

1 **Efficiency of a dual density studded fish pass designed to mitigate for impeded**  
2 **upstream passage of juvenile European eels (*Anguilla anguilla*) at a model Crump weir**

3 **ABSTRACT**

4 This study demonstrated that juvenile (glass) eels utilised a specific substrate (eel tiles) to  
5 circumvent a model Crump weir under an experimental setting. Upstream passage efficiency  
6 was 0% and 67% for the unmodified (no studded eel tiles on the downstream face; control)  
7 and modified (with studded eel tiles on the downstream face; treatment) setups, respectively,  
8 and greater for a small (59%) compared to large (41%) stud configuration. Eels were active  
9 and motivated to ascend the weir during both control and treatment setups. Approach and  
10 attempt rates were elevated during the first few minutes of the treatment compared to control  
11 trials. Eels were edge oriented under both setups, and ascended the weir through the tiles  
12 during single burst swimming events (reaching estimated speeds of 68.5 cm s<sup>-1</sup>). Eel tiles may  
13 provide a cost effective solution for mitigating impacts of anthropogenic barriers to juvenile  
14 eel migration. Further research is required to determine passage efficiencies under higher  
15 flows, for a greater size range of eel, and for other migratory anguilliform fish (e.g. lamprey,  
16 *Lampretra* spp. and *Petromyzon marinus* L.). The performance of eel tiles should be  
17 validated through robust field studies.

18 **KEYWORDS:** Barrier, behaviour, eel ladder, fish passage, flume, migration.

19

20 **Introduction**

21 The European eel, *Anguilla anguilla* (L.) is a species of high conservation concern due to a  
22 dramatic decline in recruitment (e.g. greater than 90% in some catchments) throughout its  
23 range over the last *ca.* 30 years (Dekker 2003). Adult eels migrate from rivers to oceanic  
24 spawning grounds, thought to be in the Sargasso Sea, while the larval life-stage (leptocephali)

25 utilise ocean currents to return to continental waters (Tesch 2003). As they develop into  
26 “glass eels” they move through estuaries predominately by Selective Tidal Stream Transport  
27 (McCleave & Kleckner 1982; Beaulaton & Castelnaud 2005), and embark on active upstream  
28 migration in rivers as they metamorphose into the pigmented “elver” life-stage (Chadwick *et*  
29 *al.* 2007). Anthropogenic barriers (e.g. dams, weirs, sluices, culverts) can prevent or limit  
30 juvenile eel upstream migration in freshwater, restricting access to suitable rearing habitat  
31 and contributing to population declines (Dekker 2003; Knights & White 1998; Starkie 2003).

32 The European eel stock is considered outside safe biological limits and its fishery  
33 unsustainable (ICES 2007). In 2007, the European eel was listed under Appendix II of the  
34 Convention on International Trade in Endangered Species (CITES), and the European Union  
35 adopted Council Regulation 1100/2007/EC, requiring member states to prepare eel  
36 management plans (EMPs). Mitigating the impact of anthropogenic barriers on eel migration  
37 is highlighted in many EMPs as an important strategy for aiding stock recovery.

38 Fish passes are designed to aid upstream passage of fish at anthropogenic barriers (for  
39 an overview see Clay 1995). Common technical designs include: 1. pool type passes, which  
40 provide a series of stepped pools through which water flows downstream over weirs or  
41 through vertical slots, orifices or notches; or 2. steep compact passes (such as the Denil pass)  
42 which incorporate baffles to dissipate water energy as turbulence, thus reducing mean  
43 velocities to within the swimming capabilities of the target species (Clay 1995; Armstrong *et*  
44 *al.* 2004). While such designs may work, at least partially (see Noonan *et al.* 2012), for large  
45 bodied migrants with strong swimming and leaping capabilities (e.g. adult salmonids), they  
46 tend to be less effective in facilitating the upstream passage of smaller species (MacDonald &  
47 Davies 2007; Mallen-Cooper & Brand 2007) or those with elongated anguilliform body  
48 morphologies (e.g. eels, Feunteun 2002, and lampreys, Moser *et al.* 2002; Foulds & Lucas  
49 2013). Juvenile eels have low burst swimming capabilities (e.g. in a swim chamber, 72 mm

50 elvers attained maximum burst speeds of *ca.* 50 cm s<sup>-1</sup>; McCleave 1980) and are unable to  
51 reach or maintain the swimming speeds often required to ascend traditional fish passes, while  
52 vertical differences in head between pools may pose a physical barrier as they cannot leap.  
53 Fish pass design must therefore take their small size and poor burst swimming capability into  
54 consideration. Conversely, their ability to climb wetted surfaces provides an opportunity for  
55 novel species specific solutions. The high density of barriers to migration in the UK and  
56 Europe (Kemp & O’Hanley 2010) necessitates that the fish pass design adopted must be cost  
57 effective and simple to retrofit.

58 Eel specific bristle board passes have been developed and widely used for upstream  
59 migrating juveniles, e.g. in the UK (Solomon & Beach 2004) and France (Porcher 2002).  
60 Despite their apparent effectiveness in the field (Solomon & Beach 2004), there have been  
61 few robust and controlled studies conducted to assess passage efficiency. Concerns have been  
62 raised that bristles might clog with debris over time and may be less effective during high  
63 flows. In the UK, as an alternative, ‘studded’ substrates have been developed recently as a  
64 biologically and economically effective solution. There are precedents for the use of similar  
65 designs. For example, a plastic studded substrate proved effective for inanga, *Galaxias*  
66 *maculatus* (Jenyns), and redfin bullies, *Gobiomorphus huttoni* (Ogilby), ascending a 1.5 m  
67 artificial ramp (Baker & Boubée 2006), and a *ca.* 9 m long studded eel ladder on the  
68 Richelieu River (Canada) enabled American eel, *Anguilla rostrata* (Lesueur) to pass over a 5  
69 m high weir (Verdon *et al.* 2003). In the UK, the studded boards, commonly referred to as eel  
70 tiles, are frequently designed with a novel dual diameter stud dimension set at two different  
71 densities (see ‘Materials and methods’ for detailed description) to facilitate a wide range of  
72 body lengths. To date, the efficiency of eel tiles has not been independently evaluated, and an  
73 understanding of swimming behaviour when attempting to ascend such passes is lacking.

