capability of adult Pacific lamprey and juvenile eel. For example, Pacific lamprey passes have been installed at dams on the Columbia River (USA) and consist of a series of smooth ramps interspersed by “rest boxes” (Moser et al. 2011). Bristle board passes provide a climbing substrate and have been widely implemented for eel (e.g. in the UK, Solomon & Beach 2004; France, Porcher 2002; North America, Hatry et al. 2013; and New Zealand, Jellyman & Ryan 1983). Despite seemingly large numbers of eel ascending bristle boards (e.g. Solomon and Beach 2004), one of the few mark recapture studies reported poor passage efficiencies (19.8 – 49.1%; Drouineau et al. 2015). Similarly, under controlled experimental conditions, bristle board efficiency for both European eel and river lamprey was mediocre in some instances (Kerr et al. 2015). Passage efficiency over a model Crump weir during high velocities (max. 2.4 m s-1) was improved through installation of bristle boards from 0.0 and 17.2%, to 36.7 and 76.5% for lamprey (291 – 401 mm total body length) and eel (322 – 660 mm total body length), respectively. Despite such positive improvements, it is likely efficiency of these species specific fish passes remain insufficient considering cumulative impacts of multiple barriers and further development of innovative fishway options is recommended for both species (Kerr et al. 2015).

Boss or studded material (subsequently referred to as studded tiles) are commonly installed on weirs as a robust alternative to bristle boards, which can be damaged or permanently distorted by the flow. When placed on an experimental ramp, a studded tile proved effective for inanga (*Galaxias maculatus*), redfin bullies (*Gobiomorphus huttoni*) (Baker & Boubée 2006) and juvenile (glass) eel (*A. anguilla*)(Vowles et al. 2015). On the Richelieu River (Canada) a similar material was used at a 5 m high weir to pass American eel (*A. rostrata*) (Verdon et al*.* 2003). In the UK, studded tiles have been installed oriented either horizontally (flat on a weir with upward facing studs) or vertically (and side mounted with studs protruding towards the channel wall) at numerous low-head barriers to facilitate upstream eel and lamprey passage. However, to date no controlled studies have quantified the performance of the two tile orientations for these species.

In this study the ability of yellow phase eel and adult lamprey to pass over a Crump weir using studded tiles under two velocity regimes was quantified. The objectives were to calculate: (1) passage efficiency (number that passed the weir as a percentage of those that attempted) for eel and lamprey in the absence (control) and presence of vertically- or horizontally-oriented studded tiles, (2) the number of attempts made by individual fish to ascend the weir under control and treatment conditions, (3) delay (in time)to upstream passage under control and treatment conditions, and describe (4) the responses of fish (e.g. lamprey oral disc attachments and swimming kinematics when moving over studded tiles) to the conditions encountered during both successful and failed passage events.

