1   **European eel *Anguilla anguilla* compromise speed for safety in the early marine spawning**

2   **migration**

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19

20   **Abstract**

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22   There are substantial benefits to potential fitness conferred to animals that undertake migrations.

23   However, animals must make compromises to maximize survival and compensate for the risks

24   associated with long-distance movement. European eel (*Anguilla anguilla*), a migratory

25   catadromous fish, has undergone population declines owing to changes in marine and freshwater

26   habitat and interactions with human infrastructure, instigating research to investigate the

27   mechanisms controlling their migration. Yellow-phase European eels from the local River Opo

28   and silver-phase European eels transplanted from River Imsa, Norway, were implanted with

29   acoustic transmitters and released within a network of receiver stations in the Hardangerfjord,

30   Norway. Silver-phase eels exhibited more movement within the array than yellow-phase eels,

31   signifying the onset of migration. Silver-phase eels moved through the fjord nocturnally, arriving

32   at gates predominantly at night. Els had slower rates of migration than expected based on models

33   predicting continuous movement, suggesting that movement ceased during daylight hours.

34   Reduced net rates of travel supported the hypothesis that eels compromise speed for safety during

35   the early marine migration by avoiding predators and not actively migrating during daylight. The

36   silver eels were capable of directed movement towards the ocean and were not recorded by

37   receivers in bays or dead ends. European eels must successfully transit this coastal zone, where

38   their residence is prolonged because of the relatively slow speeds. These results suggest that the

39   early marine phase of the European eel spawning migration be a focal period for European eel

40   conservation efforts.

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42   Keywords- asset protection principle, exploitation, conservation behaviour, telemetry, fjord

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44 **Introduction**
45

46   Migration is a behaviour that pervades among invertebrate and vertebrate taxa in the

47 animal kingdom (Dingle and Drake, 2007). Animals evolved migratory behaviour to cope with

48 seasonal changes in their environment and exploit highly productive areas to enhance

49 reproductive potential by accelerating growth, avoiding predators (Zaret and Suffern, 1976;

50 Gliwicz, 1986), or mitigating disease risk (Altizer et al., 2011). The behaviour confers substantial

51 resource advantages to individuals but also involves considerable risk (Hebblewhite and Merrill,

52 2007). Long-distance migration is energetically taxing and many animals forego feeding while

53 migrating, meaning that migration must be powered by limited somatic energy stores (Stephens

54 et al., 2009). Hormones associated with the glucocorticoid stress response (e.g., cortisol; Lobato

55 et al., 2010; Cornelius et al., 2013) and oxidative stress products (Bombardier et al., 2010)

56 incurred along the migration have the potential to negatively affect the individual and require

57 physiological and behavioural adaptations to manage stress and maintain fitness. The asset

58 protection principle states that animal behaviour should be increasingly cautious with

59 increasingly valuable reproductive assets (Clark 1994). Older age, larger body size, or greater

60 gonadal investment should therefore increase vigilance in animals (Lenormand et al., 2004;

61 Halttunen et al., 2013).

62   The European eel is a highly migratory fish that colonizes rivers or coastal areas

63 throughout the European continent (van Ginneken and Maes, 2005). Eel larvae recruit to coastal

64 areas and freshwater systems and may remain up to 50 years while feeding, growing, and

65 preparing to return to the Sargasso Sea (Poole and Reynolds 1998). After sufficient energetic

66   reserves have been accumulated, yellow-phase European eels transition to the migratory life

67   stage, which may be characterized by a change in colouration (Lokman et al., 2003; Durif et al.,

68   2005; Bruijs and Durif 2009). Migratory eels undergo a whitening of the ventral skin, darkening

69   of the dorsal skin, expansion of the eye width, and lengthening of the pectoral fins for marine life

70   (Durif et al., 2005; but see Pankhurst and Lythgoe, 1982). Physiological changes to the silver-

