Climbing the ladder: an evaluation of three different anguillid eel climbing substrata and placement of upstream passage solutions at migration barriers

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Abstract

Conservation programmes for endangered, long-lived and migratory species often have to target multiple life stages. The bottlenecks associated with the survival of juvenile anguillid eels migrating into inland waters, the survival and growth of the freshwater life stage, as well as the recruitment and survival of silver eels, migrating back to the ocean to spawn, must be resolved. In this study, we focus on the efficiency of passage solutions for upstream-migrating juveniles. Such solutions can consist of inclined ramps lined with wetted climbing substrata. We evaluated different commonly used substrata in a controlled experiment, recorded eel behaviour at the entrance of the ramp with infrared videography and validated the experimental results at a hydropower dam, where we also investigated the effects of ramp placement on performance. In the experiment on eel substratum selection, 40% of the eels passed in lanes with studded substratum, whereas only 21 and 5% passed using open weave and bristle substrata respectively. Video analysis revealed that the studded substratum attracted more approaches and initiated climbs than the other substrata, but once a climb had been initiated, passage success rates did not differ between substrata. Eels using the studded substratum climbed 26% faster than those using the bristle substratum and almost four times as fast as those climbing in the open weave. The superior performance of the studded substratum was supported by data from the field validation. Moreover, ramps positioned by the bank with low water velocities caught the most eels, but proximity to the dam had no effect on performance. To strengthen the European eel population, more juveniles need to reach their freshwater feeding grounds. A critical step to achieve this increase is to equip upstream passage solutions with suitable substrata and to optimize ramp placement at migration obstacles.

Introduction

The ultimate goal of the management of endangered species is for them to become self-sustaining elements in their natural ecosystems (Tear *et al.*, 1993). While there is a general positive relationship between funding for conservation projects and successful recovery (Gerber, 2016), decisions made by managers on how to spend this funding can have major effects on the probability of success. These decisions are, however, often made without consulting evidence or under uncertainty, resulting in potentially cost ineffective species conservation practices (Sutherland *et al.*, 2004; Milner-Gulland & Shea, 2017). Moreover, conservation actions need to target the most critical life stage for population growth. For instance, in amphibians, high mortality rates early in life generally act as the main population bottleneck (Semlitsch, 2002). Contrastingly, in long-lived species, such as crocodiles and ungulates, survival at both the adult and juvenile life stages play important roles for population growth dynamics (Owen-Smith & Mason, 2005; Briggs-Gonzalez *et al.*, 2017). Furthermore, programmes for conservation of migratory species that need different habitats to complete their life cycles may have to target several life stages in different geographical areas (Bowen *et al.*, 2005). For example conservation of the globally threatened anguillid eels (Jacoby *et al.*, 2015) is complicated by their complex life histories, including multiple life-history stages, catadromy and semelparity (Tesch, 2012). Since eels are panmictic and their marine spawning areas are located far from their freshwater rearing habitats (Aida, Tsukamoto & Yamauchi, 2012;

Tesch, 2012), the effects of conservation measures on recovery are difficult to evaluate (McDowall, 1992). Therefore, all life stages of anguillids should be conserved as it remains unknown where the main population bottlenecks occur.

The decline in the abundance of anguillid eels has been suggested to be caused by multiple factors, such as pollution, parasites, disease, exploitation, habitat loss, altered oceanic conditions and migration barriers (Jacoby *et al.*, 2015). In particular, migration barriers, obstructing eels from reaching their freshwater rearing grounds and subsequently the ocean on their spawning migration, constitute a major challenge (Righton & Walker, 2013). The decline of European eel *Anguilla anguilla* has been particularly severe, and during the last 45 years the recruitment has been reduced by more than 90–95% across its geographical range (Jacoby & Gollock, 2014a). The species has received the status *critically endangered* by the International Union for Conservation of Nature's Red List of Threatened Species (IUCN), and in 2007, the European Union launched a regulation (Council Regulation (EC) No 1100/2007, EU, 2007) that required the member states to develop national eel management plans. Other anguillid eel species, for example Japanese (*A. japonica*) and American (*A. rostrata*) eel, have also faced recent drastic declines, and broad conservation actions for these species have been initiated (MacGregor *et al.*, 2013; Jacoby & Gollock, 2014b; Jacoby *et al.*, 2017).

It has been suggested that the current, low recruitment of juvenile European eel to their freshwater rearing grounds may act as a population bottleneck (e.g. Bult & Dekker, 2007; Laffaille, Caraguel & Legault, 2007; Mouton *et al.*, 2014). Before the population decline, optimizing upstream passage solutions was not as imperative as it is today, as early passage solutions succeeded in transporting enough eels (due to high densities) past the barriers to reach the carrying capacity of the inland waters upstream of the barrier, at least in south-western Europe (Dekker, 2003). At present, the alarmingly low densities of upstream-migrating juvenile eels suggest that immediate actions are required to increase the proportion of eels passing upstream migration barriers. During recent years, several new upstream passage solutions have been developed, but research assessing the performance of these solutions has until recently been completely lacking, and only a handful of studies address this issue (Kerr, Karageorgopoulos & Kemp, 2015; Vowles *et al.*, 2015, 2017; Jellyman, Bauld & Crow, 2017). In particular, further studies evaluating the effects of upstream passage solution design and placement are needed.

