Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir.

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Abstract

Globally, populations of diadromous anguilliform morphotype fish, such as eel and lamprey, have experienced substantial declines, partly as a result of habitat fragmentation caused by river infrastructure. In the UK, a new configuration of hydraulically unobtrusive bristle pass (side-mounted and vertically oriented) has been developed to help upstream moving European eel (*Anguilla anguilla*) negotiate gauging weirs. The efficacy of vertically oriented bristle passes remains untested, despite their potential as a low-cost low-maintenance solution to improve habitat connectivity at low-head structural barriers worldwide. This study assessed the ability of small (82 – 320 mm) and large (322 – 660 mm) European eel and adult (291 – 401 mm) river lamprey (*Lampetra fluviatilis*) to pass upstream over an experimental Crump weir installed in a large open-channel flume with (treatment) and without (control) side-mounted vertically oriented bristle passes under three different hydraulic regimes. Both species were highly motivated to explore their surroundings and move upstream during the trials. Under flooded control conditions, passage efficiency (the total number of times fish passed the structure as a percentage of total attempts) and passage success (the number of fish that passed the structure as a percentage of those that attempted) were high, delay was short, and number of failed attempts before passage was low for both species. When difference in head was at its greatest (230 mm) and velocity and its variation downstream were high (maximum u and σ: 2.43 ms^{-1} and 0.66 ms^{-1}, respectively), the upstream movement of small eel and lamprey was blocked, and passage efficiency and success for large eel low (4.6% and 17.2%, respectively). For large eel that successfully passed, delay was long, and number of failed attempts before upstream passage was high. When bristle passes were installed, passage efficiency for small (91.5%) and large eel (56.7%), and passage success for large eel (76.5%) and lamprey (36.7%) was higher, while delay and the number of attempts before passage was lower for both species. Bristle passes helped European eel and river lamprey pass a small experimental Crump weir, although interspecific variation in efficacy was evident.

1. Introduction

Impacts of infrastructure, such as dams, weirs and barrages, on the physical and chemical processes of rivers are well established (Petts, 1980). Impoundments alter flow and sediment regimes (Nilsson *et al.*, 2005; Xu and Milliman, 2009), channel morphology (Gordon and Meentemeyer, 2006), and nutrient and oxygen availability (Bellanger *et al.*, 2004; Gresh *et al.*, 2000). Ecological impacts include changes in invertebrate communities (Boon, 1988), and for fish the loss of, or reduced access to, critical habitat (Pess *et al.*, 2008), delayed migration (Caudill *et al.*, 2007), population isolation (Morita and Yamamoto, 2002), and reduced productivity and diversity (Agostinho *et al.*, 2008; Matzinger *et al*., 2007). As a consequence, populations of riverine fish have declined worldwide (Aparicio *et al*., 2000; Dekker, 2007; Kruk, 2004; Nelson *et al.*, 2002). For diadromous species these declines are often due to impeded migration between essential habitats (Feunteun, 2002; Lucas and Baras, 2001; Ojutkangas *et al*., 1995; Yoshiyama *et al.*, 1998).

In an effort to re-establish fluvial connectivity and reverse population declines a range of mitigation strategies have been developed, including the installation of fish passes at structural barriers to migration (Beach, 1984; Clay, 1995; Larinier and Marmulla, 2004;). Unfortunately, fish passes, such as those developed for upstream migrating salmonids, often perform poorly for weaker-swimming non-salmonid species (Bunt *et al.*, 1999, 2000, 2001; Cooke *et al.*, 2005; Noonan *et al*., 2012; Slatick and Basham, 1985). For example, anguilliform morphotype fish, such as eel (*Anguilla* spp.) and lamprey (e.g. *Lampetra* spp. *and Petromyzon Marinus*), exhibit distinctly different forms of locomotion (Sfakiotakis *et al.*, 1999) and behaviour (Russon and Kemp, 2011a), compared to those with a subcarangiform morphology. Although anguilliform morphotypes have good acceleration and are highly manoeuvrable (Muller *et al.*, 2001; Sfakiotakis *et al.*, 1999), they do not leap at barriers and their burst swimming speeds are relatively low (Beamish, 1978; Clough *et al.*, 2004, Russon and Kemp, 2011b; Keefer *et al.*, 2012). Instead, if required, eel and lamprey adopt alternative strategies to ascend obstacles; juvenile eel climb wetted slopes using substrate surface irregularities (Legault, 1988; Tesch, 2003), while lamprey use their oral disk to attach to structures to rest between intermittent bouts of activity (Kemp *et al.*, 2009; Quintella *et al.*, 2004; Russon *et al.*, 2011). In recognition of these adaptations, and in response to environmental legislation (e.g. The Eels [England and Wales] Regulations 2009; CITES; European Habitats Directive [92/43/EEC]; EU Water Framework Directive [2000/60/EC]; Bern convention [COE, 1979]) enacted in an attempt to reverse population declines (Dekker, 2003; Dekker, 2007; ICES, 2012; Kelly and King, 2001; Moriarty and Tesch, 1996; Renaud, 1997), specialist fish passes have been developed and employed for several anguilliform morphotype fishes (Moser *et al.*, 2011; Solomon and Beach, 2004).

For upstream migrating juvenile eel, specialist fish passes predominantly rely on their ability to climb (Legault, 1988; Tesch, 2003). A variety of substrates have been developed to facilitate climbing (Environment Agency, 2011; Porcher, 2002), including those that incorporate clusters of bristles (usually synthetic), set at regular intervals, protruding from a solid surface (see Environment Agency, 2011). This ‘bristled substrate’, when used in a traditional configuration (where the base is oriented horizontally, or slightly off horizontal, with water flowing through the bristles), has proved effective at facilitating the upstream passage of a large number (hundreds of thousands per year) (Briand, 2005; Jellyman and Ryan, 1983; Moriaty, 1986) and a broad size range (60-500mm) (Moriaty, 1986, Robinet *et al.*, 2003) of eel worldwide. Further, there is some evidence that lamprey passage can also be enhanced by the judicial use of a bristled substrate (Laine *et al.*, 1998). Bristled substrate is now being used as a cost effective and hydraulically unobtrusive (Environment Agency, 2010) addition to low-head gauging structures, such as Crump weirs (common in the UK), to facilitate the upstream passage of eel (Environment Agency, 2011) and possibly other anguilliform morphotype species. However, to minimise flow interference and negate the need for a separate water source (i.e. as required for 'up and over' installations - see: Environment Agency, 2011), the bristled substrate is oriented vertically and attached with the bristles protruding perpendicularly towards the wing wall of a gauging structure. The efficacy of this configuration of bristle pass is currently untested, despite regional implementation and the recommendation of nationwide deployment in England and Wales (Environment Agency, 2011).

