

1 Freshwater and coastal migration patterns
2 in the silver stage eel *Anguilla anguilla*

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14 Running headline: SILVER EEL MIGRATION PATTERNS

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19 **ABSTRACT**

20 The unimpeded downstream movement patterns and migration success of small female and
21 male *Anguilla anguilla* through a catchment in North West Europe was studied using an
22 acoustic hydrophone array along the River Finn and into the Foyle estuary in Ireland. Twenty
23 silver stage *A. anguilla* (L_t range: 332-520 mm) were trapped 152 km upstream from a
24 coastal marine sea lough outlet and internally tagged with acoustic transmitters of which 19
25 initiated downstream migration. Migration speed was highly influenced by river flow within
26 the freshwater compartment. *Anguilla anguilla* activity patterns were correlated with
27 environmental influences; light, tidal direction and lunar phase all influenced initiation of
28 migration of tagged individuals. Migration speed varied significantly between upstream and
29 lower river compartments. Individuals migrated at a slower speed in transitional water and
30 sea lough compartments compared with the freshwater compartment. While 88.5% survival
31 was recorded during migration through the upper 121 km of the river and estuary, only 26%
32 of *A. anguilla* which initiated downstream migration were detected at the outermost end of
33 the acoustic array. Telemetry equipment functioned efficiently, including in the sea loch, so
34 this suggests high levels of mortality during sea lough migration, or less likely, long-term sea
35 lough residence by silver *A. anguilla* emigrants. This has important implications for Eel
36 Management Plans (EMP's).

37 Key words: Anguillidae, migration triggers, survival, sea lough, telemetry.

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INTRODUCTION

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In the last 30 years the panmictic European eel *Anguilla anguilla* (L. 1758) population (Als *et al.*, 2011) has experienced declines across its range (ICES, 2013), the causes of which are not fully understood (Kettle *et al.*, 2011). An important precursor to any effective management of the existing population is to identify bottlenecks to critical life history stages. As a result of this decline, the European Union enacted legislation (EC Reg 1100/2007) to ensure increased *A. anguilla* escapement of the freshwater feeding lifecycle stage, the aim being to raise the biomass of potential semelparous spawners leaving continental waters for the spawning migration; the presence of newly hatched larvae in the south west Sargasso Sea in the western Atlantic reveals that to be the spawning area of the species (Schmidt, 1923; Kleckner & McCleave, 1988). The growth phase for *A. anguilla* in continental waters ends with a transition called the silvering process (Tesch, 2003; Durif *et al.*, 2005), following which *A. anguilla* residing in freshwater begin migrating towards marine waters. The downstream migration patterns in *A. anguilla* are thought to vary across localities (Vøllestad *et al.*, 1994; Breukelaar *et al.*, 2009). The majority of the information on silver stage *A. anguilla* migration comes from commercial fishing data (Durif & Eile, 2008) and consequently details of silver stage *A. anguilla* behaviour as they transit from freshwater to saltwater are poorly understood.

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Tracking technologies allow detailed studies of individual migration behaviour in freshwater and inshore marine environments (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011; Verbiest *et al.*, 2012). Several studies have revealed impacts of hydropower impoundment and fisheries on riverine survival of migrating silver stage *A. anguilla* (Winter *et al.*, 2006; Travade *et al.*, 2010). The freshwater -marine transition represents an important life history stage for diadromous fishes. During the transition they experience fundamental physiological challenges at the freshwater - saltwater interface and there is evidence of increased mortality

67 risk from predators as migratory fishes enter sea water (Aarestrup *et al.*, 2010; Davidsen *et al.*, 2011; Aarestrup *et al.*, 2014). In common with other diadromous fishes, migrating silver
68 stage *A. anguilla* pass through productive estuarine habitats which often have large numbers
69 of avian, mammalian and fish predators. Predation pressures in such habitats may be high on
70 migratory fishes, for example Keller (1995) reports that cormorants (*Phalacrocorax* sp.) a
71 common species in estuarine habitats, feed heavily on smaller *A. anguilla*. Knowledge of
72 escapement success during the freshwater saltwater transition is crucial to understanding of
73 the natural dynamics of *A. anguilla* populations. Specifically, understanding migration
74 behaviour, life stage specific mortality and ultimately migration success at this important life
75 stage, is critical to effective conservation management. Recent work on downstream
76 migration patterns has indicated low survival rates during migration to the open ocean
77 (Verbiest *et al.*, 2012; Aarestrup *et al.*, 2010). However these studies were conducted in
78 catchments impacted by hydropower and fisheries thus it is it difficult to disentangle natural
79 mortality from anthropogenic mortality resulting from hydroelectric power generation or
80 fishery pressure. Furthermore the migration of male *A.anguilla*, which migrate at a smaller
81 size than female *A. anguilla* (Poole *et al.*, 1990), is particularly poorly understood. Previous
82 studies have focused solely on the behaviour of females (which are preferred for tagging as a
83 result of being large relative to tag size) and as a result, field data on the downstream
84 migration of smaller sized female and male *A. anguilla* is lacking. The aims of this study
85 were to (i) determine the progression rates and migration behaviour of small silver stage *A.*
86 *anguilla* through sequential catchment compartments; (ii) elucidate migration influences and
87 how they may differ between catchment compartments; (iii) quantify escapement success of
88 tagged individuals through freshwater and coastal sea lough habitats.