The swimming capacity of juvenile eels is normally insufficient to ascend traditional technical fishways (McCleave, 1980). Upstream passage solutions for juvenile eels instead take advantage of the eels' rheotactic and thigmotactic climbing behaviour (Jellyman, 1977; Geffroy & Bardonnet, 2012) and generally consist of an inclined ramp lined with a wetted climbing substratum (Solomon & Beach, 2004) with an attraction flow at the entrance of the ramp (Piper, Wright & Kemp, 2012). The features of the ramps, such as climbing substratum and slope, are critical, as the efficiency in aiding the ascent of juvenile eels (both in terms of passage success

rate and climbing velocity) may directly affect the performance of the passage solution (Jellyman *et al.*, 2017; Anwar, 2018). Evaluations of single substrata have shown that, for example studded plastic tiles and bristle passes improve passage success at Crump weirs (Kerr *et al.*, 2015; Vowles *et al.*, 2015, 2017), but few studies have directly compared the performance of different climbing substrata (Jellyman *et al.*, 2017). A recent study by Tamario *et al.* (2019) reports that existing upstream passage solutions targeted at juvenile eels in general have suboptimal performance, indicating a need for further research on passage design. In this study, we evaluated and compared the performances of studded, open weave geotextile and bristle climbing substrata (Solomon & Beach, 2004). We tested their efficiency in attracting and passing upstream-migrating eels in a controlled experiment, in which eels could choose climbing substratum. The behaviour of the climbing eels was analysed with infrared videography. We validated the results from the controlled experiment by carrying out a field study at a hydropower dam, where also ramp placement in relation to water flow and distance from the migration obstacle was evaluated.

Materials and methods

Controlled experiment

We conducted the experiment in two outdoor concrete pools (length × width × depth = 4.0 × 4.0 × 0.6 m) at Statkraft's fish hatchery at the River Lagan hydropower plant (N 56.516, E 13.049, Laholm, Sweden) during eight nights from 27 June to 8 July 2016 (sunset – sunrise: 22:00 – 04:30). We covered the pools with a partly light-permeable tent to avoid avian predation. Six ramps, each attached to a holding cage constructed of wood and net (length × width × depth = 1.0 × 1.1 × 0.7 m), were positioned in the concrete pools (Fig. 1). Ramps consisted of three aluminium lanes (2.0 × 0.32 m; inclination = 30°), separated by walls (10 cm high) and lined with (1) a studded, (2) an open weave and (3) a bristle climbing substratum respectively (Solomon & Beach, 2004). The positions of the three lanes with different substrata were assigned according to random permutation within each ramp. The entrances of the lanes were positioned so that water covered approximately 15 cm of their lower ends. Each lane was fed by water (0.07 L s^{-1}) from the reservoir of the nearby hydropower plant in the River Lagan, and water temperature ranged from 18.3 – 19.0°C. Water was released evenly spread over the upper end of the lanes (and wetted their full widths) and as single sprays at the entrances of the lanes (functioning as attraction water; Piper *et al.*, 2012). Eels that climbed the full length of a lane fell into a collecting bucket. We equipped two of the six ramps with infrared-sensitive video cameras and infrared lamps (NVAHD-2DN5106H/IR-1, wavelength = 850 nm; Novus, AAT Holding S.A., Warszawa, Poland). During three nights (20:00 – 08:00; 4 – 8 July 2016), eels that approached and ascended either of the three climbing substrata were recorded. The video cameras filmed the three entrance ends
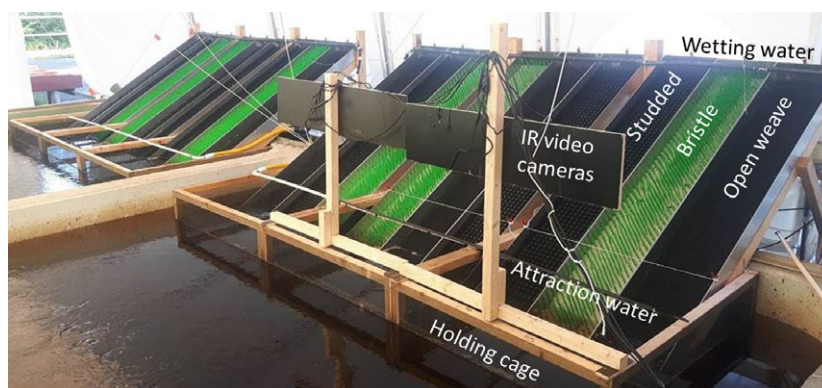
Figure 1 Experimental setup to test in which substratum juvenile eels chose to climb. Each ramp (*n* = 6, 30° inclination) consisted of three lanes lined with a studded, an open weave and a bristle substratum (Fig. 2) respectively. Substrata were wetted by pumped water over the upstream end of the lanes, and attraction water was released as single sprays in front of the lane entrances. Eels were released in each downstream holding cage and could climb the ramp in one of the lanes to end up in a collecting bucket above each lane. The behaviour of the eels was filmed with infrared cameras in two of the ramps.

of the lanes in a ramp, and videos therefore only showed eels that approach the submerged part (15 cm) and 50 cm of their climb in each wetted climbing substratum.