This study investigated the behaviour of European eel (*Anguilla anguilla*) and European river lamprey (*Lampetra fluviatilis*) as they attempted to pass an unmodified (control), or modified (treatment - with bristle passes installed) Crump weir, under experimental conditions. The experiment was repeated under three hydraulic regimes (low, medium and high velocity) that represent flow conditions similar to those encountered at Crump weirs in the field (see: National River Flow Archive). Passage and delay were quantified and the influence of hydraulic regime and treatment assessed.

2. Methodology

2.1. Experimental setup

A model Crump weir (2.38 m long, 1.38 m wide and 0.34 m high) (Figure 1a) was installed midway along an indoor recirculating flume (21.40 m long, 1.38 m wide, and 0.60 m deep) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK (50° 57’42.6”N, 1°25’26.9”W). A 14 m long experimental area, sectioned off from the rest of the channel by flow straightening devices (100 mm thick polycarbonate screens with elongated tubular porosity - 7 mm diameter), extended 7 m either side of the weir crest. Under treatment conditions, vertically oriented bristle passes (10 mm thick polypropylene board covered with 30 mm spaced orthogonally oriented clusters of *ca.* 24 synthetic fibres [70 mm long x 1.5 mm diameter]) were attached with bristles protruding towards the flume wall on each side of the channel (Figure 1b, c). The bristled substrate was installed in accordance with Environment Agency guidelines to maintain a 70 mm cavity (equal to bristle length) between the bristle board and flume wall (see: Environment Agency, 2011).

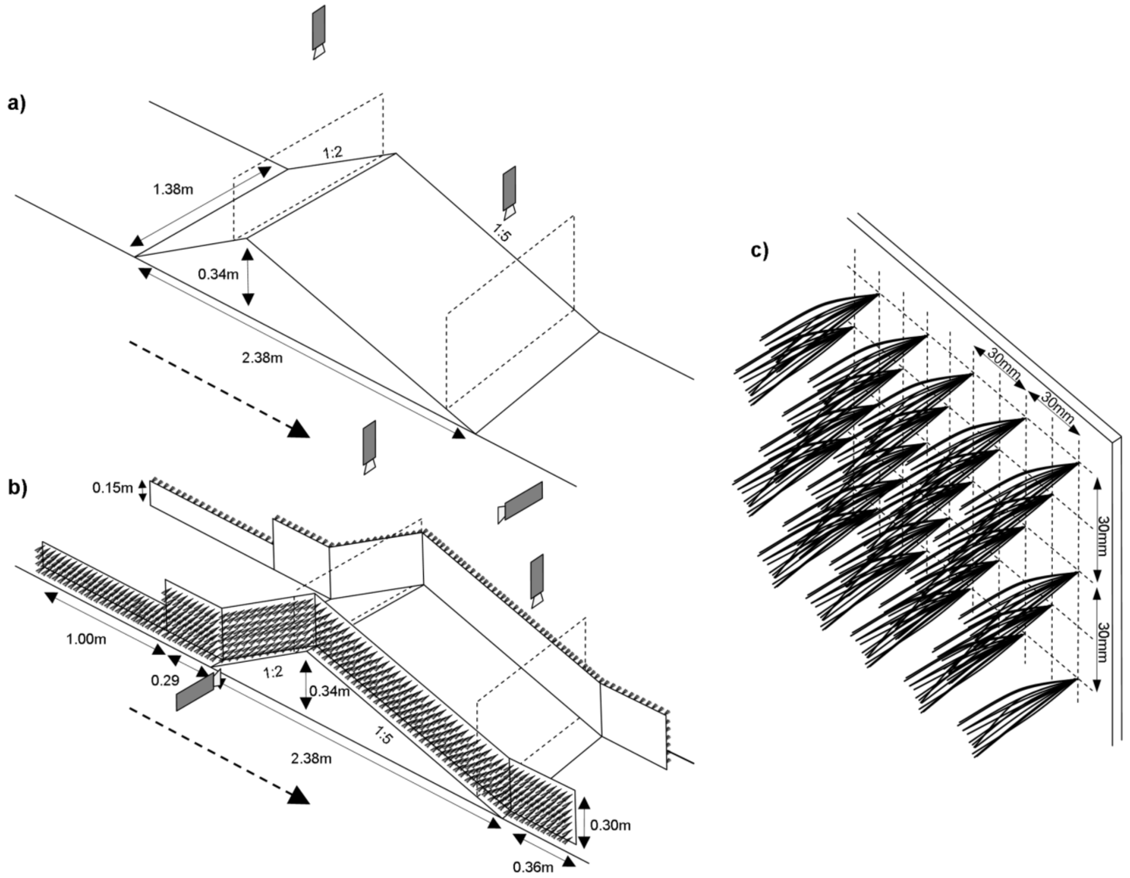

Figure 1. The Crump weir under control (**a**) and treatment (**b**) setups during which a bristled substrate (**c**) was vertically positioned against the channel walls to aid upstream movement of European eel and river lamprey under various hydraulic conditions. In **a** and **b** dashed lines indicate the position of half-duplex Passive Integrated Transponder (PIT) antennae coils and the dashed arrows indicates direction of flow.

Experiments were conducted under three hydraulic regimes: high (HV), medium (MV) and low velocity (LV) (Figure 2), created by altering the downstream water level (depth: 220, 330 and 450 mm, respectively) by adjusting an overshot weir (located at the downstream end of the channel), under a constant discharge (0.09 $m^3 s^{-1}$). The HV and MV regimes were within the modular limits of the experimental weir with upstream water level (depth: 450 mm) independent of that downstream. The LV regime was outside the modular limits of the weir (flooded conditions - upstream water depth: 455 mm). As such, head difference under the HV, MV and LV regime was 230, 120, and 5 mm, respectively. Velocities were measured using an Acoustic Doppler Velocimeter (ADV) (Vectrino, Nortek-AS, Norway - frequency 50 Hz, sample volume 0.05 cm^3, record length 60 sec), and mean velocity ($V = \sqrt{\bar{u}^2 + \bar{v}^2 + \bar{w}^2}$) and standard deviation ($S.D. = \sqrt{{\sigma_u}^2 + {\sigma_v}^2 + {\sigma_w}^2}$) calculated. Where u, v and w are the instantaneous velocity values corresponding to the x, y and z spatial coordinates, overbar denotes time-average, and σ is the standard deviation of its subscript. *S.D.* was used as a proxy for the intensity of turbulence. In conditions that precluded using the ADV, i.e. when depth was < 60 mm or air entrainment was high, an electromagnetic flow meter (Model 801 Flat, Valeport, UK - frequency 1 Hz, record length 30 sec) was used to measure *V* and *S.D.*. Spatial maps of the hydraulics associated with the Crump weir were generated in ArcMap v10 (Esri, USA) using a spline interpolation.