74 The aim of this study was to assess effectiveness of eel tiles for facilitating upstream  
75 passage of juvenile European eels at an experimental Crump weir. Crump weirs, common  
76 barriers to fish migration in the UK (Lucas & Frear 1997; Lucas & Bubb 2005; Russon *et al.*  
77 2010), are used to gauge river discharge as part of flood monitoring, and so retrofitting  
78 through installation of fish passes (Rhodes & Servais 2008) is preferred over their removal.  
79 This study used glass eels as they represent the earliest developmental stage expected to  
80 utilise eel passes, and have been observed congregating below anthropogenic barriers  
81 (Feunteun *et al.* 1998). Restricted upstream migration of this life-stage represents a  
82 bottleneck for recruitment, alleviation of which is considered a principal target for  
83 conservation efforts (Mouton *et al.* 2014). The first objective of this study was to quantify  
84 and compare upstream passage efficiency for an unmodified (no studded eel tiles on the  
85 downstream face; control) and modified (with eel tiles on the downstream face; treatment)  
86 model Crump weir. As eel tiles utilise a dual density stud design, the second objective was to  
87 determine whether stud configuration (dimension and spacing) influenced passage efficiency.  
88 The third objective was to quantify eel behaviour (in terms of activity and motivation,  
89 position reached on the weir face and swimming speed) when attempting to ascend the  
90 Crump weir.

91

## 92 **Materials and methods**

### 93 *Experimental setup*

94 Experiments were conducted in an indoor open channel flume (12.0 m long, 0.3 m wide, and  
95 0.4 m deep) at the International Centre for Ecohydraulics Research, University of  
96 Southampton (UK). Discharge was constant (approximately  $1 \text{ L s}^{-1}$ ) and plastic screens  
97 placed on the outside of the flume prevented visual disturbance to the test fish. A Crump weir  
98 (25 cm high) spanned the width of the experimental channel, with upstream and downstream

99 slopes of 1:2 and 1:5, respectively, in line with British Standards Institution (BS 3680-4B)  
100 criteria (Figure 1a). The ability of European glass eel to ascend the weir was tested under two  
101 setups: unmodified (control) and modified (treatment) with eel tiles placed on the  
102 downstream face. The tiles consisted of two 'stud' sizes (5 cm high; 3.0 and 1.5 cm max.  
103 diameter for the large and small stud, respectively), spaced 8.5 cm (large) or 4.5 cm (small)  
104 apart (measured from centre of the stud; Figure 1b).

105 Water velocities were measured (at 60% water depth) up- and down-stream of the  
106 weir using an electromagnetic flow meter (Valeport Model 801). A shallow (0.5 cm) sheet of  
107 water flowed over the downstream face of the weir, where velocity was measured only during  
108 the control treatment. Use of the flow meter was prevented when eel tiles were in place, so  
109 the time taken for 5 ml of India ink to flow down the weir face was recorded instead. Mean ( $\pm$   
110 SD) water velocity upstream (control = 1.03 [ $\pm$  0.64] cm s<sup>-1</sup>, modified = 0.80 [ $\pm$  0.61] cm s<sup>-1</sup>)  
111 and downstream (control = 7.11 [ $\pm$  8.84] cm s<sup>-1</sup>, modified = 10.00 [ $\pm$  9.52] cm s<sup>-1</sup>) of the weir  
112 were similar between setups. During the control, water velocity accelerated as it flowed down  
113 the weir face, reaching a maximum of 73.7 cm s<sup>-1</sup> (mean velocity: 57.4 [ $\pm$  17.3] cm s<sup>-1</sup>).  
114 During the treatment, average water velocity on the downstream weir face was estimated to  
115 be 34.7 cm s<sup>-1</sup>. Downstream water depth remained constant (5 cm) between setups, but  
116 upstream water depth was higher (27.8 versus 26.5 cm) when the tiles were in place.

117

### 118 *Fish maintenance*

119 Three hundred grams of glass eels (showing a small degree of pigmentation, but see Figure  
120 1c), captured from the River Severn (UK) on the night of 2 May 2013, were transported in  
121 chilled (8°C) river water to the University of Southampton the following day, and placed in a  
122 290 L holding tank under natural photoperiod. Holding tank water was chilled to 8°C and  
123 then allowed to increase by approximately 2°C per day until reaching ambient laboratory

124 temperatures before trials commenced. Mean holding tank water temperature at the beginning  
125 of the experimental period was  $18.8 (\pm 1.19) ^\circ\text{C}$ .

126

### 127 *Experimental protocol*

128 Ten 10 minute trials were conducted during daylight (10:00 to 17:00) for each of the two  
129 setups between 7 and 9 May 2013. At the start of each day, up to 10 groups of 30 fish were  
130 placed in perforated sealed tubes located at the upstream end of the flume and allowed to  
131 acclimatise for a minimum of 1 hour before the start of the first trial. Flume water  
132 temperature (mean  $\pm$  SD =  $21.8 \pm 0.96 ^\circ\text{C}$ , comparable to some UK river temperatures during  
133 late spring / summer e.g. the River Stour, East Anglia; Piper *et al.* 2012) was recorded before  
134 30 fish were released 2.2 m downstream of the weir crest at the start of each trial. At the end  
135 of each trial the fish were removed from the flume and weighed (mean mass  $\pm$  SD =  $0.35 \pm$   
136  $0.03$  g), and measured (mean total length based on a sample of 10% of the test population  $\pm$   
137 SD =  $71.73 \pm 3.87$  mm). Each fish was used in one trial only.

