

1 **Movement patterns of seaward migrating European eel (*Anguilla anguilla*)**
2 **at a complex of riverine barriers: implications for conservation**

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15 Running headline: Downstream migration patterns in European eel

16
17 **ABSTRACT**

18 River infrastructure such as weirs and hydropower stations commonly present migrating fish
19 with multiple potential passage routes. Knowledge of the cues fish use to navigate such
20 environments is required to protect migrants from hazardous areas and guide them towards
21 safe passage, however, this is currently lacking for many species. Employing high-resolution
22 positioning telemetry, this study examined movements of downstream migrating adult
23 European eel, *Anguilla anguilla*, as they encountered a complex of water control structures in
24 one location on the River Stour, southern England. The distribution of eels across five
25 potential routes of passage differed from that predicted based on proportion of discharge
26 alone. Certain routes were consistently avoided, even when the majority of flow passed
27 through them. Passage distribution was partially explained by avoidance in the vicinity of a
28 floating debris boom. Movement paths were non-randomly distributed across the forebay and
29 eels moved predominantly within a zone 2-4 m from the channel walls. Understanding of
30 avoidance and structure-orientation exhibited by eels will help advance effective guidance
31 and downstream passage solutions for adults.

32
33 Keywords: fish passage; bypass; fishway; hydropower; migratory barriers.

34 **INTRODUCTION**

35

36 Many populations of diadromous fish are threatened by anthropogenic activities, such as
37 overfishing and the construction of river infrastructure that impedes or blocks access to
38 essential habitat (Limburg & Waldman 2009; McCauley et al. 2015). The catadromous
39 European eel (*Anguilla anguilla*, Linnaeus, 1758) exhibits a semelparous life history that
40 includes an initial journey as larvae (leptocephali) across the Atlantic Ocean to the coasts of
41 Europe and North Africa followed by an inland migration to estuaries, rivers and streams,
42 where they may remain resident for between 2 and 20+ years. As adults, the eels will embark
43 on an outward final 5000–6000 km migration to spawning grounds in the Sargasso Sea
44 (Aarestrup et al. 2009; Bruijs & Durif 2009). Compared to the 1980s, juvenile eel recruitment
45 has reduced by 88 to 96% in many rivers (Dekker 2003; ICES 2014). As a result, the species
46 is considered critically endangered (Jacoby & Gollock 2014) and listed under Appendix II of
47 the Convention on International Trade in Endangered Species of Wild Fauna and Flora
48 (CITES). Accordingly, the European Union implemented the Eel Recovery Plan (2007) to
49 establish management strategies to restore stocks (Council Regulation No. 1100/2007/EC), and
50 the International Council for the Exploitation of the Sea recommended that mortality during
51 the adult eel migration as a result of human induced stressors should be reduced to zero
52 whenever possible (ICES 2014).

53

54 Several contributory factors have been attributed to the decline of European eel. These
55 include loss of habitat and reduced habitat quality (Feunteun 2002), bioaccumulation of toxins
56 (Belpaire et al. 2009), impacts of parasites (Kirk 2003; Palstra et al. 2007) and disease (van
57 Beurden et al. 2012; Van Ginneken et al. 2005), overharvest (Briand et al. 2003), and oceanic
58 climate changes such as shallowing of the mixed layer depth and reduced primary productivity

59 near the spawning grounds which may impair the survival and transport of leptocephali
60 (Friedland et al. 2007; Kettle et al. 2008; Knights 2003). Loss of hydrological continuity due
61 to the presence of river infrastructure, such as weirs and dams, limits both juvenile upstream
62 migration and adult spawner escapement (Bruijs & Durif 2009; Jansen et al. 2007; Verbiest et
63 al. 2012; White & Knights 1997). Estimates of the proportion of downstream migrating eels
64 that reach the marine environment range between 15 and 96% in regulated rivers (Aarestrup et
65 al. 2010; Breteler et al. 2007; Breukelaar et al. 2009; Feunteun et al. 2000; Verbiest et al. 2012;
66 Winter et al. 2006).

67

68 River infrastructure may delay or prevent downstream migration (Acou et al. 2008;
69 Behrmann-Godel & Eckmann 2003), while hydropower and pumping stations cause direct
70 mortality through blade strike, cavitation and pressure differences (Bruijs & Durif 2009;
71 Schilt 2007; Turnpenny et al. 1998). Mortality of adult eels at these facilities may range
72 between 10 and 100% (Calles et al. 2010; Carr & Whoriskey 2008; Larinier 2008). Physical
73 screens may be installed to prevent adult eels from entering intakes to pumps and turbines,
74 but can be expensive and cause injury and mortality through collision and impingement
75 (Calles et al. 2010; Hadderingh & Jager 2002). Screens may also guide fish to alternative
76 downstream passage routes. Guiding screens should create an attractive, or at least not an
77 unattractive, environment (e.g. structural, hydrodynamic, acoustic) that does not induce
78 avoidance and delay. Effective guidance for eel is considered lacking (Boubée 2014; Bruijs &
79 Durif 2009; Haro 2014), and for those designs tested so far, efficiencies are highly variable
80 and generally lower than expected (Calles et al. 2012; Gosset et al. 2005; Marohn et al.
81 2014). Development of effective guidance requires improved understanding of fish response
82 to environmental parameters associated with structures at realistic scales (Goodwin et al.
83 2006; Kemp et al. 2012).