The velocity at the crest of the weir was similar under each regime (*ca*. 0.83 m s^{-1}) (Figure 2). Maximum velocity (2.43, 1.91, and 0.80 m s^{-1} under the HV, MV, and LV regimes, respectively) was inversely related to head difference (Figure 2) and occurred at the weir crest under the LV and just upstream of the hydraulic jump under the MV and HV regime (Figure 2). The hydraulic jump consisted of a standing wave generated as the super-critical flow along the face of the weir rapidly decelerated on reaching the downstream water level. Despite flooded conditions under the LV regime, a small hydraulic jump occurred *ca.* 100 - 150 mm downstream of the weir crest (Figure 2). Downstream of the hydraulic jump, under all regimes, velocity gradually decreased as the channel deepened (Figure 2).

Upstream of the weir the intensity of turbulence was low and similar under each regime (*S.D.* = *ca.* 0.05 m s^{-1}). High intensities of turbulence, relative to maximum velocity, were generated at the hydraulic jump (*S.D.* = 0.66, 0.27 and 0.17 ms^{-1} under the HV, MV and LV regime, respectively), and gradually dissipated with distance downstream. At the extent of the hydraulically mapped region (3.74 m downstream of the weir crest), turbulence had almost returned to background levels (*S.D.* = 0.10, 0.08 and 0.05 m s^{-1} under the HV, MV and LV regime, respectively).

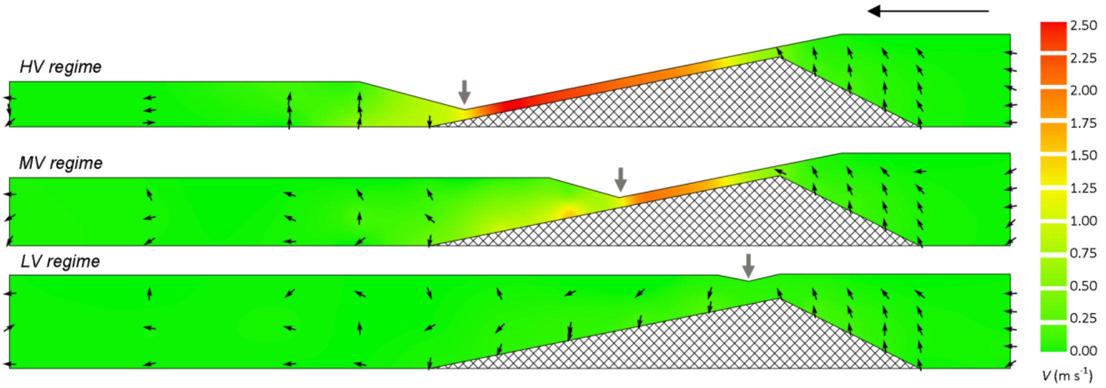

Figure 2. Velocity (m s^{-1}) profiles for a Crump weir under low (LV), medium (MV) and high (HV) velocity regimes. Small and large black arrows indicate mean and bulk flow direction, respectively. Grey arrows indicate position of a hydraulic jump.

2.2. Experimental procedure

Yellow phase European eel were collected by electric fishing from the Rivers Itchen (50° 57’ 19.2” N, 1° 20’ 15.8” W, *N* = 208, Total Length [TL]: μ = 397 mm, σ = 108 mm, Range = 149 – 660 mm), Wallington (50° 51’ 45.4” N, 1° 09’ 54.5” W, *N* = 31, TL: μ = 277 mm, σ = 58 mm, Range = 111 – 386 mm) and Meon (50° 53’ 53.2” N, 1° 11’ 14.3”

W, *N* = 32, TL: μ = 178 mm, σ = 72 mm, Range = 82 – 333 mm) by the Environment Agency between 1 May and 12 July 2011. Actively migrating adult river lamprey were trapped in the River Ouse (53° 53’ 26.2”N, 1° 5’ 36.8”W) by a commercial fisherman on 4 December 2012 (*N* = 96, TL: μ = 358 mm, σ = 21 mm, Range = 291 – 401 mm). Fish were transported to the ICER facility in sealed polyurethane bags (river water and pure oxygen atmosphere - eels) or transportation tanks (aerated river water - lamprey) and held in separate 3000 litre outdoor holding tanks (aerated and filtered, 50% weekly water change) at ambient temperature (μ = 16.2 °C, σ = 1.9 and μ = 7.6 °C, σ = 3.1 for eel and lamprey, respectively). All fish were acclimated to holding tank conditions over 2 hours via gradual water exchange. Eel >320 mm TL and all lamprey were tagged, under anaesthetic (2-Phenoxy-1-ethanol, 1 ml l^{-1}), with half-duplex Passive Integrated Transponder (PIT) tags (23 mm and 12 mm long, respectively) inserted through a small mid-ventral incision in the posterior quarter of the peritoneal cavity (mortality 0%, tag retention 99.6%,).Large eel and lamprey were weighed and measured during the tagging procedure and allowed at least 48 hours to recover from surgery before being used in experiments.

Treatment replicates were undertaken with multiple small (82 - 320 mm TL) or large (322 - 660 mm TL) eel between the 3 May and 21 July 2011 (temperature: μ = 16.2°C, σ = 0.8) or lamprey (291 - 401 mm TL) between the 24 January and 7 February 2013 (temperature: μ = 8.8°C, σ = 1.5) (Table 1). Timings and temperatures were representative of peak migration periods for both species (lamprey: Jang and Lucas, 2005; eel: Moriaty, 1986). The duration between capture and experimentation ranged from 2 - 17 and 51 - 65 days for eels and lamprey, respectively. Each replicate lasted 5.5

hours and was undertaken at night (23:00 - 04:30) (<0.1 lux) to coincide with peak eel and lamprey activity (eel: Haro and Kynard, 1997; Laffaille *et al*., 2007; Tesch, 2003, lamprey: Kelly and King, 2001; Moser *et al.,* 2002). Fish were acclimated to flume conditions in a porous container in the channel for 1 hour (22:00 - 23:00) before release into the experimental area 3 metres upstream of the downstream screen. Small eel were weighed and measured under anaesthetic (2-Phenoxy-1-ethanol, 1ml l^{-1}) after each replicate. Each fish was used only once during the study. Due to limited fish availability, passage experiments with lamprey were conducted only under the LV and HV regime. Temperature increase during experiments due to the pumps was small for both eel (μ = 0.4°C, σ = 0.5) and lamprey (μ = 0.6°C, σ = 0.5).

Table 1. Conditions encountered by European eel and European river lamprey during passage over a model Crump weir installed in a recirculating flume under either a high (HV), medium (MV) or low (LV) velocity regime with (treatment) or without (control) bristle passes installed during 2011 (eel) and 2013 (lamprey). *N* is the number of fish used per trial.