138

### 139 *Fish behaviour*

140 Three overhead CCTV video cameras were used to record eel behaviour as they attempted to  
141 ascend the weir, and analysis of the video footage allowed the following metrics to be  
142 quantified:

143

#### 144 *Passage efficiency*

145 During control trials, a passage attempt was deemed to occur when the head of an eel  
146 progressed upstream of the hydraulic jump (15 cm up the weir face). As no hydraulic jump  
147 was present during modified trials, a passage attempt occurred when the head progressed onto  
148 the most downstream tile. A successful pass was recorded when the whole body of the fish

149 progressed over the weir crest. Passage efficiency was defined as the number of successful  
150 passes expressed as a percentage of number of passage attempts, and compared between the  
151 two setups (objective 1). Under the treatment condition the two stud types (small and large)  
152 each covered 50% of the downstream weir face (Figure 1b). The number of eels that passed  
153 the weir crest above the side of flume covered by small and large studs was recorded and  
154 influence of stud configuration on passage efficiency assessed (objective 2).

155

#### 156 *Activity and motivation*

157 Approaches (when an eel came within 5 cm of the downstream weir face) and attempts to  
158 ascend the weir were used to indicate levels of activity and motivation, respectively, and  
159 quantified as approach or attempt rate (mean number per minute per fish downstream of the  
160 weir).

161

#### 162 *Position on weir face*

163 The maximum distance of ascent (the most upstream point reached on the weir face during a  
164 passage attempt, including those that succeeded) was quantified using video tracking  
165 software (Logger Pro v3.8.2, Vernier Software, Beaverton, OR, USA). At the start of each  
166 passage attempt, lateral position was categorised as being the true left (TL), true right (TR)  
167 (i.e. the left or right side of the flume when looking downstream), or centre, assuming equal  
168 channel division.

169

#### 170 *Swimming speed*

171 A conservative estimate of swimming speed (i.e. assuming the shortest possible swim path)  
172 was determined for each eel that successfully ascended the weir. Time to pass, between  
173 initiating a passage attempt and the entire body passing over the weir crest was calculated.

174 Ground speed was calculated as the quotient of weir face length (1.25 m) and time to pass.

175 Swimming speed was estimated as the sum of mean water velocity and ground speed.

176

### 177 *Statistical analysis*

178 Data were tested for normality and homogeneity of variance using a Shapiro-Wilk and

179 Levene's Test, respectively. When these assumptions were violated, data were log

180 transformed. The number of fish that passed over the small versus large stud configuration

181 and maximum distance of ascent was tested using an Independent samples *t*-test. Within each

182 setup, differences between lateral position (TL, TR or Centre) were tested using one-way

183 ANOVA with a Tukey *post hoc* test.

184 Owing to the non-linear relationship between approach (or attempt) rate and time,

185 additive modelling was used to test whether there were differences between setups. Three

186 candidate additive models were fitted which examined whether: 1. there was a relationship

187 between approach (or attempt) rate and time, 2. the mean value of the relationship differed

188 between setups, and 3. the shape of the relationship varied between setup. The models were

189 fitted using a penalized regression spline from the 'mcgv' package in R (R version 3.03; R

190 Core Team 2014; Wood 2003, 2004) which used cross-validation to determine the amount of

191 smoothing (Zuur 2012). A thin plate regression spline was used for the smoother. The final

192 model was determined as the candidate model with the lowest Akaike Information Criterion

193 (AIC) value. For approach and attempt rate the assumptions of normality, homogeneity of

194 variance, and independence were assessed by examining plots of the residuals against the

195 fitted values and covariates. As the initial model fit violated the assumption of independence,

196 the model was refitted using a Generalized Additive Mixed Model (GAMM) with an AR-1

197 auto-correlation structure. As the assumption of homogeneity was violated the GAMM was

198 extended to incorporate a variety of variance structures (see Zuur *et al.* 2009). The structure



199 that produced the lowest AIC value was selected. A combined structure that allows for  
200 different residual variation between the control and treatment, and power of the variance  
201 covariate for time produced the best fit. For attempt rate, examination of the residuals  
202 suggested a large outlier. Therefore, this trial was removed and the model re-run.

203

## 204 **Results**

### 205 *Passage efficiency*

206 Mean ( $\pm$  SD) number of passage attempts and passes were respectively 30.4 ( $\pm$  13.0) and 0.0  
207 ( $\pm$  0.0) during the control. When eel tiles were installed, an average of 29.9 ( $\pm$  6.1) and 20.0  
208 ( $\pm$  4.6) passage attempts and passes per trial were recorded, respectively (Figure 2), resulting  
209 in a mean passage efficiency of 66.9% (objective 1). More eels passed the weir crest above  
210 the small ( $11.7 \pm 2.9$ ) than large ( $8.3 \pm 2.6$ ) studs ( $t = 2.72$ , d.f. = 18,  $P < 0.05$ ), with  
211 corresponding mean passage efficiencies of 58.7% and 41.3% per trial, respectively  
212 (objective 2).

213

### 214 *Activity and motivation*

215 The third candidate additive model had the lowest AIC value, indicating the shape of the  
216 relationship between approach (and attempt) rate and time (minute) differed between setups  
217 (Figure 3). There was no relationship between approach rate and time for the control ( $F_{1, 198} =$   
218  $1.83$ ,  $P = 0.177$ ), but a strong relationship for the treatment ( $F_{6.14, 192.87} = 42.75$ ,  $P < 0.001$ ).  
219 Approach rate was initially higher for the treatment compared to the control (minutes 1, 2 and  
220 3), but approximately equal between setups thereafter (Figure 3a). The final GAMM  
221 explained 58.1 % of the variability in approach rate. A similar pattern was observed for  
222 attempt rate (Figure 3b), with no relationship with time for the control ( $F_{1, 197} = 3.70$ ,  $P =$

223 0.056), but a strong relationship for the treatment ( $F_{4.52, 194.48} = 20.88, P < 0.001$ ). The final  
224 GAMM explained 39.1 % of the variability in the number of passage attempts.

