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Behaviour of endangered European eels in
proximity to a dam during downstream
migration: Novel insights using high accuracy
3D acoustic telemetry

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Running title: Behaviour of silver European eel at a dam

Abstract

1 River infrastructures such as weirs, hydropower stations or water
2 reservoirs represent obstructions to migration for diadromous fish.
3 Knowledge of accurate behaviour of fish in front of such structures is
4 required to protect migrants from hazardous areas, guide them towards
5 safe passage or adapt structure to improve the escapement. We
6 developed and made available a method to process acoustic telemetry
7 data based on Time Difference of Arrival (TDOA) analysis to accurately
8 locate tagged fish. Improved accuracy allows the detection of escape
9 routes and description of dam-crossing tactics. Sixteen tagged eels were
10 tracked with high accuracy (1–2 m) and ~ 1 location min^{-1} frequency
11 during their exploration period on reaching the dam. Two migration
12 routes (spillways and bottom compensation flow pipe) were used by 77%
13 and 23% of eels, respectively. Spillways were the preferred route, but a
14 median of 16 days were required to pass the dam versus 1.1 days via the
15 compensation pipe. A minimal water crest of 40 cm was required for
16 passage via spillways. Eels passing through the compensation pipe were
17 exclusively nocturnal, and mainly explored the bottom of the dam. Eels
18 passing through spillways explored the whole dam area by night and day,
19 and were not attracted to the compensation pipe entrance.

20 With global warming, more frequent drought periods are expected,
21 potentially leading to decreased opportunities for eels to migrate across
22 safer dams by spillways. To conserve this endangered species, dam
23 management strategies that account for expected hydrologic conditions
24 and distinct exploration behaviours are needed.

25 **Keywords:** European eel, 3D acoustic telemetry, downstream migration,
26 dam, diadromous fish

27

28 1 Introduction

29 Diadromous fish are vulnerable because they must migrate between
30 marine and freshwater habitats to reproduce (McDowall, 1988). This
31 breeding migration involves passing through narrow ecological pathways,
32 called corridors, that are being exposed to increased anthropogenic and
33 ecological pressures. The latter has led to major population declines in
34 most diadromous fishes (Limburg & Waldman, 2009). Recruitment rate
35 of the European eel *Anguilla anguilla* is currently below 10% that of the
36 maximum level recorded in the late 1970s (ICES, 2018). Consequently,
37 this species is now far outside its safe biological limits, and is considered
38 as critically endangered by the International Union for Conservation of
39 Nature (IUCN) (Jacoby & Gollock, 2014). The European Union
40 recommends actions focused on reducing commercial fishing, limiting
41 recreational fishing, adopting restocking measures, increasing watershed
42 connectivity and quality, catching and transporting silver eels, exercising
43 predator control, implementing hydroelectrical turbine shutdowns, and
44 adopting aquaculture measures. These actions were specified to reduce
45 the effects of the most significant causes of decline. Overfishing is
46 considered to be primary cause of decline, followed by mortality induced
47 by turbines and dams (Feunteun, 2002).

48 The impacts of hydropower dams have been well studied.
49 Hydroelectric complexes can cause injuries (Bruijs & Durif, 2009), direct
50 mortality (Winter, Jansen & Bruijs, 2006; Bruijs & Durif, 2009), delays in
51 the timing of migration (Behrmann-Godel & Eckmann, 2003), and can
52 inhibit downstream migration (Durif, Elie, Gosset, Rives, & Travade,
53 2003). To date, downstream passage at non-powered dams (i.e. that are
54 not equipped with turbines) have not been considered to be a
55 particularly important issue for migrating silver eels, as the passage is
56 usually considered to be safe (Besson et al., 2016). Consequently, the
57 impact of reservoirs and dams is less studied, despite high numbers

58 existing in some European regions. In particular, non-powered dams can
59 delay migration (Besson et al., 2016; Larinier, 2000; Larinier & Travade,
60 2002) and result in lower (20%) annual migration rates when compared
61 to equivalent non-obstructed rivers (Feunteun et al., 2000; Acou, 2006).
62 In such systems, the principal route for eels to migrate seaward involves
63 waiting for the overflow during flood episodes. Unfortunately, climate
64 change might have significant consequences on the availability of water
65 resources, with the frequency of overflow periods being expected to
66 decline, particularly in areas already suffering from water stress or that
67 have low groundwater (Versini, Pouget, McEnnis, Custodio, & Escaler,
68 2016). To manage this endangered species efficiently, scientists and
69 environmental managers must adapt existing measures to enhance the
70 passage of silver eels through dams under current and future hydrological
71 conditions. As a first step, it is necessary to understand how eels behave
72 in reservoirs and their migration pathways across dams.

73 In recent years, telemetry technology has been used to study the
74 behaviour of a variety of aquatic animals (including fishes, turtles, and
75 mammals) and ecosystems (including oceans, rivers, lakes, and estuaries)
76 (Hussey et al., 2015). To study large-scale migrations (spanning several
77 hundreds or thousands of kilometres), the accuracy needed to locate
78 individuals below a hectometre is generally not an issue (e.g. Renkawitz,
79 Sheehan, & Goulette, 2012; Rechisky et al., 2013; Beguer-Pon et al.,
80 2014; Righton et al., 2016). However, greater accuracy (approx. 1 m) is
81 required to elucidate patterns in fine-scale behaviour (Løkkeborg, Fernö,
82 & Jørgensen, 2002; Rillahan, Chambers, Howell, & Watson, 2009), home
83 range movements, and habitat selection (Andrews et al., 2011; Coates,
84 Hovel, Butler, Klimley, & Morgan, 2013; Espinoza, Farrugia, & Lowe,
85 2011), and reproduction (Dulau et al., 2017).

86 Such fine-scale accuracy is required to study the behaviour of eels
87 so that effective management measures can be implemented. Accurate

88 information on movement is essential to optimize the design and
89 construction of eel passageways and to verify their efficiency (Brown,
90 Haro, & Boubée, 2007). Currently, two main methods are available and
91 widely used to track species in aquatic systems; namely, satellite and
92 acoustic tracking (Hussey et al., 2015). Although satellite tracking
93 represents the most accurate method of determining location, this
94 technology requires the regular emersion of transmitters so that they can
95 communicate with satellites, making it only suitable for species that
96 remain at, or come regularly to, the water surface (e.g. aquatic
97 mammals, birds, turtles, and some shark species). In comparison,
98 acoustic telemetry has rapidly become the most suitable technology for
99 monitoring fishes (Hussey et al., 2015).

100 Unfortunately, because sound in water propagates uniformly in all
101 directions, the locations recorded using a single fixed receiver
102 encompass a large area (up to several hundreds of meters) around the
103 receiver. The size of this area depends on factors related to: (1) the
104 characteristics of transmitters (size and type of acoustic transmitter), (2)
105 the environment (e.g. depth, salinity, current, suspended matter, and
106 substrate), and (3) anthropogenic activities that generate noise (e.g.
107 boat traffic and turbines) (Simpfendorfer, Heupel, & Collins, 2008;
108 Gjelland & Hedger, 2013; Kessel et al., 2014; Hayden et al., 2016;
109 Huveneers et al., 2016; Reubens et al., 2018). Thus, it is difficult to
110 determine the precise location of an acoustic-tagged animal, although
111 several methods have been designed and developed to improve this
112 accuracy. For example, Simpfendorfer, Heupel, and Hueter (2002)
113 developed a method using presence data from multiple receivers to
114 obtain position estimates (short-term centre of activity) based on the
115 weighted means of the number of signal receptions at each receiver
116 during a specified time period. However, this method can only determine
117 the centre of activity within a given time period, rather than a precise

118 estimate of location at a single point in time. To obtain precise location
119 estimates at a single time point, numerous companies offer accurate
120 positioning systems with metre or sub-metre resolution using acoustic
121 telemetry. Some of these methods require communication from
122 receivers to reception units with acoustic cables, which is not always
123 feasible.