Different plastic substrata with studs have recently been used in eel and elver passage solutions (Solomon & Beach, 2004; Vowles *et al.*, 2015, 2017; Jellyman *et al.*, 2017). The studded substratum used in our study (designed for eel passes; EF-16, Elghagen Fiskevård, Åstorp, Sweden) consisted of dark coloured plastic tiles with rows of circular studs (height = 14 mm; max. diameter = 28 mm) and depressions (depth = 14 mm; max. diameter = 16 mm) evenly spaced 14 mm apart (Fig. 2). Open weave geotextile mats with three-dimensionally looped polyamide monofilaments fused at their intersections, normally used for erosion control, have earlier been installed as climbing substratum in many upstream passage solutions for eel (Solomon & Beach, 2004). In this study, we used the open weave geotextile Enkamat 7020 (Colbond, Geosynthetics, Arnhem, the Netherlands; Fig. 2), the substratum legally required by the Danish eel management plan. We stapled the geotextile mats to dark coloured wood sheets fitted into the aluminium lanes. Bristle and brush passes have also been extensively used in upstream passage solutions (Solomon & Beach, 2004), and

we used bristle mats (Fish-Pass, rigid mixed substrates 1.0 × 0.32 m, Ichtyologic, Rennes, France) with green brush bundles (1 mm filaments: height = 7 cm) on a smooth white plastic surface (Fig. 2). This bristle substratum is designed to pass different size classes of eels and therefore has areas with different spacing between the brush bundles (1.6 cm apart in a 12-cm-wide central area and 2.8 cm apart in the rest of the lane).

Juvenile eels used in the experiment were collected directly below the River Lagan hydropower dam during the period 27 June – 7 July, 2016, from a refuge trap, consisting of a floating rectangle (50 × 50 cm) made from plastic tubing (diameter = 50 mm) with attached bundles (30 cm) of unwound synthetic black rope (diameter = 12 mm) underneath. In the experiment, we used eels with lengths from 60 to 110 mm and eel individuals participated only once in the experiment.

At 20:00 each experimental night, ten juvenile eels were transferred from the refuge trap to each holding cage. At 08:00 the following morning, we counted and removed the eels in each collecting bucket, as well as all individuals remaining in the holding cage. In total, data were collected during eight nights from the six ramps. We used the
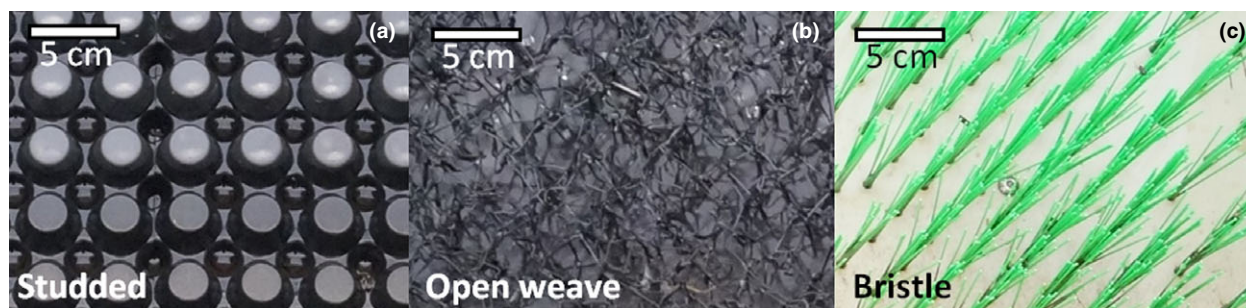
Figure 2 Three different climbing substrata were used in the study. The studded plastic substratum (a) had both studs and depressions, the open weave geotextile substratum (b) had three-dimensionally looped polyamide monofilaments and the bristle substratum (c) had green brush bundles fastened on white plastic sheets.

proportion of the ten eels found in each of the three collecting buckets in each ramp as a measure of eel choice of climbing substrata. The video recordings were evaluated for eel behaviour. We defined an 'approach' as when an eel swam into the area over the submerged part of the climbing substratum by at least half of its body length. The eel could then leave the field of view or initiate a 'climb', which started when the eel ascended the emerged part of the climbing substratum with more than half of its body length. A 'success' was defined as when the eels successfully climbed 50 cm and left the upstream end of the field of view. The time it took from an initiated to a successful climb was used to calculate climbing velocity. Eels that aborted their climbs after they had passed the field of view were not quantified, because these fallbacks generally moved fast with the water flow, making them difficult to detect.

Field validation

We validated the results from the controlled experiment by a field study in 2017. The six ramps from the controlled experiment were attached to floating devices, and we positioned these units in the tailrace of the Laholm hydropower plant in the River Lagan (Fig. 3). This tailrace runs in a relatively straight channel that connects with the old riverbed 200 m downstream of the power plant. The turbine outlet is positioned approximately 20 m from the dam on the southern side of the channel, resulting in faster water currents at this side. We chose to position the ramps along the banks (three on each side; 1–2 m from the bank at low flow conditions) because upstream-migrating juvenile eels normally avoid the channel centre (Piper *et al.*, 2012). The ramps were fixed with rope approximately 30 m apart, with the two most upstream ramps positioned within a meter from the dam wall.

Due to a dry summer in 2017, there was little water in the reservoir of the hydropower plant, and turbines were in operation at night only for 2.5 h (21:45 – 00:15; 62 m^3 s^{-1}).