**Methodology**

***Experimental setup***

Experiments were conducted in an indoor open channel flume (21.4 m long, 1.37 m wide and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER), University of Southampton, UK. Discharge was maintained constant (90 L s-1) and plastic screens placed on the outside of the flume prevented visual disturbance by the observer. A model Crump weir (as used by Kerr et al. 2015) spanned the width of the experimental channel (Figure 1). The ability of yellow phase European eel (*Anguilla anguilla*) and spawning run adult river lamprey (*Lampetra fluviatilis*)to ascend the weir was tested under two velocity regimes, designated as high or low, and corresponding to the high (max. 2.4 m s-1) and medium (max. 1.9 m s-1) velocities used by Kerr et al. (2015). Low velocity was created by increasing downstream water depth, shifting the location of the hydraulic jump (a standing wave generated where supercritical flow on the weir face reached the downstream water level) further upstream. Under low velocity the distance fish were required to burst through supercritical flow to ascend the weir was reduced and water had a shorter distance over which to accelerate. The weir was either unmodified (control), or modified with studded tiles (for stud dimensions and spacing see Figure 1a, b) oriented vertically (vertical treatment) or horizontally (horizontal treatment) on the downstream face of the weir (Figure 1 c, d). The tiles stopped short of the weir crest as is frequently required for fish passage modifications (e.g. the Low Cost Baffle) installed on gauging weirs to prevent impacts to hydrometric properties (Rhodes & Servais 2008). Due to their perceived low impact on gauging accuracy, current guidance (in England) is to extend bristle boards to at least the point where the upstream slope of a Crump weir meets the river bed (Environment Agency 2011). While this guidance may also be appropriate for vertically oriented tiles, the gap between tiles and weir crest was maintained under the vertical treatment to facilitate direct comparison between the two tile orientations. The dual density tile (i.e. containing two stud sizes/spacings) was designed to facilitate passage of a wide size range of fish. In this study, the diameter of eel (mean ± SD = 27 ± 8 mm) and lamprey (20 ± 3 mm) were similar to the small stud spacing (which due to the tapered design was 17 to 20 mm on the diagonal and 30 to 35 mm on the horizontal, relative to the direction of bulk flow). The small stud spacing was placed nearest the base of the weir and flume wall during the vertical and horizontal treatment, respectively. During experimentation, fish were contained within a test area 7 m up- and down-stream of the weir crest by polycarbonate tubular flow straightening screens.

Water depth ranged from 9.0 cm at the weir crest to 4.1 cm immediately upstream of the hydraulic jump (mean ± SD water depth on the downstream weir face was 5.5 ± 1.4 cm) during the control under the high velocity regime. Depth at the weir crest remained at 9.0 cm under all treatments and localised increases in depth were created immediately next to the tiles. Visual observations confirmed that fish were fully submerged at all times when on unmodified sections of the weir. Water accelerated under the influence of gravity as it flowed down the weir face to the hydraulic jump, an area characterised by turbulent hydraulic conditions. Under the control, maximum velocities on the downstream weir face, measured using an electromagnetic flow meter (Valeport Model 801, Valeport Ltd, Totnes, UK), was 1.99 and 2.12 m s-1 under low and high velocity, respectively (see Figure 2 in Kerr et al. 2015 for hydraulic profiles). Studded tiles deflected flow on the downstream weir face towards the opposite side of the channel causing recirculating flow downstream of the weir. Maximum velocities on sections of the downstream weir face not containing studded tiles were generally similar to the control (max. 2.20 m s-1 for the horizontal treatment under high velocity, and 2.03 and 2.15 m s-1 for the vertical treatment under low and high velocity, respectively; Figure 2), with the exception of the horizontal treatment under low velocity (max. 1.26 m s-1; Figure 2b).

***Fish capture and maintenance***

Ninety eels (mean ± SD total length and mass: 424 ± 76 mm, 139 ± 89 g) were captured from the River Stour (Dorset, UK) on 8, 11, 22 and 29 July 2013 using fyke nets. Sixty six river lamprey (mean ± SD total length and mass: 359 ± 24 mm, 80 ± 16 g) were captured from the River Ouse (Yorkshire, UK) on 3 December 2013 using un-baited commercial eel traps. All fish were transported in aerated river water to the ICER experimental facility, and maintained at ambient temperature, under natural photoperiod, in clean (nitrite < 1 mg L-1 and nitrate < 50 mg L-1) aerated water. Eel were held in perforated barrels placed in the water tank of the test flume (mean ± SD temperature = 19.5 ± 1.1 ˚C) as the ambient temperature of separate holding tanks were consistently over 2°C warmer than flume temperatures. Lamprey were placed in a 3000 L indoor holding tank (mean ± SD temperature = 9.4 ± 0.7 ˚C) prior to experiments commencing. Temperatures in which fish were held were recorded at the start of each experimental day.

