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1 **Silver eel downstream migration in fragmented rivers: use**
2 **of a Bayesian model to track movements triggering and**
3 **duration**

4
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13

14 1 Abstract

15 Obstacles in rivers are considered to be one of the main threats to diadromous fish. As a result of the
16 recent collapse of the European eel, the European Commission introduced a Regulation, requiring
17 to reduce all sources of anthropogenic mortality, including those caused by passing through
18 hydropower turbines. Improving knowledge about migration triggers and processes is crucial to
19 assess and mitigate the impact of obstacles. In our study, we tracked 97 tagged silver eels in a
20 fragmented river situated in the Western France (the River Dronne). Using the movement ecology
21 framework, and implementing a Bayesian state-space model, we confirmed the influence of river
22 discharge on migration triggering and the distance travelled by fish. We also demonstrated that, in
23 our studied area, there is a small window of opportunity for migration.
24 Moreover, we found that obstacles have a significant impact on distance travelled. Combined with
25 the small window, this suggests that assessment of obstacles impact on downstream migration
26 should not be limited to quantifying mortality at hydroelectric facilities, but should also consider the
27 delay induced by obstacles, and its effects on escapement.

28 The study also suggests that temporary turbines shutdown may mitigate the impacts of hydropower
29 facilities in rivers with migration process similar to those observed here.

30

31 keywords: *Anguilla anguilla*, silver eel, migration delay, river fragmentation, movement ecology,
32 state-space model

33

34 2 Introduction

35 Movement plays a fundamental role in a large variety of biological, ecological and evolutionary
36 processes (Nathan 2008). Migration is a specific type of movement particularly prevalent among
37 taxa (Wilcove and Wikelski 2008). The phenomenon is defined by Dingle (1996) as a continuous,
38 straightened out movement not distracted by resources. Contrary to other movements (mainly
39 foraging and dispersion (Jeltsch et al. 2013)), migration is generally a response to environmental
40 cues such as temperature or photoperiod, and not only to fluctuations in resources and the
41 availability of mates (Dingle 2006). Because of their sensitivity to habitat degradation,
42 overexploitation, climate change, and obstacles to migration, most migratory species are in decline
43 (Berger et al. 2008; McDowall 1999; Sanderson et al. 2006; Wilcove and Wikelski 2008).
44 Consequently, improving knowledge about animal migration and its relationship with the rest of the
45 life cycle is of high scientific importance.

46 Diadromous fish are species that migrate between sea and fresh water during their life cycle
47 (McDowall 1968; Myers 1949). Three types of diadromy have been described (McDowall 1988): (i)
48 catadromous species, which spawn in the sea but spend most of their growth phase in continental
49 waters, (ii) anadromous species, which spawn in continental waters but spend most of their growth
50 phase at sea and (iii) amphidromous species, which undergo non-reproductive migration between
51 fresh water and sea during their growth phase. Populations of most diadromous fish species are
52 currently in decline (Limburg and Waldman 2009). Obstacles to migration, such as dams, are
53 considered to be one of the main threats to those fish species (Limburg and Waldman 2009). They

54 are also seen as the root cause of some population extinctions or their keeping in confined areas
55 within river catchments (Coutant and Whitney 2000; Fukushima et al. 2007; Kondolf 1997; Larinier
56 2001; Porcher and Travade 1992). Obstacles can have a large variety of impacts. Direct mortality as
57 a result of water turbines has been widely studied and quantified (Blackwell et al. 1998; Buchanan
58 and Skalski 2007; Čada et al. 2006; Dedual 2007; Travade et al. 2010; Welch et al. 2008; Williams
59 et al. 2001). However, obstacles can have many other consequences (Budy et al. 2002), including
60 stress, disease, injury, increased energy costs, migration delay (Caudill et al. 2007; Marschall et al.
61 2011; Muir et al. 2006) overpredation, and overfishing (Briand et al. 2003; Garcia De Leaniz 2008)
62 of populations that often suffer intense exploitation (McDowall 1999). In view of this,
63 understanding diadromous fish migration is a critical issue for conservation (McDowall 1999) and
64 can inform biodiversity policy (Barton et al. 2015).

65 This is especially true for catadromous European eels (*Anguilla anguilla*), which spawn in the
66 Sargasso Sea (Schmidt 1923; Tesch 2003) and grow in European continental waters after a few
67 years long larval drift (Bonhommeau et al. 2009). Leptocephali metamorphose into glass eels when
68 they arrive on the continental shelf (Tesch 2003). Glass-eels then colonise continental waters, where
69 they become pigmented yellow eels and remain during their growth phase, which lasts several
70 years. Colonisation tactics are largely plastic, and eels are able to use a variety of habitats, ranging
71 from estuaries and lagoons to upstream rivers (Daverat et al. 2006). After a period varying between
72 3 and 15 years in duration, yellow eels metamorphose into silver eels, migrate back to the sea, and
73 travel across the ocean to the Sargasso Sea (van Ginneken and Maes 2005). River fragmentation can
74 therefore impact both the upstream migration of glass-eels (Briand et al. 2005; Drouineau et al.
75 2015; Mouton et al. 2011; Piper et al. 2012) and downstream migration of silver eels (Acou et al.
76 2008; Buysse et al. 2014; Piper et al. 2013). As a result of a population collapse, (Dekker et al.
77 2007, 2003), observed on both recruitment (Castonguay et al. 1994; Drouineau et al. 2016; ICES
78 2014) and spawning biomass (Dekker 2003), the European Commission introduced Council

79 Regulation N°1100/2007, which requires a reduction in all sources of anthropogenic mortality,
80 including death caused when passing through hydroelectric turbines during downstream migration.
81 Three main types of studies have been carried out to improve knowledge of silver eel downstream
82 migration. Many have focused on the behaviour of silver eels passing downstream through
83 hydroelectric power stations to estimate mortality (Boubée and Williams 2006; Carr and Whoriskey
84 2008; Pedersen et al. 2012; Travade et al. 2010) or to improve mitigation solutions (Calles et al.
85 2013; Gosset et al. 2005; Russon and Kemp 2011). Some studies have tracked silver eels along
86 fragmented watercourses to estimate escapement (Acou et al. 2008; Breukelaar et al. 2009;
87 Haraldstad et al. 1985; Jansen et al. 2007; Marohn et al. 2014; Mccarthy et al. 2014; Piper et al.
88 2013; Reckordt et al. 2014; Verbiest et al. 2012). Other studies have focused on migration triggered
89 by environmental factors, to predict migration activity and especially peaks of migration, and
90 consequently when to shutdown turbines (Durif et al. 2008; Durif and Elie 2008; Trancart et al.
91 2013; Vøllestad et al. 1986). One common aspect in these previous studies is that they make use of
92 the same two types of data: telemetric tracking or daily abundance estimates (through either
93 catching or counting). Moreover, the three key issues (mortality at hydro-electric power stations,
94 escapement, and triggers for migration) are generally addressed separately.

95 The movement ecology framework (Nathan et al. 2008) appears to be an appropriate way of
96 simultaneously studying both triggers of migration and the impact of obstacles on escapement.
97 Movement ecology is a specific field of ecology focusing on organism movements (Nathan 2008;
98 Nathan et al. 2008). More specifically, it examines the interplay between an individual internal
99 state, its motion capacity, its navigation capacity and the environment. This interplay is addressed
100 through movement analysis. Several types of questions may be addressed (Nathan et al. 2008): (i)
101 why organisms move, (ii) how they move, (iii) where and (iv) when they move, (v) how the
102 environment influences those movements, and (vi) how those components interact together (Nathan
103 et al. 2008). Depending on their objectives, studies may focus on one or several of those questions
104 (Holyoak et al. 2008).

105 The development of tracking methods during the 1990s revolutionized behavioural and movement
106 ecology (Cagnacci et al. 2010; Jonsen et al. 2003). Satellite tags (Safi et al. 2013), satellite based
107 monitoring systems (Bez et al. 2011; Joo et al. 2013; Vermard et al. 2010), and acoustic tags with
108 positioning algorithms (Berge et al. 2012) now provide fine-scale temporal and spatial position data
109 relating to fish, mammals, birds, boats, etc. Different tools have been developed to analyse such
110 trajectory data. Among these tools are state-space models (SSM) (Jonsen et al. 2013; Patterson et al.
111 2008) and, more specifically, Hidden Markov Chain models (Joo et al. 2013). These are based on
112 two distinct sub-models. The state model describes the evolution of animal states across different
113 (generally discrete) time-steps. The observation model describes the link between unobserved states
114 and observations. In movement ecology, states are generally a position and type of behaviour, while
115 observations may be an estimation of position, speed or any other monitored parameter providing
116 information on movement (Jonsen et al. 2013). In their synthesis, Patterson et al. (2008) detail the
117 advantages of SSM in movement ecology. SSM enables statistical inference, accounting for various
118 types of uncertainty. It provides many interesting outputs: state probabilities (spatial location and
119 duration of specific behaviours), process model parameters for each state/behaviour, and
120 observation model parameters. Also, the flexibility of SSM allows the effects of environmental
121 factors on state/behaviour transition to be taken into account. Consequently, SSMs are relevant tools
122 to address each of the questions of movement ecology.

123 In this paper, we used the movement ecology framework to study silver eel migration and assess the
124 impact of obstacles in a highly fragmented river in southwest France. More specifically, we
125 developed a single integrated state-space model to (i) analyse the effects of different environmental
126 factors on migration triggering and derive the corresponding environmental suitability envelopes, (ii)
127 quantify the impact of river flow on migration speed, and (iii) quantify the impact of obstacles on
128 this speed. We analysed the implications of the results from a conservation point of view. The model
129 was applied to data relating to 68 eels (among 97 tagged) tracked along 90 kilometres of the
130 watercourse, covering three successive migration seasons. Our study illustrates how a state-space

131 model may respond to the different movement ecology questions listed by Nathan et al. (2008),
132 specifically “when do they move?” (environmental triggering) and “how do they move?” (influence
133 of discharge and weirs on migration speed).

134

135

136 3 Material and methods

137 3.1 Data

138 3.1.1 Study site: Dronne River

139 The river Dronne is a 200-kilometer long low land plain river located in the southwest of France
140 (Fig. 1). Its watershed covers 2816km². It flows into the river Isle, a tributary of the Dordogne
141 River, about 80 km from the Bec d'Ambès, where the Dordogne and Garonne rivers flow into the
142 Gironde estuary. It is one of the 10 “index rivers” identified in the French Eel Management Plan
143 (Anonymous 2010) in which specific efforts are made to quantify yearly eel recruitment and
144 escapement. Oceanic-type rainfall is observed, with a 45 years average discharge of 19.6 m³/s at
145 Bonnes (Table 1). The study site covers approximately 90 km along the downstream section of the
146 river (Fig. 1). The river is highly fragmented, with 91 obstacles referenced in the French obstacles
147 inventory (ROE ® database, finalized version 5.0, [http://www.onema.fr/REFERENTIEL-DES-](http://www.onema.fr/REFERENTIEL-DES-OBSTACLES-A-L)
148 [OBSTACLES-A-L](http://www.onema.fr/REFERENTIEL-DES-OBSTACLES-A-L)), i.e. one obstacle every 2.2km (every 2.1km on the studied section) on average.
149 Most obstacles correspond to old mill weirs, with a waterfall of less than two meters. Many
150 obstacles are now disused, although a few of them (7 of the 43 obstacles located in the study area)
151 are still used for hydroelectricity production.

