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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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Abstract
River infrastructures such as weirs, hydropower stations or water reservoirs represent obstructions to migration for diadromous fish. Knowledge of accurate behaviour of fish in front of such structures is required to protect migrants from hazardous areas, guide them towards safe passage or adapt structure to improve the escapement. We developed and made available a method to process acoustic telemetry data based on Time Difference Of Arrival analysis to accurately locate tagged fish. Improved accuracy allows the detection of escape routes and description of dam-crossing tactics. Sixteen tagged eels were tracked with high accuracy (1–2 m) and ~1 location min^{-1} frequency during their exploration period on reaching the dam. Two migration routes (spillways and bottom compensation flow pipe) were used by 77% and 23% of eels respectively. Spillways were the preferred route, but a median of 16 days were required to pass the dam versus 1.1 days via the compensation pipe. A minimal water crest of 40 cm was required for passage via spillways. Eels passing through the compensation pipe were exclusively nocturnal and mainly explored the bottom of the dam. Eels passing through spillways explored the whole dam area by night and day, and were not attracted to the compensation pipe entrance. With global warming, more frequent drought periods are expected, potentially leading to decreased opportunities for eels to migrate across safer dams by spillways. To conserve this endangered species, dam management strategies that account for expected hydrologic conditions and distinct exploration behaviours are needed.

KEYWORDS
3D acoustic telemetry, dam, diadromous fish, downstream migration, European eel

1 | INTRODUCTION

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

The impacts of hydropower dams have been well-studied. Hydroelectric complexes can cause injuries (Bruijs & Durif, 2009), direct mortality (Bruijs & Durif, 2009; Winter, Jansen, & Bruijs, 2006), delays in the timing of migration (Behrmann-Godel & Eckmann, 2003) and can inhibit downstream migration (Durif, Elie, Gosset, Rives, & Travade, 2003). To date, downstream passage at nonpowered dams (i.e. that are not equipped with turbines) has not been considered to be a particularly important issue for migrating silver eels, as the passage is usually considered to be safe (Besson et al., 2016). Consequently, the impact of reservoirs and dams is less studied, despite high numbers existing in some European regions. In particular, nonpowered dams can delay migration (Besson et al., 2016; Larinier, 2000; Larinier & Travade, 2002) and result in lower (20%) annual migration rates when compared to equivalent nonobstructed rivers (Acou, 2006; Feunteun, Acou, Laffaille, & Legault, 2000). In such systems, the principal route for eels to migrate seaward involves waiting for the overflow during flood episodes. Unfortunately, climate change might have significant consequences on the availability of water resources, with the frequency of overflow periods being expected to decline, particularly in areas already suffering from water stress or that have low groundwater (Versini, Pouget, McEnnis, Custodio, & Escaler, 2016). To manage this endangered species efficiently, scientists and environmental managers must adapt existing measures to enhance the passage of silver eels through dams under current and future hydrological conditions. As a first step, it is necessary to understand how eels behave in reservoirs and their migration pathways across dams.

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

Such fine-scale accuracy is required to study the behaviour of eels so that effective management measures can be implemented. Accurate information on movement is essential to optimise the design and construction of eel passageways and to verify their efficiency (Brown, Haro, & Boubée, 2007). Currently, two main methods are available and widely used to track species in aquatic systems, namely satellite and acoustic tracking (Hussey et al., 2015). Although satellite tracking represents the most accurate method of determining location, this technology requires the regular emersion of transmitters so that they can communicate with satellites, making it only suitable for species that remain at, or come regularly to, the water surface (e.g. aquatic mammals, birds, turtles and some shark species). In comparison, acoustic telemetry has rapidly become the most suitable technology for monitoring fishes (Hussey et al., 2015).

Unfortunately, because sound in water propagates uniformly in all directions, the locations recorded using a single fixed receiver encompass a large area (up to several hundreds of metres) around the receiver. The size of this area depends on factors related to (a) the characteristics of transmitters (size and type of acoustic transmitter), (b) the environment (e.g. depth, salinity, current, suspended matter and substrate) and (c) anthropogenic activities that generate noise (e.g. boat traffic and turbines; Gjelland & Hedger, 2013; Hayden et al., 2016; Huveneers et al., 2016; Kessel et al., 2014; Reubens et al., 2018; Simpfendorfer, Heupel, & Collins, 2008). Thus, it is difficult to determine the precise location of an acoustic-tagged animal, although several methods have been designed and developed to improve this accuracy. For example, Simpfendorfer, Heupel, and Hueter (2002) developed a method using presence data from multiple receivers to obtain position estimates (short-term centre of activity) based on the weighted means of the number of signal receptions at each receiver during a specified time period. However, this method can only determine the centre of activity within a given time period, rather than a precise estimate of location at a single point in time. To obtain precise location estimates at a single time point, numerous companies offer accurate positioning systems with metre or sub-metre resolution using acoustic telemetry. Some of these methods require communication from receivers to reception units with acoustic cables, which is not always feasible.