We carried out the field validation during five nights (2 – 7 July 2017). When the turbines were in operation, pumped water (0.07 L s^{-1}) wetted the climbing substrata and was released as attraction water in the same way as in the controlled experiment, and eels should thus only have been able to climb the ramps during this period. Eels were counted in the collecting buckets at 08:00 each morning. Water velocities when the turbines were in operation, measured at 0.5 m depth in front of the entrances (downstream) of the three ramps along the northern bank, were in the upstream-downstream direction 0, 0 and 0.2 m s^{-1} respectively. The corresponding values for the ramps positioned along the southern bank were −0.2, 0.2 and 0.5 m s^{-1}. The negative velocity by the ramp positioned near the dam on the southern side of the channel was due the turbine outlet releasing its water downstream of this ramp, resulting in an eddy (Fig. 3).

Statistical analyses

Proportions were arcsine square root transformed and all other variables measured in the controlled experiment were log transformed to achieve normally distributed data. To reduce problems with autocorrelation, the proportions of eels that did not succeed in climbing the ramp were removed from the further analyses of substratum selection. Differences in the proportions among substrata were analysed with one-way ANOVAs with date included as a random factor. For the behavioural analyses from the video recordings, we included group ID as a random factor to account for the overall activity of each group of ten eels. Pairwise Bonferroni corrected post hoc comparisons were made between the substrata.

We fitted the count data from the field validation to a generalized linear mixed model with a Poisson distributed log link function. We used substrata, position north-south (i.e. near the bank with low and high water velocities respectively), position upstream-downstream and the interaction
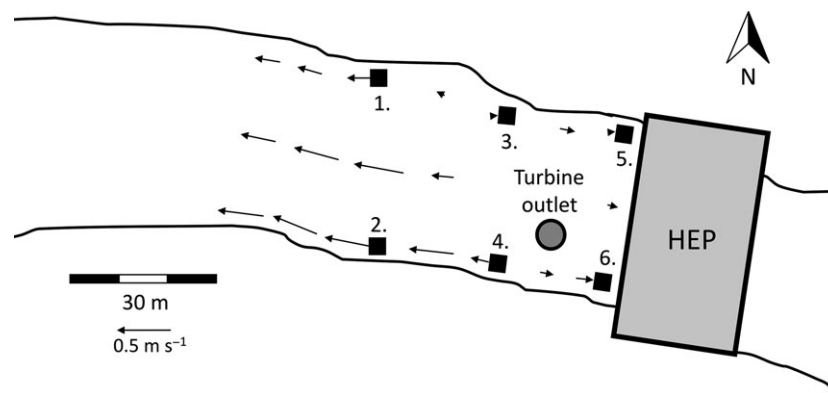
Figure 3 The ramps (1–6) used in the controlled experiment were transferred into the tailrace of the hydroelectric power plant (HEP) in the River Lagan at Laholm, Sweden, to validate the results from the experiment. The ramps were positioned by the banks near (5 and 6), approximately 30 m (3 and 4) and 60 m downstream of the HEP (1 and 2) respectively. Arrows indicate water current direction and velocity, measured at 0.5 m depth. Turbulence prevented measurements of water velocity near the turbine outlet (grey filled circle).
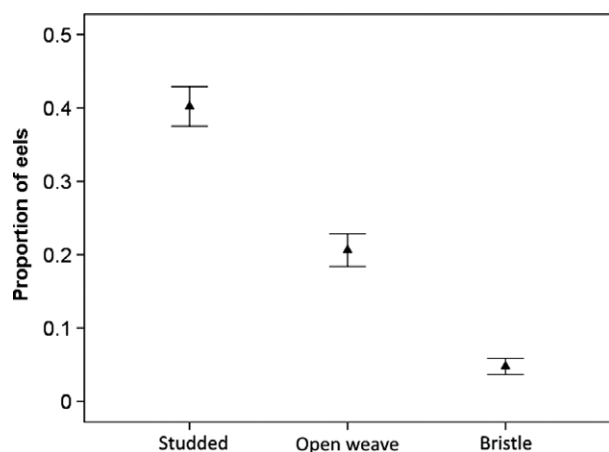
between north-south $\times$ upstream-downstream as fixed effects and date as a random factor.

Results

Controlled experiment

On average, seven of the ten eels in each cage successfully climbed the ramp in one of the three lanes and ended up in a collecting bucket during the night (mean proportion ± 1 SE $= 0.66 \pm 0.03$, $n = 48$). Eels that successfully climbed the ramps in lanes with studded substratum were approximately twice as common as those that climbed in the open weave, and more than eight times as common as those in the bristle substratum (Fig. 4). A one-way ANOVA with a Bonferroni corrected post hoc test revealed that there was a significant difference in the proportions of eels that had successfully climbed the different substrata ($F_{2, 134} = 81.0$, $P < 0.001$, $\eta_p^2 = 0.55$), and that the studded substratum had a higher mean proportion of successfully climbing eels than the open weave, which in turn had a higher proportion than the bristle substratum (all pairwise comparisons: $P < 0.001$).