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MATERIALS AND METHODS

91 STUDY AREA

92 The study was conducted in the Foyle catchment, Northern Ireland in 2013. The Foyle
93 Catchment has an area of 4450 km² and drains into the Atlantic Ocean on the North coast of
94 Ireland (55.01°N , 7.08°W).The River Finn has no man-made barriers to migration and the
95 hydrology retains high natural variability. The sea lough (Lough Foyle) located at the mouth
96 of the River Foyle is typical of an enclosed broad, but shallow, productive estuary and the
97 exit point to the open ocean at Magilligan Point is narrow (0.98 km) (Fig.1). The upper limit
98 of tidal influence is located 60 km from Magilligan Point and the salt wedge occurs
99 approximately 40 km upstream of Magilligan Point depending on the tide and river flow
100 conditions. In this study, the catchment compartments were designated as follows: freshwater
101 (95 km long), transitional (26.8 km long) and sea lough (30.2 km long). Catchment
102 characteristics are presented in Table I.

103 FISH CAPTURE AND TAGGING

104 Migrating silver stage *A. anguilla* were captured using a fixed fyke net (leader length=8.5 m,
105 depth=55 cm , mesh=10 mm) in the outflow stream from Lough Finn at the source of the
106 River Finn (54.50°N 8.05°W) between 29 September and 28 October 2013. Prior to
107 measuring and tagging, *A. anguilla* were placed in a tank and anaesthetised with clove oil
108 (0.5 mg⁻¹of freshwater). After anaesthetisation, the total body length (L_T mm), mass (g), eye
109 diameter (mm) and length of the pectoral fin (mm) were recorded to determine their
110 maturation stage and sex according to Durif *et al.* (2005) (Table II). According to this
111 classification, 17 *A. anguilla* were deemed mature males and three mature females (Table II).
112 Fat content was measured on live individuals using a Distell FM 692 fat meter (Distell
113 Meters, Scotland UK; www.distell.com). This meter has a micro strip censor which measures
114 the water content of a sample. The fat content of the fish is correlated with the water content
115 and thus the measurement of one can determine the other if the relationship between the two
116 is known. The fat meter was calibrated (company calibration) to the fat /water relationship

117 specific to *A. anguilla* prior to taking measurements. Three measurements were taken along
118 the body on both sides of the *A. anguilla*. The fat meter was then used to calculate the
119 average percent body fat for the individual based on the six readings.

120 A total of 20 silver stage *A. anguilla*, 17 males and 3 females (L_T range:332-520 mm, mass
121 range: 83-384 g) were tagged with individually coded acoustic transmitters (Model LP-7.3,
122 7.3 mm diameter, 18 mm length, 1.9 g mass in air, 139 dB re 1 μ Pa power, Thelma Biotel
123 AS, Trondheim, Norway 2013; www.thelmabiotel.com) (Table II). For each *A. anguilla* an
124 acoustic transmitter was surgically implanted through a 15 mm incision into the peritoneal
125 cavity, and the incision closed with independent sterile sutures (6-0 ETHILON, Ethicon Ltd,
126 Livingston, UK; www.ethiconproducts.co.uk). The mean tag to body mass ratio was
127 $1.53 \pm 0.5\%$ (<2% recommended, *sensu* Lucas & Baras, 2000). *Anguilla anguilla* were
128 aspirated with 100% river water throughout the procedure. Tags were programmed to have an
129 acoustic transmission repeat cycle of $30 \text{ s} \pm 50\%$, giving a tag life span in excess of 110 days.
130 This surgical procedure does not adversely affect behaviour of tagged *A.anguilla* (Thorstad *et*
131 *al.*, 2013). Once the tagging procedure was complete, *A. anguilla* were returned to a recovery
132 tank filled with highly aerated water. The entire surgical process took less than 4 minutes.
133 After complete recovery (10-15 min), defined as orientation regained and response to stimuli,
134 *A. anguilla* were released.

135 ACOUSTIC TRACKING

136 The passage of tagged *A. anguilla* was recorded using seven automatic listening stations
137 (ALS: VEMCO VR2 W (vemco.com); Fig. 1.) deployed prior to tagging (August 2013) and
138 recovered in February 2014. Detection ranges were tested for all ALSs to ensure all tagged *A.*
139 *anguilla* passing ALS sites would be recorded. Range testing was conducted in freshwater
140 and transitional compartments with varying hydromorphological conditions. No *A. anguilla*

141 were recorded on a downstream ALS which had not been previously recorded at inward
142 ALSs higher in the catchment. Extensive range tests were undertaken for ALS at Magilligan
143 Point (the sea lough sites; Fig.1.) to ensure coverage at these points was adequate to
144 determine escapement success. To test for acoustic breaches at the final ALS an acoustic
145 transmitter (Model LP-7.3, 7.3mm diameter, 18 mm length, 1.9 g mass in air, 139dB re 1 μ Pa
146 power, Thelma Biotel AS, Trondheim, Norway 2013) was immersed at 3 m depth and trolled
147 (~1500 m x 4; ebbing and flooding tide) by a drifting boat (engine off). Range tests revealed
148 an acoustic range of 450 m ensuring overlap between the two final ALS (6&7), no acoustic
149 breaches were recorded during range tests.