84

85 Downstream eel migration has previously been considered to be predominantly semi-
86 passive, with elements of both active swimming and drifting with the currents (Porcher 2002;
87 Tesch 2003), and a tendency to follow bulk flow (Breteler et al. 2007; Bultel et al. 2014; Jansen
88 et al. 2007). Similarly, downstream migration of juvenile salmonids was historically thought
89 to reflect obligate passive displacement with flow (Flagg et al. 1983; Smith 1982 for
90 *Oncorhynchus* sp.; Thorpe & Morgan 1978; Tytler et al. 1978 for *Salmo salar*). This is now
91 known not to be the case, as juvenile salmonids are capable of relatively strong swimming (e.g.
92 Peake & McKinley 1998), actively seek high velocity zones (Svendsen et al. 2007), and avoid
93 rapid accelerations of flow (Enders et al. 2009; Kemp et al. 2005; Svendsen et al. 2011). Indeed,
94 diadromous fish are likely to exhibit a complex repertoire of migratory behaviours to
95 accommodate the diversity of physical and hydrodynamic cues they encounter as they move
96 through freshwater and marine environments (Goodwin et al. 2014; Kemp et al. 2012; Smith
97 et al. 2014).

98

99 As predicted under assumptions of semi-passive downstream migration, the distribution
100 of migratory adult eels at river bifurcations and flow diversion structures may be proportional
101 to the flow passing each route (Breukelaar et al. 2009; Bruijs & Durif 2009; Calles et al. 2013;
102 Jansen et al. 2007; Piper et al. 2013). Recent studies cast doubt on the simplistic semi-passive
103 drift assumption, however, and describe a wide variety of behaviours displayed by eels when
104 approaching structures. These include active hesitation before passing trash racks (Bruijs &
105 Durif 2009), and altering of position in the water column and recurrent or searching behaviours
106 on encountering rapid velocity gradients (Piper et al., 2015) and debris screens (Brown et al.
107 2009 for *A. rostrata*; Keeken et al. 2011 for *A. anguilla*). In flumes, eels associate closely with
108 channel walls and structure (Adam et al. 1999; Russon et al. 2010) and may react to turbulent

109 flow features (Russon et al. 2010; Silva et al. in press) and reject velocity acceleration
110 (Newbold et al., 2015).

111

112 This study aimed to enhance understanding of the migratory behaviour of eels by
113 exploring fine-scale movement and route choice of actively downstream moving adults in a
114 field setting when presented with a variety of passage routes at one location. Using high
115 resolution positioning acoustic telemetry, European eel were tracked through the forebay of a
116 complex of water control structures, including both overshoot and undershot sluices at a
117 redundant hydropower site. Movement patterns were analysed and compared to those predicted
118 based on the assumption of proportional passage with the flow through five available routes.
119 Spatial distribution of eels across the forebay was examined to determine the influence of
120 structural boundaries.

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123 **MATERIALS AND METHODS**

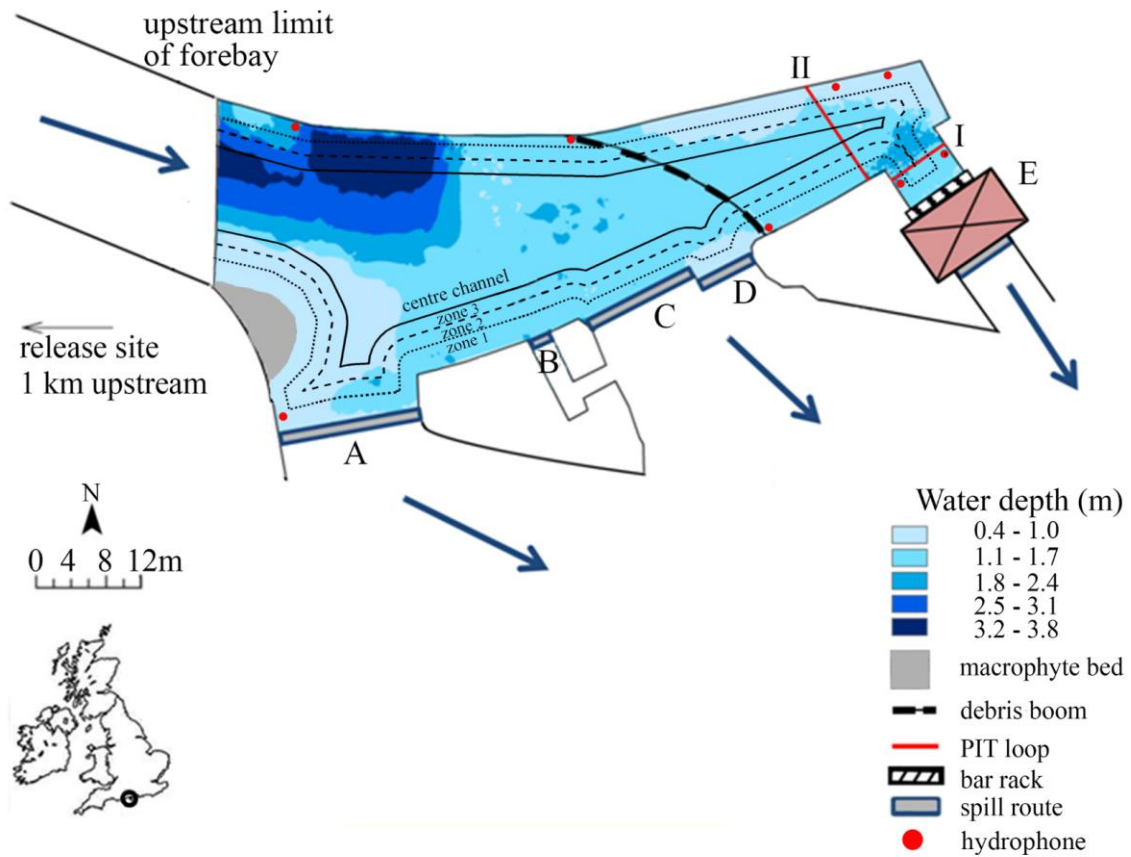
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125 **STUDY SITE**