The video analysis showed that eels generally did not initiate a climb immediately after approaching the ramp, but swam back and forth between the different substrata and the holding cage. Each batch of ten eels made in total about 50 approaches per lane entrance during a night (mean number of approaches per lane and batch ± 1 SE $= 53.2 \pm 8.0$, $n = 18$). There was a significant effect of substratum on the mean number of approaches (one-way ANOVA, $F_{2, 10} = 4.72$, $P = 0.03$, $\eta_p^2 = 0.49$), and the studded substratum attracted more approaches than the bristle substratum, but not significantly more than the open weave (Fig. 5; Bonferroni post-hoc pairwise comparisons $P_{\text{studded vs bristle}} = 0.04$, $P_{\text{studded vs open weave}} = 0.40$, $P_{\text{open weave vs bristle}} = 0.55$). More eels initiated a climb in the studded substratum than in the open weave and in the bristle substrata (one-way ANOVA, $F_{2, 10} = 12.2$, $P = 0.002$, $\eta_p^2 = 0.71$; Bonferroni post-hoc pairwise comparisons $P_{\text{studded vs bristle}} = 0.003$, $P_{\text{studded vs open weave}}$

$= 0.01$, $P_{\text{open weave vs bristle}} = 1.0$; Fig. 5). The same pattern was found when analysing the effect of substratum on the mean number of eels that successfully passed the 50-cm-long emerged section that the video camera was covering (one-way ANOVA, $F_{2, 10} = 20.2$, $P < 0.001$, $\eta_p^2 = 0.80$; Bonferroni post hoc pairwise comparisons $P_{\text{studded vs bristle}} < 0.001$, $P_{\text{studded vs open weave}} = 0.009$, $P_{\text{open weave vs bristle}} = 0.11$; Fig. 5).

Few approaches made by the eels resulted in climbs (mean proportion of climbs per approach ± 1 SE $= 0.16 \pm 0.03$, $n = 18$). The proportion of initiated climbs per approach was higher in the studded substratum than in the other substrata (one-way ANOVA, $F_{2, 10} = 8.3$, $P = 0.008$, $\eta_p^2 = 0.62$; Bonferroni post hoc pairwise comparisons $P_{\text{studded vs bristle}} = 0.02$, $P_{\text{studded vs open weave}} = 0.02$, $P_{\text{open weave vs bristle}} = 1.0$; Fig. 5). Therefore, the difference in the number of initiated climbs among the substrata can be explained both by the substrata's different capacities to attract approaches and by their capacities to attract initiated climbs once approached. When climbs had been initiated by eels, about half of these eels successfully passed the 50 cm field of view of the camera (mean proportion of successful passes per climb ± 1 SE $= 0.47 \pm 0.08$, $n = 17$). There was, however, no significant difference among the substrata in regards to this proportion (one-way ANOVA, $F_{2, 9} = 0.52$, $P = 0.61$, $\eta_p^2 = 0.10$; Fig. 5), indicating that eels climbing in the different substrata had comparable success rates after a climb had been initiated.

Eels that successfully passed the 50 cm emerged part of the video camera's field of view generally initiated this climb between 23:00 and 02:00 (Fig. 6). The mean time (± 1 SE) it took an eel to pass the field of view was 61 ± 13 s ($n = 77$). The climbing velocity differed among the eels climbing in different substrata (one-way ANOVA, $F_{2, 72} = 6.81$, $P = 0.002$, $\eta_p^2 = 0.16$; Fig. 7). A Bonferroni corrected post hoc pairwise comparison revealed that eels climbed significantly faster in the studded than in the open weave substratum ($P < 0.001$), but there was no difference between the studded and the bristle ($P = 0.34$) or between the bristle and the open weave substrata ($P = 1.0$) in this respect. The two last pairwise comparisons, however, had low statistical power since there were only four eels in total recorded from the video footage passing the camera's 50 cm field of view in lanes lined with bristle substratum.

Field validation

The mean number of eels (± 1 SE) captured per night (from 22:15 to 00:15) and lane was 1.09 ± 0.18. A generalized linear mixed model with a Poisson distributed log link function fitted to the data (Table 1) revealed that there were significant effects of substratum ($F_{2, 82} = 15.0$, $P < 0.001$) and the position of the ramp in the north-south direction (i.e. by the bank with low or high water velocities) ($F_{1, 82} = 23.5$, $P < 0.001$; Fig. 8) on the number of captured eels. In this field validation, more than twice as many eels were caught in lanes lined with studded than those lined with open weave, and more than four times as many as those lined