71   phase eel include increased muscle power output to economize energy during the non-feeding

72   migratory life stage (Ellerby et al., 2001; Lokman et al., 2003). The long-distance movements of

73   European eel in the marine environment were unknown until recently (see Aarestrup et al., 2009;

74   Righton et al., 2012, 2016) and based on field observations and fishery interceptions of migrating

75   eels (Ernst, 1977; Bast and Klinkhardt, 1988) without empirical data on the actual marine life of

76   adult eels. Advances in animal biotelemetry provide evidence that silver eels swim in excess of

77   5000 km through the marine environment to reach spawning grounds in the Sargasso Sea

78   (Aarestrup et al., 2009; Righton et al., 2016). Eels encounter competing pressures of speed and

79   safety after entering the marine environment as they must avoid predation and energetic

80   exhaustion to reach spawning grounds in time to meet with conspecifics at the appropriate time.

81   Migratory species are exposed to additional risks because of their movement through

82   multiple habitats (Hebblewhite and Merrill, 2007). Long-distance movements by European eel

83   up and down major river systems and through the open ocean exposes them to considerable

84   interference from human infrastructure that has contributed to their imperilment (Dekker, 2003;

85   ICES, 2009). An effective recovery plan for eels requires accurate knowledge of the behaviour

86   and survival throughout the life history and better information of the early marine phase is

87   needed to contribute to such a framework (Davidsen et al., 2011; Bultel et al., 2014). In Norway,

88   silver eels exit rivers into fjords, which form relatively narrow estuarine channels to the open

89   ocean. Compared to rivers that discharge into the open ocean, long networks of fjords provide an

90   opportunity for accurate tracking of the early marine phase of eel migration (e.g. Davidsen et al.,

91   2011) because they travel through a channel that can be adequately covered by arrays of acoustic

92   receivers. Yellow-phase and silver-phase eels were implanted with transmitters in Norway's

93   second longest fjord system with receiver gates positioned in the fjord en route to the North Sea

94   to track the speed, periodicity, and success of eels exiting the fjord. The array was used to

95   observe the early marine migration of acoustically tagged European eels and to test the

96   hypothesis that European eels trade off safety and speed in their migration.

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98   **Methods**

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100   The 179 km Hardangerfjord is the world's fourth longest fjord and the second longest in

101   Norway. The Hardangerfjord is a network of smaller fjords, creating a large, branching area that

102   must be navigated by migratory species that use the fjord including sea trout (*Salmo trutta*),

103   Atlantic salmon (*Salmo salar*), and European eel that enter local rivers. To study the movement

104   of eels during their spawning migration, trap nets were set from August 25 – September 15, 2006

105   in the Hardangerfjord (60.072210 °N, 6.549732 °E) near the confluence of the River Opo at the

106   town Odda to capture European eel. Seventeen female yellow-phase eel were captured (56.6 ±

107   20.2 cm SD TL, range = 47.4 – 73.7 cm TL). Because of an absence of silver-phase eel, 56

108   female silver-phase eel were captured in a Wolf trap 100 m from the sea in the River Imsa

109   (58.903324 °N, 5.963514 °E) during their downstream migration (59.7 ± 18.1 cm TL, range =

110   51.0 – 89.7 cm TL) and transported by car to the same site in the Hardangerfjord for release on

111   September 14, 2006. Eels were individually anaesthetized (40 mg L^{-1} metomidate, Aquacalm,

112   Syndel Laboratories Ltd, Canada; Iversen et al., 2013) and a 9 or 13 mm acoustic transmitter

113   (Thelma Biotelemetry, Trondheim, Norway) was implanted into the intraperitoneal cavity using

114   methods described by Økland and Thorstad (2013) and Thorstad et al. (2013). The incision in the

115   body cavity was closed with sutures and the eels were allowed to recover prior to release.