126 The study was conducted on the River Stour, Southern England, in the forebay of a
127 complex of water level control structures (50°46'31.98"N, 1°54'41.08"W) located 19 km
128 upstream of the estuary. The complex comprises of two broad-crested Crump weirs (15.2 m
129 width, A; 14.8 m width, C, Fig. 1); a pool and weir fish pass (1.8 m width, B, Fig 1); an
130 adjustable overshoot radial weir (7.5 m width, D, Fig. 1); and a set of 6 undershot sluice gates
131 on the downstream side of an intake channel (7.6 m width) that formerly led to two
132 hydropower turbines that were removed in the 1970s (Redundant Hydropower – RHP, E, Fig.
133 1). At the intake, a vertical bar rack (7.6 m width, 55° angle, 58 mm bar spacing), extends the

134 full width and depth of the channel (Fig. 1). Floating debris is diverted via the radial drop
 135 weir by a rubber floating boom that spans the width of the channel upstream of the RHP (Fig.
 136 1). The forebay channel ranges from 15 to 35 m wide, with vertical banks bounded by steel
 137 revetments.

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139

140 **Fig. 1. Forebay bathymetry and location of structures (A and C - broadcrest weirs; B - pool and weir**
 141 **fish pass; D - radial weir, and E - an intake to a redundant hydropower (RHP) facility at Longham**
 142 **water works, River Stour, Dorset, UK. Red lines show PIT antennas I and II. Structures A to D are**
 143 **overshot discharge routes, whereas E (RHP intake) is undershot. Red dots denote the positions of**
 144 **hydrophones. For spatial analysis, the site was divided into four zones at increasing distances from**
 145 **the channel walls: Zone 1 (0 to 2 m, small dashes); Zone 2 (2 to 4 m, large dashes); Zone 3 (4 to 6**
 146 **m, solid line), and centre channel (the remainder of the site)**

147

148 Adjustable water control structures were maintained at fixed positions throughout the
149 study with RHP sluice gates 50% open. An automatic flood control gate upstream of the
150 forebay diverted excess flow down an alternate channel and thereby regulated the total channel
151 discharge passing the study site.

152

153 A downward focused raft-mounted Acoustic Doppler Current Profiler with onboard GPS
154 (ADCP, Sontek M9 River Surveyor®; www.sontek.com) was used to map site bathymetry and
155 quantify discharge flowing into the study site and through each water control structure (Fig. 1).
156 For bathymetry, the ADCP measured distance to channel bed using a vertical acoustic beam
157 (0.5 MHz), and was pulled from bank-to-bank along a zig-zag transect to sample the entire
158 forebay (see Dinehart & Burau 2005 for detailed description). For discharge, daily ADCP
159 transect measurements in which the raft was pulled bank to bank perpendicular to flow were
160 conducted across the inlet channel of the forebay, 4 m downstream of the debris boom, and 2
161 m upstream of structures A to D. Discharge was calculated within processing software
162 RiverSurveyor Live v3.01 (Sontek; www.sontek.com) using established methods (Simpson
163 2001; SonTek 2010). Water level (cm) and temperature (°C) were recorded every 15 minutes
164 throughout the study period by fixed loggers located near the debris boom (HOBO® U20,
165 OnsetComp; www.onsetcomp.com). Temperature ranged from 7.9 to 8.6 (mean 8.1 ± 1.3 S.D.)
166 over the study period. Flow patterns were generated through linear interpolation based on
167 ADCP discrete transect measurements and continuously logged changes in water level.