***Experimental procedure***

For eel, 15 trials were conducted for each of the six test conditions during hours of darkness (2100 - 0400 h) from 11 July to 8 August 2013. For lamprey, 11 trials per test condition were conducted during hours of darkness (1800 – 0300 h) from 8 to 31 January 2014. The time of year and day that trials were conducted coincided with periods of peak upstream movement and activity, respectively, for each species (see Baras et al. 1998 for eel; Foulds & Lucas 2013 for lamprey). A single fish was used once only during a trial. Velocity (high or low) and treatment (control, vertical or horizontal) were alternated throughout the test periods, as was the location of the studded tiles (i.e. right or left hand side of the weir) to control for any potential bias in fish behaviour and flume hydraulics. At the start of each daily set of trials, up to 10 eel or 6 lamprey were placed into a perforated container located at the downstream end of the experimental flume and allowed to acclimatise for a minimum of 1 hour before the start of the first trial. Immediately prior to the start of each trial, flume water temperature (mean ± SD for eel = 19.4 ± 1.0 ˚C, and lamprey = 9.7 ± 0.8 ˚C) was recorded. A single fish was released 7 m downstream of the weir crest at the start of each trial which lasted until either the fish successfully passed the crest or until 2 hours had elapsed. Fish behaviour as they approached and attempted to ascend the weir was recorded using 8 low light (Swann Pro A850) video cameras (2 were placed overhead while 6 were positioned to film through the glass sides of the flume), under infrared (850 nm) illumination. At the end of each trial fish were removed from the flume, before being measured (total length and max diameter) and weighed.

***Fish behaviour***

Analysis of the video footage enabled metrics of fish passage performance and behaviour to be quantified (Table 1). Additional descriptive observations of fish behaviour, identified during video analysis, were documented (such as ease of exiting vertically-oriented tiles and swimming kinematics when using tiles to ascend the weir).

***Statistical analysis***

Assumptions of normality and homogeneity of variance were tested using a Shapiro-Wilk and Levene’s test, respectively, and if violated, attempts were made to transform the data collected. If transformation was unsuccessful, nonparametric tests were performed. For pairwise comparisons, a Bonferroni correction was used when interpreting significant differences. Percentage data were arcsine square root transformed prior to statistical analysis. Pearson’s Chi-square tests were used to assess whether observed differed from expected *passage efficiency*, *tile entrance efficiency*, *percentage tile passage* and *percentage attachments* under different velocity regimes and treatments. When expected values were less than 5, the Fisher’s exact statistic was reported. *Number of passage attempts* was assessed using a discrete-time hazard model (with Logit link function) and Wald statistic, while *delay* was evaluated using a Kaplan-Meier product-limit estimator and Log Rank (Mantel-Cox) statistic; both are methods of time to event analysis (Singer and Willett 2003). Time to event analysis provides unbiased estimates by including fish that fail to pass the weir (right-censored individuals) in a probability function (in this instance, cumulative probability of passage) after any given number of attempts or time (Castro-Santos and Haro 2003). Mann-Whitney U and Kruskal-Wallis tests were used to quantify differences in *number of attachments* and *mean duration of attachments* between velocity regimes and treatments, respectively. As eel size appeared to influence their ability to progress through the vertically oriented tile, an Independent sample *t*-test determined if mean eel diameter differed between individuals passing via the tile or weir. This comparison was not performed for lamprey as only passage via the tile occurred. Statistical analysis were performed in SPSS v22 (IBM, USA).

**Results**

Fish were active and motivated to progress upstream with all eels and 98.5% of lamprey approaching the weir during the 2 hour trials.

***Passage efficiency***

For eel, passage efficiency was lower under high (68.9%) compared to low (93.3%) velocity when considering all treatments (χ2 = 8.78, d.f. = 1, *p* < 0.01). Under high velocity, passage efficiency was higher under the horizontal treatment (93.3%) than the control (46.7%; Fisher’s exact: *p* = 0.014; Figure 3a). Tiles did not improve passage efficiency under low velocity (Fisher’s exact: *p* = 1.00; Figure 3a).

For lamprey, passage efficiency was low (Figure 3b) and did not differ between the high (14.1%) and low (23.9%) velocity regime when considering all treatments (χ2 = 0.26, d.f. = 1, *p* = 0.609). Lamprey did not pass the weir under the control. Passage efficiency was higher when tiles were provided, but there was no difference between vertical (20.0% and 27.3% during high and low velocity) and horizontal (22.2% and 44.4% during high and low velocity) treatments (χ2 = 0.43, d.f. = 1, *p* = 0.510; Figure 3b).