124 To position tagged aquatic animals accurately without links to
125 receivers, analysis of time difference of arrival (TDOA) has been
126 developed by telemetry manufacturers. Unfortunately, scientific studies
127 using this methodology have not provided sufficient details of the
128 technical methods and calculations to enable reported experiments to
129 be reproduced (see for instance Espinoza et al., 2011; Roy et al., 2014;
130 Guzzo et al., 2018). Moreover, until recently, access to this methodology
131 was via a paid service or software, not via open access services (Baktoft,
132 Gjelland, Økland, & Thygesen, 2017).

133 Thus, the current study proposed and described the use of a complete
134 methodology to locate tagged silver eels accurately (~1 m) using TDOA
135 within the Fremur River (north-western France). Using this method, eel
136 behaviour during downstream migration (i.e. exploratory behaviour and
137 avoidance behaviour) was analysed. It is important to understand how
138 silver eels behave and explore their environment in the context of
139 blocked migration. Therefore, the method described here is expected to
140 help advance our understanding of how, how many, where, and when
141 silver eels cross dams. Based on our results, we provide
142 recommendations for conservation managers to facilitate the passage of
143 silver eels blocked upstream of dams by defining optimal escapement
144 routes.

145 **2 Methods**

146 **2.1 Study site**

147 The *Bois-Joli* dam is located on the Frémur River, north-western France,
148 and was built in 1992. It is a 150 m long and 15 m high dam that creates
149 a reservoir of 0.4 km², with a maximum volume of 3 000 000 m³. The
150 water level upstream of the dam is monitored and recorded every 10 min.
151 However, this dam is not equipped for downstream eel migration.
152 Downstream migration is possible over the six spillways of the dam (each
153 6.8 m in width) during overflows (Legault et al., 2003; Acou et al., 2008),
154 or through a compensation flow pipe (Figure 1). One of these spillways
155 (spillway 1) is located 10 cm below the other five spillways. The other
156 five spillways are all at the same level (Figure 2). A 40 cm diameter
157 compensation pipe is present to ensure a minimum instream flow in the
158 Frémur River (Figure 1), which is consistent year-round. The
159 compensation pipe is also used for freshwater intake in a pumping station
160 supplying a water treatment plant. The compensation pipe has five
161 different entrances at five different depths (Figure 2), which are located
162 in a concrete tower at the middle of the dam. Although the pipe has
163 been fitted with a fine metallic grid (20 mm mesh size) to prevent eel
164 passage and mortality, this grid has proved to be inefficient, as numerous
165 eels have been found dead in the filter located beyond the grid.

166 2.2 Silver eel collection and tagging method

167 Silver eels were captured using fyke nets in the fall of 2017 (October-
168 december). The fyke nets were positioned in the upstream part of the
169 Bois-Joli Reservoir, and were checked three times a week. Sixteen silver
170 eels were selected using classical external characteristics (Acou et al.,
171 2005), anaesthetised with benzocaine (150 mg l⁻¹), and tagged with
172 acoustic transmitters (ID-LP9L-69 kHz Thelma Biotel, Trondheim, Norway,
173 9 mm diameter, 24 mm long, 4 g in air, transmission interval 30-90
174 seconds), respecting the 2% transmitter/body mass ratio (Winter, 1996).
175 Incisions were closed with absorbable sterile sutures (3-0 ETHICON

176 MONOCRYL™, Ethicon Ltd, Livingston, UK) and disinfected with
177 bactericidal antiseptic (0.05% chlorhexidine). After a recovery period in
178 a large aerated tank and when all anaesthetic effects had dispersed (full
179 recovery of locomotor movements, usually under 1h), the fish were
180 released 100 m downstream of the fishing site, which was located about
181 3 km upstream of the dam. Previous survival tests with eels from the
182 same study site that were tagged with the same method showed no death
183 or injury (Trancart et al., 2017); thus, based on the endangered status
184 of European eels and the very low number of silver eels in Fremur River,
185 we chose not to perform survival test for this experiment. The
186 institutional and national guides for the care and use of laboratory
187 animals were followed. Tagging was conducted under the authority of
188 the “certificat capacitaire pour l’expérimentation animale”
189 (experimental animal certificate) no. A29-039-1 of the Museum National
190 d’Histoire Naturelle, Dinard

191 **2.3 Acoustic array**

192 Twenty-three acoustic receivers (Thelma Biotel TBR 700) were deployed
193 in three parallel lines along the front of the *Bois-Joli* Dam (Figure 3). The
194 Thelma Biotel receivers provide time of reception in milliseconds, which
195 is required for the positioning determination method. These receivers
196 were located at 20 m intervals from each other, covering a 150 x 50 m
197 area. The accurate horizontal location (latitude, longitude) of each
198 receiver was determined to the nearest centimetre using a theodolite.
199 The hydrophone depth (Z, vertical position) was measured to the nearest
200 centimetre using a tape measure. To ensure time synchronization
201 between all receivers, a synchronization transmitter (ST) was placed in
202 the reservoir (using the precise theodolite determined latitude,
203 longitude, and depth to the nearest centimetre) (Figure 3). Each receiver

204 had an internal temperature sensor that recorded the temperature every
205 10 min, enabling us to determine the speed of sound in water accurately.

206 To monitor whether the departure of tagged eels from the study area
207 was up- or downstream, additional receivers were placed downstream of
208 the dam and upstream the reservoir (Figure 3).

209 **2.4 Location estimation in the reservoir**

210 **Horizontal positioning determination method**

211 The horizontal positioning determination method is based on Time
212 Difference Of Arrival (TDOA). In this method, the location of an acoustic
213 transmitter is calculated from the relative time of acoustic emission
214 received by different hydrophones surrounding the transmitter and
215 according to their relative distance. Time registration by the receivers
216 uses an internal clock based on crystal oscillators. The frequency of
217 these oscillators varies slightly between receivers, inducing temporal
218 drift specific to each receiver. Consequently, the accuracy of an acoustic
219 transmitter location depends both on the accuracy of the time of signal
220 reception by receivers (to the nearest millisecond) and the accuracy of
221 the location of the hydrophones themselves (to the nearest centimetre).
222 This issue required relatively precise synchronization of the different
223 receivers (to the nearest millisecond), and a precise knowledge of their
224 locations (to the nearest centimetre). The method used in the present
225 study involved three steps: (1) database synchronisation and time drift
226 removal, (2) multilateration, and (3) filtering of aberrant results (i.e.
227 positions located out of the study site range), if required. All of the
228 treatments (synchronization, multilateration, and filtering) were
229 performed using R 3.5.0 software (R Development Core Team, 2008).
230 Details on the methods used are provided in Annex 1 to allow the free
231 method to be reproduced by the whole scientific community.

232 **Vertical positioning determination method**

233 To determine vertical positioning (depth), we used the internal pressure
234 sensor of the Thelma Biotel acoustic depth transmitters (D-LP9).
235 Preliminary tests in an artificial basin (10 x 10 x 10 m) showed the perfect
236 accuracy (to the nearest 10 cm) of these sensors, for three test depths
237 (2, 5, and 8 m) over a 7-day period.

238 **Evaluation of the accuracy for horizontal location**
239 **determination**

240 To validate the method presented here, two stationary reference
241 transmitters were placed at known X-Y-Z positions (to the nearest cm)
242 in the reservoir, with a 10 min mean interval between two successive
243 signals throughout the study period. The first test transmitter was
244 located close to the spillways (Figure 3), just in front of the possible
245 routes to exit the reservoir. A second test transmitter was placed close
246 to the shore (Figure 3). The second test transmitter remained in the
247 water throughout the course of the experiment, whereas, due to drought
248 conditions, neighbouring receivers were out of the water during the first
249 part of the experiment in the autumn of 2017. For this test transmitter,
250 the validation period was limited to the period when neighbouring
251 receivers were submerged in the water. The distance between the real
252 position and the calculated positions was calculated to evaluate the
253 accuracy of the method (in metres).