168

169 TELEMETRY CONFIGURATION AND VALIDATION

170 Acoustic telemetry (Hydroacoustic Technology Inc.; www.htisonar.com) was employed
171 to track 2-dimensional movements (x and y) of tagged eels within the study site. Eight
172 hydrophones (300 kHz) were positioned around the perimeter of the study area (Fig. 1) and

173 detections were logged by a receiver (HTI, Model 290). As it was not possible to accurately
174 determine the position of the fish in the shallow water column from acoustic detections alone,
175 Passive Integrated Transponder (PIT) telemetry (Model LF-HDX-RFID, Oregon RFID;
176 www.oregonrfid.com) was employed to indicate eel depth. A pass-over antenna was positioned
177 across the full width of the intake channel (7.6 m length, 0.5 m width) (I, Fig 1), with a second
178 antenna positioned across the channel 6.0 m upstream (14 m length, 0.5 m width) (II, Fig 1,).

179

180 The detection range of the acoustic tags was assessed at various positions throughout the
181 study site. This enabled optimal positioning of the hydrophones and quantification of detection
182 efficiency. Known tag locations demonstrated a minimum accuracy of < 1m which is
183 comparable to other studies (Brown et al. 2009; Svendsen et al. 2011). Similarly, PIT antenna
184 range testing indicated consistent detection (> 99 %) for depths < 0.2 m across both antennas.
185 Both telemetry systems logged continually throughout the study period.

186

187 FISH CAPTURE AND TAGGING PROCEDURE

188 Actively migrating adult eels ($n = 25$) were trapped downstream of the RHP on five
189 consecutive nights in November 2009, within the typical migration period for this river (Roger
190 Castle, pers. comm.). Fish were transferred to in-river perforated holding barrels and held for
191 a maximum of 8 h before being individually anaesthetised (Benzocaine 0.2 g l^{-1}). Morphometric
192 measurements were collected: wet mass (M , g); total length (L_T , mm); left pectoral fin length
193 from insertion to the tip (mm), and maximum vertical and horizontal left eye diameter (mm).
194 All individuals captured exceeded 450 mm (L_T) and were therefore presumed to be female
195 (Durif et al. 2005). Degree of sexual maturation was quantified prior to tagging using two
196 metrics; the Ocular index (I_O), according to Pankhurst (1982), and Fin Index (I_F), according to
197 Durif *et al.* (2009). European eel with $I_O \geq 6.5$, and $I_F \geq 4.3$ (females only) were considered to

198 be at the migratory silver stage. The first five eels fulfilling these criteria were selected for
199 tagging each night. Tagged eels ranged from 635 to 827 mm L_T , 596-1049 g M , with median
200 I_O 8.9 (range 6.8-12.3) and median I_F 4.6 (range 4.4 to 5.0).

201

202 An acoustic tag (HTI model 795G, 11mm diameter, 25mm length, 4.5 g mass in air,
203 300kHzs, 0.7 – 1.3 s transmission interval), and Passive Integrated Transponder (PIT) tag
204 (HDX, 3.65 mm diameter, 32 mm length, 0.8 g mass in air, Texas Instruments; www.ti.com)
205 were surgically implanted into the peritoneal cavity of each eel following methods similar to
206 Baras and Jeandrain (1998) under UK Home Office licence. No individual surgical procedure
207 exceeded 3 minutes.

208

209 After tagging, eels were transported to the release location (1 km upstream of the study
210 site) and held for 10-12 hours in a barrel to allow post-operative recovery and acclimation
211 before release. No mortality was observed. To reduce bias in route choice, the holding barrel
212 was tethered in the centre of the channel following previous studies (Piper et al. 2013; Svendsen
213 et al. 2010). On each study night in darkness (20:00 h), the barrel lid was removed remotely
214 with rope and pulley to minimise disturbance and allow individuals to leave volitionally.

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216

217 DATA ANALYSIS

218 Acoustic tag detections were manually marked to remove background noise, then
219 processed and corrected for speed of sound using MarkTag v5 and AcousticTag v5 software
220 (Hydroacoustic Technology Inc., www.htisonar.com). Only detections within the perimeter of
221 the hydrophone array were used (Ehrenberg & Steig 2003; Svendsen et al. 2011). Time-
222 stamped Universal Transverse Mercator (UTM) designated detections (eel tracks) were

223 imported into ArcMap v10 (ESRI; www.esri.com). Fish were deemed to have entered the study
224 domain when tracks crossed a hypothetical cross-channel line between the two most upstream
225 hydrophones at the upstream entrance to the forebay (Fig. 1). Passage was deemed to have
226 occurred at the last detection point before an individual passed downstream of one of the five
227 structures (A to E, Fig. 1). Residence time was calculated as the duration between first and last
228 detection in the study domain before downstream passage. PIT records were examined for
229 detections at the times when acoustic tracks intersected antenna locations. Positive detection
230 provided a surrogate measure of near-bed (≤ 20 cm) movement.