Figure 4 Mean proportions of eels, from batches ($n = 48$) of ten eels climbing the full length (2 m) of lanes lined with studded, open weave and bristle substrata (Fig. 2). Error bars indicate ± 1 SE.
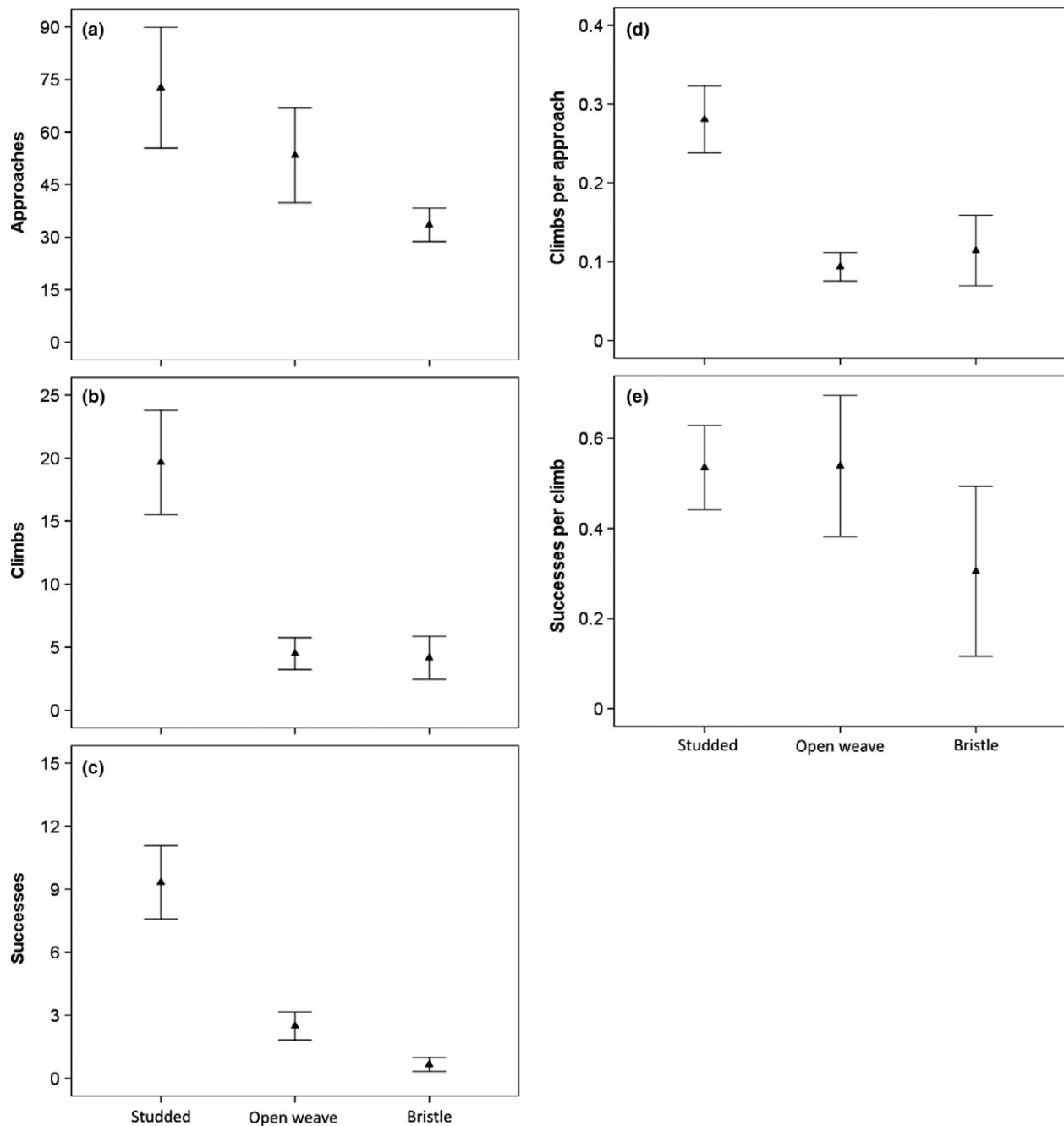
Figure 5 Mean number of approaches (a), initiated climbs (b), successful passes through the video camera's 50 cm field of view (c), proportions of climbs per approach (d) and successful climbs per initiated climb (e) made by eels from batches (n = 18) of ten eels presented with ramps lanes lined with studded, open weave and bristle substrata (Fig. 2). Eel behaviour was recorded with infrared videography. Error bars indicate ± 1 SE.

with bristle substratum (Fig. 8), supporting the results from the controlled experiment. Ramps positioned by the northern bank of the tailrace with low water velocities caught about three times as many eels as ramps positioned by the southern bank with high velocities. There were no significant effects of position in the upstream-downstream direction ($F_{2, 82}$ = 1.94, P = 0.151) or the interaction between position

in the north-south × upstream-downstream position ($F_{2, 82}$ = 1.81, P = 0.171).

Discussion

Increasing the number of juvenile eels that reach their inland freshwater feeding grounds may be a critical step towards
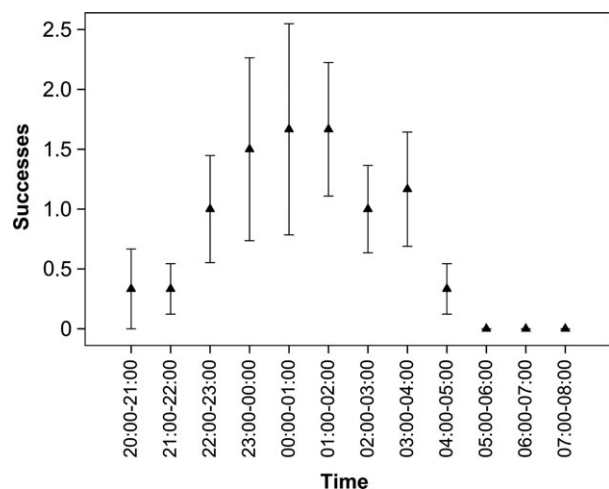
Figure 6 Mean successful passes through the video camera's 50 cm field of view per ramp and hour between 20:00 and 08:00 by eels from batches (n = 6; pooled data from three lanes) of ten eels. Eel behaviour was recorded with infrared videography. Error bars indicate ± 1 SE.
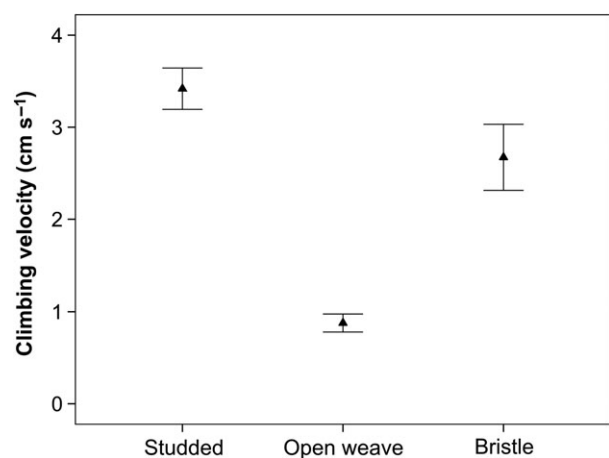
Figure 7 Mean climbing velocities of juvenile eels ($n_{studded}$ = 59, $n_{open\ weave}$ = 14, $n_{bristle}$ = 4) in ramp lanes lined with studded, open weave and bristle substrata (Fig. 2). Eel behaviour was recorded by means of infrared videography. Error bars indicate ± 1 SE.