254 **2.5 Data analysis**

255 **2.5.1. Estimation of escapement**

256 Individual escapement was estimated using the positioning method
257 previously described and confirmed by the detection of a transmitter by
258 the receiver immediately downstream of the dam. Escapement rate was

259 defined as the number of silver eels detected below the Bois-Joli Dam
260 against the total number of marked silver eel in the Bois-Joli Reservoir.
261

262 **2.5.2. Estimation of migration routes to pass over** 263 **the dam**

264 Method 1: Observed route using a compensation pipe survey and
265 one acoustic receiver

266 The exit of the compensation pipe was equipped with a net (6.5 m long,
267 0.5 m large, 2 mm mesh size) to control silver eel escapement. Over the
268 study period, the net was inspected approximately once every three days.
269 All captured eels were inspected for the presence of a tag and signs of
270 trauma. All eels that were caught alive were released downstream of the
271 dam. The compensation pipe operates throughout the year and is
272 protected by a grid, but this grid is not fully effective, as silver eels were
273 caught in net.

274 We considered that a silver eel had succeeded in passing the *Bois-*
275 *Joli* dam via the compensation pipe if it was observed in the net. We
276 considered that a silver eel had succeeded in passing this dam via the
277 spillway if it was not observed in the net and it was recorded on the
278 acoustic receiver just downstream of the dam.

279

280 Method 2: Estimated route using the TDOA method

281 A second method was employed to estimate the most probable escape
282 route from the *Bois-Joli* Reservoir (i.e. compensation pipe versus
283 spillways). For each eel, the 10 last estimated positions, given by the
284 previous method (see 3.4 Horizontal positioning determination method),
285 were retained to trace the most probable route used. The most probable

286 exit route was attributed to a given individual, only if the route and the
287 final estimated location clearly indicated one of the two possible ways
288 of escapement. With this method, the most probable date/time of the
289 passage can be inferred, and was used to obtain the water level in front
290 of the dam and the height of the water crest (when overflowing) during
291 the passage of the eels.

292

293 **2.5.3. Exploratory behaviour and efficiency in** 294 **passing**

295 To evaluate the efficiency of eels in passing the dam, four metrics
296 were calculated for each eel:

- 297 i. The time to pass (TTP, in days), which was defined as the time
298 difference between the first detection recorded in close proximity
299 to the upstream part of the dam (<10 m) and the observed passage
300 recorded on the receiver downstream of the dam;
- 301 ii. The time to pass after overflow (TTP-O, in days), which was
302 defined as the time difference between the first detection
303 recorded in close proximity to the dam (<10 m) once the overflow
304 period had begun and the observed passage recorded on the
305 receiver downstream of the dam;
- 306 iii. The total number of detections (TND), which was defined as all
307 records in close proximity to the dam (<10 m) over the entire
308 period of presence;
- 309 iv. The number of detections close to the dam (<10 m) per day
310 (TND/d).

311

312 To identify potentially different exploration tactics, another metric was
313 used. For this metric, we only considered presence close to the dam (<10
314 m). The period of presence close to the dam was defined as the period

315 of the day when an eel was observed close to the dam (<10 m). This
316 period was analysed. Two periods were defined according the natural
317 luminosity occurring at the study site during the experiment: night
318 (17:00–07:59) and the day (08:00–16:59 PM).

319 Finally, to characterise spatial patterns in exploration, the locations
320 of the individuals were represented from two perspectives: above and
321 frontal. In the view from above, a 30 × 20 cells raster (resolution = 0.1
322 and 0.3 cell m⁻¹ in x and y axes, respectively) was created and
323 superposed to the aerial view of all locations for a given eel. The value
324 of each cell corresponded to the number of detections observed in this
325 cell. In the frontal view facing the dam, a 30 × 15 cells raster (resolution
326 = 0.1 and 1 cell m⁻¹ in the x and y axes, respectively) was used. Eel
327 locations were projected according to an orthogonal projection. The
328 value of each cell corresponded to the number of detections observed in
329 this cell. In both views, percentages were computed afterwards to
330 improve readability.

331

332 **3 Results**

333 **3.1 Validation of estimated horizontal locations using** 334 **test transmitters**

335 The median errors of location obtained from the stationary reference
336 transmitters located at fixed positions were 1.14 and 1.64 m, and ranged
337 from 0.07 to 36.76 m (n = 3413 locations over 169 d) (Table 1). The
338 cumulative frequencies in the distribution of the error locations of the
339 two reference transmitters indicated that the positioning error was less
340 than 2 m for 80% and 70% of locations for stationary reference
341 transmitter 1 and 2, respectively, and less than 5 m for 100% and 93% of

342 locations for transmitters 1 and 2, respectively (Figure 4). For both
343 transmitters, inframetric accuracy was reached for 30% of locations.

344 **3.2 Estimation of the most probable routes of exit**

345 Based on the first method, 13 silver eels were observed downstream the
346 *Bois-Joli* Dam, and only three were captured in the net, suggesting that
347 the other ten passed over the dam via the spillways.

348 Based on the second method, the principal migration route was
349 the spillways, because 10 eels used it. Nine eels crossed the dam by the
350 first spillway (Figure 5). The other three eels used the compensation pipe
351 (Figure 6). The migration pathways used by tagged silver eels determined
352 from the two methods (surveys and TDOA alone) were identical (Table
353 2). This method allowed us to elucidate the probable time and date of
354 the passage, and the water level in front of the dam. The water crest
355 height above spillway #1 ranged from 40 cm to 53 cm (table 2) during eel
356 passage. These heights were rapidly reached after the onset of the
357 overflow (48 hours at 40 cm level).

358

359 **3.3 Efficiency in crossing the dam**

360 The Time To Pass (TTP) the *Bois-Joli* Dam ranged from 0.29 to 65 d (Table
361 3 and Fig. 7). The median time for eels to pass through the compensation
362 pipe was shorter (1.1 d) than those passed through the spillways (18.53
363 d). When considering the date and time when the dam began to overflow
364 (15 December, at 15:00), the time to pass (TTP-O) the spillways was
365 16.53 days (Table 3 and Fig. 7). Eels that passed through the
366 compensation pipe had the highest number of detections close to the
367 dam per day (TND/d). Yet, the Total Number of Detections (TND) close
368 to the dam was similar for both groups (Table 3 and Fig. 7).

369 **3.4 Behaviours during escape attempts**

370 **Behavioural differences between eels passing through the**
371 **spillways and eels passing through the compensation pipe**

372 A very strong behavioural difference was observed between silver eels
373 that used spillways versus the compensation pipe. In the final period of
374 movement (just before passing), those passing through the spillways had
375 a higher swimming speed, beginning their final displacement further
376 from the dam (Figure 5). In comparison, those passing through the
377 compensation pipe had lower swimming speeds and visited the entrance
378 for a long duration (Figure 6). Although the number of eels that passed
379 through the compensation pipe was too low (three) to allow for
380 statistical comparison, their body weights were equivalent to those of
381 eels that passed through the spillways (554.1 ± 193.56 g and 515 ± 225.3
382 g for spillways and compensation pipe, respectively).

383 Eels that passed through the compensation pipe only explored the
384 waterways at night. In comparison, eels that used the spillways explored
385 the dam during day for 10–40% of records. A strong difference was also
386 documented for the locations of detections close to the dam (<10 m)
387 between eels that passed through the compensation pipe and eels that
388 passed through spillways. The first ones were mainly located close to the
389 compensation pipe. The right side of the dam was also explored, while
390 the left side was explored less (Figure 8).