Date	*Hydraulic regime*	*Setup*	*Water depth (mm)* [a]		*Maximum velocity ($m\ s^{-1}$)*	*Maximum S.D. of velocity ($m\ s^{-1}$)*	*Mean water temp (°C)*	*N*	*Length range (mm)*	*PIT tagged*
			Upstream	*Downstream*						
Small European eel										
9 May	HV	Control	450	220	2.43	0.66	16.5	10	195-290	No
10 May	MV	Control	450	330	1.91	0.27	16.8	10	215-317	No
11 May	LV	Control	455	450	0.81	0.17	16.6	10	149-314	No
7 June	LV	Control	455	450	0.81	0.17	15.4	10	220-302	No
8 June	MV	Control	450	330	1.91	0.27	15.8	10	149-290	No
21 June	HV	Treatment	450	220	2.43	0.66	16.0	8	222-297	No
15 July	HV	Control	450	220	2.43	0.66	17.5	10	113-290	No
17 July	HV	Treatment	450	220	2.43	0.66	17.5	12	82-315	No
18 July	MV	Treatment	450	330	1.91	0.27	17.2	10	98-320	No
19 July	LV	Treatment	455	450	0.81	0.17	17.1	10	111-315	No
20 July	MV	Treatment	450	330	1.91	0.27	17.2	10	211-317	No
21 July	LV	Treatment	455	450	0.81	0.17	17.2	10	205-320	No
Large European eel										

3 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*14.7*	*10*	*437-660*	*Yes*
4 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.0*	*10*	*361-582*	*Yes*
8 May	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*16.2*	*10*	*366-575*	*Yes*
12 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*16.3*	*10*	*360-585*	*Yes*
16 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.3*	*10*	*357-630*	*Yes*
17 May	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*15.9*	*10*	*365-540*	*Yes*
18 May	*MV*	*Control*	*450*	*330*	*1.91*	*0.27*	*15.8*	*10*	*325-481*	*Yes*
19 May	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*16.3*	*10*	*333-501*	*Yes*
9 June	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*15.8*	*10*	*347-549*	*Yes*
13 June	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*15.1*	*10*	*405-544*	*Yes*
14 June	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*15.9*	*10*	*322-585*	*Yes*
15 June	*MV*	*Treatment*	*450*	*330*	*1.91*	*0.27*	*16.6*	*10*	*335-543*	*Yes*
16 June	*MV*	*Treatment*	*450*	*330*	*1.91*	*0.27*	*16.7*	*10*	*373-520*	*Yes*
19 June	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*15.6*	*10*	*326-510*	*Yes*
22 June	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*16.2*	*10*	*338-537*	*Yes*
River lamprey										
24 January	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*5.5*	*8*	*329-384*	*Yes*
26 January	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*6.8*	*8*	*320-395*	*Yes*
27 January	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*7.7*	*8*	*320-379*	*Yes*
28 January	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*8.7*	*8*	*320-373*	*Yes*
29 January	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*10.2*	*8*	*338-401*	*Yes*
30 January	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*10.6*	*8*	*340-388*	*Yes*
31 January	*HV*	*Control*	*450*	*220*	*2.43*	*0.66*	*10.6*	*8*	*339-395*	*Yes*
1 February	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*10.2*	*8*	*291-388*	*Yes*
2 February	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*9.2*	*8*	*322-379*	*Yes*
3 February	*HV*	*Treatment*	*450*	*220*	*2.43*	*0.66*	*9.0*	*8*	*314-391*	*Yes*
4 February	*LV*	*Treatment*	*455*	*450*	*0.81*	*0.17*	*9.3*	*8*	*324-371*	*Yes*
6 February	*LV*	*Control*	*455*	*450*	*0.81*	*0.17*	*7.6*	*8*	*327-388*	*Yes*

a: Measured 5 metres upstream or downstream of the weir crest.

Due to staggered eel availability, source location could not be randomised among treatments. For the purpose of this study it was assumed that there were no differences in behaviour / swimming ability among sources. Mean water temperature did not differ among treatments for any group. Mean TL did not differ among treatments for small and large eel. Despite random allocation, the mean TL of lamprey differed among treatments (one-way ANOVA: $F(3, 8) = 4.578$, $p<0.05$), being higher under the HV control. Across treatment comparisons were considered acceptable as the difference was deemed small from a biological perspective (8.7 mm).

2.3. Fish behaviour

Fish behaviour was monitored using 2-4 low-light digital video cameras (AV-TECH Sony Effio 580TVL CCD) under infrared illumination, enabling visual assessment of movement and differentiation of route selection by individuals. The field of view of the two overhead cameras (control + treatment conditions) spanned the width of the flume at the crest and downstream extent of the weir. The two side cameras (treatment conditions only) monitored fish movement in the bristle passes at the crest of the weir through the glass walls (for camera locations, see Figure 1). Video footage was recorded and reviewed using split-screen multi-channel acquisition and playback software (NUUO ltd., Taiwan). Individual large eel or lamprey were identified during movement over the weir using Half Duplex PIT telemetry (antennae installed at the trailing edge and crest of the weir, Figure 1a, b). Each antenna (3 coils of 2.5 mm^2 stranded 0.25 mm copper wire) was connected to a PIT detection system incorporating a single reader and two external dynamic tuning units (DEC-HDX-MUX-LOG 134.2 kHz, Wyre Micro Design Ltd., UK), powered using a 110Ah 12v leisure battery, and connected to an external data logger (AntiLog RS232, Anticyclone Systems Ltd., UK). The antenna wiring was attached directly to the face of the weir and had minimal impact on flow due to its low profile. The PIT system was tested by ensuring that tags (either size) held in a clenched fist were consistently detected when passed through each loop at any angle or location.

For each replicate the video footage and/or PIT data were interrogated and relevant passage events recorded (Table 2). As fish could move freely both up and downstream of the weir throughout the experimental period, multiple upstream passage events per fish were possible during each replicate. Based on the passage events the following metrics were calculated for all fish groups: 1) *number of failed attempts,* 2) *number of upstream passes,* 3) *bristle pass use,* and 4) *passage efficiency* (Table 2). For large eel and lamprey, to which passage events could be attributed to individual tagged fish, additional metrics were calculated: 5) *percentage attempts*, 6) *passage success*, 7) *number of attempts before upstream passage*, and 8) *delay* (Table 2). Tagged fish not detected at the downstream PIT antenna during the experiments (3 lamprey: 2 LV treatment, 1 LV control), were considered not to have explored their surroundings or sampled treatment conditions, and were not included in these metrics. For lamprey, which have the ability to attach to surfaces using their oral disc (Kemp *et al.*, 2009), specific attachment metrics were also calculated: 9) *percentage attachment*, 10) *number of attachments*, and 11) *mean duration of attachment* (Table 2).

Table 2. Definition of the passage events and metrics obtained for the small eel, large eel (*LE*), and/or lamprey (*L*) as they passed over an experimental Crump weir, and the statistical tests used.