150 MIGRATION DESCRIPTORS

151 The ALS array was used to examine behavioural differences in migration patterns of *A.*
152 *anguilla* during their downstream migration. Nineteen out of the 20 *A. anguilla* transmitters
153 were detected at ALS1 (0.5km from release), it is assumed that these *A. anguilla* had initiated
154 downstream migration. Freshwater compartment (FW) migration is defined as movement of
155 tagged fish from the most upstream receiver ALS 1 downstream to ALS 2 at the point of tidal
156 interface. It was assumed that *A. anguilla* which were detected at the first upstream receiver
157 (ALS 1) but not detected entering the estuary (ALS 2) either terminated their migration or
158 suffered mortality or tag failure in the freshwater compartment. Transitional water
159 compartment migration was defined as the movement of *A. anguilla* between ALS 2 and ALS
160 4&5. Similarly *A. anguilla* which were detected at ALS 2 but not at ALS 4 and 5 were
161 assumed to have terminated their migration, suffered mortality or tag failure in the
162 transitional compartment. Sea lough compartment migration was defined as movement
163 between ALS 4 and 5 and the lough exit at ALS 6 and 7. Tagged individuals were deemed
164 successful migrants (*i.e* successful transit between the freshwater, transitional and sea lough
165 compartments) if they were detected passing ALS 6 or 7 and thus entering the open ocean.

166 For migrating *A. anguilla*, transit time and travel speed between ALSs were calculated. The
167 transit time corresponds to the time elapsed between the departure from an ALS, i.e, the last
168 detection at that ALS, and arrival at the next, i.e, the first detection at the successive
169 downstream ALS. Distance travelled between detection sites was calculated using the centre
170 line of the river using ARC GIS software and was expressed in km day⁻¹.

171 ENVIRONMENTAL DATA

172 River discharge data were provided by the Office of Public Works, Ireland. Mean daily
173 discharge from the River Finn was used to assess flow conditions for the study period in
174 2013. Tidal range data were obtained from published data (www.tidetimes.org.uk). Light
175 level was defined as day or night, based on the times of sunrise and sunset, these were
176 calculated using the NOAA sunrise/sunset calculator (NOAA, 2014). The lunar cycle was
177 categorised into eight phases: new moon, waxing crescent, 1st quarter, waxing gibbous, full,
178 waning gibbous, 3rd quarter, waning crescent based on the percentage of the moon
179 illuminated using the R package lunar (Lazaridis, 2015).

180 DATA ANALYSIS

181 Differences in the number of successful migrants moving through successive compartments
182 were tested using a Pearson chi-square test. Migration speed was log₁₀ transformed to reduce
183 heterogeneity of variances. Differences in migration speed through compartments were tested
184 by ANOVA. To investigate the potential factors influencing migration speed of individuals
185 through the catchment a general linear model approach was taken. Migration speed (log₁₀ km
186 d⁻¹) in freshwater, transitional water and sea lough compartments was modelled using *A.*
187 *anguilla* L_T , body fat and water discharge as predictor variables. Final models were generated
188 with non-significant variables being dropped. Model diagnostics were assessed graphically
189 by examining the residuals for heterogeneity. A *t*-test was used to test for significant

190 differences between migration speeds of successful and unsuccessful migrants. Pearson chi
191 square tests were used to test for differences in diurnal, lunar phases and tidal cycle (ebb or
192 flood) effects on movement activity. Movement activity times were defined as the difference
193 between detection time when entering receiver range and the time of the last detection before
194 leaving receiver range. All analyses were performed using R statistical software 3.1 (R Core
195 Team 2014).

196 RESULTS

197 MIGRATION SUCCESS

198 The 19 tagged *A. anguilla* which initiated downstream migration (detection at ALS 1) were
199 all detected at the lower end of the freshwater compartment (ALS 2), thus 100% of migrants
200 made successful passage through the freshwater compartment (Fig. 2, and 3). Seventeen *A.*
201 *anguilla* (89%) were detected at the lower end of the transitional water compartment (ALS4-
202 5). Of the 17 *A. anguilla* that entered the sea lough compartment, five *A. anguilla* (29%) were
203 detected at ALS6-7 indicating successful passage through this zone (Fig. 2). Thus, overall
204 there was 26% escapement of tagged *A. anguilla* to the open sea. There was a non-significant
205 difference in migration success (assuming that non-detected tags at downstream loggers
206 represent successful passage of tagged *A. anguilla*) between freshwater and transitional water
207 compartments ($\chi^2= 0.054$, $df=1$, $P >0.05$). Estimated survival rates of tagged individuals were
208 significantly lower in the sea lough compartment compared to the transitional compartment
209 ($\chi^2 = 10.31$, $df=1$, $P <0.001$) (Fig. 2).