To position tagged aquatic animals accurately without links to receivers, analysis of Time Difference Of Arrival (TDOA) has been developed by telemetry manufacturers. Unfortunately, scientific studies using this methodology have not provided sufficient details of the technical methods and calculations to enable reported experiments to be reproduced (see for instance Espinoza, Farrugia, Webber, Smith, & Lowe, 2011; Guzzo et al., 2018; Roy et al., 2014). Moreover, until recently, access to this methodology was via a paid service or software, not via open access services (Baktoft, Gjelland, Økland, & Thygesen, 2017).

Thus, the current study proposed and described the use of a complete methodology to locate tagged silver eels accurately (~1 m) using TDOA within the Fremur River (north-western France). Using this method, eel behaviour during downstream migration (i.e. exploratory behaviour and avoidance behaviour) was analysed. It is important to understand how silver eels behave and explore their environment in the context of blocked migration. Therefore, the

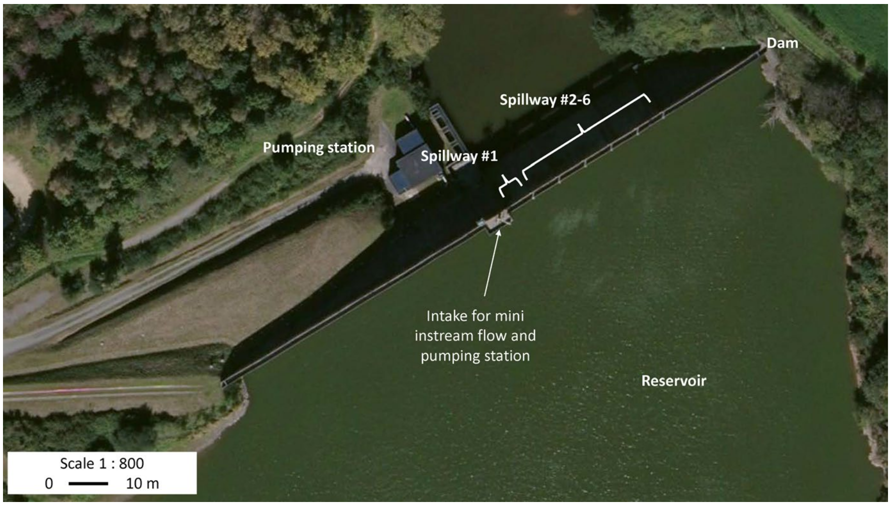

FIGURE 1 Details of the study site: In the vicinity of the dam

method described here is expected to help advance our understanding of how, how many, where and when silver eels cross dams. Based on our results, we provide recommendations for conservation managers to facilitate the passage of silver eels blocked upstream of dams by defining optimal escapement routes.

2 | METHODS

2.1 | Study site

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

2.2 | Silver eel collection and tagging method

Silver eels were captured using fyke nets in the fall of 2017 (October–December). The fyke nets were positioned in the upstream part of the Bois Joli Reservoir and were checked three times a week. Sixteen silver eels were selected using classical external characteristics (Acou, Boury, Laffaille, Crivelli, & Feunteun, 2005), anaesthetised with benzocaine (150 mg/L) and tagged with acoustic transmitters (ID-LP9L-69 kHz Thelma Biotel, Trondheim, Norway, 9 mm diameter, 24 mm long, 4 g in air, transmission interval 30–90 s), respecting the 2% transmitter/body mass ratio (Winter, 1996). Incisions were closed with absorbable sterile sutures (3-0 ETHICON MONOCRYL™, Ethicon Ltd) and disinfected with bactericidal antiseptic (0.05% chlorhexidine). After a recovery period in a large aerated tank and when all anaesthetic effects had dispersed (full recovery of locomotor movements, usually under 1 hr), the fish were released 100 m downstream of the fishing site, which was located about 3 km upstream of the dam. Previous survival tests with eels from the same study site that were tagged with the same method showed no death or injury (Trancart et al., 2017); thus, based on the endangered status of European eels and the very low number of silver eels in Fremur River, we chose not to perform survival test for this experiment. The institutional and national guides for the care and use of laboratory animals were followed. Tagging was conducted under the authority of the "certificat capacitaire pour l'expérimentation animale" (experimental animal certificate) no. A29-039-1 of the Museum National d'Histoire Naturelle, Dinard.