Event/metric	**Definition**	**Group**	**Statistical test for variable:**	
			Hydraulic regime	Treatment
	Events			
Attempt	*Progression upstream, of any part of the body onto the downstream face of the weir upstream of the hydraulic jump.*	All	N/A	
Upstream pass over the weir	*Passage of whole body upstream beyond the weir crest.*	All	N/A	
Upstream pass via a bristle pass	*Passage of whole body upstream beyond the weir crest via a bristle pass.*	All	N/A	
Attachment	*Attachment using oral disk on the downstream face of the weir upstream of the hydraulic jump.*	L	N/A	
	Metrics			
1. Number of failed attempts	*Total number of attempts not resulting in upstream passage normalised by the number of fish per replicate.*	ALL	*One-way ANOVA*[a]	*Student t tests*
2. Number of upstream passes	*Total number of upstream passes normalised by the number of fish per replicate.*	ALL	*One-way ANOVA*[a]	*Student t tests*
3. Bristle pass use	*Quotient of the number of upstream passes via a bristle pass and total number of upstream passes per replicate.*	ALL	*Not assessed*	*Not assessed*
4.Passage efficiency	*Total number of times fish passed the weir as a percentage of total attempts per replicate.*	ALL	*One-way ANOVA*[a]	*Student t tests*

5. Percentage attempts	*Number of fish that attempted as a percentage of the total per treatment.*	LE, L	*Pearson's Chi-square (X^2) tests.*[b]
6. Passage success	*Number of fish that passed the weir as a percentage of those that attempted per treatment.*	LE, L	*Pearson's Chi-square (X^2) tests.*[b]
7. Number of attempts before upstream passage	*Number of attempts before first upstream passage event for each fish.*	LE, L	*Discrete-time hazard model (Logit function) and the Wald statistic (W).*[c]
8. Delay	*Time between the first detection at the downstream PIT antennae and first upstream passage for each fish.*	LE, L	*Kaplan-Meier product-limit estimator and the Log Rank (Mantel-Cox) statistic (X^2_{mc}).*[c]
9. Percentage attachments	*Total number of fish that attached as a percentage of the total that attempted per treatment.*	L	*Pearson's Chi-square (X^2) tests.*[b]
10. Number of attachments	*Number of attachments normalised by the number of fish per replicate.*	L	*Two-way ANOVA*
11. Mean duration of attachment	*Quotient of total duration and number of attachments per replicate.*	L	*Two-way ANOVA*

a: Brown and Forsyth F ratio used in cases that violated homogeneity of variance.
b: Fisher's exact tests (FET) used if expected frequencies were < 5.
c: Event time analysis (Singer and Willet, 2003).

Discrete attempts (see Table 2) were delineated by a fish drifting back downstream of the hydraulic jump for > 1 second or by an attachment (see Table 2) on the downstream face of the weir (lamprey only). Any further upstream progression observed on the downstream face of the weir was considered a separate attempt as it involved an observable increase in swimming speed to counter the high velocity flow. All statistical analysis was undertaken in SPSS v20 (IBM, USA). Due to low replicate numbers it was not possible to assess interaction effects. Hence, the influence of hydraulic regime was assessed under control conditions only and the influence of treatment was assessed separately under each hydraulic regime. Percentage data were arcsine square root transformed prior to statistical analysis (*see:* Sokal and Rohlf, 1995). *Delay* and *number of attempts before upstream passage* were assessed using time to event analysis (Singer and Willet, 2003) (Table 2). This method provides unbiased estimates by including fish that fail to pass the weir (right-censored individuals) in a probability function (Cumulative Probability of Passage [CPP]) at any given time or number of attempts (see: Castro-Santos and Haro, 2003).

3. Results

A high percentage of the observed passage events were detected by the PIT system (Large eel: 97.2%, Lamprey: 93.0%) allowing identification of the majority of individuals. Passage events with no directly associated PIT data were assigned to individuals with a high degree of confidence by assessing historic and future detections combined with visual tracking of the fish over time.

Number of failed attempts was not influenced by hydraulic regime or treatment for any group (μ ± S.E.: small eel = 1.87 ± 0.64, large eel = 3.74 ± 1.10, and lamprey = 5.24 ± 1.47).

Number of upstream passes was negatively related to maximum velocity for all groups (small eel: $F(1, 3) = 157.984$, $p < 0.01$, large eel: $F(1, 6) = 19.020$, $p < 0.01$, and lamprey $F(1, 4) = 91.240$, $p < 0.01$), but was not influenced by treatment (Figure 3).

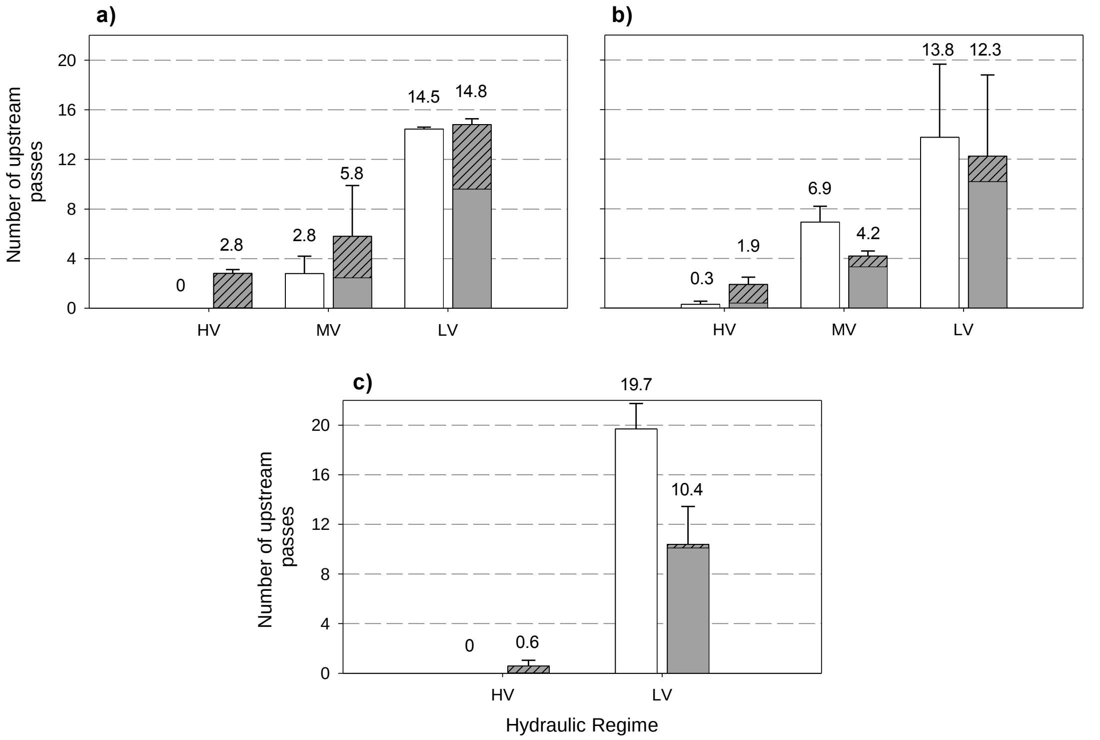

Figure 3. Mean *number of upstream passes* per fish for (**a**) small eel, (**b**) large eel, and (**c**) lamprey without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydraulic regimes. Hatched sections of the grey bars indicate the proportion of upstream passes that occurred via the bristle passes. Error bars represent ± 1 S.E..