116   Thorstad et al. (2013) found tag expulsion rates after six months of 12% using similar methods.

117   Following tagging, eels were recovered for 1-6 h such that all were released simultaneously on

118   two tagging days, either September 14, 2006 at 20:25 or September 15, 2006 at 15:34.

119   Underwater acoustic telemetry receivers (VEMCO VR2, Halifax, NS, Canada) were

120   deployed in a gate configuration (see Donaldson et al. 2014) at six points in the fjord and in

121   some bays and dead ends. The gates, G1 (N = 2 receivers), G2 (N = 6), G3 (N = 6), G4 (N = 2),

122   and G5 (N = 8), were placed 2.0, 9.6, 34.8, 73.6, and 94.7 km from the release location and

123   remained active from September 2006 to March 2007. The first gate was placed 2.6 km from the

124   confluence of the River Opo (Figure 1). This receiver network permitted the identification of

125   migratory activity through the fjord and a determination of survival. Calculating survival was

126   only possible up to Gate 4 because of gaps in coverage at subsequent gates. Migration speed

127   wase calculated between Gates to determine the average rate of movement through the fjord.

128

129   *Data Analysis*

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131   Time to enter the array was compared between silver-phase and yellow-phase eels with a

132   Welch's two-sample t-test, implemented with the *t.test* function in R (R Core Team, 2017).

133   Lunar phases were determined using the *lunar.phases* function in the R package lunar (Lazaridis,

134   2014). Diel migratory activity was tested by the Rayleigh test of uniformity, implemented with

135   the *r.test* function in the R package CircStats by converting hour of the day to degrees (Lund and

136   Agostinelli, 2012). To determine whether eels arrived at gates predominantly at nighttime, the

137   onset and cessation of darkness were determined using the *getSunlightTimes* function in the R

138   package suncalc returning the time of night and nightend (Agafonkin and Thieurmel, 2017).

139   Migratory behaviour of yellow-phase and silver-phase eels was modeled using time to event

140   analysis. Visual comparison of the migration of yellow-phase and silver-phase eels was plotted

141   with Kaplan-Meier Survival curves using the *ggsurvplot* function in the survminer package

142   (Kassambara and Kosinski, 2016). Cox proportional hazards regression was then applied using

143   the *cph* function in the survival package (Therneau, 2015) to compare the migratory behaviour of

144   yellow-phase and silver-phase eels in the Hardangerfjord. Proportionality of hazards assumption

145   was tested by extracting Schoenfeld residuals from the model and testing for violation at $\alpha =$

146   0.05. Time to event analysis relies on a continuous response variable associated with the time at

147   which an event is recorded (or censorship is assigned); for our purposes, we used the spatial

148   variable (Gate number) instead of time as the response variable. The model was therefore

149   comparing the migratory activity of yellow-phase and silver-phase eels based on detections at the

150   Gates. For example, eels that were detected up to Gate 4 were coded as having an event occur at

151     $t(4)$. Time to event analysis also allows individuals to be censored when they drop out of a study,

152   eels not detected at Gate 5 could not be determined to have died but instead were censored at

153 Gate 4. The dataset is therefore right censored because eels that were detected at all gates never

154 experienced an event but instead were censored at $t(5)$. Censorship of eels with unknown fate

155 allowed us to account for the uncertainty associated with incomplete receiver array coverage of

156 Gates 4 and 5 while maximizing the amount of data available for modeling (i.e. because we did

157 not have to entirely remove fish with unknown fate).

158   Average migration rates were calculated for eels as the time between last detection at a

159 gate to the first detection at the subsequent gate in kilometers per day. Detection efficiencies

160 were calculated by Plantalech Manel-La et al. (2011) between 100 and 500 m depending on the

161 environmental conditions at the time of tag transmission, with 99% efficiency at G2 and 94% at

162 G3. Rate of movement was compared among gates with a linear model (*lm* function in R) to

163 determine whether distance between gates influenced the time taken to migrate within the array

164 with multiple comparisons calculated by a Tukey HSD test with the *glht* function in the

165 multcomp package (Hothorn et al., 2008). Figures were plotted using ggplot2 (Wickham, 2008)

166 and the extension ggridges (Wilke, 2017).