231

232 Randomization tests of goodness of fit (200 replicates) (McDonald 2009) were used to
233 assess whether: 1) the number of fish that passed varied between nights, and 2) passage through
234 the five available routes was proportional to flow. Where assumptions of normality and
235 homogeneity of variance were met, one-way ANOVAs were used to test for differences in the
236 body length, ocular index and fin index of eels that passed the five available downstream routes.
237 Buffer analysis was conducted on mapped tracks in ArcMap to explore spatial patterns of eel
238 movement across the forebay. Three edge zones (buffers) of 2 m width (to encompass the
239 maximum possible error in fish positioning i.e. ± 1 m) were imposed inside the structural site
240 perimeter (zone 1: 0 – 2, zone 2: 2 – 4, and zone 3: 4 – 6 m from channel walls) and a fourth
241 zone (centre channel) encompassed the remainder of the site (Fig. 1.). For each eel, the length
242 of track falling within each of the four zones was calculated and weighted to account for the
243 difference in area covered by each zone (20.9, 18.9, 17.2 and 43.0% of total site area,
244 respectively). Weighted lengths were compared between zones using a one-way repeated
245 measures ANOVA with pairwise comparisons and Tukeys post-hoc test. The Greenhouse-
246 Geisser correction was applied where data violated the assumption of sphericity. Values are

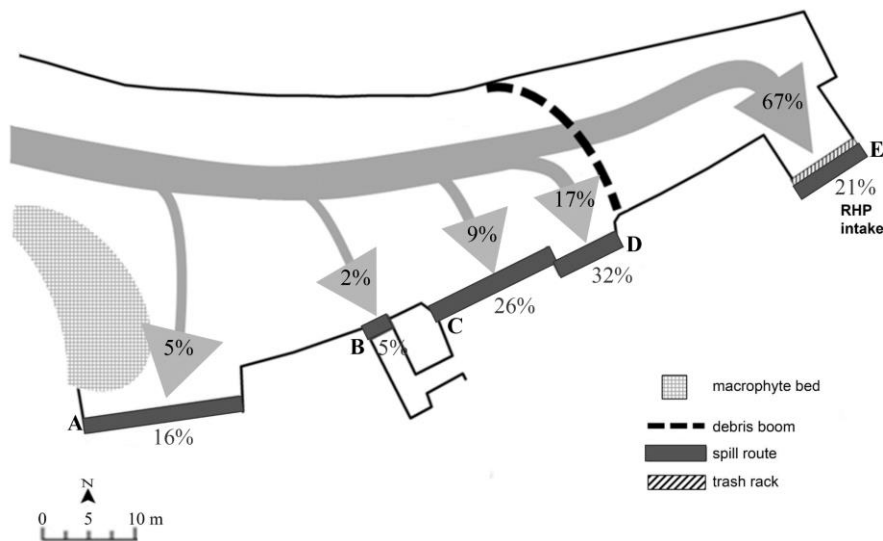
247 quoted as mean \pm S.E. The significance level was 0.05. Statistical analyses were carried out
248 using IBM SPSS v21 (IBM; www-01.ibm.com/software/uk/analytics/spss).

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250 RESULTS

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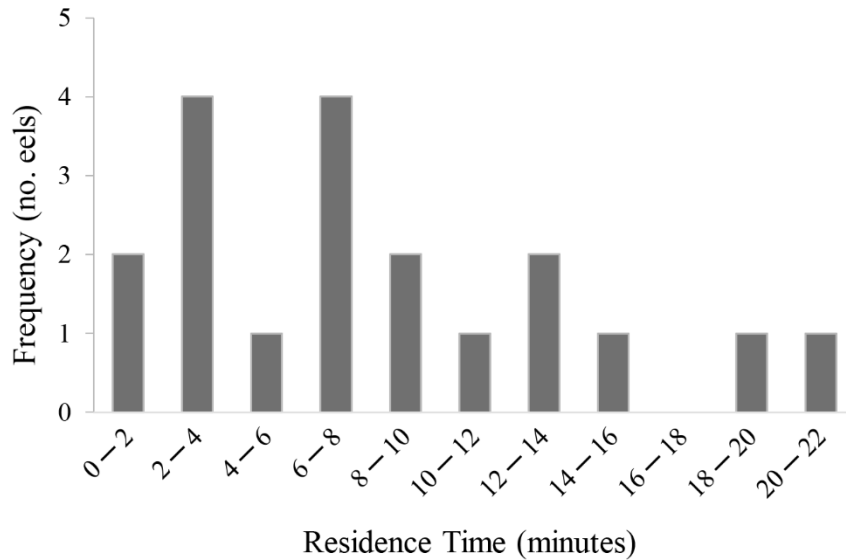
252 Of the 25 fish released, 19 passed downstream via the five available routes (Fig. 2). Three
253 individuals remained undetected, and a further three were detected briefly in the forebay
254 entrance, but returned upstream and were thus excluded from further analysis. The number of
255 fish that passed did not vary between nights (randomisation test, $p = 0.82$). Fish took between
256 1.67 and 53 h to enter the forebay after release, and mean residence time was $8.2 \text{ min} \pm 1.35$
257 min (Fig. 3). Passage always occurred during the hours of darkness.



259

259 **Fig. 2.** Passage routes of downstream migrating adult eel (*Anguilla anguilla*) ($n = 19$) (%) via two
260 broad crested weirs (A,C), a pool and weir fish pass (B), a drop weir (D) and a redundant
261 hydropower (RHP) intake (E) at Longham Water Works, river Stour, UK. Arrows indicate water
262 discharge routes, with percentages (in arrow heads) indicating total mean channel flow through
263 each route. The proportion of eels that passed the routes differed ($p < 0.01$) from that predicted
264 based on the distribution of flow through the routes.