152

153 3.1.2 Environmental data

154 The study took place during three successive eel downstream migration seasons: 2011-2012, 2012-
155 2013, 2013-2014.

156 Daily river flow data were obtained from the French “Banque Hydro” (website:

157 <http://www.hydro.eaufrance.fr>). Discharge was collected in three different stations of the studied

158 area, however only discharge measured at Bonnes (just downstream RAG, Fig. 1 and 2 - Table 1)
159 was considered for this study, since the three series were perfectly correlated.

160 Mean daily air temperatures were provided by Météo-France® and collected in Saint-Martial, a
161 station located a few kilometres from Bonnes (Fig. 1 - Fig. 2).

162 Water conductivity (WTW TetraCon®), turbidity (WTW VisoTurb®), temperature and dissolved
163 oxygen (WTW FDO® 700 IQ) were collected every hour in three stations (PAU, NAD and MON -
164 Fig. 1). Because strong correlations were observed between environmental variables (Spearman
165 correlation coefficients: 0.90 between discharge and turbidity; 0.80 between water temperature and
166 air temperature, 0.62 between air temperature and oxygen), we restricted the dataset to 5 variables:
167 average daily river discharge (Q), relative variation of average daily river discharge (ΔQ measured
168 as discharge at day d minus discharge at day $d-1$ divided by the discharge at time $d-1$), daily average
169 air temperature (T_{air}), squared average daily discharge (Q^2), and squared average temperature
170 (T_{air}^2). Using both factor and squared factors allow mimicking dome-shaped environmental
171 windows (i.e. a nonlinear relationship passing through a maximum). We chose to use discharge and
172 air temperature because (i) they do not present any gaps contrary to other variables and (ii) those
173 two variables are easily accessible in most rivers. Though less correlated (Spearman correlation
174 coefficient 0.41 between conductivity and air temperature); we did not consider conductivity
175 because records displayed abrupt and unexplainable changes (perhaps due to hydropower
176 operations), timely inconsistent between the three monitoring stations, therefore we considered they
177 were not reliable enough. We also tested relative variation of daily discharge because increasing
178 discharge phase tends to be more favourable than decreasing discharge phase for eel migration
179 (Haro 2003). The 5 variables are summarized in Table 2.

180 The three migration seasons were hydrologically contrasted, with a first season of low run-off
181 compared to the reference period (1970-2014), and two seasons with more intense discharges (Table
182 1 - Fig. 2). This contrast was visible both in terms of average discharge ($14.7 \text{ m}^3/\text{s}$ in 2011/2012
183 versus 26.9 and $34.9 \text{ m}^3/\text{s}$ in the two following seasons – Table 1) and in the number of discharge

184 peaks (three short peaks in 2011/2012 versus 5 peaks of longer duration in the two following
185 seasons – fig. 2). The first migration season was also characterised by a period of very low
186 temperature in January and February.

187

188 3.1.3 Fish sampling and tracking

189 Fish were collected during moderate discharge events in two filter traps incorporated in two old
190 mills (similar to the description by Tesch (2003)) located in station REN and POL (Fig. 1). Traps
191 were visited every 12 hours and caught eels were then placed in a tank supplied with river water.
192 Eels were tagged according to the protocol proposed by Baras and Jeandrain (1998) that had already
193 been successfully used by Travade et al. (2010) and Gosset et al. (2005). Eels were anaesthetized in
194 a solution of acetylugenol (~1.1mL/L), measured, and weighed. Their head lengths and heights,
195 eyes (vertical and horizontal lengths) and pectoral fins were measured and their stages of maturity
196 was checked according to Durif et al. (2005) and Acou et al. (2005) indices. A coded ATS
197 (Advanced Telemetry System) radio-transmitter with a pulse rate of 45 ppm (F1820 frequency
198 48–49 MHz, length 43 mm, diameter 12 mm, weight 8 g, minimum battery capacity 95 days or
199 F1815 frequency 48–49 MHz, length 36 mm, diameter 12 mm, weight 7 g, minimum battery
200 capacity 65 days) was implanted in the body cavity by surgical incision as described by Baras and
201 Jeandrain (1998). Intracoelomic implantation limits the risk of tag expulsion (Bridger and Booth
202 2003; Brown et al. 2011) and has a more limited impact on fish behaviour and survival (Koeck et al.
203 2013). Baras and Jeandrain (1998) had specifically validated the tag retention for eels while Winter
204 et al. (2005) confirmed good tag retention and survival, and limited behavioural impact using
205 intracoelomic implantation. The advocated threshold of 2% (weight of tag in air/weight of fish) was
206 carefully checked (Brown et al. 1999; Winter 1983) (see also (Jepsen et al. 2005; Moser et al. 2007)
207 for anguiliforms). High tag emission rates (45ppm) were required to ensure efficient detections rates
208 by autonomous receivers but decreased drastically batteries life. Consequently, we had to tag fishes
209 that were expected to move fairly soon after tagging, that's why we used eels caught by a filter trap

210 (this type of trap mainly catch active migrant). All eels fulfilling the 2% ratio rule were tagged
211 except a few individuals that had been injured during the catching process (other individuals were
212 in good health). According to Durif et al. (2005) and Acou et al. (2005), they were all silver eels
213 (table S1) and consequently expected to migrate in the short terms.

214 Similarly to Gosset et al. (2005), an exit hole was made for the antenna with a hollow needle
215 through the body wall 2 cm behind the incision and closed up with cyanoacrylate adhesive. The
216 incision was then closed up using a monofilament absorbable suture (Ethicon PDS® II 2-0, 3/8c vc
217 tr 24mm Z453H model) and a cyanoacrylate adhesive with antimicrobial effect (3M™ Vetbond™
218 Tissue Adhesive) to speed up healing (<10s). Following a veterinary advice, a broad course and
219 long-lasting antibiotics was also injected to reduce the risk of infection (Shotapen 1.0mL/kg). Eels
220 were released a few hours after surgery in three different places (Fig. 1). The protocol was
221 developed to limit the time between eel catch and release and to limit the transportation between
222 catch point and release point in order to limit behavioural biases due to tagging or infection in
223 holding tanks. More specifically, all the work was designed to respect animal welfare and to
224 minimize suffering. Finally, 97 silver eels were tagged and tracked during the 3 migration seasons.
225 Given that their total lengths were largely greater than 45 cm, we can assume that they were all
226 females (Durif 2003; Tesch 1991). Their complete biometry is presented in supplementary material.

227 Eleven R4520 ATS® autonomous receivers with low frequency antenna loop were installed at
228 different points along the river to detect passing fish (Fig. 1 - Table 3). The receivers were listening
229 continuously the only frequency used with a fast setting (2 s time out, a 10 s scan time and 1mn
230 store rate). This setting combined with a full gain setting that provides 200 m detection range
231 (validated by field tests) ensured that no fish were missed. In addition, active tracking was carried
232 out on a weekly basis to try locating eels more precisely. Unfortunately, the river is not easily
233 accessible along the whole study so active tracking provided sparse data that were not included
234 latter in the study, except to check whether the transmitters were still working. It also confirmed that
235 autonomous receivers had successfully detected all passages.

236 Radiotracking had already been used to study eel downstream migration (Durif 2003; Travade et al.
237 2010; Winter et al. 2006) and had proved efficient in freshwater systems such as ours. It is well
238 suited in shallow waters and when working close to river obstacles because not sensitive to
239 turbulences contrary to many acoustic systems. Moreover, active tracking can be carried out by car
240 (in a fragmented river such as the Dronne river, a tracking by boat required by acoustic telemetry
241 would be impossible).

242 For each day t and each tagged eel f , we calculated the distance between the most downstream
243 detection before the end of day t and the most downstream detection recorded before the end of day
244 $t-1$. This indicator, denoted $I(t,f)$, gave a rough approximate of the distance travelled each day t by
245 fish f . The daily average over all eels still in the studied area at time t is denoted $I'(t)$.

246

247 3.2 Model

248 A state-space model was developed to analyse our results. It is based on a state-model that describes
249 migration triggering and an observation model that describes fish movement (Fig. 3).

250

251 3.2.1 Behavioural states transitions and migration triggering

252 The model has a daily time-step. In each time-step t , a fish f can be in three different unobserved
253 states $S(f,t)$: 1 pause, 2 active migrant, 3 definitive stop (either mortality or definitive withdrawal).

254 In the first state, fish are not moving and are waiting for favourable conditions to migrate. In the
255 second state, fish are actively migrating (i.e. migrating downstream) and will continue to move as
256 long as conditions are favourable. In the third step, fish have definitively abandoned migration or
257 are dead.

258 State at time step t is assumed to follow a Markovian process: the state at time t depends only on the
259 state at time $t-1$ and vector of transition probabilities which depend mainly on environmental

260 conditions (transition to state 3 is considered to be independent of environmental conditions and
 261 may be due to predation, diseases...), through a categorical distribution:

$$262 \quad S(f, t) \sim \text{Cat}(\{q_{S(f, t-1), 1}(t), q_{S(f, t-1), 2}(t), q_{S(f, t-1), 3}(t)\}) \quad (1)$$

263 $q_{i,j}$ denotes the probability of switching from state i to state j . Consequently,

264 $\{q_{S(f, t-1), 1}(t), q_{S(f, t-1), 2}(t), q_{S(f, t-1), 3}(t)\}$ is a vector that contains the probabilities that fish f

265 switches to each possible state given that it was in state $S(f, t-1)$ at time step $t-1$. Those

266 probabilities are assumed to be a function of environmental conditions:

$$267 \quad q_{1,2}(t) = (1 - p_e) \cdot \left(\frac{1}{1 + \exp(-\mu_s + \langle \vec{\alpha}_{sd}, E(t) \rangle)} \right)$$

$$268 \quad (2)$$

$$269 \quad q_{1,1}(t) = (1 - p_e) \cdot (1 - q_{1,2}(t)) \quad (3)$$

$$270 \quad q_{2,1}(t) = (1 - p_e) \cdot \left(\frac{1}{1 + \exp(-\mu_w + \langle \vec{\alpha}_w, E(t) \rangle)} \right)$$

$$271 \quad (4)$$

$$272 \quad q_{2,2}(t) = (1 - p_e) \cdot (1 - q_{2,1}(t)) \quad (5)$$

$$273 \quad q_{1,3}(t) = q_{2,3}(t) = p_e \quad (6)$$

$$274 \quad q_{3,3}(t) = 1 \quad (7)$$

$$275 \quad q_{3,1}(t) = q_{3,2}(t) = 0 \quad (8)$$

276 with $E(t)$ a vector that contains the environmental factors at time step t

277 The table of environmental factors was previously scaled and centred to decrease the correlation

278 between regression parameters (Bolker et al. 2013). $\vec{\alpha}_s$ and $\vec{\alpha}_w$ denote the vector regression

279 coefficients associated with each environmental factor while μ_s and μ_w denote the intercept in

280 the regression between transition probabilities and environmental factors. $\langle \vec{A}, \vec{B} \rangle$ denotes the

281 inner product between vectors \bar{A} and \bar{B} . Finally, p_e denotes the daily probability of
282 definitive abandon (a fish that will definitively not move anymore).