210 MIGRATION INFLUENCES

211 Migration patterns of individuals were significantly related to environmental factors in some
212 compartments. A general linear model revealed a significant relationship between discharge
213 and migration speed in the freshwater compartment ($F_{1,17}=8.761$, $r^2=0.35$, $P<0.05$) and

214 transitional water compartment ($F_{1,15}=5.058$, $r^2=0.26$, $P<0.05$) but not through the sea lough
215 compartment ($F_{1,4}=8.761$, $r^2=0.02$, $P>0.05$). The number of downstream movements was
216 also significantly higher at night than during the day through all three compartments;
217 freshwater compartment ($\chi^2=35.103$, $df=1$, $P<0.001$), transitional compartment ($\chi^2=36.250$,
218 $df=1$, $P<0.0001$) and sea lough compartment ($\chi^2=5$, $df=1$, $P<0.05$). The number of
219 downstream movements was significantly different between tidal phases; a higher proportion
220 of movements occurred during ebb tides (92.3%) in comparison to flood tide (7.6%) ($\chi^2=$
221 32.362 , $df=1$, $P<0.001$). A significantly higher number of *A. anguilla* movements (77.7%)
222 were observed in the three moon phases which represent the least illumination during the
223 lunar phase, waning crescent, new moon and waxing crescent compared with higher
224 illuminated phases ($\chi^2=135.067$, $df=7$, $P<0.001$).

225 MIGRATION SPEEDS

226 Of the 19 tagged *A. anguilla* for which directional migration was recorded, all progressed
227 downstream, no individuals detected at ALS 1 were recorded moving back upstream. Time
228 spent from release to last detection on the outermost receivers ranged from 11 to 80 days for
229 migrants. Overall the mean migration speed (km d^{-1}) of individuals was not found to be
230 significantly influenced by *A. anguilla* L_T ($F_{3,37}=1.905$, $P>0.05$). Mean migration speeds were
231 significantly different between compartments (ANOVA; $F_{2,38}=13.77$, $P<0.001$, Table III),
232 specifically, slower migration speeds were observed in the transitional compartment
233 compared with the freshwater compartment (Tukey HSD $P<0.001$) and between the sea
234 lough compartment and the freshwater compartment (Tukey HSD $P<0.001$). However there
235 was no difference in migration speeds between transitional and sea lough compartments
236 (Tukey HSD $P>0.05$) (Fig. 3). Mean migration speed of migrants successfully reaching the
237 open sea was not significantly different from unsuccessful migrants in the transitional
238 compartment, freshwater compartments or sea lough ($P>0.05$ in all cases). Overall the level

239 of fat deposition did not significantly influence migration speed through freshwater and
240 transitional compartments ($P>0.05$). The level of fat deposition was found to have a
241 significant positive effect on migration speed of migrants through the sea lough ($t=5.204$, $_{1,3}$,
242 $P<0.001$).

243 DISCUSSION

244 This study details differences in migration success and behaviour of small silver stage *A.*
245 *anguilla* as they migrate down a freshwater river reach, through a transitional zone and into a
246 coastal marine sea lough. The *A. anguilla* in this study (L_T range: 332-520 mm) exhibited a
247 marked decline in migratory speed in the lower reaches of the catchment. Also shown are
248 substantially higher losses of migrating *A. anguilla* in the sea lough compartment compared
249 with freshwater and transitional water zones. While high mortality has been reported for
250 downstream migrating larger female silver stage *A. anguilla* (Aarestrup *et al.*, 2010;
251 Davidsen *et al.*, 2011), it has not been recorded for male and smaller female *A. anguilla*, nor
252 in a catchment exhibiting a natural hydrology and free of anthropogenic influences
253 (hydropower facilities and fisheries). These results strongly suggest that passage through a
254 coastal marine sea lough imposes a high mortality rate on the seaward escapement of smaller
255 *A. anguilla*

256 MIGRATION SUCCESS

257 The detection of 26% of the tagged individuals which initiated downstream migration at the
258 final array is a minimum estimate of successful escapement of tagged individuals. There are
259 three possible explanations for the very low rate of detection of tagged *A. anguilla*.

260 *Acoustic equipment failure or tag loss by A. anguilla*; It is plausible that low detection
261 efficiency resulting from poor receiver performance and or tag failure / performance may
262 have resulted in low detection of tagged *A. anguilla* that reached ALS 6 or 7. The former is