***Number of passage attempts***

For eel, the number of passage attempts was higher under the high (50% median probability of passage [PP] after 2 attempts) compared to low (50% PP after 1 attempt) velocity (χ2ws = 13.18, d.f. = 1, *p* < 0.001) when considering all treatments. When velocity was low, the number of attempts prior to passage was lower during the horizontal (75% PP after 1 attempt) compared with vertical treatment (75% PP after 3 attempts; χ2ws = 5.23, d.f. = 1, *p* < 0.05; Figure 4a). When velocity was high, number of attempts was lower for the horizontal treatment (50% PP after 1 attempt) compared to the control (50% PP of passage after > 10 attempts, χ2ws = 7.28, d.f. = 1, *p* < 0.01) and vertical treatment (50% PP of passage after 3 attempts, χ2ws = 5.09, d.f. = 1, *p* < 0.05) (Figure 4b).

Number of attempts prior to passage was not influenced by velocity regime (χ2ws = 0.334, d.f. = 1, *p* = 0.563) or treatment (χ2ws = 1.76, d.f. = 2, *p* = 0.184) for lamprey (Figure 4c and d). For the horizontal treatment, 50% PP occurred after 18 attempts under high velocity, for all other treatments there was < 50% PP despite up to 31 attempts.

***Delay***

For eel, delay was longer under the high (50% PP after 15.8 mins) compared to low (50% PP after 5.6 mins) velocity (χ2mc = 9.89, d.f. = 1, *p* < 0.01) when considering all treatments. While there was no difference in delay between treatments when velocity was low (χ2mc = 0.89, d.f. = 2, *p* = 0.640; Figure 5a). When velocity was high, delay was longer for the control (50% PP after > 120 mins) compared with the horizontal treatment (50% PP after 12.9 mins) (χ2mc = 4.98, d.f. = 1, *p* < 0.05; Figure 5b).

Delay was high for lamprey, with < 50% PP after 120 mins under all conditions tested. There was no difference in delay between high compared to low velocity (χ2mc = 1.66, d.f. = 1, *p* = 0.197). However, it took longer to pass the control when compared to the vertical (χ2mc = 4.60, d.f. = 1, *p* < 0.05) or horizontal treatment (χ2mc = 6.17, d.f. = 1, *p* < 0.05; Figure 5c and d).

***Tile entrance efficiency and Percentage tile passage***

For eel, tile entrance efficiency did not differ between velocity regime (χ2 = 0.13, d.f. = 1, *p* = 0.721), but was higher under the vertical compared to horizontal treatment when velocity was low (χ2 = 4.78, d.f. = 1, *p* < 0.05; Table 2). For lamprey, tile entrance efficiency was higher under high (66%) compared to low (47%) velocity (χ2 = 11.35, d.f. = 1, *p* = 0.001), but did not differ with tile orientation (Table 2).

For eel, percentage tile passage did not differ between velocity regime (χ2 = 0.73, d.f. = 1, *p* = 0.392) but was higher under the horizontal compared to vertical treatment when velocity was high (χ2 = 10.36, d.f. = 1, *p* = 0.001; Table 2). When velocity was low, eel used both tile treatments to ascend the weir around half the time (Table 2). For lamprey, percentage tile passage did not differ between velocity regime (Fisher’s exact: *p* = 0.491). Lamprey passage was only via the tiles, with the exception of the horizontal treatment when velocity was low (Table 2), where some lamprey passed the weir when swimming directly next to the tiles.