283 Equations 2 (respectively 4) means that probability for a fish to switch from state pause to active
284 migrant (respectively active migrant to pause), given it has not definitively abandoned, is similar to
285 a logistic regression of environmental conditions (with intercept μ and regressions coefficients α).

286 Equations 3 (respectively equation 5) is the probability that a fish remains in state 1 (respectively 2)
287 and is the complement of equation 2 (respectively 4). Equation 6 mean that the probability to switch
288 to state 3 is constant through time, i.e. do not depend on initial state nor on environmental
289 condition, while equation 7 and 8 mean that a fish in state 3 always remain in state 3.

290

291 3.2.2 Movement and observation model

292 Considering that eel migration speed increases with water velocity, and since water velocity
293 increases as a function of river flow (Leopold and Maddock 1953), we assumed that the average
294 theoretical distance that an actively migrating fish would travel within 24 hours at time step t
295 without any obstacles $L_{th}(t)$, was dependent on flow conditions:

$$296 \quad L_{th}(t) = \exp[\mu_{mig} + \alpha_{mig} \cdot \log(Q(t-1))] \quad (9)$$

297 with $\exp(\mu_{mig})$ the distance that an eel would travel in absence of discharge and

298 $\exp(\alpha_{mig} \cdot \log(Q(t-1)))$ the influence of the water velocity on this distance.

299 We defined a reach as a portion of the studied area between two successive autonomous receivers.

300 For each day, we know exactly in which reach each eel is located because autonomous receivers

301 were settled to detect all fish passages. Fish movement is modelled through a reach transition matrix

302 composed of the daily transition probability of moving from a reach r_1 to a reach r_2 . To simplify the

303 computation of the reach transition matrix, we assumed that fish were located at the middle of the

304 departure reach at the beginning of each time-step, which is a usual approximation for growth

305 transition matrix (DeLong et al. 2001; Sullivan et al. 1990). We denote d_{r_1, r_2} the maximum distance

306 that a fish has travelled to move from reach r_1 to reach r_2 . Similarly, we denote nb_{r_1,r_2} the maximum
 307 number of weirs that a fish must pass through in order to move from reach r_1 to reach r_2 . d_{r_1,r_2} and
 308 nb_{r_1,r_2} are directly calculated using Table 3.

309 Assuming that passing an obstacle acts as a penalty equivalent to w kilometres, and that the
 310 effective distance covered by an eel in 24 hours follows a lognormal distribution, we can then
 311 compute the transition probability to move from a reach r_1 to a reach r_2 :

$$312 \quad p_{r_1,r_2}(t) = \begin{cases} 0 & \text{if } r_1 < r_2 \\ \int_0^{d_{r_1,r_2} + w \cdot nb_{r_1,r_2}} \frac{1}{2 \cdot \sigma_m^2 \cdot \sqrt{2 \cdot \pi}} \cdot e^{-\frac{1}{2} \cdot \left(\frac{x - \ln(L(t))}{\sigma_m}\right)^2} dx & \text{if } r_1 = r_2 \neq 11 \\ \int_{d_{r_1,r_2-1} + w \cdot nb_{r_1,r_2-1}}^{d_{r_1,r_2} + w \cdot nb_{r_1,r_2}} \frac{1}{2 \cdot \sigma_m^2 \cdot \sqrt{2 \cdot \pi}} \cdot e^{-\frac{1}{2} \cdot \left(\frac{x - \ln(L(t))}{\sigma_m}\right)^2} dx & \text{if } r_2 > r_1 \wedge r_2 \neq 11 \\ \int_{d_{r_1,r_2-1} + w \cdot nb_{r_1,r_2-1}}^{+\infty} \frac{1}{2 \cdot \sigma_m^2 \cdot \sqrt{2 \cdot \pi}} \cdot e^{-\frac{1}{2} \cdot \left(\frac{x - \ln(L(t))}{\sigma_m}\right)^2} dx & \text{if } r_2 > r_1 \wedge r_2 = 11 \\ 1 & \text{if } r_1 = r_2 = e \end{cases} \quad (10)$$

313 with r_1 and r_2 a reach index (1: DRO->PAU, 2: PAU->RIB, 3: RIB->EPE, 4: EPE->RAG, 5: RAG->
 314 >NAD, 6: NAD->STA, 7: STA->CHA, 8: CHA->PAR, 9: PAR->ROC, 10: ROC->MON, 11:
 315 escaped – see Table 3 and Fig. 1)

316 The observed transition from reach r_1 to a reach r_2 for fish f at time t follows a categorical
 317 distribution:

$$318 \quad P(f,t) \sim \text{Categorical}(\{p_{P(f,t-1),1}(t), \dots, p_{P(f,t-1),11}(t)\}) \quad (11)$$

319 where variable $P(f,t)$ denotes the position of fish f at time step t , i.e. the reach in which the fish is
 320 located.

321

322 3.2.3 Bayesian inference and priors

323 The model was fitted using JAGS (Plummer 2003), an application dedicated to Bayesian analysis

324 that uses a Gibbs Sampler. The runjags library (Denwood n.d.) was used as an interface between R

325 (R Development Core Team 2011) and jags. Three chains were run in parallel for 60000 iterations
326 with a thinning period of 3 (resulting in 20000 samples per chain), after a burn-in period of 100000
327 iterations.

328 The convergence was checked using the usual Gelman and Rubin tests (Gelman and Rubin 1992)
329 using library coda (Plummer et al. 2010) and by visual inspections of the chains.

330 Uninformative priors were used on most parameters:

$$331 \quad w \sim Unif(0, 10) \quad (12)$$

$$332 \quad \mu_s \sim Unif(-6, 6) \quad (13)$$

$$333 \quad \mu_d \sim Unif(-6, 6) \quad (14)$$

$$334 \quad p_e \sim Beta(0.5, 0.5) \quad (15)$$

$$335 \quad \sigma_{mig} \sim Unif(0.01, 2)$$

$$336 \quad (16)$$

$$337 \quad \mu_{mig} \sim Unif(-6, 6) \quad (17)$$

$$338 \quad \alpha_{mig} \sim Beta(0.5, 0.5) \quad (18)$$

339 The prior for α_{mig} (equation 18) is due to the fact that mean water speed increases as a function of
340 river flow with a power between 0 and 1 (Leopold and Maddock 1953). Assuming that migration is
341 passive or semi-passive, migration speed should then be power function of river discharge with a
342 power between 0 and 1.

343

344 For the effects of environmental variables on migration triggering, spike-and-slab priors were used
345 (Ishwaran and Rao 2005; Mitchell and Beauchamp 1988). Those priors are appropriate for selecting
346 relevant explanatory variables in a model. The prior is constructed as follows:

$$347 \quad \alpha_{s,i} \sim Normal(0, \sigma_{s,i}^2) \quad (19)$$

348
$$\sigma_{s,i}^2 = 0.001 \cdot (1 - \Gamma_{d,i}) + 10 \cdot \Gamma_{s,i} \quad (20)$$

349
$$\Gamma_{s,i} \sim \text{Bernouilli}(0.5) \quad (21)$$

350 where $\alpha_{s,i}$ is the i -th component of vector α_s . $\Gamma_{s,i}$ is an indicator variable with a value of 0
351 or 1 which can be interpreted as posterior probabilities that the variables should be included. When

352 $\Gamma_{s,i}$ has a value of 0, the environmental factor is not selected, the variance $\sigma_{s,i}^2$ is small and

353 consequently $\alpha_{s,i}$ is close to 0. Conversely, when $\Gamma_{s,i}$ has a value of 1 (factor selected),

354 $\sigma_{s,i}^2$ is strong and $\alpha_{s,i}$ may take any values. The same approach is used for $\alpha_{d,i}$, $\Gamma_{d,i}$ and

355 $\sigma_{d,i}^2$.

356 To limit the risk of possible behavioural bias due to surgery, we fitted the model to a restricted
357 dataset including only eels movements after they had passed at least one detection station (MDR for
358 eels released in REN, RIB for eels released in PAU and NAD for eels released in POL), i.e. moved
359 at least 8 kilometres after surgery. This restricted the dataset to 68 eels among the 97 eels that had
360 been initially tagged. Daily eels reach locations were used to fit the model from those first
361 detections to the last detections recorded for each eel (either from autonomous receiver or active
362 tracking) to ensure that transmitters were still working. This resulted in a 2595 days x eels dataset.

363

364 4 Results

365 From now, we defined escapement as the successful migration from release point to the most

366 downstream autonomous receiver, i.e. MON. Consequently, an escaped fish was detected at every

367 detection station between its release point and MON.

368

369 4.1 Global results

370 Escapement was nil in the first migration season, probably because of unsuitably low river flow

371 conditions (Table 1), while it was about 55% of tracked eels escaped during the next two seasons

372 (Table 4) if considering all tagged eels, and between 60% and 70% if considering only the 68 eels

373 that had travelled at least 8 km. There was no significant difference in escapement between REN
374 and POL release points. We also observed that nearly 1/3 of the eels that did not escape stopped in
375 the first 10 km. Interestingly, there is no significant difference between whole tagged eels length
376 distribution and successfully escaped eels length distribution (Wilcoxon test p-value 0.53), nor
377 between non-escaped and escaped eels (Wilcoxon test p-value 0.11)

378 The transfer rates seemed slightly higher downstream the studied area than upstream (Table 5),
379 especially downstream STA station. This result was possibly due to a lower density of obstacles
380 downstream the studied area. However, it was also possibly due to the decreasing influence of
381 environmental conditions at fish release while fish moved downstream. The model we developed
382 was appropriate to disentangle between those two effects.