167

168 **Results**

169

170   Seventeen yellow-phase eels (62.2 ± 7.5 cm TL) were captured from the River Opo and

171 fifty-six (64.7 ± 7.1 cm TL) silver-phase eels were imported from the River Imsa; both groups

172 were released between September 14 and 15, 2006. No detections were recorded on receivers in

173 dead ends or bays. Among 73 eels tagged, 26 were not detected on the first gate, most ($N = 16$)

174 of which were yellow-phase eels from Opo. However, six silver-phase eels and one yellow-phase

175   eel were later detected at Gate 4 (having never been detected at any prior gates). Five silver-

176   phase eels were never detected in the array (9%) and 22 (39%) were detected at the final gate;

177   however, this gate did not have complete coverage and therefore the fate of eels that did not

178   make it beyond Gate 3 is unknown. There was a significant difference in movement of the silver-

179   phase eels of River Imsa origin compared to the movement of local yellow-phase eels according

180   to Cox proportional hazards ($z = 6.22$, $p < 0.01$). Odds of movement within the array were 9.48

181   higher for silver-phase eels than yellow-phase eels.

182   Average silver-phase eel speed from release to Gate 1 was 4.2 ± 13.7 km d^{-1}, 44.5 ± 25.4

183   km d^{-1} Gate 1-2, 19.5 ± 18.8 km d^{-1} Gate 2-3, 9.8 ± 8.2 km d^{-1} Gate 3-4, and 13.9 ± 9.6 km d^{-1}

184   (Gate 4-5; Figure 4). Modeled travel times between gates were significantly different from Gates

185   1-2 and all other gates (all Tukey $|t| > 5.78$, $P < 0.01$) and between Release and Gate 1 and Gates

186   1-3 (Tukey $t = 3.89$, $P < 0.01$) such that shorter distances were transited faster.

187   Eels moved nocturnally and were first detected at each gate predominantly during

188   nighttime hours (r-bar $= 0.99$, $P < 0.01$; Figure 1). Based on nighttime hours calculated from the

189   suncalc package, eels arrived at gates predominantly during the night at Gates 1 (71% of those

190   arriving), 2 (91%) and 3 (88%) Gate 4 (79%), and Gate 5 (95%). Arrivals at each gate were

191   recorded predominantly on waxing (51%) and full (23%) moon phases, with a minority when the

192   moon was waning (15%) or new (12%).

193

194   **Discussion**

195

196   The marine migration of Anguillid eels has presented one of the great mysteries of fish

197   biology but the secrets are slowly being revealed by electronic tagging technologies (Righton et

198   al., 2012). Considerable effort has been expended to characterize the routes used by silver-phase

199   eels migrating in the open ocean as they progress towards spawning grounds (Aarestrup et al.,

200   2008, 2010; Davidsen et al., 2011; Righton et al., 2016). However, movement through nearshore

201   coastal areas such as fjords may be a significant bottleneck with disproportionately high

202   mortality (as in Atlantic salmon smolts; Thorstad et al., 2012). Here, we used the branching

203   geology of a long fjord complex to establish a receiver array in which acoustically implanted

204   European eel can migrate and reveal the early marine migration through coastal waters towards

205   the open ocean. Our findings suggest a nocturnal migration that slows the average rate of

206   progress out of the fjord, may prolong the overall migration, and could even delay the arrival at

207   breeding grounds if there is no compensation later in the migration. We interpret this adaptation

208   as supporting the asset protection principle (Clark, 1994) wherein the eels compromise speed for

209   safety from predation during this phase of migration. Typical eel predators include marine

210   mammals, sharks, and probably large bony fishes (Béguer-Pon et al. 2012; Wahlberg et al.,

211   2014), which may be more effective predators during diurnal periods.