***Lamprey attachments***

Approximately half of lamprey that attempted to pass the weir attached to its downstream face with their oral disc. Propensity to attach was not influenced by velocity (high: 46.3%, low: 58.9%; χ2  = 2.23, d.f. = 1, *p* = 0.135) or treatment (control: 55.6%, vertical treatment: 52.3%, horizontal treatment: 50.0%; χ2  = 0.87, d.f. = 2, *p* = 0.648). Similarly, number (median [IQR] = 3.5 [1.3 – 8.0]) and duration (4.24 mins [3.26 – 4.80]) of attachments per fish were not influenced by velocity (number: *U* = 58.5, z = -1.67, *p* = 0.096; duration *U* = 84, z = -0.45, *p* = 0.655) or treatment (number: *H* = 5.04, d.f. = 2, *p* = 0.081; duration: *H* = 1.36, d.f. = 2, *p* = 0.506).

***Other behavioural observations***

During the vertical treatment, eel and lamprey often had difficulty navigating through the small stud size/spacing, which due to water depth was the only density available for them to use. Consequently, 85.7 and 81.1% of attempts to ascend the weir using the tiles resulted in eel and lamprey abandoning the passage effort and exiting the fish pass at the downstream entrance. The vertical treatment was size selective for eel with those passing via the weir being wider in diameter (mean ± SD: 3.1 ± 0.7 cm) than those that used the studded tiles to ascend (mean ± SD = 2.3 ± 0.6 cm; *t* = 2.60, d.f. = 18, *p* < 0.05; Figure 6). Eel width did not differ between those passing via the tiles versus weir during the horizontal treatment (*t* = 0.11, d.f. = 19, *p* = 0.916; Figure 6). Individuals of both species that did progress to the upstream exit of the vertical tiles had some degree of difficulty exiting and bursting over the remaining (24 cm) section of unmodified weir (Supplementary material A). Thirty-three and 80.0% of eel and lamprey respectively, failed to successfully pass during that attempt because they were either washed back down the weir or eventually turned around in the tiles and moved back downstream. During the horizontal treatment, eels appeared to more readily weave between the submerged studs (Supplementary material B) compared to lamprey which typically attempted to burst over the top (Supplementary material C). This resulted in frequent failed attempts, and in some instances impingement on the surface of the studded substrate.

**Discussion**

Restoring habitat connectivity is an important conservation strategy for migratory fishes. Despite wide-scale implementation of anguilliform specific fish passes, robust information on their performance is limited. This study quantified the performance of a vertically- and horizontally-oriented studded tile for facilitating upstream movement of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) under controlled experimental conditions. In the absence of studded tiles, high water velocity generated at a model Crump weir limited passage of eel and prevented upstream movement of lamprey. The studded design improved upstream passage and reduced delay for both species under some scenarios. The inter-specific differences in passage performance observed during this study support those of Kerr et al. (2015) where side-mounted vertically-oriented bristle boards were more effective for eel than for lamprey.

Studded tiles improved passage efficiency for eel and lamprey under conditions that were difficult to ascend (i.e. where less than 50% of fish that attempted were capable of passing under control conditions). For eel, installation of horizontally oriented tiles on the downstream face of the weir improved passage efficiency to levels observed under low velocity when studded tiles were absent, a condition which eel could pass with relative ease. For lamprey, which were unable to pass the weir under control conditions, passage efficiency improved through installation of vertical and horizontal tiles to 20% and 22%, respectively, during the high velocity regime. Under the same velocity regime, Kerr et al. (2015) observed a passage efficiency of 37% for bristle boards.

At barriers to migration fish may be required to stage multiple upstream passage attempts, e.g. if they fail to burst through areas of high water velocity or need to ascend multiple traverses within fishways. However, accommodating multiple attempts into fish passage metrics is rare (for relevant exceptions see Castro-Santos 2004 and Keefer et al. 2014). In this study, analysis of the number of upstream passage attempts provided interesting insight into the performance of studded tiles for eel and lamprey passage. Overall, number of attempts was higher for eel under the more challenging high velocity regime. However, when the velocity was high, the number of attempts to pass the weir was lower when horizontally-oriented tiles were installed relative to the vertical configuration or control. Interestingly, under low velocity, where passage efficiency was over 90% for all treatments tested, number of attempts was higher when vertically oriented tiles were installed relative to the horizontal configuration. This suggests that sub-optimally designed and/or located fish passage solutions may act as a hindrance. In a field setting, where barriers are larger and occur in combination, a higher number of attempts prior to successful passage may result in elevated energetic costs, delay to upstream movement, and reduction in individual fitness.