383 The detailed behaviours of monitored eels are presented in supplementary material.

384 The analysis of $I'(t)$ (Fig. 4 - left panel) showed that movements were concentrated in river
385 discharge peaks, especially during rising phases. Some movements were observed at low discharge
386 and some eels did not move even at very high discharges, however, despite a great variability, the
387 probability of long travelled distance increased with the discharge (Fig. 4 - right panel).

388 Interestingly, 75% of eels' first or last detection in an antenna field (i.e. when eels entered or left an
389 antenna field without considering the time when they remain in the field) occurred at night between
390 20:00 and 07:00 am.

391

392 4.2 Efficiency of autonomous receivers

393 Analysis of autonomous receivers records showed that in 96% of cases, a fish passage at a station
394 was recorded at least twice, i.e. fishes stayed long enough in the antenna field to be recorded at least
395 twice. Moreover, we validated that fish located by active tracking was successfully detected by
396 upstream autonomous receivers. Therefore, we considered that our autonomous receivers were
397 totally efficient.

398

399 4.3 Model results

400 The model was fitted on 68 eels (Table 4).

401

402 4.3.1 Model convergence

403 \hat{R} values for Gelman and Rubin tests were less than 1.05 for all variables. Visual inspection of

404 the posterior distributions confirmed the limited influence of the priors on the results, except for

405 $\alpha_{mig} \sim Beta(0.5, 0.5)$ which posterior distribution is concentrated around the prior upper bound.

406 However, a larger value would be hydrologically a non-sense (Leopold and Maddock 1953).

407

408 4.3.2 Selected environmental variables on migration triggering and reaction norms

409 The spike-and-slab procedure confirms the importance of river discharge in migration triggering

410 (Table 6). The main factor triggering the migration was relative change in river discharge (Fig. 5 -

411 left column): movements can be triggered even at low discharge when relative change is high.

412 However, the transition probability from “active migrant” (state 2) to “pause state” (state 1)

413 increased rapidly at low discharge (Fig. 5 - right column). These results mean that eels start their

414 migration during a rising river phase event and continue as long as the river flow remains at a

415 sufficient level. Small movements are possible, even at low discharge if the relative change is high.

416 For example, the probability for an eel to turn into active migrant is superior to 40% if the discharge

417 increases from 5 m³/s to 10 m³/s (Fig.5, left column, T=4°C first line), which corresponds to half the

418 yearly mean discharge, while this probability is equal to 56% if the discharge increases from 25 to

419 50 m³/s (Q90 of the spawning season – Tab. 1). However, high levels of discharge are required for

420 long-term movements: in our previous example the eel would pause a movement the following day

421 with probability 92% if the discharge remains at 10 m³/s (Fig.5, second column, T=4°C first line),

422 while this probability is equal to 33% if the discharge remains at 50 m³/s. This results in a rather

423 limited environmental window suitable for downstream migration.

424 Regarding transition from state 2 to state 1, the model predicts a decreased probability at very high
425 discharge, however this corresponds to discharges greater than $100\text{m}^3/\text{s}$, i.e. greater than Q99 so
426 very rare. Therefore, in this zone, the model is fitted on a very number of observations and
427 predictions are very uncertain.

428 Temperature had a much more limited influence on our results, although it may have an influence
429 on the transition from state 2 to state 1 (Table 6 - Fig. 5 right column).

430

431 4.3.3 Travelled distance and impact of obstacles

432 The model predicts that an active eel should theoretically travel tens of kilometres in 24 hours (Fig.
433 6) but this distance is significantly decreased by the presence of obstacles.

434 The posterior distribution of the penalty equivalent of an obstacle w is a way to quantify the impact
435 of obstacles. The median value of 3.84 km would mean that each obstacle represents an additional
436 3.84 kilometres. Given that there is an obstacle every 2 kilometres, this would imply that the
437 distance covered by active migrant in 24 hours is divided by 2.86 because of obstacles. However,
438 because the river is very fragmented and there is little contrast between reaches (Table 3), this
439 impact was difficult to estimate as demonstrated by the flat posterior distribution of w (standard
440 deviation: 2.4 km). It should also be noticed that this penalty is an average covering a wide range of
441 impacts: some fish may suffer little impact while others may definitively stop their migration.

442

443 4.3.4 Activity indices

444 The model may be used to estimate (i) the proportion of actively migrant eels and (ii) the expected
445 travelled distance (multiplication of the proportion of active migrant by the predicted travelled
446 distance) to derive activity indices for each day of the three migration seasons (Fig. 7, we set p_e to
447 zero, i.e. no definitive stop since it would require knowing the date at which each eel starts to
448 migrate and our estimate of p_e might include post-tagging effects). The low run-off in 2011-2012
449 resulted in a limited activity. Fig. 7 confirms that migratory activity is concentrated within limited

450 windows of opportunity, especially in terms of expected distance travelled. Summing or averaging
451 those indices illustrates the inter-annual contrast due to environmental conditions. For example, the
452 average daily proportion of migrants was equal to 5.8% in 2011/2012, to 10.8% in 2012/2013 and
453 14.8% in 2013/2014. Regarding the total travelled distance (without accounting for definitive stop),
454 it was equal to 47km in the first season, 279km in the second season and 433km in the last season.
455 Another way to display the results consists in plotting the number of days in which the activity
456 (proportion of migrants or travelled distance) was superior to a given level (Fig.8). We observed
457 that high activity is limited to a limited number of days, especially during the first season. The
458 number of days in which half the eels were active was close to zero in 2011/2012 and around 20
459 days in the two following seasons. This was even worse regarding travelled distance: the number of
460 days for which travelled distance was superior to 5 km was close to 0 in 2011/2012, close to 20 in
461 2012/2013 and about 40 in 2013/2014.

462

463 4.3.5 Final states of non-escaped eels

464 It is interesting to analyse the estimated final states of the 31 eels that did not escape the studied
465 area (Table 7). For 14 eels, a pause in the migration (state 1) was the most credible state, or had
466 credibility similar to a definitive abandon (state 3). For those 14 eels, mostly from the first
467 migration season, unsuitable environmental conditions, especially low river flow, may account for
468 the fact that they did not continue moving.

469 On the other hand, for 17 eels, the most credible states were either abandon (state 3) or still active
470 migration (state 2), i.e. when migration had stopped completely (with no further movement, even in
471 suitable conditions) or when eels were still actively migrating when last detected, but no further
472 detections were registered. For those 17 eels, environmental conditions can hardly explain that they
473 have not escaped the study site. Interestingly, 13 of those 17 eels were detected for the last time just
474 a few kilometres downstream from one of hydropower plants, suggesting possible impacts caused
475 by a passage through turbines (i.e. they may have been killed, injured or disoriented by turbines).

476

477 5 Discussion

478 Various environmental factors have been proposed as triggering factors of the downstream
479 migration of silver eels (Bruijs and Durif 2009): turbidity (Verbiest et al. 2012), wind direction
480 (Cullen and McCarthy 2003), pH (Durif et al. 2008), conductivity (Durif 2003; Verbiest et al. 2012),
481 rainfall (Durif 2003; Trancart et al. 2013), temperature (Reckordt et al. 2014; Vøllestad et al. 1986),
482 atmospheric pressure (Acou et al. 2008), moon phase (Acou et al. 2008; Cullen and McCarthy
483 2003; Poole et al. 1990), river flow (Acou et al. 2008; Bau et al. 2013; Cullen and McCarthy 2003;
484 Jansen et al. 2007; Reckordt et al. 2014). Most of those parameters are strongly linked: rainfall
485 directly influences river discharge which in turn impacts turbidity and conductivity. As anywhere
486 else, it is difficult in the River Dronne, to disentangle the respected effects of these correlated
487 factors. Using controlled experiments, Durif et al. (2008) demonstrated that eels can display
488 migratory behaviour while not exposed to river flow. They concluded that the main trigger is
489 probably physico-chemical in nature. However, it is easier to predict rainfall than turbidity or
490 conductivity. Consequently, Trancart et al. (2013) used rainfall in their model to forecast migration
491 activity and subsequently propose periods of turbine shutdowns. River flow can also be predicted
492 using rainfall-runoff models (Beven 2011) as illustrated by flood prediction models (Nayak et al.
493 2005; Toth et al. 2000). River flow is especially relevant, since it influences water speed and
494 consequently affects migration speed. It also influences route selection when faced with an obstacle
495 (Bau et al. 2013; Jansen et al. 2007; Piper et al. 2015), therefore also affecting the probabilities of
496 passing through alternative routes (weirs or by-pass devices for example). Consequently, this is a
497 key factor in any model aimed at quantifying mortality caused by hydropower plants at both the
498 obstacle and the river basin scales, as illustrated by the Sea-Hope model (Jouanin et al. 2012).
499 Interestingly, it was not river discharge itself, but the relative variation of river discharge which was
500 selected by the model as the main triggering factor. This result is consistent with Trancart et al.
501 (2013), whose study showed that rainfall triggers migration. It is indeed logical to assume that

502 increased precipitation leads to a rising river flow phase. It may also be consistent with Durif et al.
503 (2003; 2008): sediment concentration is often higher during a rising runoff phase than at an
504 equivalent runoff during the falling phase. Williams (1989) refers to this as clockwise hysteresis.
505 Such a hysteresis may explain why turbidity and conductivity, suggested as triggering factors by
506 Durif (2003) and Durif et al. (2008), are different during rising and falling phases, and that the
507 relative flow change selected in our model is just a distal mechanism that influences turbidity and
508 conductivity which would be the proximal triggering factors. This significant direct or indirect
509 influence of river flow on migratory behaviour raises questions about the consequences of
510 streamflow modification due to climate change (Arnell 1999; Milly et al. 2005) and the impact of
511 flow regulation due to different anthropogenic activities which smooth river flow variations, (this is
512 especially true when dam reservoirs have high storage capacities and smooth variations at low
513 discharges, though it is not the case in the Dronne River).