Bristle pass use (μ ± S.E.) was highest under the HV, and lowest under the LV regime for small eel (100 ± 0.0%; 35.1 ± 6.0%), large eel (78.3 ± 6.3%; 16.7 ± 6.1%), and lamprey (100 ± 0.0%; 2.6 ± 1.1%) (Figure 3).

Passage efficiency was negatively related to maximum velocity for small eel ($F(1, 3) = 43.841$, $p < 0.01$), large eel ($F(1, 5) = 24.961$, $p < 0.01$) and lamprey ($F(1, 4) = 145.462$, $p < 0.001$) (Figure 4). Under the HV regime, passage efficiency was higher for small

(91.5%; $t(1) = -31.658$, $p < 0.05$) and large eel (56.7%; $t(3) = -5.057$, $p < 0.05$) when the bristle passes were installed (Figure 4). Treatment did not significantly influence *passage efficiency* for lamprey under the HV regime, or for any group under the MV or LV regime.

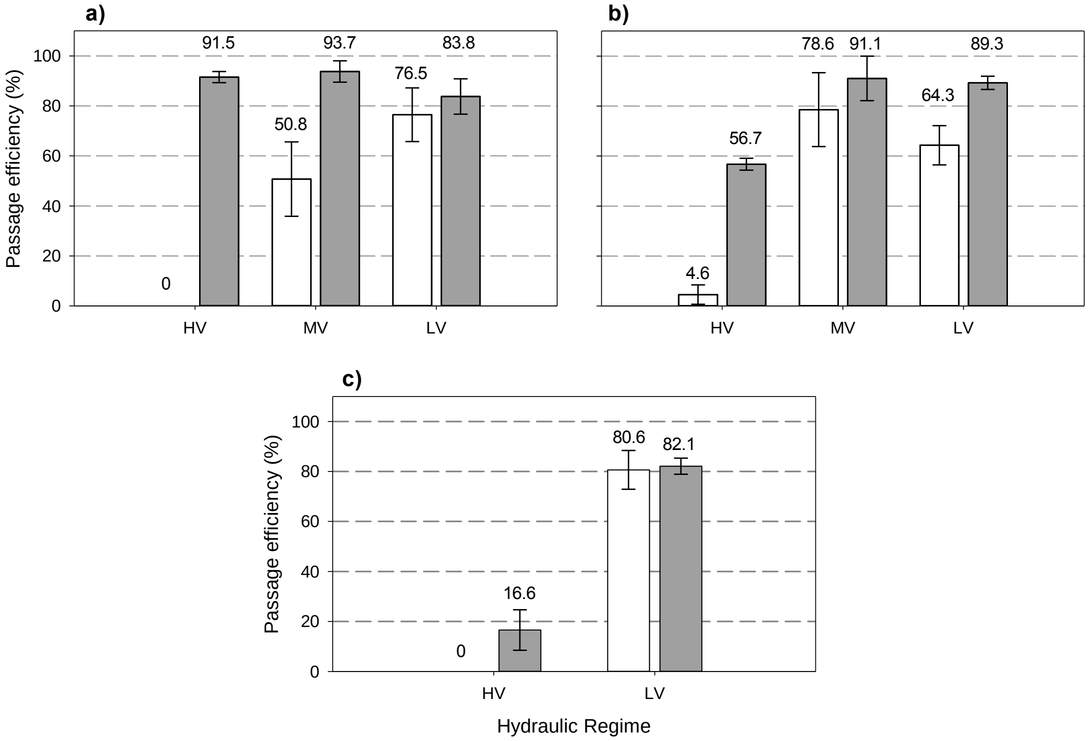

Figure 4. Mean p*assage efficiency* (%) for (**a**) small eel, (**b**) large eel, and (**c**) lamprey without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydraulic regimes. Error bars represent ± 1 S.E..

Percentage attempts for large eel was not influenced by hydraulic regime or treatment, and was consistently high (>85%). For lamprey, *percentage attempts* was not influenced by treatment but was lower under the HV (62.5%) compared to the LV (95.6%) regime ($X^2(1) = 15.034$, $p < 0.001$).

For large eel, *passage success* was lower under HV (17.2%) than the MV (92.3%) ($X^2(1) = 41.85$, $p < 0.001$) and LV control (100%) ($X^2(1) = 30.99$, $p < 0.001$), but not different between the MV and LV control (Figure 5a). For lamprey, *passage success* was lower under the HV (0%) than LV control (100%) ($X^2(1) = 37$, $p < 0.001$) (Figure 5b). *Passage success* was higher under the HV treatment than control for both large eel (76.5%; $X^2(1) = 5.785$, $p < 0.001$) and lamprey (35.7%; *FET*: $p < 0.05$) (Figure 5). There was no influence of treatment under the MV or LV regime (Figure 5).

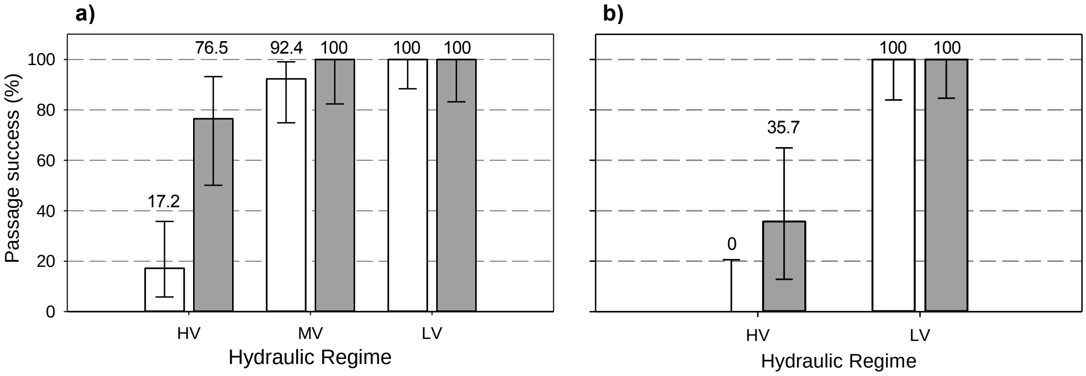

Figure 5. *Passage success* (%) for (**a**) large eel and (**b**) lamprey without (control: clear bars) and with (treatment: grey bars) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydraulic regimes. Error bars are 95% confidence intervals calculated using the Clopper-Pearson exact method.