391 In contrast, the areas close to the compensation pipe were not
392 explored more than other areas by eels that passed through the spillways.
393 Most detections were recorded the right side, close to the bottom. No
394 clear difference was observed between the periods before (Figure 9,
395 upper slide) and during overflow (Figure 9 lower slide). During overflow,
396 the range of explored areas seemed to be higher than before overflow.
397 However, this phenomenon was just an artefact linked to the number of
398 detections during both periods (1880 and 3347 detections for periods
399 before and during overflowing, respectively).

400

401 **4 Discussion**

402 This study demonstrate the behaviour of endangered silver European eel
403 attempting to cross a dam using high accuracy 3D acoustic telemetry
404 based on Time Difference Of Arrival analysis. This method is described
405 in the annex so it may be reproduced without the need for payment of
406 software and services. The method developed here produced sufficiently
407 accurate location (<2 m), allowing the precise description of eel
408 behaviour. Eels used two escape routes, with some behavioural
409 differences being detected between these two groups.

410

411 **4.1 Accuracy of the location determination method**

412 The method presented in the current study showed a median location
413 error of approximately 1.14 m for test transmitter #1 and approximately
414 1.64 m for test transmitter #2. The first test transmitter was located
415 very close to the potential exit routes for eels. For this test transmitter,
416 the location accuracy was constant throughout the study period
417 (12/09/17–28/02/18). The second test transmitter was placed close (<10
418 m) to the shore. At the beginning of the experiment, the receivers close
419 to this transmitter were out of the water and, therefore, not operational
420 until the water level had risen and submerged the receivers. Given that
421 Espinoza et al. (2011) showed the error was significantly lower inside
422 than outside an array, errors were only calculated for the period (after
423 15th December), when all the receivers were submerged.

424 The accuracy in the present study was better than, or equivalent
425 to, that reported in comparable studies using commercial positioning
426 systems. For example, Espinoza et al. (2011) showed that the mean
427 positional accuracy of Vemco Positioning System (VPS) estimates from a

428 stationary transmitter deployed at several locations within the receiver
429 array was 2.64 ± 2.32 m. In comparison, Guzzo et al. (2018) found that
430 the accuracy estimates of HR-VPS positions for all stationary trials was
431 5.6 m. Biesinger et al. (2013) demonstrated a positional accuracy of
432 approximately 2 m. This improved accuracy could be explained by: (i)
433 the positioning of the receiver to the nearest centimetre using a
434 theodolite for x and y coordinates, and using a decametre for z, and (ii)
435 the real-time measurement of water temperature to continuously
436 correct the speed of sound in water at the exact moment of acoustic
437 signal reception. This was possible using the intern thermic sensor
438 included in Thelma Biotel receivers.

439 A novel positioning method has recently been presented, involving
440 Maximum Likelihood analysis of a state-space model applied directly to
441 time of arrival (Baktoft et al., 2017). This method is free, unlike vendor-
442 supplied solutions, and it is transparent and accurate. However, the
443 accuracy of the location determination method presented and used in
444 the present study was sufficiently good for the fine-scale analysis of
445 movements, as required in the present context of silver eel downstream
446 migration.

447

448 4.2 A paradox in the choice of escape routes

449 The two methods used produced the same results (three eels by
450 compensation pipe, 10 eels by spillways). However, the second method
451 using TDOA provided a greater level of accuracy. The second method
452 showed that, for nine eels, the most probable route out of the six
453 spillways was the first one (with a lower overflow crest). For one eel,
454 the last detection was too far from the spillway to determine the
455 spillway used.

456 Seventy seven percent of individuals used spillways to successfully
457 cross the *Bois-Joli* dam. When both routes were available at the same

458 time (i.e. during the overflow period), no eel passed through the
459 compensation pipe. Although spillways were the principal route used, it
460 is still not clear if it is a beneficial one. For instance, the downstream
461 movement of eels predominantly occurs close to the river bed (Brown &
462 Castro-Santos, 2009; Gosset, Travade, Durif, Rives, & Elie, 2005),
463 therefore eels may prefer bottom fishways over surface ones. However,
464 the compensation pipe might induce strong rejection, resulting in most
465 eels using a surface route (spillway). The limited diameter of the intake
466 pipe is highly restrictive, accelerating flow (Legault, Acou, Guillouët, &
467 Feunteun, 2003), which might also deter eels. Finally Piper et al. (2015)
468 observed that eels tend to move rapidly back upstream when exposed to
469 high velocity gradients downstream. Although the grid covering the
470 compensation pipe was not fully effective at preventing eels from
471 entering, visual inspection is required to evaluate its impact on eel
472 migration.

473 From when the overflow started operating, the delay in eels using
474 the spillway was quite long, ranging from 3 to 22 days. In comparison,
475 the delay in using the compensation pipe was shorter (maximum 2 days),
476 but was less used. Thus, a paradox was generated between a “slow”
477 principal route and a “fast” incidental one. Spillways also probably
478 induced a form of repulsion, which could be linked to several factors,
479 including the water current speed and their positioning (surface). The
480 depth of water passing over the crest could be another factor slowing
481 their use, because all tagged eels only used the spillways when the water
482 crest height exceeded 40 cm, which was a minimum of 48 h after the
483 onset of the overflow period.

484 Eels that passed through the compensation pipe exhibited a long
485 final period of exploration (time spent within 10 m of the dam), slow
486 movements before passing, nocturnal activity, and narrow exploration
487 areas located close to the compensation pipe, at around 6–7 m depth

488 (i.e. depth of the pipe mouth). In comparison, eels that passed through
489 the spillways showed a short final period of exploration, fast movement
490 before passing, were active both day and night, and explored large areas.

491 Even if the total time to pass (time difference between the first
492 detection at the front of the dam and effective passage) was shorter for
493 eels that passed through the compensation pipe, their final time of
494 exploration was similar to that of eels that passed via spillways. Eels
495 passing through the compensation pipe were faster, but not more
496 efficient, since they exhibited more exploratory behaviour. Finally,
497 differences in depth use by eels was detected. Eels that passed through
498 the spillways preferentially explored surface areas. This phenomenon
499 might be linked to individual differences in the perception of the
500 environment and migration cues.

501

502 **4.3 Behaviour during escape attempts**

503 Very few studies have analysed the behaviour of eels in front of dams.
504 Comparative studies have mostly been conducted at hydroelectric
505 project intakes, not reservoirs, as in the present study. For instance,
506 Brown, Haro, and Boubée (2007) conducted a 3D-telemetry experiment
507 to track 21 silver eels that encountered a hydroelectric power station
508 during the downstream migration. Brown et al. (2007) showed that
509 longfin eels (*A. dieffenbachia*) and shortfin eels (*A. australis*) primarily
510 migrated at night, and that most eels entered the reservoir in the mid-
511 channel section. Residence time in the reservoir ranged from several
512 minutes to 10 hours. Several eels swam back upstream before returning
513 and continuing to search for a route through. The only downstream
514 passage outlets in the reservoir were the turbine intakes. Two types of
515 behavioural responses were observed when eels encountered the power
516 station intake trash racks, with these responses being species-specific.

517 Eels either passed directly through the trash racks or intakes on their
518 first encounter, or they immediately rejected entrainment and began
519 searching for an alternative passage route in the forebay or upstream of
520 the detection zone. Shortfin eels were the only species that exhibited
521 this behaviour. Longfin eels made a significantly greater number of
522 attempts to pass downstream via the turbines, which corresponded with
523 significantly longer residence times in the reservoir than shortfin eels,
524 possibly searching for alternate passage locations.