212   Silver-phase eels in the Hardangerfjord were slower migrating between longer distances.

213   It is unlikely that they were moving more slowly owing to physiological limits on swimming

214   capacity. Experimental studies of eel swimming suggest that eels are capable of efficient

215   swimming at higher speeds, with an optimum proposed by Palstra and van den Thillart (2010) of

216   0.80 bl s^{-1}. Correspondingly, we calculated average displacement of 0.81 bl s^{-1} across a short

217   distance between Gates 1 and 2 (7.60 km). Between Gates that were farther apart, rates of transit

218   were slower, not likely because they were swimming more slowly but most likely because they

219   were only moving at night. Similar rates were observed by Davidsen et al. (2011), who

220   calculated a speed of 0.25 bl s^{-1} across a 31-km fjord reach. Righton et al. (2016) also calculated

221   speeds of 0.25 ± 0.12 bl s^{-1} for eels travelling in the open ocean. These speeds are lower than

222   predicted by van den Thillart et al. (2004), who observed eels capable of steady swimming at

223   0.50 bl s^{-1} for long intervals, albeit at a temperature (19 °C) higher than would be expected in the

224   Hardangerfjord. At speeds ≤ 0.50 bl s^{-1}, eels power movement with posterior red muscle fibres

225   without anaerobic white muscle (Gillis, 1998), which would avoid oxygen debt (Lee et al.,

226   2003). An alternate explanation for these observations would be inefficient migration by eels

227   between gates if eels failed to find the correct route. If this were the case, movement would be

228   slow but detections would be expected to be equally distributed throughout the day. Given that

229   movements on receivers were recorded at night, the most likely explanation for our observations

230   is that eels migrate predominantly during nighttime and have periods of diurnal inactivity that

231   slow the average rate of movement as measured between gates.

232   Nocturnal movement of eels during the early marine migration results in slower average

233   swimming speed and a prolonged migration through the fjord relative to the capabilities. Other

234   research has identified risk averse behaviours by eels that have been interpreted as adaptations to

235   mitigate predation. Downstream migrating silver-phase eels, for example, exit rivers on longer,

236   dimmer nights when their visibility to predators would be lower and also tend to move

237   preferentially with other conspecifics as a strategy for predator saturation (Bruij and Durif, 2009;

238   Sandlund et al., 2017). Studies that have observed European eel migration in three dimensions

239   have noted diel vertical migration, finding eels in warm, shallow water at night and cool, deep

240 water during the day (Aarestrup et al., 2009; Righton et al., 2016). Aarestrup et al. (2009)

241 suggested that this vertical migration serves to behaviourally thermoregulate rather than to avoid

242 predators. However, Amilhat et al. (2016) found that eels exhibited diel vertical migration in the

243 Mediterranean Sea in the absence of temperature stratification, suggesting that thermoregulation

244 is not the primary motivation for daily dives. Temperature stratification in the Hardangerfjord is

245 expected to be minimal and vertical movements would more likely allow eels to access different

246 salinities or photic conditions rather than temperatures. Sjøtun et al. (2015) measured the

247 halocline in the fjord and identified temperature stratification that might influence eel physiology

248 and movement. However, we did not specifically measure depth or microhabitat of eels and this

249 is an area for future research. In support of the predator avoidance hypothesis, several studies

250 have described predation on tagged eels, suggesting that the predator burden during the spawning

251 migration is considerable (Wahlberg et al., 2014; Amilhat et al., 2016), which would drive

252 evolution of behaviour. There may be benefits to eels using colder bottom water to delay

253 maturation as they make slow progress towards the Sargasso Sea (Aarestrup et al., 2009), but it

254 seems likely that predator avoidance is an important driver of the behaviour of eels during their

255 migration, including, as we have observed, diurnal inactivity.