263 highly unlikely as no acoustic breaches were recorded during range tests at the outer ALS
264 array, ruling out the likelihood of potential non detection at the final listening stations.
265 Additionally all receiver detections of individual *A. anguilla* recorded more than one signal.
266 All *A. anguilla* transmitters had an estimated battery end life in late February and given that
267 *A. anguilla* are estimated to arrive at spawning grounds from March-June (Tesch, 2003; van
268 Ginneken & Maes, 2005; Aaerstrup *et al.*, 2009) it was expected that tag life should have
269 been long enough to allow tagged *A.anguilla* to have emigrated before battery failure.
270 Manufactures reported tag failure rate in tests are <1% and studies using the same tags, over
271 the same period, have reported control tag failure rates in field environments of 0% (Gauld *et*
272 *al.*, 2013). There was no evidence of impaired migration related to tagging with ~90% of
273 tagged *A. anguilla* successfully migrating through the freshwater compartment and
274 transitional compartments. Silver stage *A. anguilla* have been successfully surgically tagged
275 in numerous other studies (Aaerstrup *et al.*, 2008, 2010; Davidsen *et al.*, 2011; Verbiest *et al.*,
276 2012; Bultel *et al.*, 2014) and surgical tagging of *A. anguilla* in a similar manner to the
277 present study was not deemed to significantly affect behaviour post tagging of *A.anguilla*
278 (Thorstad *et al.*, 2013) although osmotic stress encountered by tagged *A. anguilla* when
279 moving from fresh to salt water warrants further research.

280 *Settlement*; A possible interpretation of migration patterns shown here, which has been raised
281 by other studies is that sea migration could be a two-step migration process (Durif *et al.*,
282 2005; Aaerstrup *et al.*, 2008; Béguer-Pon *et al.*, 2014; Stein *et al.*, 2015). It has been reported
283 that *A. anguilla* maturation may be more flexible than originally thought (Svedäng &
284 Wickström, 1997) and that individuals may have the ability to interrupt migration and begin
285 feeding again. Crook *et al.* (2014) demonstrated extended estuarine residence time for
286 *Anguilla australis*, highlighting the possibility of more complex migration behaviour instead
287 of the rapid and direct seaward migration originally assumed. Stein *et al.* (2015) also

288 highlighted the possibility that *A.anguilla* may need more than one migratory season to reach
289 the sea and may temporally revert to a non-migratory stage. Therefore, it is possible that a
290 proportion of the tagged *A. anguilla* in this study ceased their migration in the lower Foyle
291 and began feeding again to commence migration at a later date.

292 *Mortality*; The most probable explanation is that *A. anguilla* in this study experienced high
293 mortality in the sea lough and the low escapement rate observed in this study represents true
294 escapement of migrating *A. anguilla* (or a combination of the above factors). Thus, the results
295 from this study strongly suggest substantial mortality of silver stage *A. anguilla* during the
296 period they are in coastal marine habitat, even in the absence of a fishery. These findings are
297 similar to those of Aarestrup *et al.* (2010) who also reported significant losses of tagged
298 female *A. anguilla*, interpreted as mortality during the early marine phase. Due to the high fat
299 content (van Ginneken *et al.*, 2000) and their relative abundance, *A. anguilla* are a very
300 profitable prey source for avian, fish and mammalian predators (Keller, 1995; Knöesche,
301 2003; Britton *et al.*, 2006; Lundström *et al.*, 2010; Béguer-Pon *et al.*, 2012). Productive
302 estuarine habitats are home to numerous potential fish predators, and such predators could
303 represent an important and unappreciated source of *A. anguilla* mortality which has important
304 management implications.

305 MIGRATION INFLUENCES

306 An important environmental influence initiating migration in both freshwater and transitional
307 compartments was increased water discharge. Increased discharge has been identified as
308 initiating downstream movement in *A. anguilla* (Vøllestad *et al.*, 1986; Feunteun *et al.*,
309 2000). In the study presented here, this effect was clearer for *A. anguilla* migrating through
310 the freshwater reaches and although evident also in the estuary (transitional compartment) the
311 effect was considerably less pronounced. In the sea lough, the effect of water discharge on

312 movement disappeared. Aarestrup *et al.* (2010) noted a similar effect of declining migration
313 responses to river discharges with passage downstream of the silver stage *A. anguilla*
314 suggesting that tidal currents may possibly buffer the effect and this is consistent with the
315 pattern in the current study. Selective tidal stream transport (STST) has been proposed as a
316 mechanism influencing *A. anguilla* migration (McCleave & Arnold, 1999) which allows *A.*
317 *anguilla* to quickly move through areas utilising tidal currents. The study presented here
318 indicates that *A. anguilla* may exploit outgoing tidal currents while migrating in the
319 transitional and sea lough compartments with 92% of migration initiations occurring at these
320 times. This concurs with findings by Béguyer-Pon *et al.* (2014) who reported that American
321 silver eels (*Anguilla rostrata* L.) use nocturnal ebb tide transport to migrate out of the St.
322 Lawrence estuary. The *A. anguilla* in the present study also exhibited increased movement
323 activity on phases around a new moon, with the majority of movements occurring in the lead
324 up to a new moon, suggesting that migration is preferred on nights of the lowest lunar
325 illumination.