525 Twenty American silver eels (*A. rostrata*) were tracked using the
526 same technology (HTI©) in the Connecticut River (Massachusetts, USA)
527 (Brown & Castro-Santos, 2009). Tracked eels were detected at all depths,
528 but mostly occurred near the bottom, with occasional vertical
529 movements. This behaviour was interpreted as downstream searching
530 behaviour. A large number of eels was detected re-entering the acoustic
531 array on multiple dates before passing the dam, with many passing
532 through the dam via the turbines.

533 In another study, nine European eels were tagged using acoustic
534 transmitters (Sonotronics ©) in the Mosel River (Germany) (Behrmann-
535 Godel & Eckmann, 2003). When migrating eels arrived at the dam, they
536 either immediately passed through the turbines or remained upstream
537 of the powerhouse for up to 8 d. During this period, they exhibited a
538 repeated behaviour: approaching the trash rack, sprinting upstream, and
539 finally passing through the turbines. This phenomenon was also clearly
540 present in our study. The lag between two successive transmissions was
541 approximately 60 seconds, suggesting that the number of detections
542 close to the dam could be used as a proxy of the time spent in the area
543 closest to the dam (<10 m). The strong difference between the time
544 spent close to the dam and the total time to pass suggests repeated entry
545 to the area in close proximity to the dam. Moreover, the detailed analysis
546 of eel trajectories before passing indicated repeated movement from the

547 mouth to the reservoir, and following the right-hand shore of the basin,
548 until they finally escaped via the spillways.

549 The movement patterns detected close to hydroelectric intakes
550 from the aforementioned studies were similar to those documented by
551 the present study, including repeated behaviour, bottom prospecting,
552 occasional vertical movement, nocturnal activity, and repulsion. Thus,
553 equipped and non-equipped dams should be managed in the same way.

554

555 **4.4 Proposed management under global change**

556 The present study showed that the two available routes for the
557 downstream migration of silver eel are not fully suited for this purpose,
558 leading to delays in migration and repulsion from the openings. Moreover,
559 global change and expected recurrent drought periods might compromise
560 the possibility for eels to use spillways to cross dams. For instance, the
561 overflow period has been increasingly delayed each year (over the last
562 25 years of observations), with no overflow period occurring in 2018-2019.
563 If eels are not able to use spillways, the only route available is the
564 compensation pipe. This route is, however, dangerous with high rates of
565 trauma and mortality (Legault et al., 2003). Suggested solutions to
566 improve the management of eels include: (i) removing the repulsion
567 effect of both the compensation pipe and spillways, e.g. reducing the
568 water velocity and increasing the depth of spillways, and (ii) adapting
569 the spillways to severe drought periods expected in the future (e.g. with
570 mobile spillway crests). Further studies are required to design viable
571 escape routes that encompass the different behaviours observed in this
572 study and previous studies.

573

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581

582 **6 Data Availability Statement**

583 The data that support the findings of this study are available from the
584 corresponding author upon reasonable request.
585

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871
872

873 **8 Authors' Contribution Statement**

874 TT, AA, AC and EF conceived and designed the investigation. VD and TT
 875 performed the field work. TT wrote the R script and analysed the data.
 876 AA, EF and AC interpreted the data. All authors discussed the results and
 877 contributed to the final manuscript.

878

879 **9 Tables**

880 Table 1. Validation results of the estimated horizontal locations for test transmitter #1 (close
 881 to the possible exit routes) and test transmitter #2 (close to the shore)

	Test transmitter #1	Test transmitter #2
Number of estimated locations	2355	1058
Period	12 September to 28 February	12 December to 28 February
Number of aberrations (out the receiver array)	3 (0.12%)	1 (0.09%)
Median error (m)	1.14	1.64
Minimum error (m)	0.33	0.07
Maximum error (m)	18.38	36.76
75%, 90%, and 95% quantile (m)	2.00, 2.78, 3.32	2.42, 4.54, 6.41

882

883 Table 2. Determination of the migration route selected by silver eels (*Anguilla anguilla*)
 884 according to the observed migration route (first method) and estimated migration route using
 885 TDOA (second method), and estimation of the height of the water crest during passage using
 886 the second method.

Eel number	Observed migration route (first method)	Estimated migration route using TDOA (second method) + estimation of the height of the water crest during passage
#17	Spillway	Spillway / 47 cm
#18	Spillway	Spillway #1 / 44 cm
#21	Spillway	Spillway #1 / 52 cm
#22	Compensation pipe	Compensation pipe

#23	Compensation pipe	Compensation pipe
#24	Spillway	Spillway #1 / 46 cm
#25	Spillway	Spillway #1 / 43 cm
#26	Spillway	Spillway #1 / 50 cm
#27	Compensation pipe	Compensation pipe
#28	Spillway	Spillway #1 / 40 cm
#29	Spillway	Spillway #1 / 43 cm
#30	Spillway	Spillway #1 / 46 cm
#31	Spillway	Spillway #1 / 41 cm

887

888 Table 3. Statistics of migration efficiency for the 13 silver migrating eels that passed the
889 Bois-Joli Dam *via spillways (SW) or the compensation pipe (CP)*. The negative number in the
890 second column indicates passage before the overflow was operational.

	Median number of days to pass through the dam (all period)	Median number of days to pass through the dam (after overflow)	Median number of detections close to the dam (<10 m)	Median number of detections close to the dam per day
Compensation pipe	1.10	-2.40	118	106.33
Spillways	18.53	16.53	126.5	11.73

891

892

893 10 Figure Legends

894 Figure 1. Details of the study site: In the vicinity of the dam.

895 Figure 2. Details of the study site: Downstream view of the six spillways (left)
896 and compensation pipe mouths during 10-years of draining (right). Spillway 1
897 is actively spilling water in the photograph.

898 Figure 3. Location of the acoustic receivers with millisecond accuracy (green
899 points) used to obtain accurate positions, and those without millisecond
900 accuracy (red points) used to monitor the downstream or upstream movement

901 of eels in Bois-Joli Reservoir. Blue squares represent the location of the two
902 test transmitters and blue triangle represent the position of the
903 synchronization transmitter (ST) and reference receiver.

904 Figure 4. Cumulative quantile of error location distribution for test
905 transmitter #1 (blue line) and test transmitter #2 (red line). The two dashed
906 lines represent the 50% and 90% quantiles.

907 Figure 5. Example of the 10 last estimated locations (~10 min) of four silver
908 eels that swam through the first spillway. These individuals were
909 representative of all eels that swam through the spillways. The colour of the
910 dots represents the temporal evolution (yellow for the first, red for the last).
911 If less than 10 points are visible, the missing points are out of the frame.

912 Figure 6. Ten last estimated locations (~10 min) for the three eels that swam
913 through the compensation pipe. The colour of the dots represents the
914 temporal evolution (yellow for the first, red for the last). If less than 10
915 points are visible, the missing points are out of the frame.

916 Figure 7. Efficiency at passing through the dam evaluated via four metrics:
917 time to pass, time to pass after overflow, number of detections close to the
918 dam (<10 m), number of detections close to the dam (<10 m) per day,
919 according the final route. CP: compensation pipe in orange, SW: spillways in
920 green.

921 Figure 8. Detections close to the dam (<10 m) for eels that passed through the
922 compensation pipe, viewed from above (left) and in front (right). In the
923 frontal view, the tower of the compensation pipe and spillways are depicted
924 by vertical and horizontal black dashed rectangles, respectively.

925 Figure 9. Detection of eels located close to the dam (<10 m) after passing
926 through the spillways, from above (left) and in front (right), for the period
927 before (upper slide) and during (lower slide) overflow. In the frontal view, the
928 compensation pipe and spillways are depicted by the vertical and horizontal
929 black dashed rectangles, respectively.

930 Supplementary figure 1: Schematic of the synchronization process. The
931 number of digits after a number indicates the accuracy.