265



266

267 **Fig. 3. Residence time of downstream migrating adult eel (*Anguilla anguilla*) (n = 19) within the**
 268 **forebay of a complex of water control structures at Longham, UK, prior to passage downstream via**
 269 **one of five flow spill routes.**

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Mean total flow into the forebay was $12.88 \pm 0.2 \text{ m}^3 \text{ s}^{-1}$. The proportion of flow spilling via each passage route remained reasonably consistent throughout the study period, irrespective of minor fluctuations in total discharge entering the study site. Eels passed the structures in proportions that differed from the division of flow through the five routes (randomisation test, $p = 0.01$). The majority of individuals (63%) (n = 12) initially swam downstream with a relatively direct path towards the debris boom, although most (8 individuals) trajectories diverted on encountering it. Although 67% of river flow passed through the RHP intake, only 21% of fish descended via this route (Fig. 2). There was no relationship between eel body length, ocular index and fin index and the passage route used by downstream migrants ($F_{4,14} = 0.356$, $p = 0.836$; $F_{4,14} = 0.316$, $p = 0.862$; $F_{4,14} = 0.292$, $p = 0.878$, respectively).

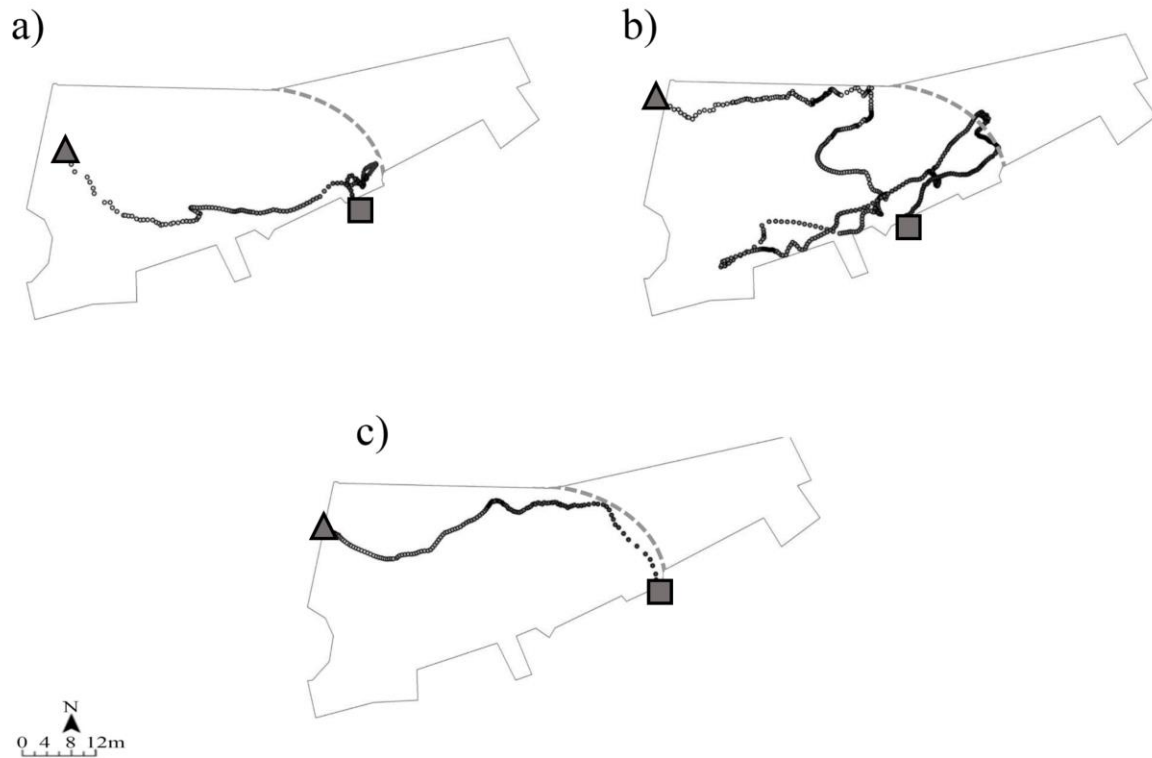
Sixteen percent of individuals showed comparatively direct paths to the point of passage. The remaining eels either explored, making lateral movements transverse to the direction of

286 flow with a non-direct path, or initially rejected a structure, i.e. abrupt switch from downstream
287 to upstream swimming ($>90^\circ$ turn angle) before subsequently passage. The highest depth
288 averaged velocity (derived from ADCP measurements) directly upstream of any structure was
289 0.62 m s^{-1} (radial drop weir) and within the burst swim speed capability of adult migrating eel
290 ($\geq 450 \text{ mm } L_T$) ($1.30 - 1.75 \text{ m s}^{-1}$) (Russon & Kemp 2011; Solomon & Beach 2004), indicating
291 that movements were volitional.