514 Our model quantifies the influence of different environmental factors, as well as making it possible
515 to generate suitability envelop for migratory activity (Fig. 5 – Fig. 8). The windows of opportunity
516 for active migration are very limited (Fig. 7 - 2nd line – Fig. 8 left column) and even more limited
517 when considering expected distance travelled (Fig. 7 - 3rd line – Fig.8 – right column). This has two
518 main consequences. First, it confirms that, as proposed by Trancart et al. (2013), temporary and
519 targeted turbines shutdowns can be a useful means of mitigating the impact of hydroelectric power
520 stations in systems in which the hydrology and migration process are similar to the Dronne River. In
521 practice, such a measure requires two additional tools: a tool that predicts migration peaks 12 to 24
522 hours in advance to comply with the operational delay for turbine shutdowns and a tool that
523 estimates the distribution of eels within the river catchment to assess the number of eels likely to
524 pass the obstacles. If such tools are available, turbine shutdowns have the advantage of not
525 requiring any work on the obstacles. Therefore, this measure can be implemented quickly and has a
526 limited cost if the number of migration peaks is limited. Turbine shutdowns should be considered as
527 a possible solution among others such as fish-friendly trashracks (Raynal et al. 2014, 2013) or other

528 physical devices which are more multispecific and less site-dependent. Moreover, 75% of the time,
529 eels entered or left our antenna fields between 20:00 and 07:00 am in our dataset. This type of
530 nycthemeral behaviour was also observed by Durif and Elie (2008) and Riley et al. (2011). In view
531 of this, shutting down turbines at night, when demand for power is lower, may or may not suffice
532 depending on escapement targets. In all cases, simulation exercises are required to assess the
533 ecological benefits of different management options, and costs-benefits (Dupuit 1844; Snyder and
534 Kaiser 2009) or costs-effectiveness analysis (Crossman and Bryan 2009) should be carried out to
535 support decision making on each site or river.

536 Regarding migration triggering, a limit of our protocol is that our fish trapping devices caught
537 already migrant eels and that may hinder our ability to work on migration triggering by
538 environmental conditions. This was required for practical reason (existing trapping systems in the
539 context of the "index river" system) but also for a question of battery life. However, eels are known
540 to alternate between active migration and sometimes several weeks long waiting phases during their
541 downstream migration depending on environmental conditions (Aarestrup et al. 2008; Durif 2003;
542 Reckordt et al. 2014; Verbiest et al. 2012; Vøllestad et al. 1994; Watene et al. 2003). So even if
543 catching active migrant eels, we were able to observe those switches between active migration and
544 pause phases (the tables presented in supplementary material illustrates those switching) and then to
545 derive the influence of environmental conditions on switching probabilities. Our study does not
546 provide any information on the environmental triggering of silvering process, but on the
547 environmental triggering of silver eels movements. In our opinion, silver eel downstream migration
548 should be considered as a three steps process: (i) silvering that occurs when eels have accumulated
549 enough energy stores and after which eels wait for favourable conditions, (ii)
550 activation/deactivation of migration due to favourable environmental conditions and (iii) travelled
551 distance that depends on speed velocity and obstacles. It will be interesting in the future to catch
552 and tag yellow eels and then track their downstream migration to explore the environmental
553 triggering of silvering process and then of migration. However, this implied to have long-life tags,

554 small enough to tag smaller fishes, with a large enough detection range and easily implantable to be
555 able to tag a sufficient number of individuals. Unfortunately, it seems that such tags are not
556 currently available.

557 In addition to environmental triggering of fish migration, the models also quantifies the impact of
558 obstacles on travelled distance though the credibility intervals are very large, probably because of
559 the lack of contrast between reaches. In an obstacle free estuary, Bultel et al. (2014) observed mean
560 directional migration of 48.6 km per day, a distance consistent with our estimates though the two
561 systems are rather different. However, obstacles significantly impact the distance covered by eels
562 and may lead to stops or delays in migration and, subsequently, potential mismatches between
563 spawners arriving in the Sargasso Sea, notably between individuals located in the lower and upper
564 parts of river catchments. It is more likely that the delay induced by obstacles impairs escapement
565 success when there is a limited suitable window for migration, even though some silver eels are
566 able to delay migration by up to a year to await favourable conditions (Feunteun et al. 2000;
567 Vøllestad et al. 1994). Consequently, quantifying the impact of obstacles should not be restricted to
568 the quantification of turbine mortality as in the Sea-Hope approach (Jouanin et al. 2012) but also
569 consider escapement failures due to delays induced by all kinds of obstacles (not only hydroelectric
570 power stations, which represent about 5% of the obstacles listed in the French obstacles inventory).
571 To achieve this quantification, a better knowledge on the time required to migrate to spawning
572 grounds and on the continental escapement deadline would be necessary. The pattern of sex-ratio
573 between the downstream (male biased) and upstream (more or exclusively females) area of a river
574 catchment (Drouineau et al. 2014; Oliveira and McCleave 2000; Tesch 2003) combined with the
575 impact of obstacles may also lead to arrival mismatch between males and females or to gender
576 disparities in terms of escapement success. Increased energy costs and injuries caused by passing
577 through downstream obstacles may also impair escapement success for silver eels, which stop
578 feeding during reproduction migration (Bruijs and Durif 2009).

579 In our study, a preliminary statistical analysis do not demonstrate any effect of fish length on
580 escapement success, consequently, we did not include fish length in our model. Palstra and van den
581 Thillart (2010) demonstrated in a previous study that fish length is a main determinant of fish
582 swimming capacity. Two reasons may explain this discrepancy. First, in our study, we only tagged
583 silver eels large enough to tolerate the tag. It resulted in a restricted length distribution biased
584 towards large individuals, limiting the contrast between individuals and impairing our ability to
585 depict an influence of individual length. Secondly, Palstra and van den Thillart (2010) carried out in
586 swim-tunnel and consequently on active swimming. In our field experiment, it is likely that silver
587 eels have a passive or semi-passive swimming behaviour using river flow to carry out their
588 migration and that consequently, fish length have a more limited impact on migration velocity and
589 travelled distance.

590 We developed a Bayesian hierarchical model (or state-space model) to analyse the movements of
591 tagged spawning eels. This kind of model has previously proved useful in analysing movements
592 (Patterson et al. 2008), notably in the framework proposed by Nathan et al. (2008). The model
593 enabled us to evaluate simultaneously the influence of environmental factors on migration
594 triggering and the influence of river discharge on distance travelled in a unique integrated model
595 (Fig. 3), while quantifying uncertainties. As mentioned in the introduction, the two aspects have
596 generally been analysed independently depending on the type of available data. Analysis of
597 migration from captures in a specific trap is suitable to analyse migration triggering (Acou et al.
598 2005; Trancart et al. 2013) while radiotracking data are appropriate for analysing movements both
599 in terms of distance travelled (Verbiest et al. 2012) and behaviour at specific dams (Bau et al. 2013;
600 Jansen et al. 2007). The main strength of our study is that it analyses three elements simultaneously:
601 migration triggering, distance travelled and the impact of obstacles. The model may be used in the
602 future to predict proportion of active migrants and expected distance travelled by eels (Fig. 7, 3rd
603 column – Fig. 8). Combined with a model of eels distribution within the catchment, they can be
604 used to determine river discharge thresholds for turbine shutdown or to derive yearly indices of

605 escapement success. The indicators proposed in section “activity indices” can be a first step towards
606 such an escapement success index and show that in years of low discharges, the expected travelled
607 distance is very limited, even without considering any source of mortality (Fig. 8). As mentioned
608 earlier, simulation and cross-validations exercises would be necessary to validate the model
609 prediction ability and to assess the relevance of such a mitigation measure.

610 One possible bias of most telemetry studies is the risk of misinterpretation due to mortality of
611 tagged individuals and that could explain our limited escapement. Our protocol aimed at reducing
612 post-surgery mortality (use of cyanoacrylate adhesive and antibiotic to limit the risk of post-surgery
613 infection, limitation of time between catching and releasing fishes, limitation of fish transport and
614 protocol that limit the risk of tag expulsion). Given the limited numbers of available eels for the
615 experiment, it was not possible to carry out a true post-surgery experiment, however three eels were
616 tagged with a similar protocol (but bigger tags) and kept in a tank with river water for 19, 25 and 44
617 days. They all survived and displayed normal healing of their incision. Though silver eel fishing is
618 strictly forbidden in this river, mortality can also be induced by predation or hydropower plants
619 during the migration. Contrary to traditional statistical approaches used to analyse telemetry data,
620 the model allow to overcome this bias by introducing a third stage “definitive stop” that accounts
621 for mortalities. Fishes that did not move at all despite favourable conditions were classified as
622 “definitive stop” by the model and therefore were not “considered” when inferring the transition
623 probabilities between active migration and pause states. Interestingly, the analysis of estimated final
624 states by the model suggested a possible impact of hydropower plants.

625 The model predicts that small scale movements are possible at low level of discharge in a period of
626 rising flow, but high levels of discharge are required to maintain migration activity and to increase
627 travelled distance. As a consequence, estimated activity indices were nearly nil below $20 \text{ m}^3 \cdot \text{s}^{-1}$.
628 This value should not be directly applied to rivers other than the Dronne. However, carrying out a
629 meta-analysis of the different radio-telemetry experiments on silver eel migration would be a
630 relevant way of identifying invariants between rivers, even though in large rivers and downstream

631 systems, migratory behaviour patterns could be more difficult to interpret (and to link to
632 environmental parameters) as they should be the consequence of different upstream behaviours
633 linked to different hydrologies. Nevertheless, state-space models are flexible enough to be applied
634 in a wide range of situations and fitting such models to the other experiments would facilitate
635 results comparisons and derive invariants. Using exceedance discharges rather than basic discharges
636 would appear to be a suitable way of carrying out such a meta-analysis.

637 Generally, state-space models have been used on movement data with high spatial and temporal
638 resolution (Jonsen et al. 2013; Joo et al. 2013; Patterson et al. 2008), however they can still be used
639 with sparser data (such as ours) to explore the interplay between individual internal state,
640 environmental conditions, and resulting individual movements. More generally, it confirms that the
641 movement ecology framework is an appropriate approach to explore this interplay in many fish
642 radiotracking experiments in rivers.

643

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658

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662

663 8 Tables

664 **Table 1.** River discharge characteristics at Bonnes monitoring station, measured from 1970 to 2014

665 for the entire year (first column) and for the months from October to May (second column) which

666 correspond to the tracking period. Q99, Q97.5, Q95, Q90, Q80, Q75 correspond to daily flows

667 extracted from flow duration curve and exceeded 99, 97.5, 95, 90, 80, 75% of the time respectively

668

	1970-2014 (whole year)	1970-2014 (Oct-May)	2011-2012 (Oct-May)	2012-2013 (Oct-May)	2013-2014 (Oct-May)
mean	19.6	25.2	14.7	26.9	34.9
median	12.1	17.6	10.4	22.1	28.3
Q75	24.2	30.9	15.8	31.4	44.9
Q80	28.4	35.8	18.0	36.0	48.2
Q90	42.5	51.5	28.4	59.0	71.4
Q95	59.9	72.0	40.1	70.6	88.3
Q97.5	83.0	97	66.4	81.0	99.9
Q99	115.0	129	114.0	103.9	110.1

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670

671 **Table 2.** Characteristics of the 5 environmental variables during the whole three migration seasons.