225

### 226 *Position on weir face*

227 Maximum distance of ascent was greater under the treatment ( $t = -25.63, \text{d.f.} = 18, P <$   
228  $0.001$ ), frequently culminating in successful passage (Figure 4). Under the control, the  
229 maximum distance of ascent was greatest at the channel edges (Figure 4a). Eels were  
230 generally edge oriented, with more passage attempts (control:  $F_{2,25} = 28.87, P < 0.001$ ;  
231 treatment:  $F_{2,27} = 25.14, P < 0.001$ ) along the channel sides (Table 1).

232

### 233 *Swimming speed*

234 Swimming speed was not calculated for the control as no eels successfully ascended the weir.  
235 Eels were not observed climbing or crawling through the eel tiles; instead they used  
236 anguilliform swimming to rapidly ascend the weir (mean  $\pm$  SD time to pass the 1.25 m weir  
237 was  $11.4 \pm 3.53$  sec, excluding 2 outliers where eels impinged on studs). Average swimming  
238 speed was estimated to be  $50.02 \text{ cm s}^{-1}$  during passage (range =  $38.9 - 68.5 \text{ cm s}^{-1}$ ).

239

### 240 **Discussion**

241 This experimental study is the first to quantify fish passage efficiency for juvenile European  
242 eels utilising eel tiles to circumvent barriers to migration. The results support the findings of  
243 others; Crump weirs can pose a barrier to upstream migration, e.g. as for barbel, *Barbus*  
244 *barbus* L. (Lucas & Frear 1997), European grayling, *Thymallus thymallus* L. (Lucas & Bubb  
245 2005), and river lamprey, *Lampetra fluviatilis* L. (Russon *et al.* 2010). Eel tiles facilitated  
246 upstream movement, improving passage efficiency from 0% to 67%.

247           The dual density of eel tile studs was intended to facilitate passage of a wide size  
248 range of eels. Under the conditions described in this study, eels tended to pass the weir crest  
249 above the side that contained small rather than large studs. For glass eels and similar sized  
250 elvers, the small stud design would likely be most effective at facilitating upstream passage at  
251 river infrastructure. In studies with similar synthetic substrates, stud (or bristle) density was  
252 often reported to be size selective, with high densities favouring smaller individuals (for an  
253 overview see Solomon & Beach, 2004). Accordingly, previous research has recommended  
254 adapting bristle / stud density according to the size distribution of eels expected to utilise the  
255 pass (Legault, 1992). The passage efficiency of the stud configurations tested in this study for  
256 larger eels requires further investigation. It appears that above a certain threshold body size,  
257 the smaller density studs become challenging for eels to navigate through (Vowles,  
258 unpublished).

259           Overall, glass eels were highly active and motivated to swim upstream, repeatedly  
260 approaching and attempting to ascend the weir under both setups. The high water  
261 temperatures observed during this study likely contributed to activity levels, with previous  
262 research demonstrating a positive relationship between water temperature and upstream  
263 movement for juvenile eel (White & Knights, 1988). Although at lower temperatures passage  
264 attempt rate will likely be lower, passage efficiency should not be compromised as long as  
265 water velocity remains within the swimming capability of the fish.

266           Although eels were motivated to progress upstream, for the first minute of the trials  
267 both approach and attempt rate were on average 4 fold greater during the treatment than the  
268 control. This difference in behaviour could be driven by hydrodynamic differences between  
269 setups. Eels may have been attracted to turbulence generated by water flowing around the  
270 staggered array of studs. Turbulence has been suggested as a potential attractant to eel passes  
271 (Solomon & Beach 2004), and in a field study elvers were twice as likely to use a bristle pass

272 with a more turbulent plunging, rather than streaming attraction flow (Piper *et al.* 2012).  
273 Higher levels of turbulence may be expected under field scenarios, potentially enhancing  
274 attraction and reducing delay for upstream migrating juvenile eels. However, benefits of  
275 turbulence as a possible attractant should be considered in light of potential costs of impaired  
276 passage performance, e.g. due to increased energetic costs of swimming (Enders *et al.* 2003)  
277 and destabilisation (Tritico & Cotel 2010). Further, levels of attraction are likely to vary  
278 between sites, due to volume of competing river discharge, or positioning of the pass. Indeed,  
279 ensuring adequate attraction may well represent the largest challenge for juvenile eel passes,  
280 which are typically designed to be narrow (30 – 45 cm) in width (Solomon & Beach, 2004).  
281 Eel tile attraction and passage efficiency should be quantified and compared with suitable  
282 alternatives through robust field studies.

283         Water accelerated as it flowed down the face of the unmodified weir, reaching  
284 velocities in excess of the maximum burst swimming capabilities previously reported for  
285 juvenile eels (e.g. 50 cm s<sup>-1</sup>; McCleave 1980). Despite this, eels were able to progress 83 cm  
286 up the weir face by taking advantage of lower velocities towards the channel sides. Indeed,  
287 eels were edge oriented during both setups, an observation documented in other studies  
288 (Tesch 2003; Piper *et al.* 2012). As a result, eel passes are typically situated at the edge of  
289 barriers to maximise passage (Porcher 2002; Solomon & Beach 2004). In rivers, low-head  
290 structures not traditionally considered to be major barriers to fish movement are likely to  
291 impede upstream migrating juvenile eels unless velocities are sufficiently low, they have the  
292 opportunity to climb suitable wetted margins (Linton *et al.* 2007), or eel specific passes are  
293 provided (Solomon & Beach 2004).

294         Based on previous observations of behaviour at bristle passes, juvenile eels were  
295 expected to ascend the tiles by climbing between the protruding studs. In this study, glass eels  
296 used anguilliform swimming to ascend the weir, typically in one rapid burst. Relatively high

297 water temperatures likely increased swimming activity and ability (see Edeline *et al.* 2006),  
298 leading to a greater propensity to burst swim against the flow. Alternatively, the gaps  
299 between studs may have been too large and / or water velocities too great to enable climbing.  
300 Eels that failed to pass in a single attempt were typically washed back downstream,  
301 seemingly unable to maintain position on the face of the tile. When weir length and / or water  
302 velocity is greater than the critical threshold for successful passage in a single burst of  
303 activity, resting locations may be required to ensure tile performance is maintained.