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327 In this study, most (94%) migratory movements of tagged *A. anguilla* occurred during the
328 night, even when moving through the relatively turbid lower reaches of the river and estuary.
329 Resident *A. anguilla* tracking studies have also shown activity peaks at night (Hedger *et al.*,
330 2010, Walker *et al.*, 2014). This pattern for smaller females and male *A. anguilla* has been
331 found in other studies in freshwater (Vøllestad *et al.*, 1986; Tesch, 2003) and for coastal
332 marine habitats in large female *A.anguilla* (Davidsen *et al.*, 2011; Aarestrup *et al.*, 2008,
333 2010). Predation has long been implicated as a major selective force in the evolution of
334 several behavioural characteristics of animals (Lima & Dill, 1990). The migration influences
335 noted in this study are probably an evolutionary response to predation pressures. *Anguilla*
336 *anguilla* are an important food source for predators (Keller, 1995; Knöesche 2003; Britton *et*

337 *al.*, 2006; Lundström *et al.*, 2010; Béguer-Pon *et al.*, 2012). One such predator, cormorants
338 (*Phalacrocrax* sp.) are visual foragers, feeding during daylight and twilight hours (Siegfried
339 *et al.*, 1975) and higher *A. anguilla* movements on nights with reduced lunar illumination
340 observed in this study are probably indicative of predator avoidance behaviour, which
341 reduces the likelihood of encountering predators when undertaking their downstream
342 migration (Fuiman & Magurran, 1994).

343 MIGRATION SPEED

344 The migration speed of individuals through the catchment was not influenced by L_T . This
345 contrasts with findings by Verbiest *et al.* (2012) and Bultel *et al.* (2014) who reported faster
346 migration progression of larger individuals. Inter- individual variability in migration speeds
347 was apparent across compartment types, however ultimate migration success was not affected
348 by individual migration speed through the catchment. Overall migration speed was found to
349 be significantly higher in the upper reaches in comparison to the lower reaches of the study
350 catchment. This contrasts with the findings of Aaerstrup *et al.* (2010) who found slower
351 progression rates upstream in comparison to downstream reaches in large female *A.anguilla*.
352 Given that tagged *A. anguilla* in this study ranged from 332-520 mm in comparison to
353 Aaerstrup's study (560-840 mm), the contrasting results may be due to size or sex differences
354 of tagged *A. anguilla*. Thus, the fresh-saltwater transition may possibly take longer for
355 smaller sized *A. anguilla*. Bultel *et al.* (2014) also noted a slower migration speed in the
356 downstream catchment compartments and suggested reduced progression may be a result of
357 very strong salinity gradients. Such gradient transfers can be found in large estuaries similar
358 to that in this study. The salinity gradient changes quickly in the lower Foyle ranging from
359 0.14- 25.50 over 20 km, which may explain the reduced migration speed. Thus one can
360 postulate that reduced migration speed in lower compartments could be related to an

361 acclimatization process due to increased salinity levels, and potential physiological size
362 related factors.

363 CONCLUSIONS

364 This study strongly suggests previously unreported poor survival through coastal marine
365 habitat of small female and male silver stage *A. anguilla* (340-520 mm), though with the
366 possibility that low recorded escapement could reflect long-term sea lough residency by a
367 high proportion of small silver stage *A. anguilla* emigrants. More detailed research is needed
368 to differentiate between these possibilities. If the low level of recorded escapement is due to
369 mortality, coastal sea loughs may be a potential bottleneck to *A. anguilla* escapement and
370 potential mortality through such zones should be considered in models estimating production
371 from a system. Given the smaller size of tagged *A. anguilla* in this study, it is hypothesised
372 that predation pressure may be high on this size component and thus significantly influence
373 escapement success. Given the likely scale of the effects identified here, estuarine and coastal
374 migration processes may be having very significant effects on the long term dynamics of *A.*
375 *anguilla* populations if this pattern is replicated elsewhere. More information is urgently
376 needed.

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396 **REFERENCE**

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542 FIGURE 1. Map of study site, compartment types marked with grey boundary line,
543 FW=freshwater, TW=transitional. ALS refers to Acoustic Listening Station outlined by solid
544 dots.

545 FIGURE 2. Proportion of tagged *A. anguilla* detected through catchment compartments
546 defined as freshwater (FW), transitional water (TW), and sea lough (SL). Distance 0 is the
547 release point.

548 FIGURE 3. Migration speed (km d^{-1}) through catchment compartments. FW= freshwater,
549 TW= Transitional compartment, SL=Sea lough.

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551 TABLE I. Environmental variables in compartments through catchments.