	Q ($\text{m}^3 \cdot \text{s}^{-1}$)	Q ² ($\text{m}^3 \cdot \text{s}^{-1}$) ²	Tair (°C)	Tair ² (°C ²)	ΔQ (%)
Range (min ; max)	1.94 ; 144.00	3.76 ; 20736.00	-8.3 ; 23.9	0.04 ; 571.21	-36.4 ; 170.4
Mean	25.49	1180.61	9.7	120.6	2.2
Median	18.6	345.96	9.6	92.16	-0.5

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674 **Table 3.** Relative positions of the different monitoring stations (Fig. 1)

Stations	Distance from previous site (km)	Distance from REN release point (km)	Distance from PAU release point (km)	Distance from POL release point (km)	Number of obstacles from previous station
REN		0	-	-	
DRO	8.2	8.2	-	-	5
PAU	7.4	15.6	0	-	4
RIB	7.3	22.9	7.3	-	3
EPE	5.7	28.6	13	-	6
POL	10.3	38.9	23.3	-	4
RAG	1.2	40.1	24.5	1.2	1
NAD	8.2	48.3	32.7	9.4	5
STA	6.9	55.2	39.6	16.3	3
CHA	8.5	63.7	48.1	24.8	5
PAR	2.1	65.8	50.2	26.9	1
ROC	10.1	75.9	60.3	37	4
MON	12.8	88.7	73.1	49.8	2

675 **Table 4.** Last detected position of tagged eels depending on the release location (Fig. 1) and
 676 migration season. * indicates eels that were not considered in the model (i.e. 29 specimens that
 677 moved less than 8 km).

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Last detection	Release REN	Release PAU		Release POL			Total considered in the model
	2011/2012	2012/2013	2013/2014	2011/2012	2012/2013	2013/2014	
before DRO	7*						0
before PAU	2						2
before RIB	3	3*	1*				3
before EPE	1	4	0				5
before RAG	1	1	2	3*	1*	0*	4
before NAD	0	0	2	8*	5*	1*	2
before STA	0	0	1	4	3	1	9
before CHA	0	0	0	0	1	0	1
before PAR	0	0	0	1	0	0	1
before ROC	0	0	0	0	0	0	0
before MON	0	0	1	1	0	2	4
escapment	0	11	9	0	10	7	37
TOTAL	14	19	16	17	20	11	
Total considered in the model	7	16	15	6	14	10	68

679

680 **Table 5.** Escapement rate (number of eels that escaped a reach / number of eels that entered the
 681 reach) for each reach and each eel downstream migration season.

	2011-2012	2012-2013	2013-2014	TOTAL
REN-DRO	7/14 (50%)			7/14 (50%)
DRO-PAU	5/7 (71%)			5/7 (71%)
PAU-RIB	2/5 (40%)	16/19 (84%)	9/16 (56%)	27/40 (68%)
RIB-EPE	1/2 (50%)	9/16 (56%)	9/9 (100%)	19/27 (70%)
EPE-RAG	0/1 (0%)	8/9 (89%)	13/15 (87%)	21/25 (84%)
RAG-NAD	6/14 (43%)	24/30 (80%)	21/24 (88%)	51/68 (75%)
NAD-STA	2/6 (33%)	20/24 (83%)	19/21 (90%)	41/51 (80%)
STA-CHA	2/2 (100%)	19/21 (90%)	19/19 (100%)	40/42 (95%)
CHA-PAR	1/2 (50%)	19/20 (95%)	18/19 (95%)	38/41 (93%)
PAR-ROC	1/1 (100%)	20/20 (100%)	18/18 (100%)	39/39 (100%)
ROC-MON	0/1 (0%)	21/21 (100%)	16/19 (84%)	37/41 (90%)

682
 683

684 **Table 6.** Proportion of samples in which the environmental factors were selected as explanatory
685 variables of states transition (state 1= pause, state 2=active migration).

	State 1 to state 2	State 2 to state 1
Q	0.58	0.94
ΔQ	1.00	0.37
$Tair$	0.24	0.43
Q^2	0.31	0.80
$Tair^2$	0.28	0.46

686

687 **Table 7.** Credibility of the three behavioural states estimated by the model for eels that have
 688 travelled more than 8 km but not escaped the studied area.

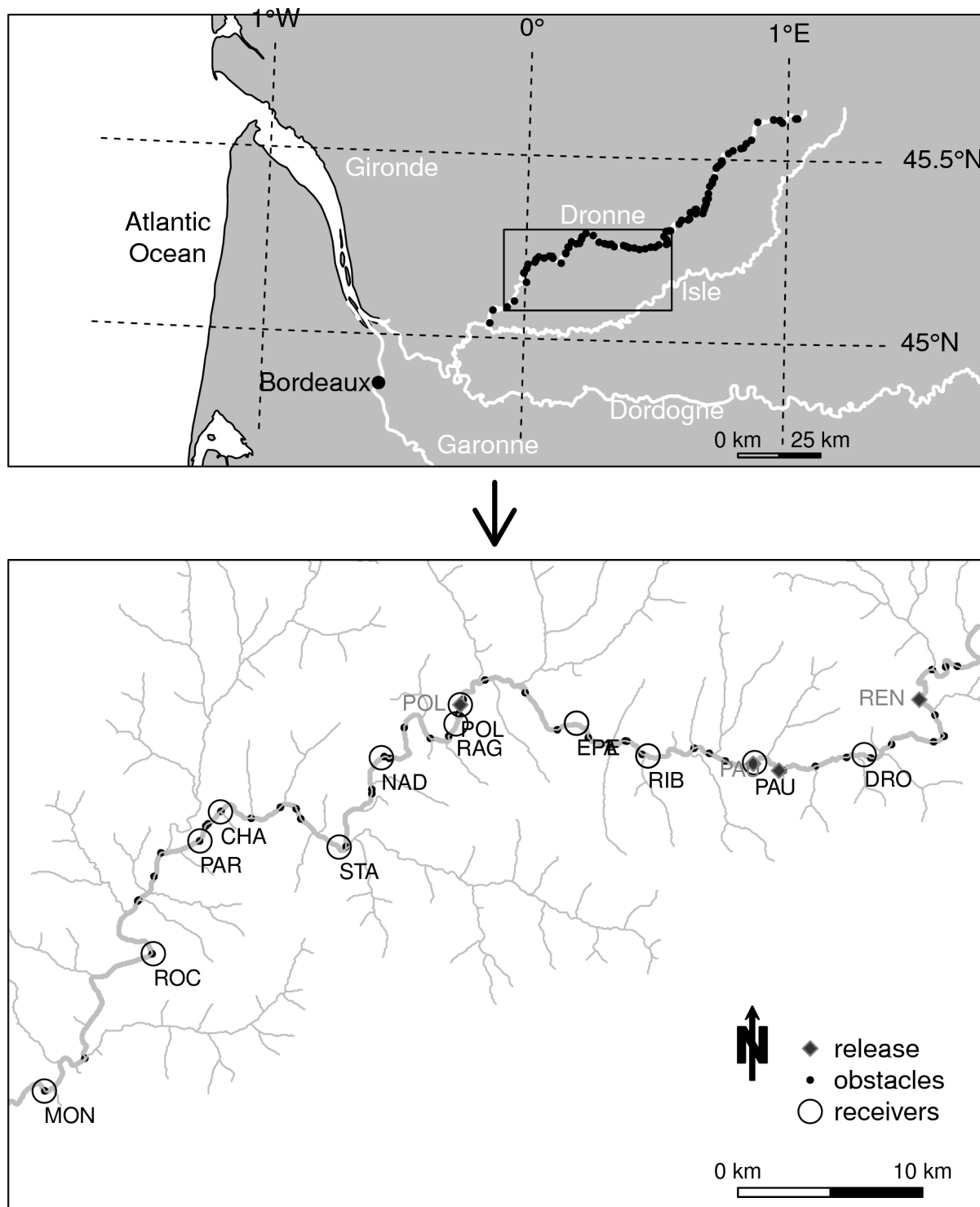
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possible causes	migration season	eel id	wait	active	stop
unsuitable conditions	2011/2012	1112_14	91%	2%	7%
	2011/2012	1112_15	74%	2%	25%
	2011/2012	1112_16	71%	1%	28%
	2011/2012	1112_22	48%	1%	51%
	2011/2012	1112_24	63%	2%	35%
	2011/2012	1112_25	52%	47%	1%
	2011/2012	1112_27	58%	3%	39%
	2011/2012	1112_28	52%	1%	47%
	2011/2012	1112_29	91%	2%	7%
	2011/2012	1112_34	44%	1%	55%
	2011/2012	1112_37	44%	1%	55%
	2011/2012	1112_38	49%	1%	50%
	2012/2013	1213_16	49%	2%	49%
	2012/2013	1213_80	48%	1%	51%
unknown	2011/2012	1112_18	28%	1%	71%
	2012/2013	1213_11	10%	1%	89%
	2012/2013	1213_13	33%	5%	63%
	2012/2013	1213_31	14%	85%	1%
	2012/2013	1213_32	0%	0%	100%
	2012/2013	1213_34	10%	0%	90%
	2012/2013	1213_35	1%	0%	99%
	2012/2013	1213_76	2%	0%	98%
	2013/2014	1314_17	36%	63%	1%
	2013/2014	1314_19	0%	0%	100%
	2013/2014	1314_20	0%	0%	100%
	2013/2014	1314_22	27%	72%	1%
	2013/2014	1314_26	6%	0%	94%
	2013/2014	1314_30	67%	3%	30%
2013/2014	1314_32	43%	3%	54%	
2013/2014	1314_33	8%	0%	92%	
2013/2014	1314_36	35%	64%	1%	