304         The conservative estimate of swimming speed ( $50 \text{ cm s}^{-1}$ ) calculated during this study  
305 closely matched the maximum burst capability of elvers (of an equivalent size) quantified  
306 using a swim chamber (McCleave 1980). However, some glass eels attained speeds as high as  
307  $68.5 \text{ cm s}^{-1}$ , indicating that they are able to reach higher swimming speeds than previously  
308 reported when motivated to move upstream. Indeed, the swimming performance of other  
309 species is greater than expected when the exhibition of volitional swimming is facilitated in  
310 open channels, rather than when fish are forced to swim in confined chambers (Peake 2004;  
311 Castro-Santos 2005; Russon & Kemp 2011). Nevertheless, swimming performance of glass  
312 eels is low when viewed from a traditional fish passage perspective, where design velocities  
313 are frequently around  $250 - 300 \text{ cm s}^{-1}$  (Clay 1995).

314

## 315 **Conclusions**

316 Given the conservation status and legislative protection afforded to European eels it is  
317 important that potential barriers to their migration are assessed and impacts mitigated for. The  
318 small size and low swimming performance of juvenile eels often renders traditional fish  
319 passes ineffective for facilitating their upstream migration, necessitating development of  
320 species specific passage solutions. This study quantified the efficiency of a dual density and  
321 dimension ‘studded’ substrate (eel tiles) for glass eels. Passage efficiency over eel tiles was

322 67%, with the small stud spacing being more effective than the large. However, as successful  
323 eels had to burst swim upstream in a single attempt, resting locations may be required for  
324 larger barriers and / or when greater velocities are encountered. Further research is needed to  
325 assess passage efficiencies under higher flows, for a wider size range of eel, and for other  
326 migratory anguilliforms such as lampreys, for which traditional fishways are often ineffective  
327 (Foulds & Lucas 2013). The performance of eel tiles should be validated through robust field  
328 studies to advance the development of cost effective methods of alleviating habitat  
329 fragmentation.

330

### 331 **References**

- 332 Armstrong G.S., Aprahamian M.W., Fewings G.A., Gough P.J., Reader N.A. & Varallo P.V.  
333 (2004) *Environment Agency Fish Pass Manual: Guidance Notes on the Legislation, Selection*  
334 *and Approval of Fish Passes in England and Wales*. Environment Agency, Pembrokeshire,  
335 Wales.
- 336 Baker C.F. & Boubée J.A.T. (2006) Upstream passage of inanga *Galaxias maculatus* and  
337 redfin bullies *Gobiomorphus huttoni* over artificial ramps. *Journal of Fish Biology* **69**, 668-  
338 681.
- 339 Beaulaton L. and Castelnaud G. (2005) The efficiency of selective tidal stream transportation  
340 in glass eels entering the Gironde (France). *Bulletin Français de la Pêche et de la*  
341 *Pisciculture* **378-379**, 5-21.
- 342 Castro-Santos T. (2005) Optimal swim speeds for traversing velocity barriers: an analysis of  
343 volitional high-speed swimming behavior of migratory fishes. *The Journal of Experimental*  
344 *Biology* **208**, 421-432.

345 Chadwick S., Knights B., Thorley J.L. & Bark A. (2007) A long-term study of population  
346 characteristics and downstream migrations of the European eel *Anguilla anguilla* (L.) and the  
347 effects of a migration barrier in the Girnock Burn, north-east Scotland. *Journal of Fish*  
348 *Biology* **70**, 1535-1553.

349 Clay C.H. (1995) *Design of Fishways and Other Fish Facilities, 2nd edition*. Lewis  
350 Publishers, Boca Raton.

351 Dekker W. (2003) Status of the European eel stock and fisheries. In: K. Aida, K. Tsukamoto,  
352 & K. Yamauchi (eds) *Eel Biology*. Springer-Verlag, Tokyo, pp. 237-254.

353 Edeline E., Lambert P., Rigaud C. & Elie P. (2006) Effects of body condition and water  
354 temperature on *Anguilla anguilla* glass eel migratory behavior. *Journal of Experimental*  
355 *Marine Biology and Ecology* **331**, 217-225.

356 Enders E.C., Boisclair D. & Roy A.G. (2003) The effects of turbulence on the cost of  
357 swimming for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and*  
358 *Aquatic Science* **60**, 1149-1160.

359 Feunteun E. (2002) Management and restoration of European eel population (*Anguilla*  
360 *anguilla*): an impossible bargain. *Ecological Engineering* **18**, 575-591.

361 Feunteun, E., Acou, A., Guillouët, J., Laffaille, P. & Legault, A. (1998) Spatial distribution of  
362 an eel population (*Anguilla anguilla* L.) in a small coastal catchment of Northern Brittany  
363 (France): consequences of hydraulic works. *Bulletin Français de la Pêche et de la*  
364 *Pisciculture* **349**, 129-139.

365 Foulds W. L. & Lucas M.C. (2013) Extreme inefficiency of two conventional, technical  
366 fishways used by European river lamprey (*Lampetra fluviatilis*). *Ecological Engineering* **58**,  
367 423-433.

368 ICES (2007) *Report of the 2007 Session of the Joint EIFAC/ICES. Working Group on Eels,*  
369 *FAO European Inland Exploration of the Sea, Bordeaux, 3-7 September 2007.*

370 Kemp P.S. & O'Hanley J.R. (2010) Procedures for evaluating and prioritising the removal of  
371 fish passage barriers: a synthesis. *Fisheries Management and Ecology* **17**, 297-322.

372 Knights B. & White E.M. (1998) Enhancing immigration and recruitment of eels: the use of  
373 passes and associated trapping systems. *Fisheries Management and Ecology* **5**, 459-471.