932 **11 Annex**

933 **Step 1: Database synchronization and removal of** 934 **drift**

935 Before the analysis, it was necessary to synchronize the data from each
936 receiver to the nearest millisecond, and to correct the mechanical drift
937 in the internal clock (this phenomenon is systematically observed for
938 each receiver). These two biases were corrected using synchronization
939 transmitters located in the centre of the reservoir (Figure 2), at a position
940 5 cm below a receiver (hereafter, referred to as the reference receiver
941 (RR). This transmitter was set up to emit to the nearest millisecond, every
942 600.000 seconds. Each synchronization acoustic signal was separately
943 identified (# of the sync signal; Supplementary figure 1). These two
944 elements provided the theoretical emission time (TET, in milliseconds)
945 (Supplementary figure 1). Given that sound velocity in water is
946 temperature-dependent, temperature recorded by the RR for each TET
947 was used to correct the sound velocity in real-time.

948

949 Distances between the ST and each acoustic receiver were calculated to
950 the nearest centimetre, as shown in the distance between ST and
951 receiver (DSR) table presented in Figure 10.

952 From the TET and DSR tables, the theoretical reception time (TRT)
953 was calculated for each synchronization signal and each receiver
954 (Supplementary figure 1). The TRT was defined as follows:

955

956 Equation 1:

957

$$TRT = TET + t(RR - receiver)_{Temp}$$

958

959 where $t(\text{RR-receiver})_{\text{Temp}}$ is the time taken for a signal to travel from
960 the RR to a given receiver at a particular water temperature. The time
961 taken for the signal to travel to the given receiver was calculated as
962 follows:

963

964 Equation 2:

965
$$t(\text{RR} - \text{receiver})_{\text{Temp}} = \frac{d(\text{RR} - \text{receiver})}{v_{\text{Temp}}}$$

966

967 where $d(\text{RR-receiver})$ is the distance between the RR and a given
968 receiver, and v is the sound velocity in water. The velocity of the sound
969 in water was calculated as follows:

970

971 Equation 3:

972
$$v_{\text{Temp}} = 1449.2 + 4.6 \times \text{Temp} - 0.055 \times \text{Temp}^2 + 0.00029 \times \text{Temp}^3 + (1.34 - 0.010 \times \text{Temp}) \times (S$$

973
$$- 35) + 0.016 \times z$$

974

975 where z is the depth and Temp is the temperature. Z is the mean value
976 between the depth of the RR and the depth of each receiver for each
977 synchronization signal. Temp is the mean between the temperature
978 close to the RR and the temperature close to each receiver for each
979 synchronization signal. For each synchronization signal (identified based
980 on the consistency between # of the sync. signal in the TRT Table and #
981 of the sync. signal in the ORT Table), the difference between TRT and
982 the observed reception time (ORT) (i.e. the recording downloaded from
983 receivers) was calculated (Supplementary figure 1). This value was the
984 correction factor (only for sync. signals).

985 For all acoustic detection values in the ORT Table, it was necessary
986 to interpolate the correction factors. The correction for the actual
987 signals (that is not a synchronization signal) was calculated based on a
988 linear regression using the correction factors corresponding to the two

989 closest synchronization signals. The reception time was modified
 990 according to these correction factors to yield the real reception time,
 991 without drift and with perfect synchronization (Supplementary figure 1).
 992

993 **Step 2: Multilateration**

994 The synchronized database was used to determine accurate locations
 995 using the multilateration technique, as described by Andersen (2011).
 996 Multilateration is a technique that uses multiple omnidirectional sensors
 997 to isolate the unknown position of a signal in two- or three-dimensional
 998 Euclidian space. In the present method, this technique was only used for
 999 horizontal positioning, X and Y (longitude and latitude). The signal from
 1000 an emitter is registered by all receivers, as the signal wave expands
 1001 spherically in all directions with constant propagation speed. The time
 1002 difference when two receivers register the signal event is called the time
 1003 difference of arrival (TDOA) (Andersen, 2011). Based on TDOA and the
 1004 location of each registration (i.e. sensor positions), it is possible to
 1005 deduce the location of the signal emitter through a set of hyperbolic
 1006 equations described by pairwise TDOA at four hydrophones. The linear
 1007 predictor function for a pairwise hydrophone Hn and Hm was defined for
 1008 each i detection as follows:

1009

1010 Equation 4:

1011 $\mu TDOA(H_n, H_m, t(i))$

$$1012 = \frac{\left((x_{H_n} - x(t(i)))^2 + (y_{H_n} - y(t(i)))^2 \right)^{0.5} - \left((x_{H_m} - x(t(i)))^2 + (y_{H_m} - y(t(i)))^2 \right)^{0.5}}{v}$$

1013

1014 where x and yHm/Hn are the hydrophone positions, x and yt(i) are the
 1015 estimated position of the transmitter at time t for detection I, and v is
 1016 the sound velocity as determined from Equation 3.

1017 To solve this equation system, we used an R version of the Matlab
1018 "mldivide" function.
1019

1020 **Step 3: Filtering**

1021 Having determined the locations, all estimations that were not located
1022 in the study site were removed.
1023
1024
1025