For large eel, *number of attempts before upstream passage* was higher under HV control (20.5% CPP after 3 attempts) than the MV (>50% CPP after the 1st attempt)

($W_s(1) = 26.729$, $p < 0.001$) and LV control (>50% CPP after the 1st attempt) ($W_s(1) = 31.593$, $p < 0.001$), but was not different between the LV and MV control (Figure 6a). For lamprey, *number of attempts before upstream passage* was higher under HV control (0% CPP despite up to 50 attempts) than the LV control (>50% CPP after the 1^{st} attempt) ($W_s(1) = 29.176$, $p < 0.001$) (Figure 6b). *Number of attempts before upstream passage* was lower under the HV treatment than control for both large eel (>50% CPP after the 2^{nd} attempt; $W_s(1) = 18.275$, $p < 0.001$) and lamprey (30.6% CPP after the 2^{nd} attempt; $W_s(1) = 45.702$, $p < 0.001$) (Figure 6). There was no influence of treatment under the MV or LV regime (Figure 6).

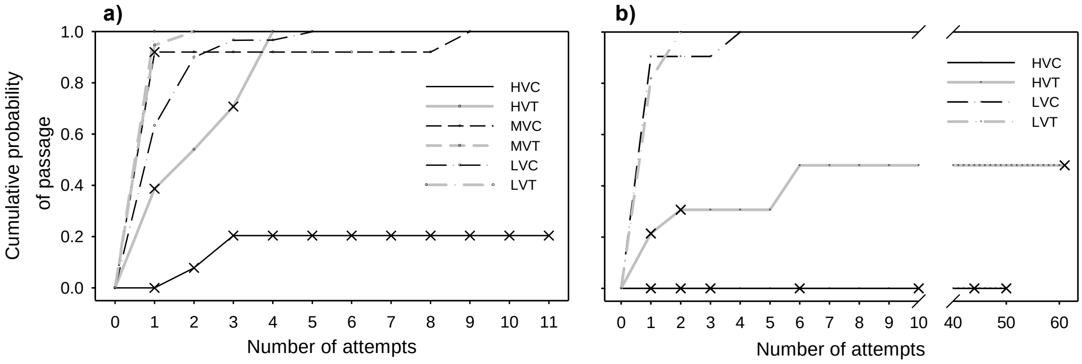

Figure 6. Cumulative Probability of Passage (CPP) upstream with number of attempts for (**a**) large eel and (**b**) lamprey with (treatment: grey lines) and without (control: black lines) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity regimes. Crosses represent right censored data.

For large eel, *Delay* was longer under the HV control (17.2% CPP after 330 minutes) than the MV (50% CPP after 13.3 minutes) ($X^2_{mc}(1) = 44.974$, $p < 0.001$) and LV control (50% CPP after 5.36 minutes) ($X^2_{mc}(1) = 69.399$, $p < 0.001$), and longer under

MV control than the LV control ($X^2_{mc}(1) = 22.837$, $p < 0.001$) (Figure 7a). For lamprey, *Delay* was longer under HV control (0% CPP after 330 minutes) than the LV control (50% CPP after 19.28 minutes) ($X^2_{mc}(1) = 38.767$, $p < 0.001$) (Figure 7b). *Delay* was shorter under the HV treatment than control for both large eel (50% CPP after 115 minutes: $X^2_{mc}(1) = 16.260$, $p < 0.001$) and lamprey (35.7% CPP after 330 minutes: $X^2_{mc}(1) = 6.730$, $p < 0.01$) (Figure 7). There was no influence of treatment under the MV or LV regime (Figure 7).

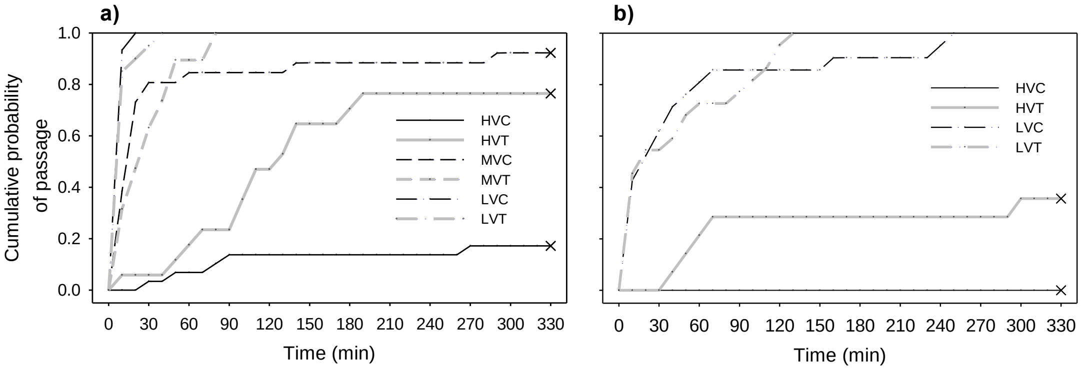

Figure 7. Cumulative Probability of Passage (CPP) upstream against time for (**a**) large eel and (**b**) lamprey with (treatment: grey lines) and without (control: black lines) bristle passes installed under the low (LV), medium (MV), and high (HV) velocity hydraulic regimes. Crosses represent right censored data.

Neither *percentage attachments* (34.2%) nor *number of attachments* (µ ± S.E.: 16.0 ± 6.8) were influenced by hydraulic regime or treatment. *Mean attachment duration* was influenced by hydraulic regime ($F(1, 8) = 7.807$, $p < 0.05$), being longer under the HV (150.7 ± 27.0s) than LV regime (46.5 ± 19.6s), but not by treatment.

Lamprey were not as proficient at navigating the bristled substrate as eel, often struggling to make progress through the passes. Lamprey were observed to have striated marks along the length of their body after exiting the bristle passes (Figure 8).These were temporary and disappeared within 24 hours. Eel showed no obvious physical external effects of bristle pass use.

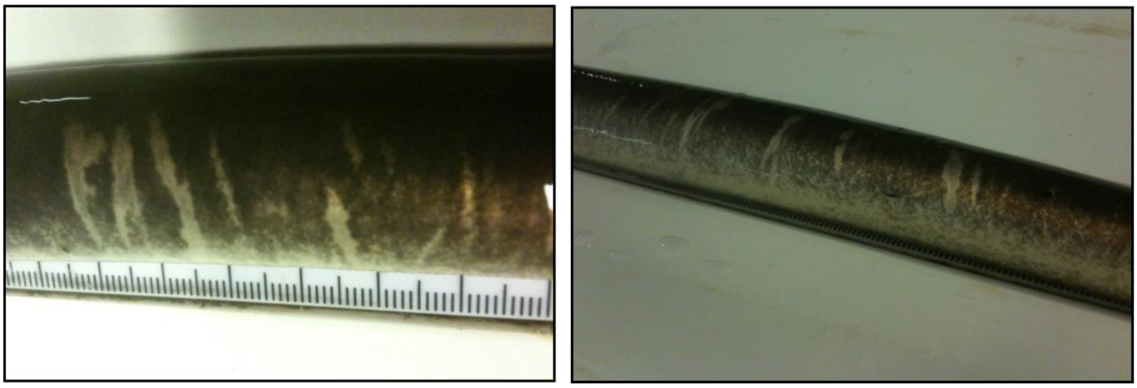

Figure 8. Two examples of striated marks on the flanks of lamprey caused by bristle pass use. Scale is in mm.