374 Legault, A. (1992). Etude de quelques facteurs de sélectivité de passes à anguilles (Study of  
375 some selectivity factors in eel ladders). *Bulletin Français de la Pêche et de la Pisciculture*  
376 **325**, 83-91.

377 Linton E.D., Jónsson B, & Noakes D.L.G. (2007) Effects of water temperature on the  
378 swimming and climbing behaviour of glass eels, *Anguilla* spp. *Environmental Biology of*  
379 *Fishes* **78**, 189-192.

380 Lucas M.C. & Bubb D.H. (2005) *Seasonal Movements and Habitat Use of Grayling in the*  
381 *UK.* Environment Agency, Almondsbury, Bristol.

382 Lucas M.C. & Frear P.A. (1997) Effects of a flow-gauging weir on the migratory behaviour  
383 of adult barbel, a riverine cyprinid. *Journal of Fish Biology* **50**, 382-396.

384 MacDonald J.I. & Davies P.E. (2007) Improving the upstream passage of two galaxiid fish  
385 species through a pip culvert. *Fisheries Management and Ecology* **14**, 221-230.

386 Mallen-Cooper M. & Brand D.A. (2007) Non-salmonids in a salmonid fishway: what do 50  
387 years of data tell us about past and future fish passage? *Fisheries Management and Ecology*  
388 **14**, 319-332.



389 McCleave J.D. (1980) Swimming performance of European eel (*Anguilla anguilla* (L.))  
390 eelers. *Journal of Fish Biology* **16**, 445-452.

391 McCleave J.D. & Kleckner R.C. (1982) Selective tidal stream transport in the estuarine  
392 migration of glass eels of the American eel (*Anguilla rostrata*). *Journal du Conseil, Conseil*  
393 *International pour l'Exploration de la Mer* **40**, 262-271.

394 Moser M.L., Ocker P.A., Stuehrenberg L.C. & Bjornn T.C. (2002) Passage efficiency of  
395 adult Pacific lampreys at hydropower dams on the lower Columbia River, USA. *Transactions*  
396 *of the American Fisheries Society* **131**, 956-965.

397 Mouton A.M., Huyssecom S., Buysse D., Stevens M., Van den Neucker T. & Coeck J. (2014)  
398 Optimisation of adjusted barrier management to improve glass eel migration at an estuarine  
399 barrier. *Journal of Coastal Conservation* **18**, 111-120.

400 Noonan M.J., Grant J.W.A. & Jackson C.D. (2012) A quantitative assessment of fish passage  
401 efficiency. *Fish and Fisheries* **13**, 450-464.

402 Peake S. (2004). An evaluation of the use of critical swimming speed for determination of  
403 culvert water velocity criteria for smallmouth bass. *Transaction of the American Fisheries*  
404 *Society* **133**, 1472-1479.

405 Piper A.T., Wright R.M. & Kemp P.S. (2012). The influence of attraction flow on upstream  
406 passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering* **44**,  
407 329-336.

408 Porcher J.P. (2002) Fishways for eels. *Bulletin Français de la Pêche et de la Pisciculture*  
409 **364**, 147-155.

410 R Core Team. (2014) R: A language and environment for statistical computing. R Foundation  
411 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

412 Rhodes D.G. & Servais S.A. (2008) *Low-cost Modifications of the Crump Weir to Improve*  
413 *Fish Passage*. Environment Agency, Almondsbury, Bristol.

414 Russon I.J. & Kemp P.S. (2011) Experimental quantification of the swimming performance  
415 and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla*  
416 *anguilla*. *Journal of Fish Biology* **78**, 1965-1975.

417 Russon I.J., Kemp P.S. & Lucas M.C. (2010) Gauging weirs impede the upstream migration  
418 of adult river lamprey *Lampetra fluviatilis*. *Fisheries Management and Ecology* **18**, 201-210.

419 Starkie A. (2003) Management issues relating to the European eel, *Anguilla anguilla*.  
420 *Fisheries Management and Ecology* **10**, 361-364.

421 Solomon D. & Beach M.H. (2004) *Fish Pass Design for Eel and Elver (Anguilla anguilla)*. R  
422 & D technical report W2-070/TR1. Environment Agency, Bristol.

423 Tesch F.W. (2003) *The Eel*. 5<sup>th</sup> Ed. Blackwell Publishing, Oxford.

424 Tritico H.M. & Cotel A.J. (2010) The effects of turbulent eddies on the stability and critical  
425 swimming speed of creek chub (*Semotilus atromaculatus*). *The Journal of Experimental*  
426 *Biology* **213**, 2284-2293.

427 Verdon R., Desrochers D. & Dumont P. (2003) Recruitment of American eels in the  
428 Richelieu River and Lake Champlain: provision of upstream passage as a regional-scale  
429 solution to a large-scale problem. In: D.A. Dixon (ed) *Biology Management, and Protection*  
430 *of Catadromous Eels*. American Fisheries Society Symposium 33, Bethesda, Maryland, USA,  
431 pp. 125-138.

- 432 Wood S.N. (2003) Thin-plate regression splines. *Journal of the Royal Statistical Society (B)*  
433 **65**, 95-114.
- 434 Wood S.N. (2004) Stable and efficient multiple smoothing parameter estimation for  
435 generalized additive models. *Journal of the American Statistical Association* **99**, 673-686.
- 436 Zuur A. F. (2012) *A Beginner's Guide to Generalized Additive Models with R*. Highland  
437 Statistics Limited, Newburgh, UK.
- 438 Zuur A., Ieno E.N., Walker N., Saveliev A.A. & Smith G.M. (2009) *Mixed Effects Models*  
439 *and Extensions in Ecology with R*. Springer, New York.



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**Table 1.** Lateral position of eels as they initiate an attempt to ascend an experimental Crump weir. Categories are true left (TL), true right (TR) or Centre, assuming equal channel division. Tukey *Post hoc* comparisons illustrate significant differences.