Eels passed the weir more rapidly (50% probability of passage after 13 mins) when tiles were oriented horizontally when compared to the control (> 120 mins). The greater passage performance of horizontally-oriented tiles, in terms of both number of attempts and delay, suggests that the configuration is more compatible with eel behaviour, and/or that the vertical treatment is a suboptimal design, perhaps because the high density of small studs located nearest the weir face impeded the movement of the large eel, or because the tiles did not extend to the weir crest. At the upstream tile exit approximately 30% of eels fell back down the weir or turned back in the tile, behaviours that were less common during the horizontal treatment. Where possible (e.g. weirs not used for gauging purposes), extending tiles beyond the crest, as is currently recommended in England for bristle boards (Environment Agency 2011), may reduce the number of eel failing to ascend barriers using vertically oriented tiles.

In contrast to eel, the weir substantially impeded and delayed the movement of lamprey under all conditions tested. There was less than 50% probability of passage despite more than 30 attempts per individual during most trials. The high attempt rate indicated a strong motivation to progress upstream and yet passage was blocked in the absence of the studded tiles. As was observed for eel, a large proportion of lamprey that reached the top of the vertical tiles failed to ascend the weir because they were either washed downstream or turned around within the tile and moved back to below the weir. Extending studded tiles beyond the crest of a weir may help improve passage performance for lamprey as well as eel.

An ideal fishway should attract fish to its entrance, enable entry and upstream progression with minimal delay or increased predation risk and energetic cost (Castro-Santos et al. 2009). In this study, tile entrance efficiency was typically greater than 50% for both species. However, in some instances (e.g. for eel during the vertical treatment) entry was high while passage over the weir crest having used the studded tiles was low. This indicates that despite using the tiles many failed, and instead ultimately passed by bursting directly over the weir through supercritical flow. It is likely that the density of small studs which was available for eel to pass through under this orientation was too high for some large eel. This is supported by the observation that eels (diameter > 25 mm) were less capable of passing the vertically oriented tiles. Provision of lower density studs would have enabled a wider size range of eel to ascend via this route, likely improving passage efficiency. Percentage tile passage was high for lamprey as they were only able to pass over the weir via the modified route, except under low velocity, when tiles were oriented horizontally. Under this treatment, some lamprey passed the weir while positioned directly next to the tiles, presumably taking advantage of lower water velocity or drag created near the boundary (see Kerr et al. 2016).

In this study, tile entrance efficiency for both species was high, and for lamprey greater than that observed in one field study (see Tummers et al. 2016). This may be for two reasons. First, the flume was narrow (1.37 m wide), and thus the probability of locating the tile entrance was likely higher than in the field where channel width may be substantially larger (e.g. the study by Tummers et al. 2016 was conducted at a 20 m wide Crump weir). Second, the tiles deflected water as it flowed down the weir face creating a recirculating flow downstream that may have made it easier for fish to locate the entrance. Additional cues e.g. hydraulic (Piper et al. 2012) or olfactory (Briand et al. 2002) may be needed to improve attraction to the tile entrance under field scenarios.

Anguilliform species are able to adopt a variety of behavioural strategies to aid upstream migration. In this study approximately half of all lamprey exhibited burst-attach-rest behaviour while attempting to ascend the downstream weir face, behaviour commonly used to facilitate passage through high velocity regions (Quintella et al. 2004; Kemp et al. 2011). Nevertheless, this behaviour did not aid passage with fish failing to progress up the weir face between attachments, suggesting water velocities exceeded thresholds of lamprey burst swimming performance. Observations of lamprey behaviour provide some explanation for the mediocre passage performance associated with studded tiles. Lamprey more readily burst over the horizontal tiles rather than weave between the studs, a behaviour commonly observed for eel. Such difference in behaviours, despite similarities of body morphology, are important considerations when designing fish passage modifications for anguilliform species.