the recovery of the critically endangered European eel. Dams used for hydropower production, irrigation and flood control pose one of the largest threats to inland migration of juvenile eels, thus reducing recruitment. Upstream passage solutions for eels have been installed in many places, but their performance has rarely been evaluated. Not using the best available technology results in suboptimal restoration efforts that may be both cost ineffective and insufficiently efficient for recovery of the European eel. This study shows that the climbing substratum in passage solutions for upstream-migrating juvenile eels has a major effect on the efficiency of the solution. Eels were more attracted to, initiated more climbs and climbed faster in the studded substratum than the

widely used open weave and bristle substrata, resulting in a superior efficiency as shown in both the controlled experiment and the field validation.

Studded, open weave geotextile and bristle substrata have been used throughout Europe and North America in upstream eel passage solutions, for example in the River Thames (UK), the East River (Ireland), the Sebasticook and Shetucket Rivers (USA) and the St. Lawrence and Richelieu Rivers (Canada) (Solomon & Beach, 2004; Schmidt, O'Reilly & Miller, 2009). While most national eel management plans do not explicitly recommend a certain climbing substratum for upstream passage solutions, the Danish eel management plan (2008), for instance stipulates that the open weave geotextile substratum Enkamat must be used. In view of our results, other substrata, such as plastic studs, likely function better in terms of attracting and passing juvenile eels at high climbing velocities, at least for ramps with slopes and flows similar to those used in this study. In other countries, such as Sweden, eel managers have until recently stocked elvers collected at the coasts of UK and France into Swedish lakes and rivers to increase the production of silver eels (instead of targeting connectivity issues). There is, however, a decline in and shortage of glass eels in their entire geographical range (Jacoby *et al.*, 2015), as well as indication that translocated eels may have reduced ability to navigate and are thus less likely to reach their spawning ground as mature silver eels (Westin, 1998, 2003; Svedäng & Gipperth, 2012). Therefore, efficient eel passages that promote natural immigration of juvenile eels may increase the amount of surviving and maturing eels in inland freshwaters, and these eels may have a greater chance of reaching their spawning grounds in the Sargasso Sea compared with mature eels that origin from stocked translocated juveniles.

Few published studies have previously experimentally tested the performance of different climbing substrata for glass eels and elvers. Vowles *et al.* (2015) showed that upstream passage efficiency for juvenile European eel at a Crump weir increased from 0 to 67% when studded tiles were installed. Jellyman *et al.* (2017) compared the performance of a gravel and a studded substratum for different slopes. Both substrata passed approximately 80% of the eels at 30° of inclination, but at 50° the studded outperformed the gravel substratum (57 vs. 13% success rate). We used a fixed slope (30°), and it is possible that the substrata evaluated in our study would perform differently for other slopes. Nevertheless, the difference among different climbing substrata's performances seems to be accentuated with steeper slopes (Jellyman *et al.*, 2017; Anwar, 2018), indicating that the studded substratum may outperform the other substrata used in our study to an even greater degree when mounted on ramps with inclinations higher than 30°. To optimize future eel ramps, further studies are needed to evaluate the design of the substratum, as well as potential interaction effects with, for example flow, water temperature, slope, surrounding hydraulic conditions at the ramp and eel size.

Fishways in general cannot be evaluated only by their performance in passing fish once fish are in the fishway; attraction efficiency and time associated with passage (delay)

Table 1 Parameter estimates for explanatory variables in a generalized linear mixed model with a Poisson distributed log link function affecting number of captured upstream-migrating juvenile eels per night (ramps were in operation between 21:45 and 00:15). Date was included as a random factor