292

293 Rejection behaviour was exhibited by five individuals in the vicinity of the debris boom.
294 Eels rejected either at a point directly upstream ($< 2.5 \text{ m}$) of the boom (Fig. 4a), or shortly after
295 passing underneath it (Fig. 4b). Several individuals showed less abrupt changes in direction
296 and followed along the upstream edge of the boom (Fig. 4c). Only four individuals passed
297 downstream of the boom, of which three exhibited an initial rejection between 0.9 and 2.8 m
298 upstream of RHP bar rack, although all ultimately passed through the intake. Four eels
299 recaptured at a trap downstream were alive and had no sign of external damage.

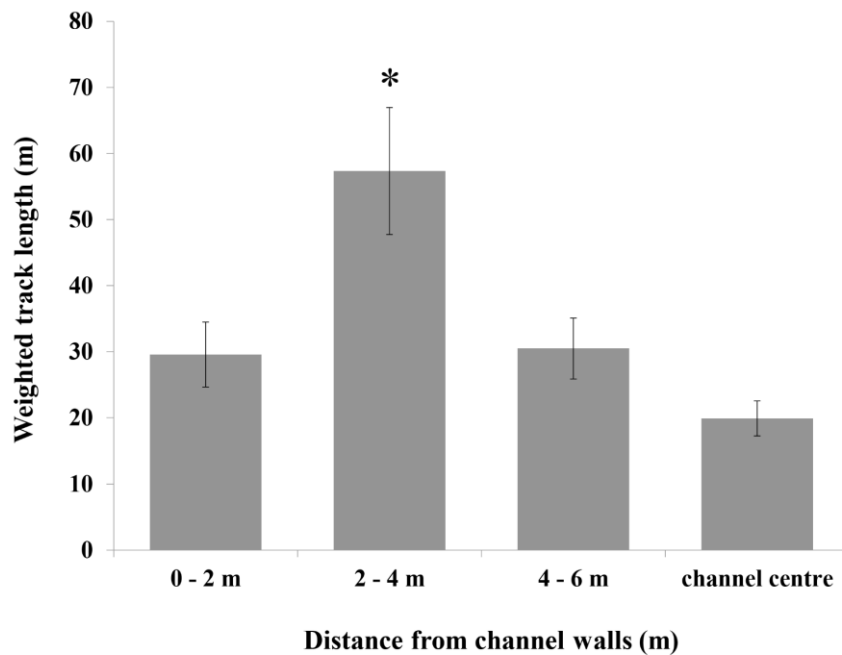
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302 **Fig. 4.** Examples of tracks of three downstream migrating adult eels (*Anguilla anguilla*) that a)
 303 rejected immediately upstream of a debris boom (dashed line), b) rejected immediately
 304 downstream of the boom, and c) changed direction at the boom and swam parallel to it before
 305 passing the radial weir. Grey triangle and square denote the start and end of tracks, respectively.
 306

307 Track length ranged from 36 to 267 m and tracks were not randomly distributed within
 308 the site ($F_{1.53, 27.47} = 10.02, p < 0.01$). Instead, eels predominantly moved within a zone
 309 extending 2 to 4 m inside of the channel walls (Fig. 5). Less than 19% of total track lengths
 310 (unweighted) were potentially in contact with structures (< 2 m).



311

312 **Fig. 5. Mean weighted track length of tagged eels (*Anguilla anguilla*) within 2 m wide zones**
 313 **extending between 0 and 6 m inside the site boundary, and a fourth zone which encompassed the**
 314 **channel centre (grey bars) \pm 1 standard error. * denotes significant difference from all other**
 315 **groups ($p < 0.05$).**

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317

318 Eel swim depth determined by PIT telemetry on the approach to, and within, the RHP
 319 intake channel was within 0.2 m of the channel bed for all individuals that descended via this
 320 route ($n = 4$). Water depth in the vicinity of the antennas ranged from 0.4 to 1.7 m, indicating
 321 that eel movements were within the lower 12 – 50% of the water column.

322

323 **DISCUSSION**

324 Facilitating effective protection, guidance and passage of seaward migrating adult eel at
 325 river infrastructure is an important component of their conservation and management
 326 (Feunteun 2002; Han et al. 2008; Haro et al. 2000; Jellyman et al. 2002). The distribution of
 327 European eel passing five water control structures did not coincide with the predominant flow

328 direction, demonstrating that individuals were not passively transported downstream with the
329 current. The principal spill route (RHP) passed only 21% of eels, with many showing avoidance
330 behaviour at a cross-channel debris boom upstream. Further, swim paths were not evenly
331 distributed across the study site; eels predominantly moved within a zone 2-4 m from the
332 channel walls. The highly variable movement patterns revealed by fine-scale telemetry
333 demonstrated a strong behavioural component to eel descent at riverine structures.