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9 Figures



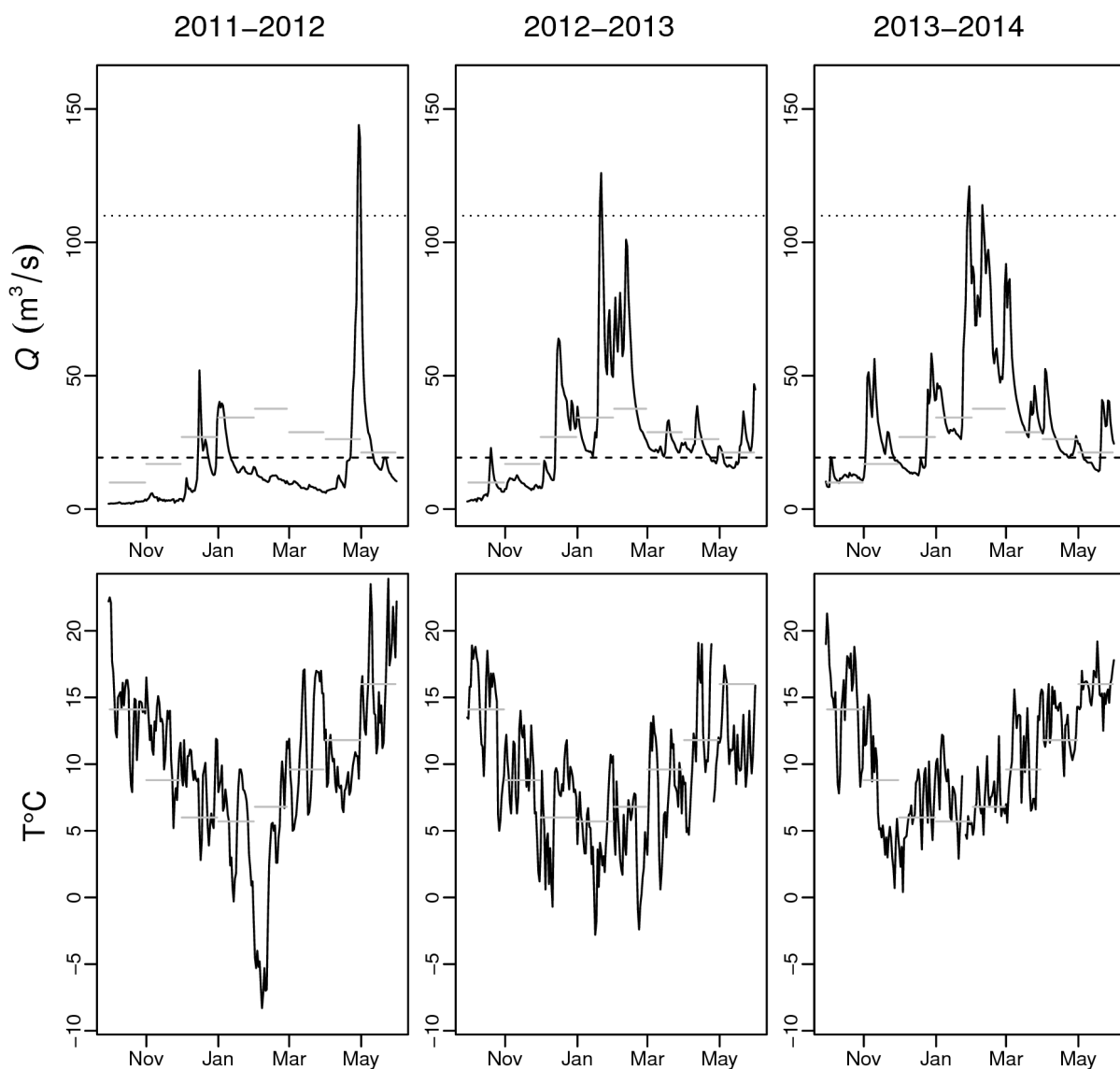
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Fig. 1. Maps of the Dronne River. Black circles represent obstacles referenced in the French ROE
database. White circles represent the fixed radio-telemetry receivers (Table 2). Diamonds represent
eels release locations (Table 2). River flow is measured at Bonnes, immediately downstream the
radio-telemetry receiver RAG. Physico-chemical parameters were monitored closed to the ATS
receivers PAU, NAD and MON. Acronyms refer to towns or sites (REN: Renamon, DRO: Maison

700

701 de la Dronne, PAU: Moulin de la Pauze, RIB : Ribérac, EPE : Epeluche, POL : Moulin de Poltot,
702 RAG : Ragot, NAD : Nadelin, STA : Saint-Aulaye, CHA : Chamberlanne, PAR : Parcou, ROC : La
703 Roche-Chalais, MON : Monfourat).

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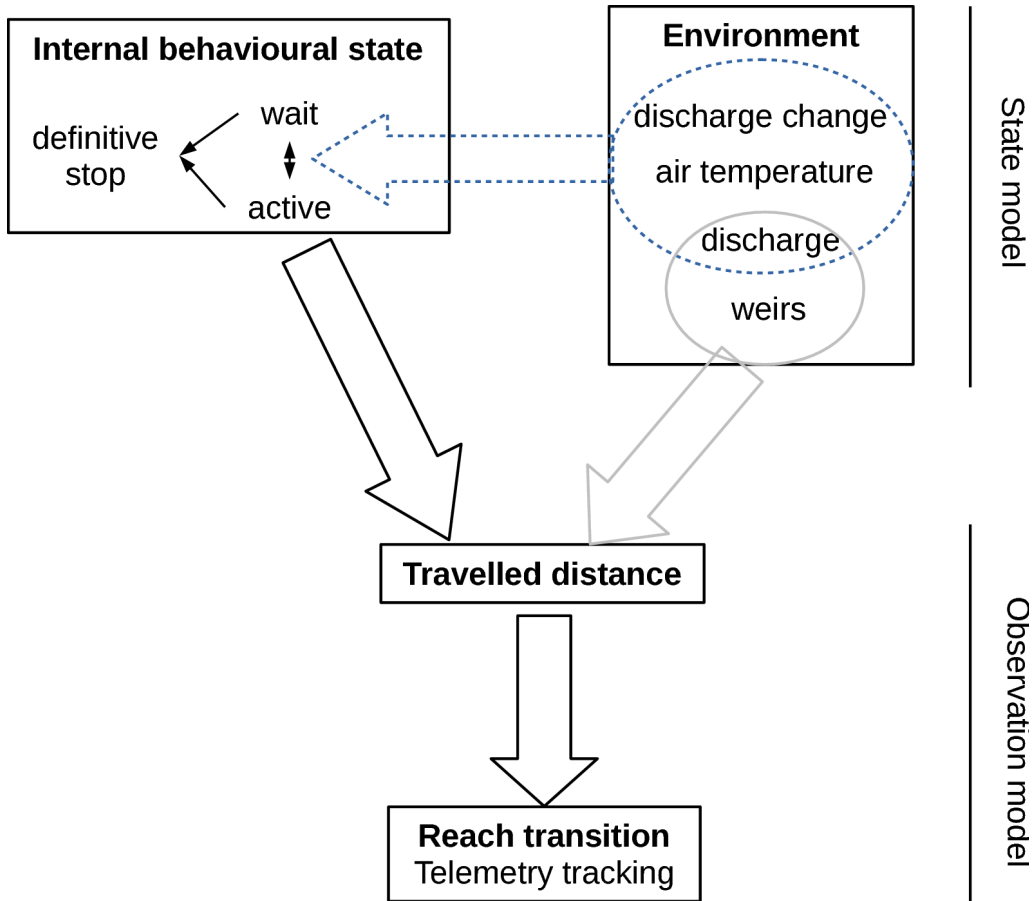


705

706 **Fig. 2.** Daily discharge (first line – solid black line) and air temperature (second line – solid black
707 line) during the three eel downstream migration seasons (in columns). Solid grey lines indicated
708 monthly means over 45 years (flow) and 30 years (air temperature monitored in Bergerac, a station
709 located 40km from our studied area which has a longer time-series). For river flow, dashed lines

710 represent the average discharge over a 45 years long period, and the dotted line represents the 2-
711 year flood.