Model term	Estimate	SE	t	P	95% CI lower	upper
Intercept	−0.536	0.372	−1.441	0.153	−1.275	0.204
Studded	1.513	0.306	4.937	<0.001	0.903	2.12
Open weave	0.693	0.34	2.041	0.045	0.017	1.369
Bristle	0	–	–	–	–	–
Downstream	0.266	0.277	0.959	0.341	−0.286	0.817
Further downstream	−0.044	0.298	−0.149	0.882	−0.638	0.549
Near dam	0	–	–	–	–	–
High velocity bank	−2.0037	0.614	−3.318	0.001	−3.258	−0.816
Low velocity bank	0	–	–	–	–	–
Downstream × high velocity bank	0.0833	0.722	1.154	0.252	−0.603	2.269
Further downstream × high velocity bank	1.344	0.716	1.878	0.064	−0.081	2.769
Near dam × high velocity bank	0	–	–	–	–	–
Downstream × low velocity bank	0	–	–	–	–	–
Further downstream × low velocity bank	0	–	–	–	–	–
Near dam × low velocity bank	0	–	–	–	–	–
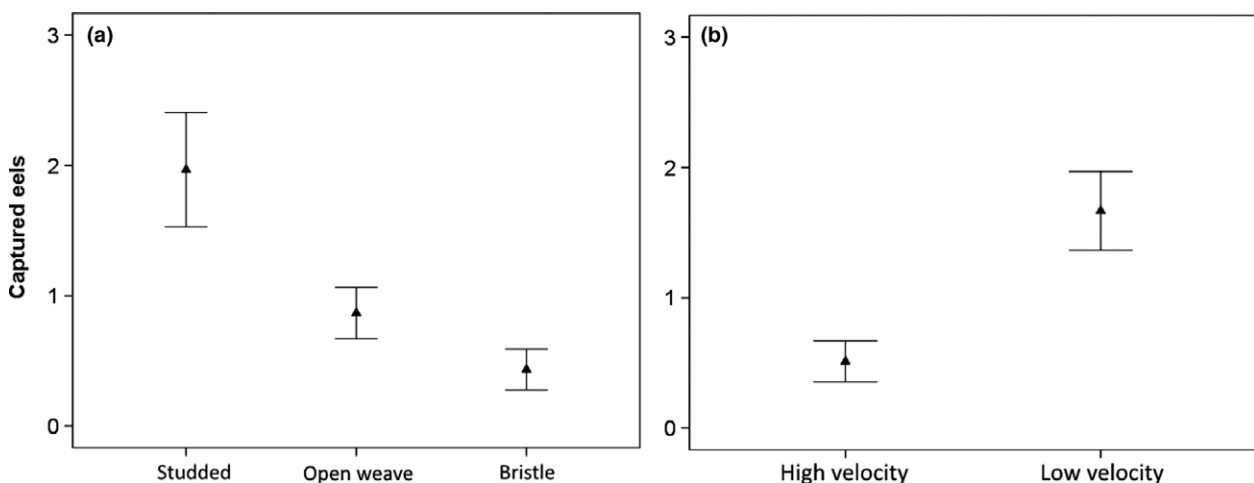
Figure 8 Mean number of juvenile eels captured per night (ramps were in operation between 21:45 and 00:15) by substratum type (studded, open weave and bristle, Fig. 2) (a) and by ramp position (i.e. by the southern bank with high or northern bank with low water velocities) (b) in the field investigation in the River Lagan. Error bars indicate ± 1 SE.

must also be taken into account (Roscoe & Hinch, 2010; Bunt, Castro-Santos & Haro, 2012). For passage solutions for juvenile eels, we showed that the climbing substratum in the ramp affects the probability of an eel approaching and entering the passage (i.e. initiating a climb) which had large effects on overall efficiency. Once in the ramp, the probability of a successful pass was not influenced by the substratum in our study, but there was a significant difference in the climbing velocity, indicating an effect on passage time. This effect would be particularly important for long eel ramps and rivers with multiple obstacles equipped with passage solutions. Minimizing delay in the passage possibly reduces both energy consumption and predation risk (McLaughlin *et al.*, 2013).

The eels in our study had a relatively narrow size range, and it is possible that the density of studs matched this size range, while the density of bristles did not (Solomon & Beach, 2004). There were, however, qualitative differences in the hydraulic conditions between the studs and the bundles of bristles. In the bristle substratum, water flowed evenly over the smooth plastic bottom, whereas turbulence was created by the depressions in the studded substratum, resulting in short waves of water wetting the substratum of these lanes (Video S1). Microturbulence also occurred in the open weave, but did not create this wave pattern. The waves resulted in a pulsed flow over the studded substratum, which may partly explain the large number of approaches at the entrance of lanes lined with this substratum, and, in addition, possibly attracted eels

to initiate climbs (Vowles *et al.*, 2015). The low performance of the bristle substratum to attract approaches may further be explained by its white plastic bottom surface, which potentially could have repelled eels from entering. However, this issue probably had minor effects on the results, because most climbs were initiated at night when eels likely could not discern the colour of the climbing substratum.

Eels migrating upstream generally prefer to swim near the banks (Piper *et al.*, 2012), where shallow water and structural elements may aid orientation and offer refuges against high water velocities (Barbin & Krueger, 1994). In our study, ramps positioned by the northern bank with low water velocities indeed caught more than three times as many eels as ramps by the southern bank, indicating that water velocity may play an important role in migration route selection. This spatial heterogeneity of the density of upstream-migrating juveniles (Piper *et al.*, 2012) should require mapping of local densities with electrofishing or mobile traps (Watz *et al.*, 2017) or, at least, the hydraulic conditions downstream the barrier, before a permanent fish passage is installed.

In conservation projects for endangered species, thorough quantitative evaluation of restoration technology is imperative for ensuring that the best available technology is used to resolve recruitment bottlenecks for key life stages. To recover endangered migrating species, enhancing the performance of passage solutions at barriers between habitats is a critical factor. For all anguillid eels, this means that safe downstream routes must be ensured along with optimization of upstream passages according to best knowledge and practice. Our results on climbing substratum and ramp positioning for juvenile eel passage solutions enhances such knowledge and practice, and hereby also facilitates the ultimate management goal of self-sustaining global anguillid eel populations.

Acknowledgements

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Video S1. A juvenile eel climbing in a lane lined with studded substratum.