**Figure 1.** Dimensions of a model Crump weir used at the ICER experimental facility, University of Southampton (UK), to assess the ability of glass eels to pass upstream when unmodified (control) and modified with eel tiles on the downstream face (treatment) (a), a plan view of the eel tile stud sizes and configuration (b), and a sample of European glass eels (*Anguilla anguilla* L.) used during the trials to illustrate degree of pigmentation (c).

**Figure 2.** Mean (+1 SE) number of approaches (black bars), attempts (grey bars), and successful passes (clear bars) over a model Crump weir in 10 minutes.

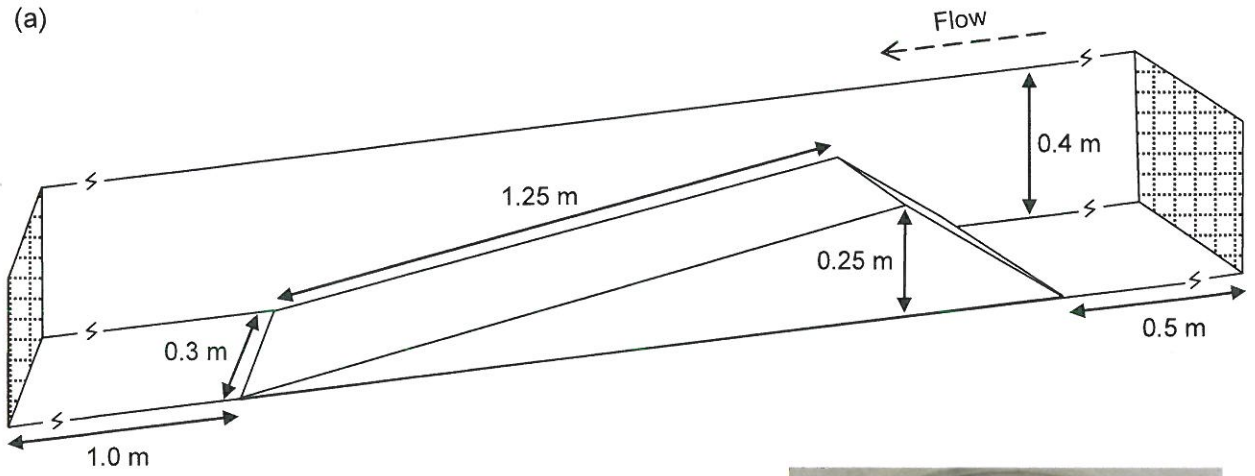
**Figure 3.** The relationship between time and, (a) approach and (b) attempt rate. The shape of the relationship in both (a) and (b) varies between the control (dashed line, open circles) and treatment (solid line, filled triangles). N.B. the relationship between time and the control was not significant at  $\alpha < 0.05$  (line added for interpretation).

**Figure 4.** Maximum distance and lateral position of glass eels that attempted to ascend an experimental Crump weir during (a) control (light grey dashed line indicates location of the hydraulic jump), and (b) treatment setups.

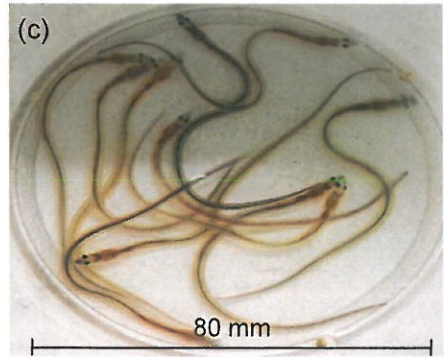
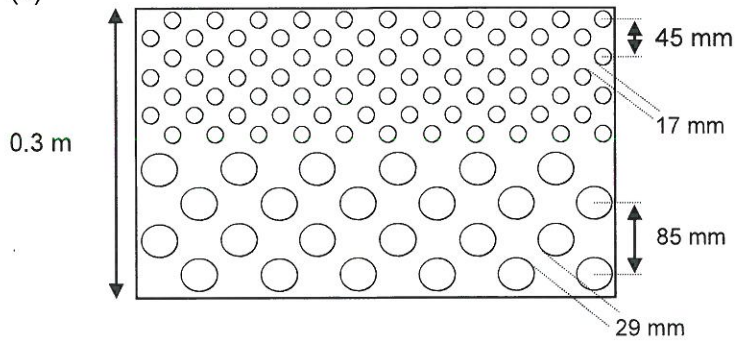




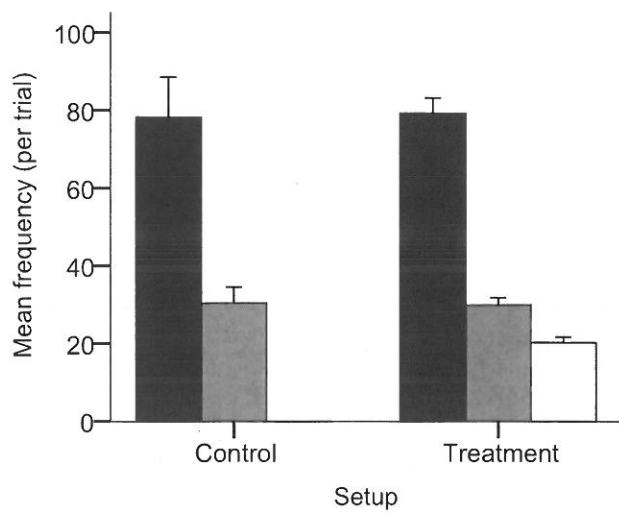
(a)