4. Discussion

This study experimentally assessed the efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel and river lamprey at a low-head gauging weir. Eel and lamprey were highly motivated to explore their surroundings and move upstream. Bristle passes improved their ability to do so when high flow velocities and turbulence restricted passage. Interspecific variation in efficacy was apparent with the passes being more effective for eel than for lamprey.

Barriers can block or impede the movement of fish between essential rearing and spawning habitat (Lucas and Baras, 2001). Excessive energetic costs during migration can compromise the physiological and behavioural processes necessary for sexual maturation and successful reproduction (Mesa *et al.*, 2003). Delayed migration can increase predation risk (Peake *et al.*, 1997; Rieman *et al.*, 1991), physiological stress, and susceptibility to disease (Loge *et al.*, 2005). For adult lamprey, as for most anadromous species, additional energetic costs during upstream movement to spawning grounds cannot be compensated as feeding ceases during migration (Lucas and Baras, 2001). In this study, bristle passes mitigated to some extent these negative effects by providing higher passage success and efficiency, shorter delay, and fewer failed attempts for both eel and lamprey as they passed the model crump weir.

A key concern in the design of the experiment was to allow fish sufficient time to pass the obstruction. As such, a single 5.5 hour long trial was undertaken per night. This, in combination with the limited duration of the experimental period, resulted in a low number of replicates. As such, the statistics presented could be considered conservative with a high chance of a type II error (i.e. only large effects being detected as significant). Although not statistically significant the measured mean and variance values indicate that bristle passes may also be affecting the number of upstream passes per night and having further beneficial influences on passage efficiency outside of those identified through the inferential statistics. For example, in addition to the bristle passes significantly improving passage efficiency for small and large eel under the HV regime, the data indicate they may have also improved passage efficiency for lamprey, and for small and large eel under the medium and low velocity regime. Further experimental data would have to be collected to validate these trends.

This study provides: 1) evidence that bristle passes improve the upstream passage of both eel and lamprey under experimental conditions and 2) a mechanistic understanding of how they function which will help improve future pass design. However, the majority of barriers where bristle passes are likely to be installed are larger than the model weir used in this experiment (e.g. increased head difference and distance for traversal). Larger scale flume trials would provide useful information of the effects of increased barrier size but the facilities to undertake such experiments are rare. In addition, flume trials cannot adequately account for the numerous confounding variables that occur in situ. The next step in validating the effectiveness of side-mounted vertically oriented bristle passes is to undertake robust field studies at larger barriers.

In good years, juvenile European eel are recruited into the lower catchment of freshwater systems in large numbers (Moriaty, 1990). As there is a causal relationship between body length and absolute swimming performance (Beamish, 1978; Clough *et al.*, 2004) small juvenile eel are particularly susceptible to velocity barriers. In this study, bristle passes facilitated the upstream passage of eel as small as *ca.* 100mm. Enhanced dispersal of this life-stage is particularly important as it is likely that density-dependent mortality (see: Vøllestad and Jonsson, 1988) would limit system productivity unless early upstream colonisation is achieved.

In comparison to small eel, a higher percentage of large eel passed over the weir directly, rather than via a bristle pass under each hydraulic regime. Possibly because bristle spacing was less appropriate for larger eel (restricted manoeuvring space) or their higher absolute swimming capability enabled them to more easily ascend the weir. Similarly, a lower percentage of both large and small eel passed the weir via the bristle passes under the low compared to high velocity treatment. Probably due to it being easier for all sizes to ascend the weir directly under these conditions. Few lamprey passed through the bristle passes under any treatment. Those that did exhibited cutaneous abrasions, which can increase a fish's susceptibility to bacterial infection (Bader *et al.*, 2006). For this species, further research to investigate how design alterations, such as increasing bristle spacing, may improve passage success and reduce abrasion is warranted. The implication of such design modifications on eel passage should be considered in parallel.

Poor attraction efficiency is known to limit the overall effectiveness of fish passes (Bunt *et al.*, 2001; Moser *et al.*, 2002). In this study, limited downstream area, long trial duration, and the highly active nature of both species resulted in a very high chance of individuals encountering the entrance of a bristle pass. In addition, both eel and lamprey tended to move upstream along the flume walls further increasing their chances of encountering a pass entrance. Actively migrating juvenile eels tend to migrate on mass in the shallow low velocity regions along the banks of estuaries and rivers (Tesch, 2003), and passes located along channel boundaries generally catch more individuals than those in the centre (Piper *et al.*, 2012). As such, the configuration of bristle pass tested in this study (attached directly to the wing wall of a gauging structure) probably represents the optimal location to maximise attraction efficiency. However, it is acknowledged that at complex sites the low flow through this type of pass may limit attraction. In such cases extra attraction flow should be provided (see: Piper *et al.*, 2012).

Unlike eel, lamprey lack paired fins and struggle to maintain stability in turbulent conditions (see: Liao, 2007). A lower percentage of lamprey attempted to pass the weir under the high compared with low velocity regime, possibly because turbulent conditions associated with the hydraulic jump inhibited upstream movement. Lamprey also frequently attached to the face of the weir and attempted to pass using a burst-attach-rest mode of locomotion thought to enhance performance (Kemp *et al.*, 2011; Quintella *et al.*, 2004). Previous studies indicate that lamprey vary their attachment behaviour in response to hydraulic conditions (Kemp *et al.*, 2011), an observation supported by the results of this study in which mean duration of attachment was longer under the high velocity regime, presumably to facilitate recovery.

In this study, when high velocity and turbulence restricted passage, bristle passes increased the passage success of large eel and lamprey to 76.5 and 36.5%, respectively. For catadromous European eel, such levels may be adequate to maintain a stable population due to the extended duration of their diffusive upstream migration (i.e. a high probability of being able to pass during a high-flow event). For anadromous river lamprey, which are energetically and temporally constrained during their upstream migration, such levels will likely limit system productivity. It is recommended that new fish passage technologies for both species continue to be investigated. However, for a small barrier the configuration of bristle pass tested would seem to represent a viable low-maintenance and low-cost option to improve habitat connectivity for European eel. For river lamprey, while the wing-wall bristle media shows potential for assisting passage, further studies over a wider range of obstacle heights and bristle spacing are needed to determine whether this approach has merit.

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