256   The prevailing hypothesis is now that eels exit rivers predominantly before September-

257 December and most spawning is completed in the early winter and springtime, with half the

258 spawning complete by February (Righton et al., 2016). Constant swimming at speeds of 0.5 bl s^{-1}

259 (van den Thillart et al., 2004) would be sufficient to place eels in the Sargasso Sea after six

260 months (Ellerby et al., 2001; van Ginneken, 2006) during the winter and spring when spawning

261 is believed to occur (Righton et al., 2016). However, this is likely after the peak spawning time

262   (Righton et al., 2016). Moreover, eels do not necessarily travel directly towards the Sargasso

263   Sea, meaning that models predicting the travel time and distance are underestimates by using

264   straight-line distances (Righton et al., 2016). Our observation that eels migrate slower in the

265   fjord suggests that silver-phase eels moving through fjords compromise speed for safety during

266   their fjord migration; rather than making it to the Sargasso Sea as quickly as possible, migrating

267   eels seem to take extra time, which we interpret as a means to improve safety. Given the speeds

268   recorded in the open ocean (Righton et al., 2016) and fjords (Davidsen et al., 2011; this study),

269   most eels must begin migrating to spawning grounds over a year in advance of their spawning

270   time.

271   Individual variation in these data show that some European eels may have a plastic

272   migration, with some migrating more quickly than counterparts or migrating more than others

273   during the day. This is consistent with the asset protection principle insofar as lower quality

274   individuals (e.g. lower energetic reserves, less gonadal investment) are likely to accept more

275   risky behaviour (Clark, 1994; Halttunen et al., 2013). Migration is a highly plastic behaviour and

276   many other species of fish exhibit intraspecific adaptations in timing and speed (e.g. Jonsson et

277   al., 1990; Olsson and Greenberg, 2004). Although we were not able to test for mechanisms

278   driving differences among individuals within our sample, our observations of variation suggest

279   that future studies should compare somatic and gonadal energies for migrating eels to investigate

280   what drives intraspecific differences in movement.

281   Silver-phase eels migrated farther in the acoustic array than yellow-phase eels, which

282   aligns with predictions based on previous literature differentiating between life stages. Although

283   the use of eel colouration as a predictor of migratory activity has been criticized (Pankhurst and

284 Lythgoe, 1982), we found there was a significant difference between silver-phase and yellow-

285 phase coloured eels. However, not all silver-phase eels migrated to the end of the array.

286 Although the eels that did not continue in the array may have died, there is considerable

287 plasticity in eel migration such that silver-phase eels should not necessarily be expected to

288 migrate rapidly out of the fjord (Simon et al., 2012). If the eels did perish, then the survival rate

289 was still comparable to a 28.7 km stretch of a Danish fjord measured by Aarestrup et al. (2008,

290 2010), who tracked 17 and 43 eels entering the Randersfjord and 3 (18%) and 17 (40%) exiting

291 the fjord in 2008 and 2010 respectively. In Randersfjord, these mortalities were attributed to

292 fishery removals given that manual tracking failed to identify any tags remaining the fjord and

293 that transmitters from predated eels would be detected from within the predator on the array. In

294 the Hardangerfjord, no manual tracking was performed so eels could have been in areas between

295 the arrays. If mortality did occur, natural mortality including predation would be the most likely

296 cause; fisheries are not active in the Hardangerfjord and no significant tag effects are anticipated

297 because Winter et al. (2005) studied transmitter implantation on silver-phase eels and identified

298 10% mortality but limited impacts on behaviour. The 10% tagging mortality could not account

299 for the five silver-phase eels that never entered the array after release but is unlikely to explain

300 the number of eels with unknown fate.