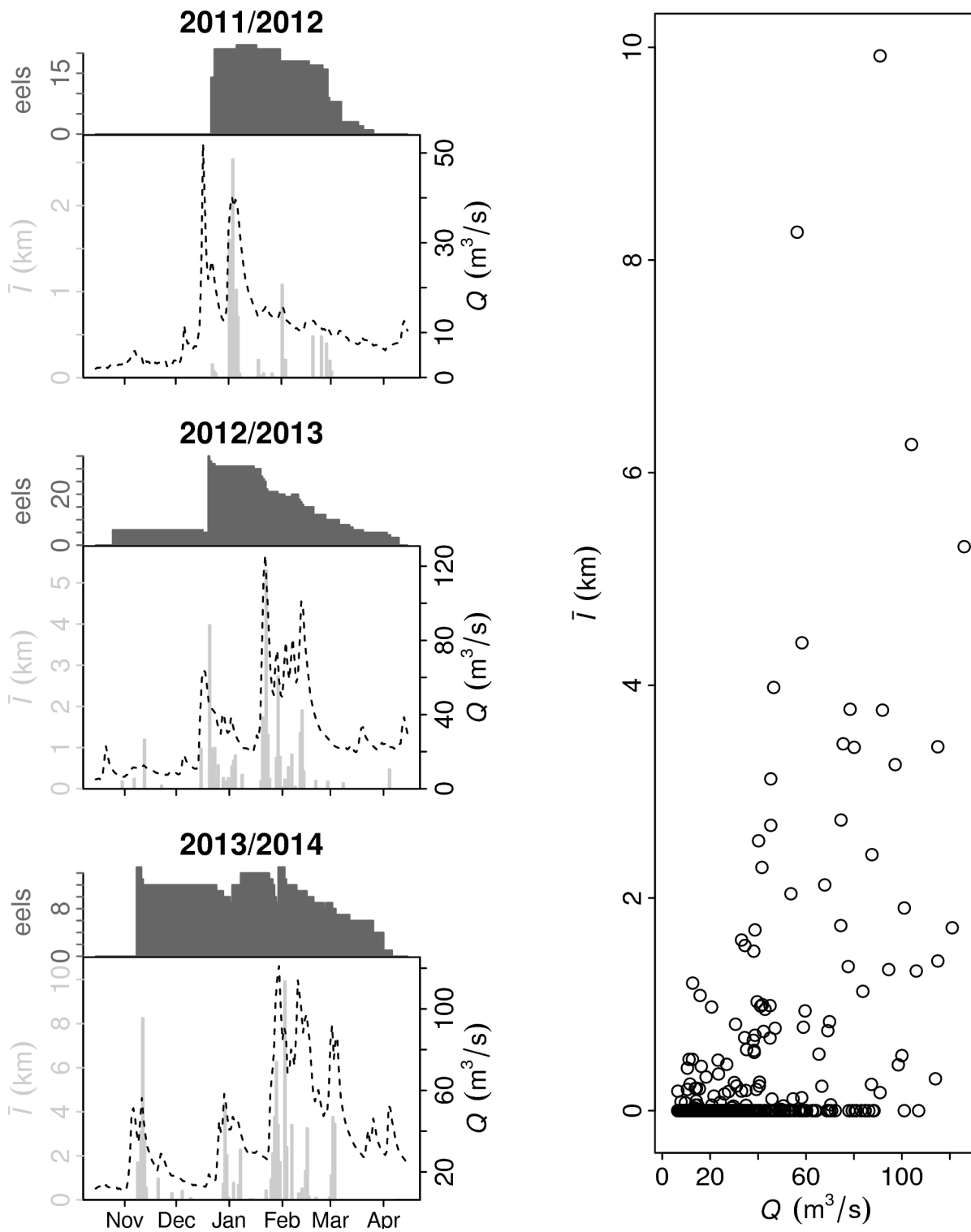
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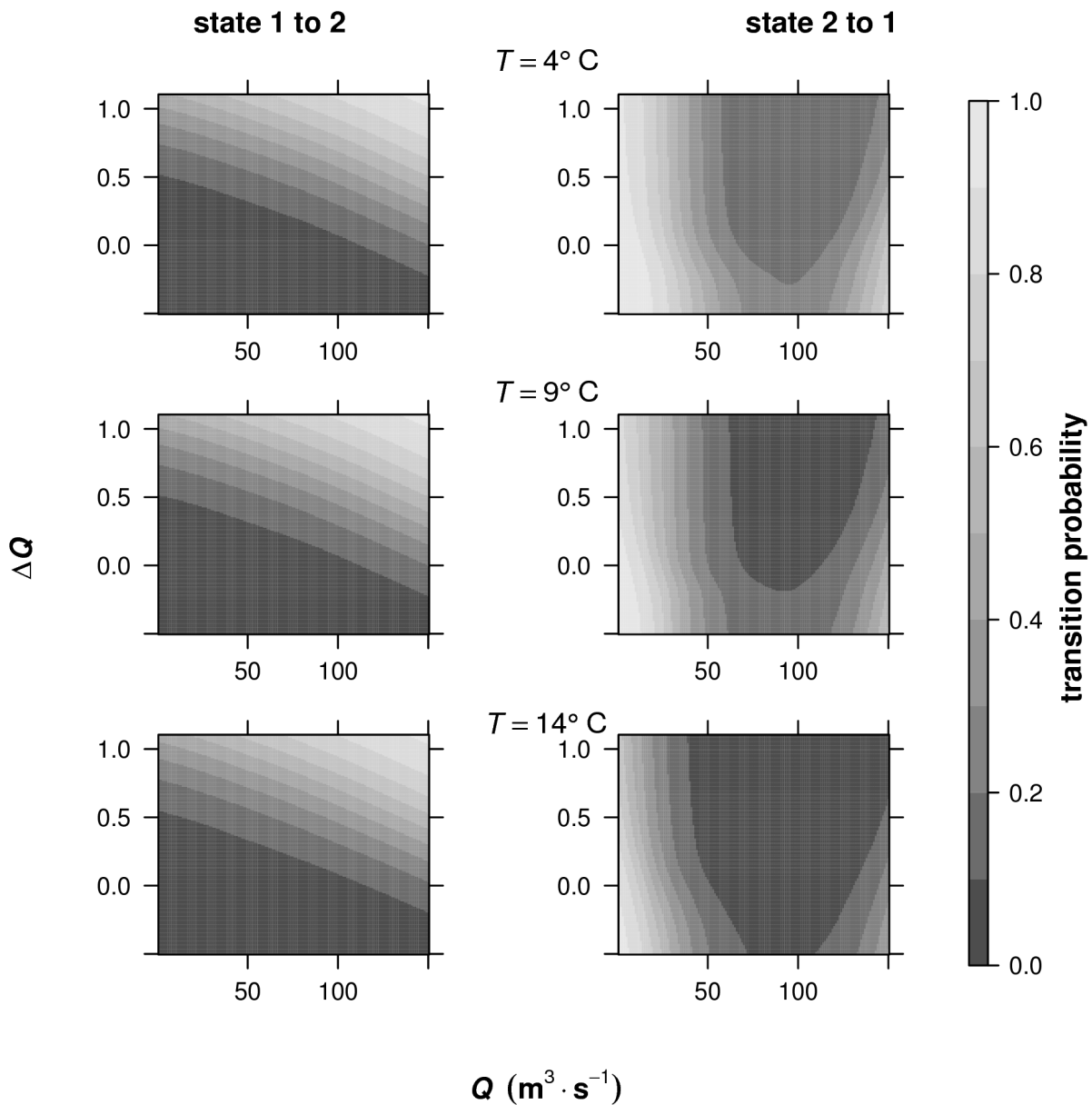
714 **Fig. 3.** Structure of the state-space model illustrating the influence of environmental conditions on
715 the internal behavioural state and their links with eels movements and resulting observations.

716



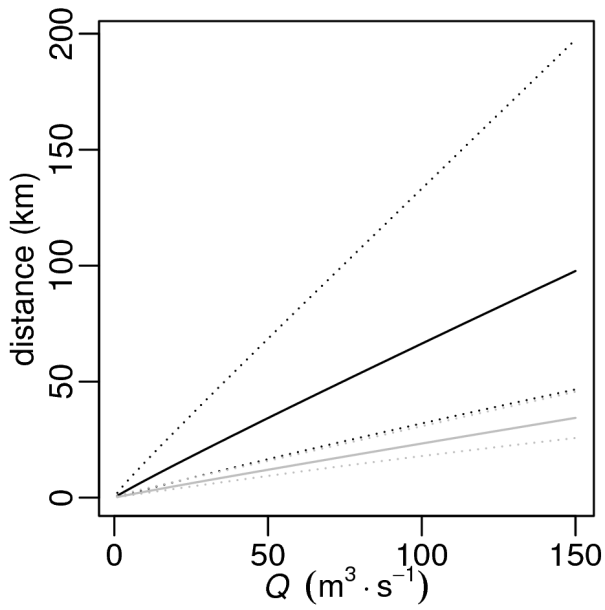
717

718 **Fig. 4.** Daily $I'(t)$ (light grey bars) for the three migration seasons (left panel) and corresponding
719 river discharge (dashed lines). Dark grey bars represent the number of tagged eels used to calculate
720 $I'(t)$. Right panel represents the daily $I'(t)$ over the 3 seasons (when at least one tagged eel
721 was available) as a function of river discharge.



722

723 **Fig. 5.** States (state 1= pause, state 2=active migration) transition probabilities predicted by the
724 model at different level of Q and ΔQ and different temperatures (4°C , first line – 9°C which
725 corresponds to the observed average, second line – 14°C , third line).

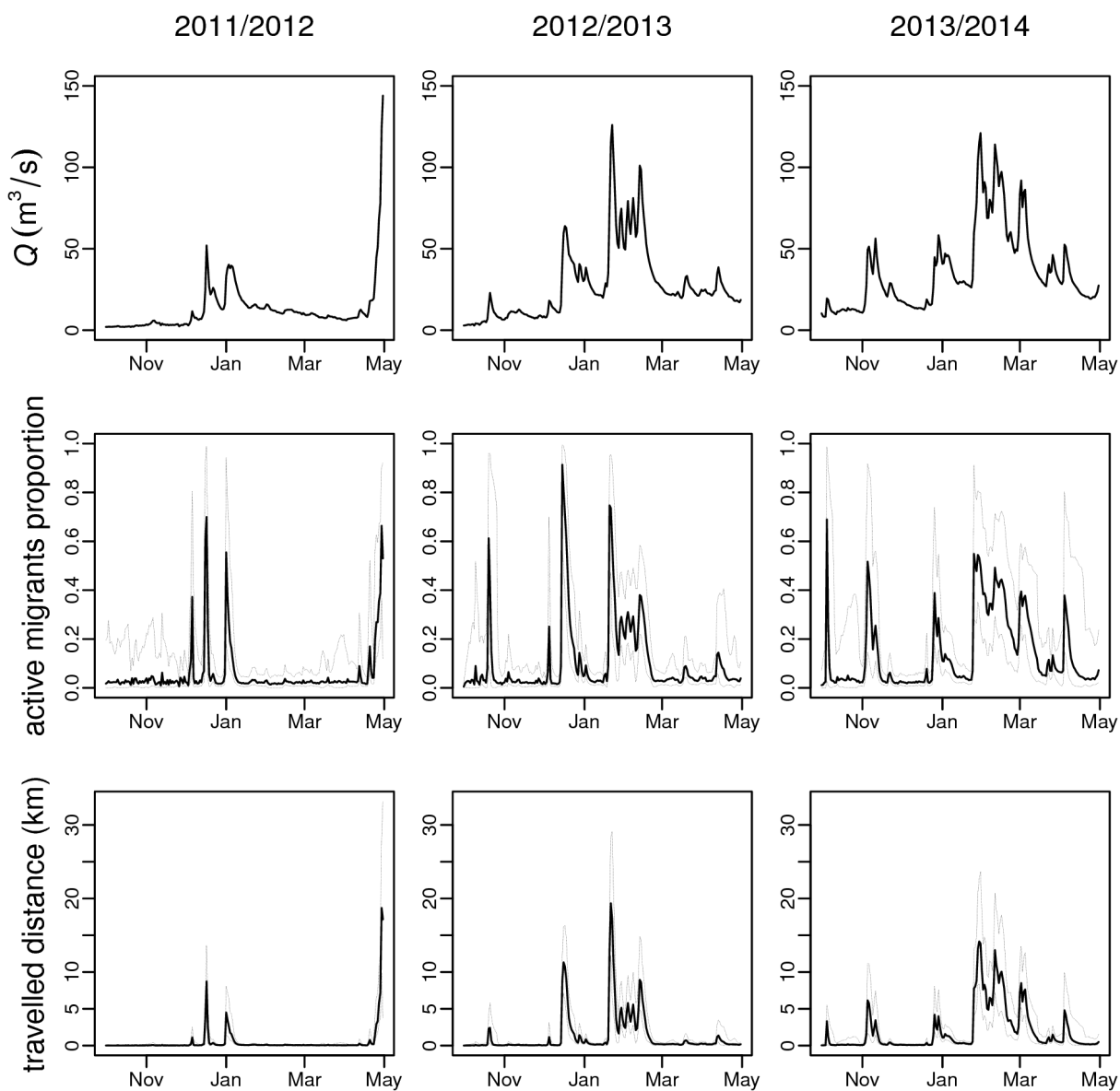


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727

728 **Fig. 6.** Theoretical distance that an active eel should travel in 24 hours without any obstacle
729 (median = solid black line, dotted black lines indicate the corresponding 95% credibility intervals)
730 and distance travelled by an eel given the weirs density in the Dronne river (median = solid grey
731 line, dotted grey line indicate the corresponding 95% credibility intervals) as estimated by the
732 model as a function of daily discharge.

733



734

735 **Fig. 7.** Average daily discharge (first line), daily proportions of active migrants (2nd line) and
736 average expected travelled distance by eels (3rd line, the product of the proportion of active migrants
737 multiplied by the predicted distance travelled by an active migrant gives an average distance
738 travelled by eels) for each migration seasons (in columns). Thin dotted lines correspond to the 95%
739 credibility intervals.

740

741

742 **Fig. 8.** Number of days (y-axis) in which the proportion of active migrants is superior to a given lev

744 axis) for each season (1st column) and number of days (y-axis) in which the expected travelled
745 distance is superior to a given level (x-axis) for each season (2nd column). Dashed lines correspond
746 to the 95% intervals and solid line to medians.