334

335 Eel movements in the forebay upstream of the debris boom initially coincided with
336 the route of bulk flow, as predicted (Breukelaar et al. 2009; Bruijs & Durif 2009; Calles et al.
337 2013; Jansen et al. 2007; Piper et al. 2013); however, final downstream passage routes did not
338 reflect this pattern. Studies that report proportion of discharge as the main determinant of eel
339 route selection were typically conducted in large, relatively uniform approach channels with
340 limited variation in passage route (Gosset et al. 2005; Jansen et al. 2007; Travade et al. 2010).
341 In the current study site, which encompassed multiple passage routes including undershot and
342 overshot spill structures in close proximity, movement patterns were highly variable. The
343 debris boom influenced eel distribution across passage routes, apparently modifying
344 behaviour in the upstream vicinity with clear rejection observed in five individuals and less
345 abrupt changes in direction in three others. Mark and recapture studies conducted at the same
346 location by the Environment Agency in 2010 and 2011 in which a sample of downstream
347 migrating adult eels were floy tagged and released upstream of the study site (n = 87 & 194,
348 ranging from 356 to 815 & 480 to 790 mm in 2010 and 2011, respectively) indicated a
349 recapture rate of 29 and 17 % of tagged individuals in the RHP trap in 2010 and 2011,
350 respectively. This is broadly comparable with the 21% which descended via this route in the
351 current acoustic telemetry study suggesting that the observed migration patterns are typical

352 for this site. The debris boom effectively diverted eels towards the two structures
353 immediately upstream (C and D) which spilled only 26% of flow, but passed 58% of fish.

354

355 The boom projected 40 cm down from the water surface (total water depth: 1 to 1.6
356 m), while the eels tended to be benthic-oriented, in common with previous studies (Brown et
357 al. 2009; Gosset et al. 2005). Rejection at the debris boom was, therefore, unlikely to be a
358 consequence of physical contact with the structure. It was not possible to decouple the
359 physical influence of the debris boom from other environmental factors within this area. Eels
360 have been shown to react to hydrodynamic features independent of physical contact with
361 structures. In a recent flume study, 46% of eels switched from downstream to upstream
362 swimming as they encountered an accelerating velocity gradient created by a flow
363 constriction (Newbold et al. 2015). In a manipulated flow experiment at the RHP intake,
364 Piper et al. (2015) observed that downstream migrating tagged eel predominantly rejected
365 rapid water velocity gradients created by flow constriction, yet showed slower, exploratory
366 movements on encountering low gradients. The boom likely induced a downstream sweeping
367 flow parallel to the upstream face (Odeh & Orvis 1998) and flow distortion with turbulent
368 upwelling in the area immediately downstream (Toniolo 2014). Such hydrodynamic
369 conditions may have deterred some eels, causing them to return upstream, and guided others
370 towards structures C and D.

371

372 Surface guidance devices such as floating booms, louvers and guide walls have been
373 used with some success for diverting downstream migrating juvenile salmonids (smolts)
374 towards safe passage routes (Adams et al. 2001; Hanson 1999; Odeh & Orvis 1998; Scruton
375 et al. 2008). For example, a floating louver installed at a hydroelectric facility on the Exploits

376 River, Canada, achieved a fish guidance efficacy of 54 to 73.3% (Scruton et al. 2003) and an
377 angled surface wall at Bellows Falls power station, Connecticut River, US, guided 84% of
378 smolts to a sluice gate (Odeh & Orvis 1998). In contrast to eels, smolts typically travel higher
379 in the water column when migrating downstream (Ruggles 1980). Nevertheless, observed
380 rejection by eels at the debris boom suggests that surface structures may also have application
381 for eel guidance in shallow water sites.

382

383 Eels predominantly followed paths that aligned with the structural perimeter of the study
384 site, maintaining a distance of on average 2-4 m from the channel walls or water control
385 structures. It is unclear how eels navigated along this route without making contact with the
386 channel wall. There was little reduction of water depth near the vertical engineered perimeter
387 walls with no distinctive topographic feature (e.g. trench or ridge) that would explain the bias
388 in the distribution. Although the dark and highly turbid conditions in the forebay likely limited
389 the visual field, it is recognised that eels, like other fish, derive navigational cues from flow
390 field distortion created by fixed structures, detected through the mechanosensory system
391 (Kalmijn 1989; Montgomery et al. 2000; Montgomery et al. 1995; Nestler et al. 2000).

392

393 Fine scale observations in the current study revealed that downstream migrating eels do
394 not necessarily 'go with the flow'. Avoidance and structure-oriented behaviours provide
395 optimism for the development of eel passage solutions in situations where demands for
396 hydroelectric generation and water abstraction dictate that only a relatively small amount of
397 flow is available to pass down alternate routes (e.g. bypasses). Effective guidance measures
398 to divert eels away from the bulk flow passing deleterious routes (e.g. turbines and pumps)
399 and towards safe passage is urgently needed to aid their conservation. As the mechanisms

400 that underpin the behaviours observed in this study remain unclear, further investigation is
401 needed to examine the fine scale response of eel to specific and well defined cues (Anderson,
402 1988; Schilt, 2007; Williams *et al.*, 2012), especially to relatively simple structures like
403 surface booms in shallow water. Given the results presented and other recent advances (e.g.
404 Newbold *et al.*, 2015, Piper *et al.*, 2015, Russon *et al.*, 2010), further investigation of eel
405 reponse to hydrodynamic features synonymous with water control structures is likely to prove
406 valuable in the development of guidance devices.

407

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