**Conclusions**

Boss or studded substrates improved upstream passage of yellow phase European eel and adult river lamprey under challenging experimental conditions. For eel, passage efficiency values for studded tiles (67 – 93%) were similar to those observed for bristle boards (mean 77%; Kerr et al. 2015). For lamprey, passage efficiency values in the region of 20 – 22% may be considered poor when considering up to 100% efficiency through nature-like fish passes in some instances (e.g. Aronsuu et al. 2015). However, efficiencies of 20 – 22% do represent a substantial improvement over the performance of some more common conventional fishways. For example, 0 and 5% passage efficiency were observed for PIT tagged river lamprey at Denil and pool-and-weir passes, respectively (Foulds and Lucas 2013). Modification of a Larinier super active baffle pass with vertically-oriented studded tiles on the River Derwent (UK) improved passage efficiency from 0.3 to 17% (Tummers et al. 2016). Results from both controlled flume (presented here) and robust field studies (Tummers et al. 2016) suggest further design optimisation of studded tiles is warranted, particularly for lamprey.

**Acknowledgements**

This study was funded by the Environment Agency, UK. We thank M Berwick, J Bloomer, M Deleau, J De Bie, J Kerr, M Short and S Vowles for assistance during experimental periods, R Castle and P Bird for capture and supply of fish, and Berry and Escott Engineering for providing the eel tiles. Data published in this paper are available from the University of Southampton repository at DOI:10.5258/SOTON/400560

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**Table and Figure captions:**

Table 1. Metrics used to determine fish passage performance and behaviour at a model Crump weir installed in an open channel flume when unmodified (control) and modified with vertically- and horizontally-oriented studded tiles for European eel and river lamprey.

 Table 2. Number of European eel and river lamprey that attempted to pass a model Crump weir using a studded tile as a percentage of the total number of passage attempts (tile entrance efficiency) and number of fish successfully passing the weir while using the tiles as a percentage of total number of passes (percentage tile passage).

Figure 1.a. A studded tile (manufactured from a high density co-polymer) used to facilitate the upstream passage of yellow phase European eel and adult river lamprey over a model Crump weir installed in an open channel flume at the International Centre for Ecohydraulics Research (University of Southampton) facility, b. the dimensions of the small and large stud configurations, c. the dimensions of the Crump weir used during experiments with the location of the horizontally- and d. vertically-oriented studded tiles illustrated on the true right side of the weir.

Figure 2. Velocity profile on the downstream face of a Crump weir under high and low velocity with horizontally-oriented tiles installed (a and b, respectively), and high and low velocity with vertically-oriented tiles installed (c and d, respectively). The arrow, dashed lines and crosses denote the direction of bulk flow, and locations of the hydraulic jump and velocity measurement points, respectively.

Figure 3. Passage efficiency for European eel (a) and river lamprey (b) at a model Crump weir. Black, grey and clear bars represent the control, vertical and horizontal treatments, respectively.

Figure 4. Cumulative probability of successfully passing a model Crump weir installed in an open channel flume in relation to number of attempts for eel under low (a) and high velocity (b), and lamprey under low (c) and high (d) velocity. Solid, small dashed and large dashed lines represent the unmodified (control), vertical and horizontal treatments, respectively. Symbols (cross, circle, triangle, for the control, vertical and horizontal treatment, respectively) represent right censored data.

Figure 5. Cumulative probability of successfully passing a model Crump weir installed in an open channel flume in relation to time for eel under low (a) and high velocity (b), and lamprey under low (c) and high (d) velocity. Solid, small dashed and large dashed lines represent the unmodified (control), vertical and horizontal treatments, respectively. Symbols (cross, circle, triangle, for the control, vertical and horizontal treatment, respectively) represent right censored data.

Figure 6. Mean diameter of European eel that successfully passed a model Crump weir in an experimental flume using either studded tiles (clear bars) or via the unmodified weir face (black bars). Error bars are +1SE.