301

302 **Conclusion**

303

304   Mortality during the early marine migration has the potential to be a significant

305 contributor to declines in European eel. Further research is needed to determine the actual fate is

306   of eels that disappeared within our array, whether they were predated, died of other causes, or

307   were more simply no longer actively migrating. Indeed, the plasticity in the migration of

308   European eel requires more attention to compare the exceptional individuals that travel slow or

309   fast through the marine environment. A relatively high rate of disappearance by tagged silver-

310   phase eels during this phase of the migration would be supported by other studies that have

311   identified migration through fjords to be a risky phase in what is ultimately a small percentage of

312   the total distance to spawning grounds. Even if mortality is not high, we found that the early

313   marine migration through fjords is similar to rates observed in the marine environment.

314   Transitional habitats such as estuaries and fjords are often overlooked phases of anadromous

315   migration (Levings 2016); however, the fjord migration is an important phase of eel migration

316   and should be a focal point for eel conservation to improve overall spawning escapement.

317

318   **Acknowledgments**

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325   **References**

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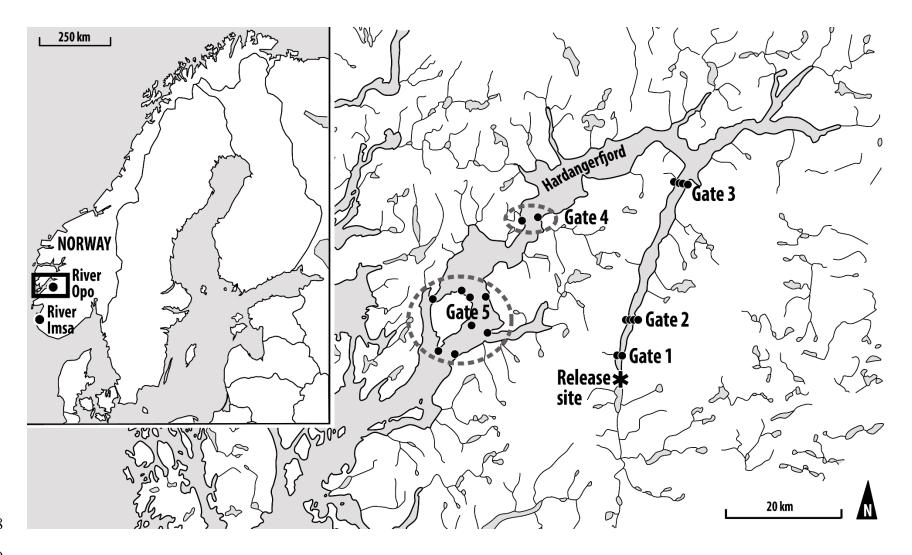
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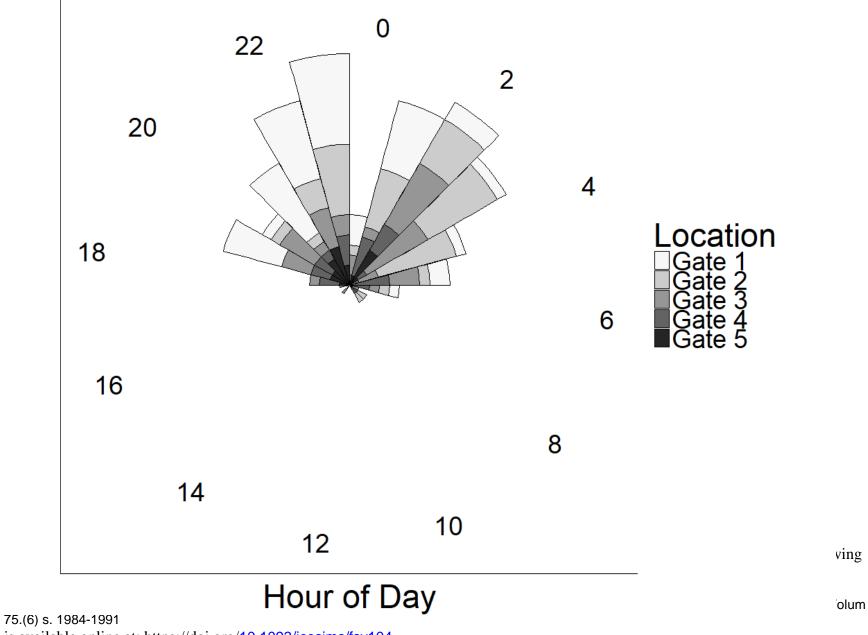
496   **Figures**