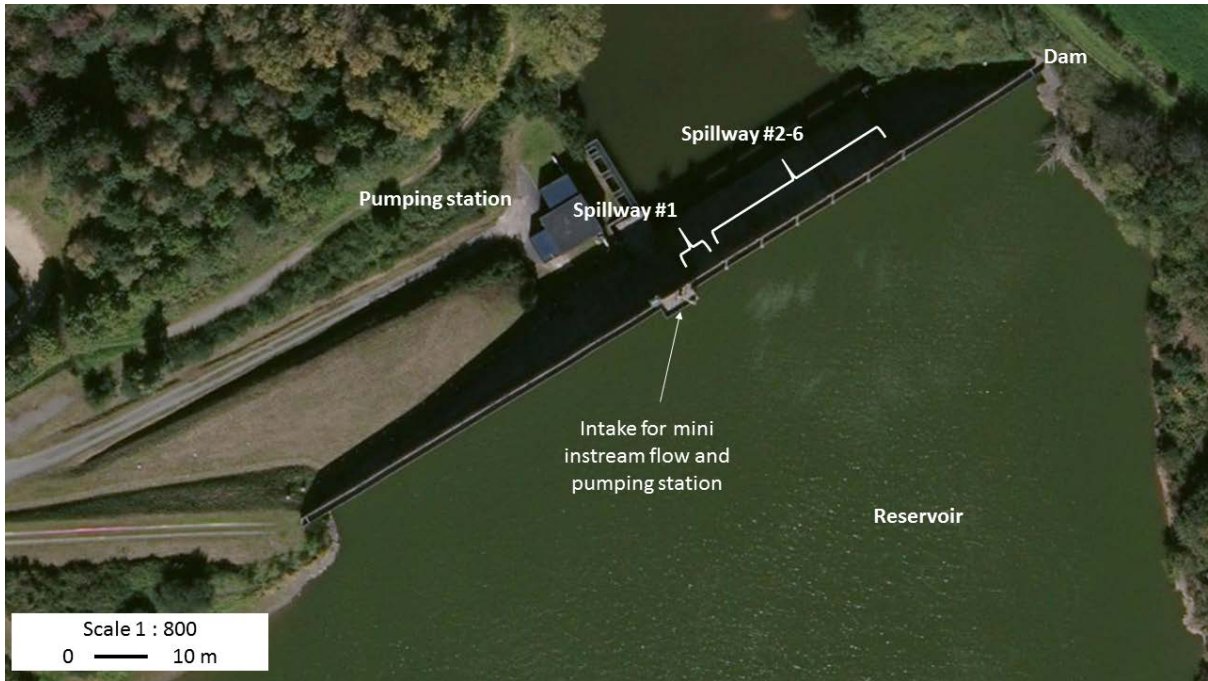


Fig. 1

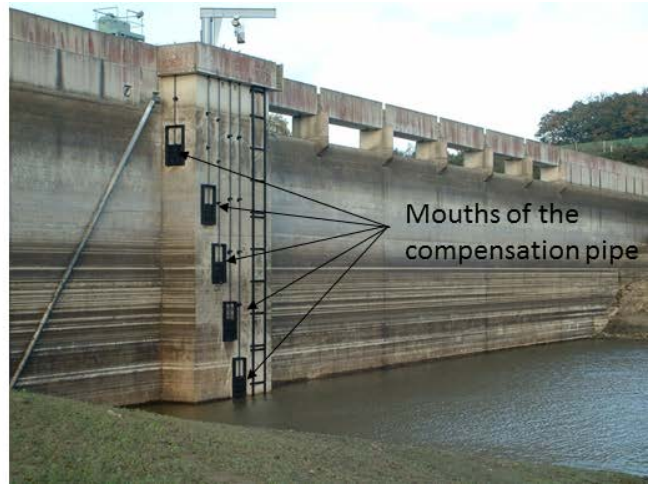


Fig. 2

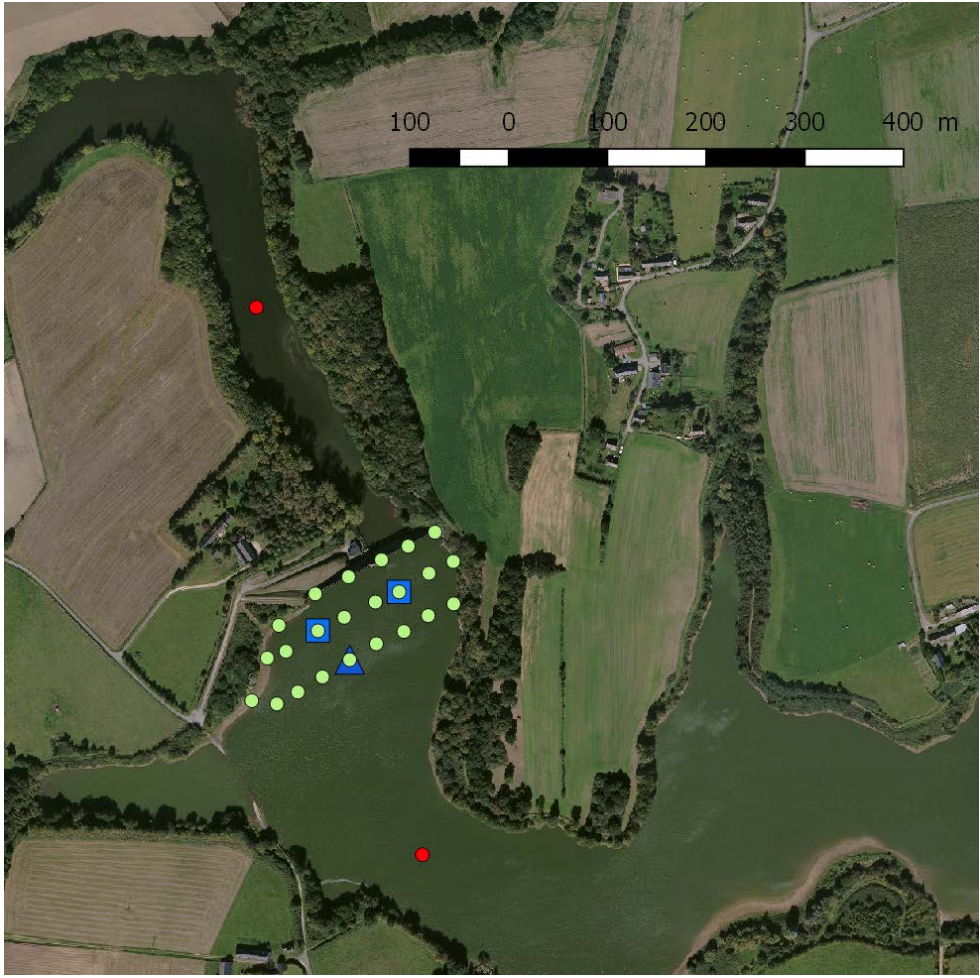


Fig. 3

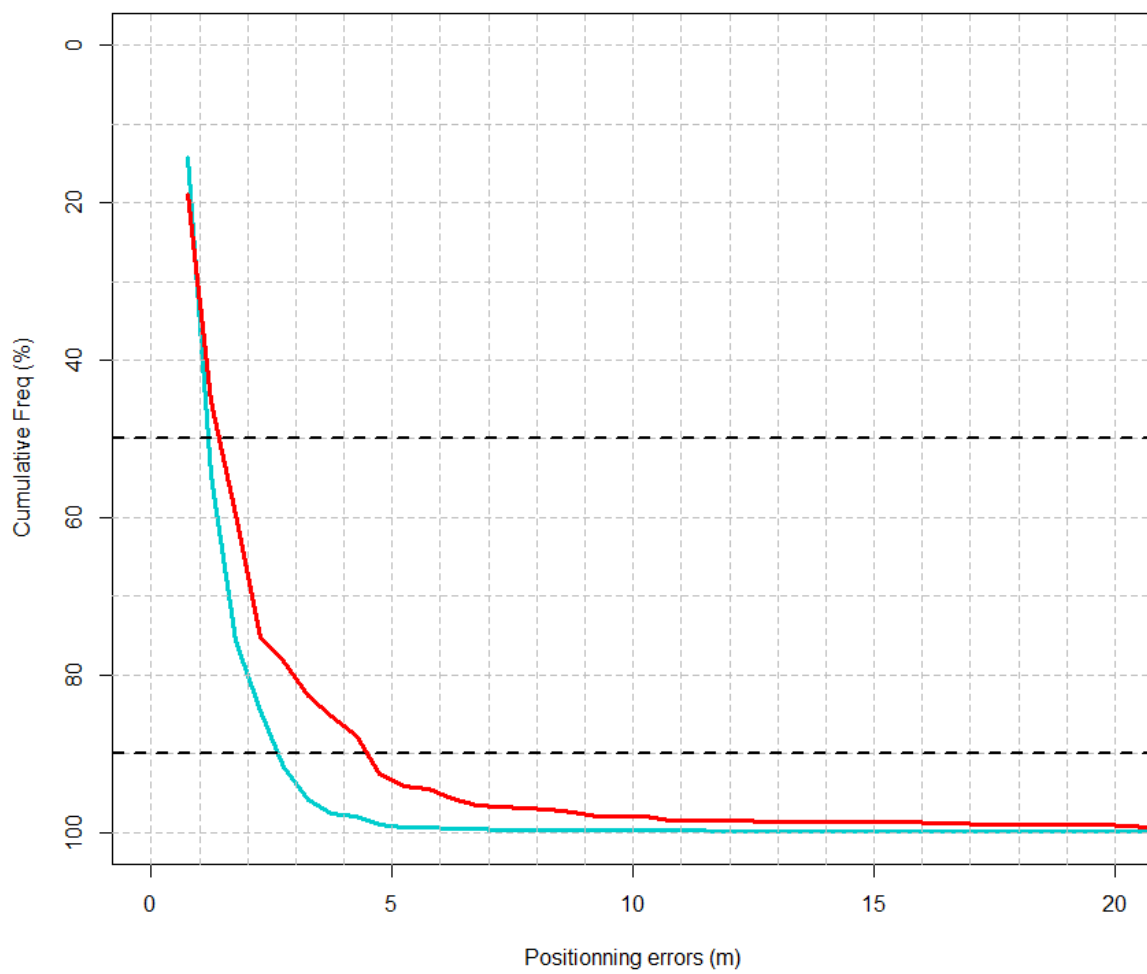


Fig. 4

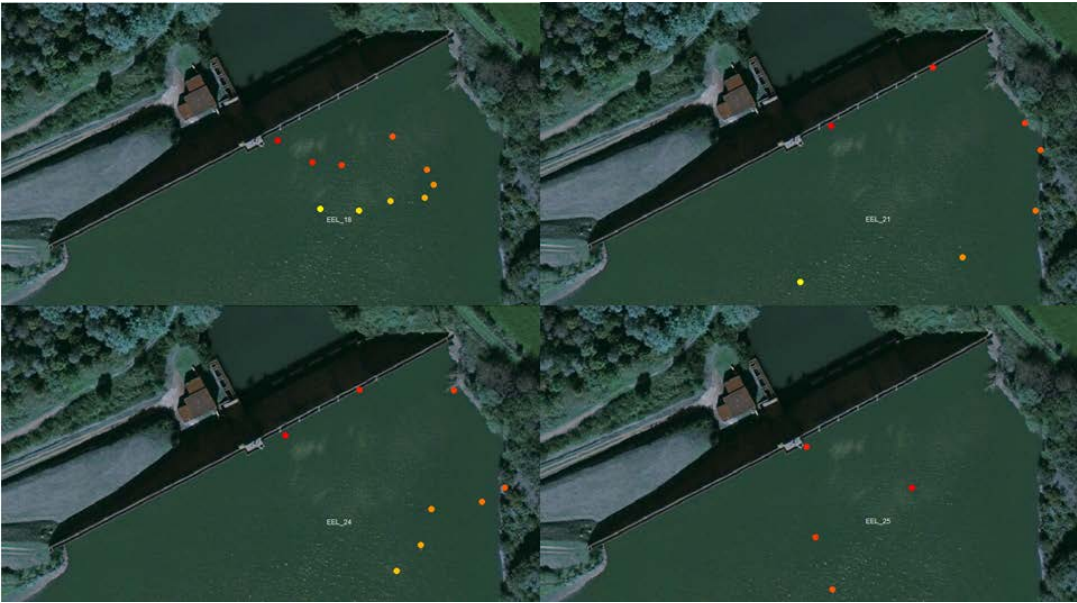


Fig. 5



Fig. 6