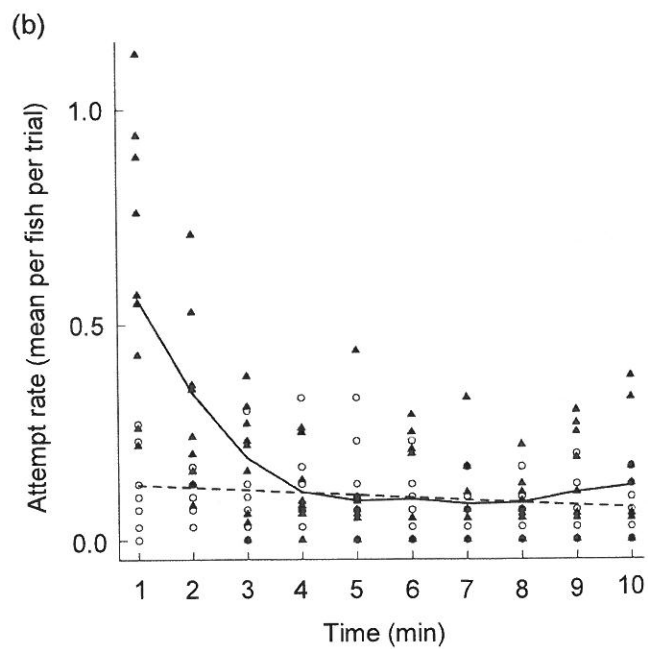
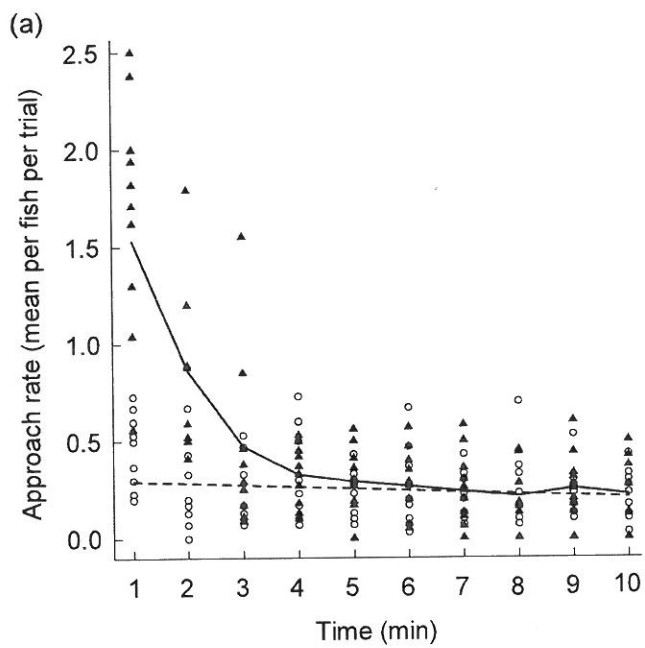
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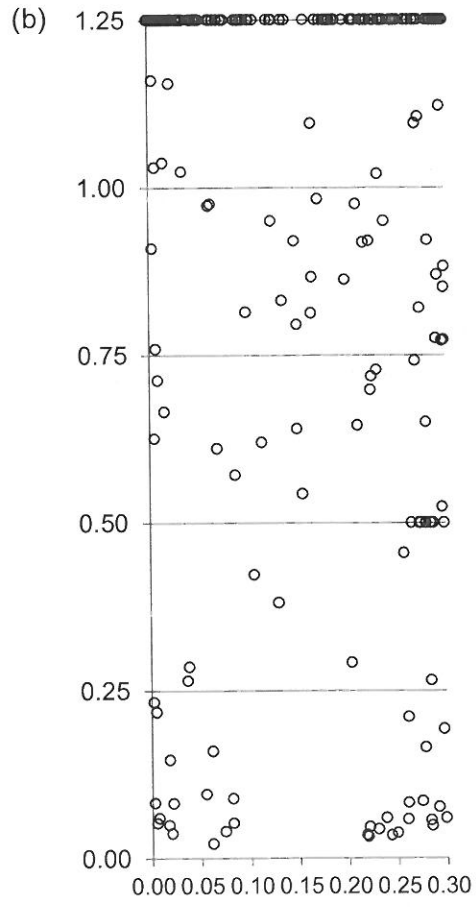
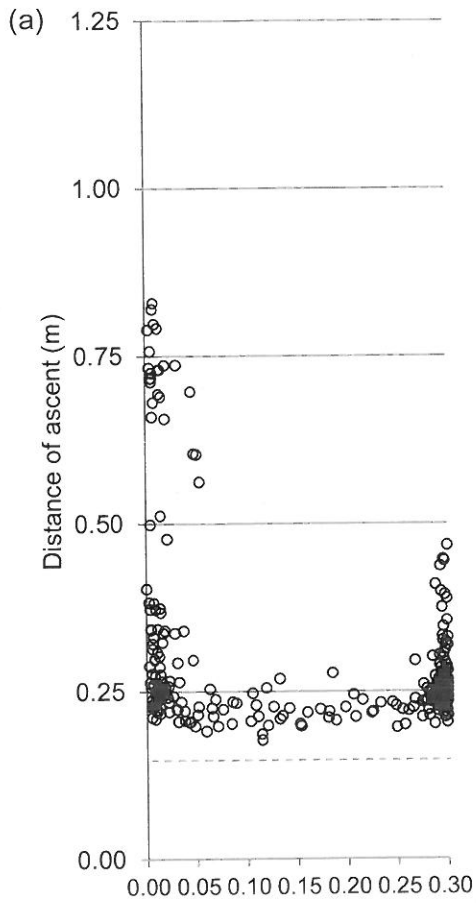












Width across weir (m)





Setup	Lateral position	Mean ( $\pm$ SD) number of attempts per trial	<i>Post hoc</i> comparisons
Control	TR	11.8 (5.22)	TR vs. Centre: $P < 0.001$
	Centre	2.2 (1.81)	TR vs. TL: $P = 0.338$
	TL	16.5 (9.63)	TL vs. Centre: $P < 0.001$
Treatment	TR	14.1 (4.86)	TR vs. Centre: $P < 0.001$
	Centre	3.5 (1.65)	TR vs. TL: $P = 0.722$
	TL	12.3 (3.47)	TL vs. Centre: $P < 0.001$