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500   Figure 1. Site diagram of the migration arena used to investigate the estuarine progress of European eels (*Anguilla anguilla*). Yellow

501   eels were captured from the River Opo and silver-phase eels were captured and transported from the River Imsa (inset). Gates are shown

502   in the main figure consisting of Vemco VR2-W type acoustic receivers to detect movements of eels out of the fjord towards the Atlantic

503   Ocean.

Hour of Day

Location
Gate 1
Gate 2
Gate 3
Gate 4
Gate 5

505 Figure 2. Polar histogram of entrance times recorded (i.e. first detection) for European eels (*Anguilla anguilla*) at Gates 1-5 in an array

506 of acoustic receivers in the Hardangerfjord, Norway. For the Rayleigh test of uniformity, hours were converted to degrees by dividing
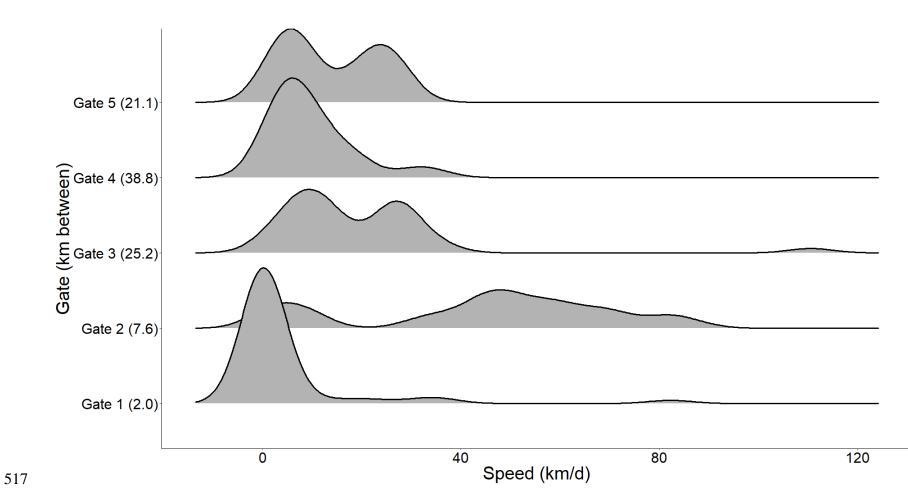
507 hour by 24 and multiplying by 360°.

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511   Figure 3. Kaplan-Meier survival curves comparing the marine migration of European eel from River Opo (yellow-phase eel) and from
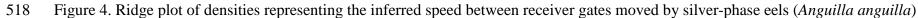
512   River Imsa (silver-phase eel). Gates are used in lieu of time in the analysis; therefore, survival curves suggest the probability for an eel

513   from each river (or of each colour) to be detected at each Gate (note- 0 is the point of release). Hashed marks indicate times at which

514   censorship (i.e. removal because the fate beyond this time was unknown) was taken into account by the model given that Gates 4 and 5

515   had incomplete coverage of area in the fjord.

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Figure 4. Ridge plot of densities representing the inferred speed between receiver gates moved by silver-phase eels (*Anguilla anguilla*)

in the Hardangerfjord. Speeds were calculated based on the first and last detection at each gate, if detections were missing for a gate it

520   is excluded (i.e. if an eel was recorded at Gate 1 and 3 there is no speed reported for Gate 1-2 or 2-3). Note that Gate 1 represents the

521   speed between the release site and Gate 1 and subsequent values are between gates (i.e. not cumulative).