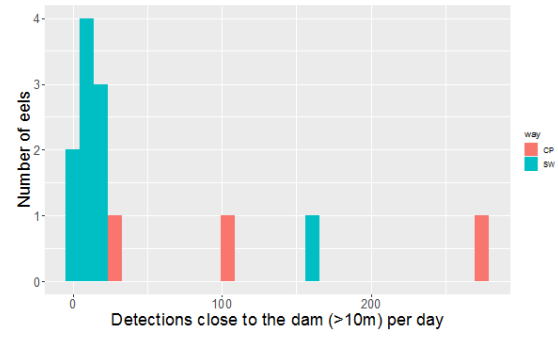
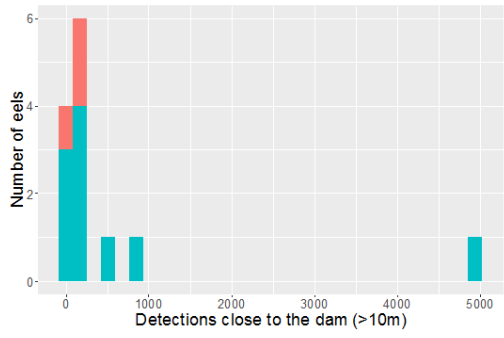
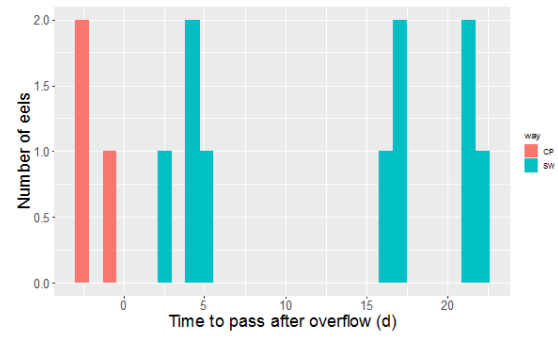
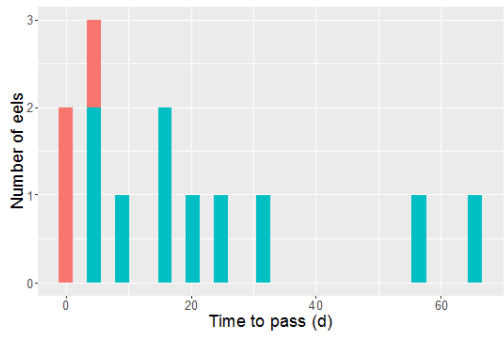


Fig. 7

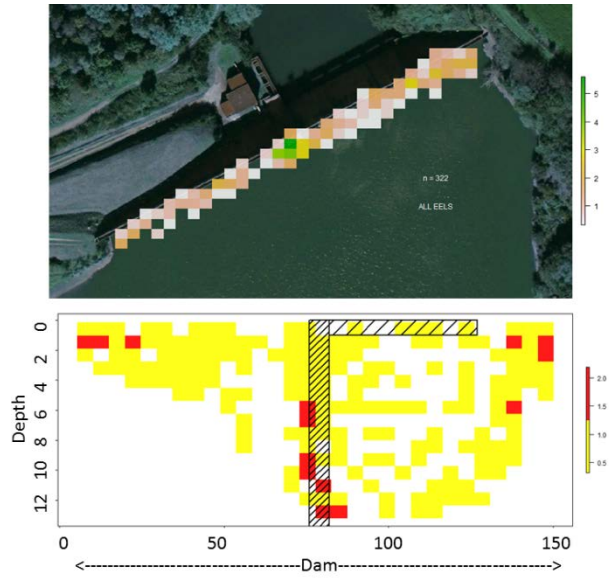


Fig. 8

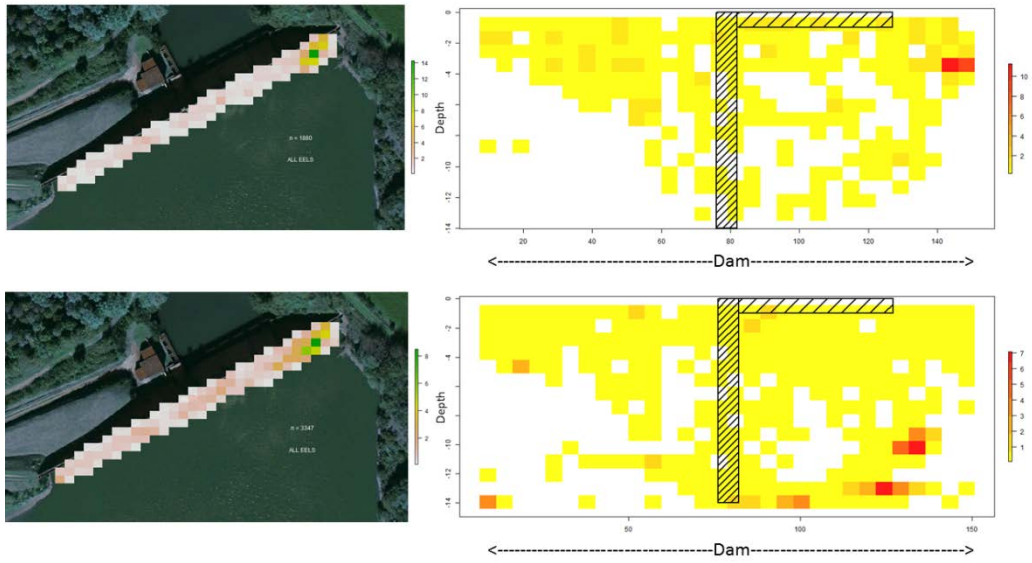


Fig. 9