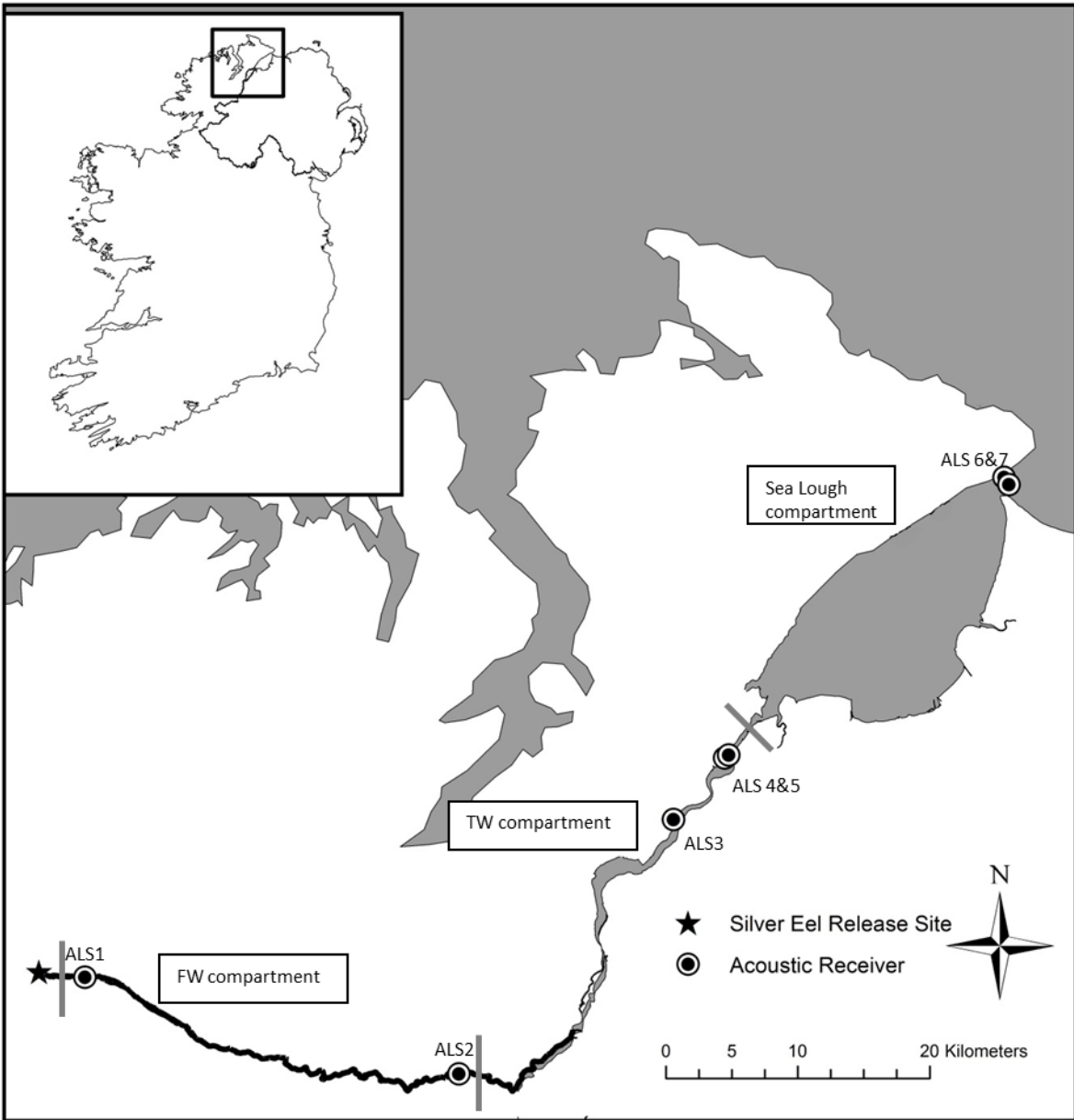
Variable	Freshwater	Transitional	Sea Lough
Salinity PSU (range)	-	0.14- 28.41	29.63- 32.20
Dissolved oxygen (mg l^{-1}) \pm S.D	-	8.10 \pm 0.65	8.04 \pm 0.15
Mean Depth (m) \pm S.D	-	2.58 \pm 0.86	3.12 \pm 1.49
Length (Km)	95	26.88	30.22

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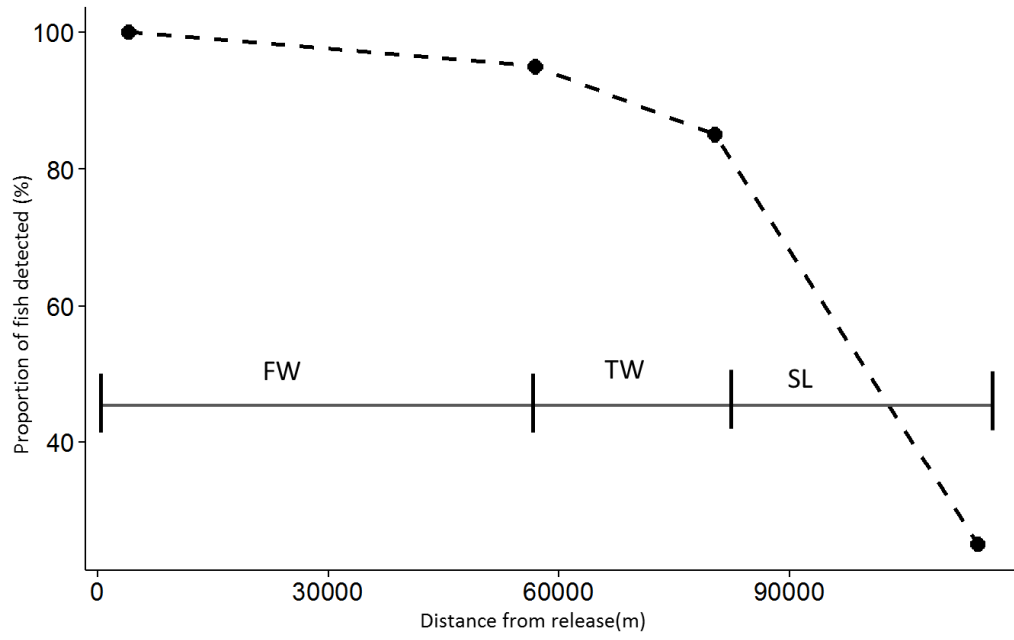
554 TABLE II. Characteristics of tagged individuals. **Successful migrants detected passing final array.
 555 Silver Index (*sensu* Durif *et al.*, 2005) MII = mature males, FV = mature female. ALS 1 refers to
 556 Acoustic Listening Station 1.

I.D	L_T (mm)	Mass (g)	Fat (%)	Silver Index	Release date	Detection span from ALS 1 (days)
2585	354	72	29.8	MII	06/10/2013	5.14
2577	365	79	30	MII	05/10/2013	8.14
2575	354	82	22.9	MII	05/10/2013	80.14**
2592	332	83	28.4	MII	08/10/2013	5.15
2583	360	84	22.9	MII	06/10/2013	5.06
2581	360	86	30.6	MII	08/10/2013	5.97
2586	365	92	26.6	MII	28/10/2013	11.27**
2593	365	96	21.9	MII	04/10/2013	2.91
2576	350	97	26.3	MII	08/10/2013	43.15**
2578	384	99	23.6	MII	08/10/2013	62.87
2579	400	100	28.0	MII	28/10/2013	16.59
2588	394	105	26.0	MII	28/10/2013	3.01
2582	401	110	28.0	MII	29/09/2013	3.95
2587	395	115	30.0	MII	05/10/2013	19.69
2589	410	126	22.6	MII	08/10/2013	22.93**
2584	435	129	26.8	MII	05/10/2013	-
2580	442	249	29.6	MII	28/10/2013	10.17
2590	530	280	21.7	FV	29/09/2013	36.43
2591	520	320	22.0	FV	29/09/2013	2.99
2574	515	384	24.5	FV	02/10/2013	48.9**



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559 FIGURE 1



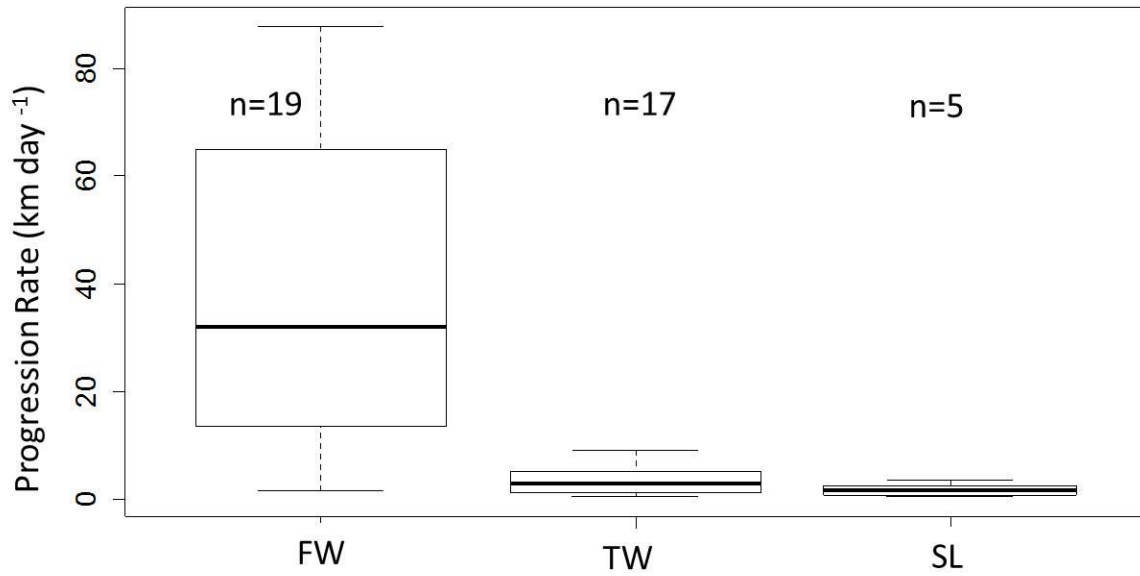
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561 FIGURE 2.

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566 FIGURE 3.

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570 TABLE III. Mean migration speed (mean ± S.D; parentheses: range) in compartment types, n=

571 number of *A. anguilla* monitored in a given compartment.

	<i>n</i>	Distance (km)	m/s ⁻¹	km/day ⁻¹
Freshwater	19	95	0.45±0.36 (0.01-1.01)	39.18±31.84 (1.58-87.7)
Transitional	17	26.88	0.04±0.03 (0.005-0.11)	3.42±2.68 (0.42-9.21)
Sea lough	5	30.22	0.019±0.015 (0.006-0.04)	1.64±1.34 (0.55-3.48)

Total

0.19 ± 0.27 (0.005-1.01)

16.68 ± 23.97 (0.42-87.74)

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