2.3 | Acoustic array

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

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

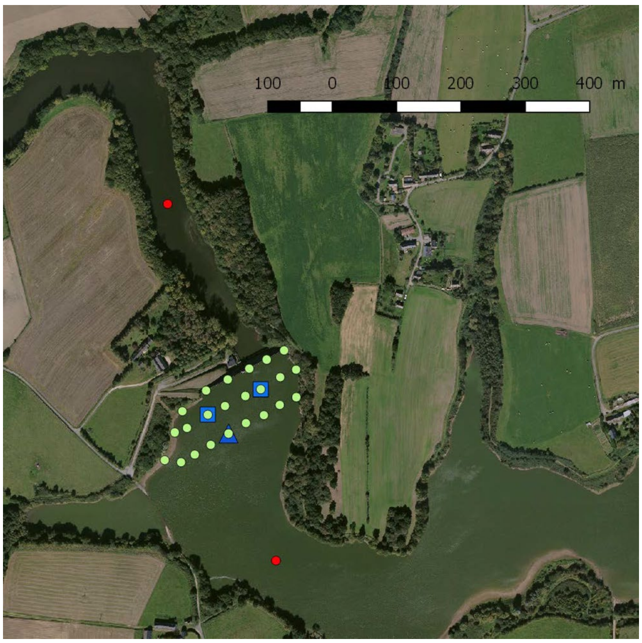

FIGURE 3 Location of the acoustic receivers with millisecond accuracy (green points) used to obtain accurate positions, and those without millisecond accuracy (red points) used to monitor the downstream or upstream movement of eels in Bois Joli Reservoir. Blue squares represent the location of the two test transmitters and blue triangle represents the position of the synchronisation transmitter (ST) and reference receiver

the nearest centimetre; Figure 3). Each receiver had an internal temperature sensor that recorded the temperature every 10 min, enabling us to determine the speed of sound in water accurately.

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

2.4 | Location estimation in the reservoir

2.4.1 | Horizontal positioning determination method

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

2.4.2 | Vertical positioning determination method

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

2.4.3 | Evaluation of the accuracy for horizontal location determination

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

2.5 | Data analysis

2.5.1 | Estimation of escapement

Individual escapement was estimated using the positioning method previously described and confirmed by the detection of a transmitter by the receiver immediately downstream of the dam. Escapement rate was defined as the number of silver eels detected below the Bois Joli Dam against the total number of marked silver eel in the Bois Joli Reservoir.

2.5.2 | Estimation of migration routes to pass over the dam

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

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

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

Method 2: Estimated route using the TDOA method

A second method was employed to estimate the most probable escape route from the *Bois Joli* Reservoir (i.e. compensation pipe vs. spillways). For each eel, the 10 last estimated positions, given by the previous method (see Section 2.4.1), were retained to trace the most probable route used. The most probable exit route was attributed to a given individual, only if the route and the final estimated location clearly indicated one of the two possible ways of escapement. With this method, the most probable date/time of the passage can be inferred and was used to obtain the water level in front of the dam and the height of the water crest (when overflowing) during the passage of the eels.

2.5.3 | Exploratory behaviour and efficiency in passing

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

1. The time to pass (TTP, in days), which was defined as the time difference between the first detection recorded in close proximity to the upstream part of the dam (<10 m) and the observed passage recorded on the receiver downstream of the dam;
2. The time to pass after overflow (TTP-O, in days), which was defined as the time difference between the first detection recorded in close proximity to the dam (<10 m) once the overflow period had begun and the observed passage recorded on the receiver downstream of the dam;
3. The total number of detections (TND), which was defined as all records in close proximity to the dam (<10 m) over the entire period of presence;
4. The number of detections close to the dam (<10 m) per day (TND/day).

To identify potentially different exploration tactics, another metric was used. For this metric, we only considered presence close to the dam (<10 m). The period of presence close to the dam was defined as the period of the day when an eel was observed close to the dam (<10 m). This period was analysed. Two periods were defined according the natural luminosity occurring at the study site during the experiment: night (17:00–07:59) and the day (08:00–16:59 p.m.).

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

3 | RESULTS

3.1 | Validation of estimated horizontal locations using test transmitters

The median errors of location obtained from the stationary reference transmitters located at fixed positions were 1.14 and 1.64 m, and ranged from 0.07 to 36.76 m (n = 3,413 locations over 169 days; Table 1). The cumulative frequencies in the distribution of the error locations of the two reference transmitters indicated that the positioning error was less than 2 m for 80% and 70% of locations for stationary reference transmitter 1 and 2, respectively, and less than 5 m for 100% and 93% of locations for transmitters 1 and 2 respectively (Figure 4). For both transmitters, inframetric accuracy was reached for 30% of locations.

3.2 | Estimation of the most probable routes of exit

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

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

3.3 | Efficiency in crossing the dam

The TTP the *Bois Joli* Dam ranged from 0.29 to 65 days (Table 3; Figure 7). The median time for eels to pass through the compensation pipe was shorter (1.1 days) than those passed through the spillways (18.53 days). When considering the date and time when the dam began to overflow (15 December, at 15:00), the time to pass (TTP-O) the spillways was 16.53 days (Table 3; Figure 7). Eels that passed through the compensation pipe had the highest number of detections close to the dam per day (TND/day). Yet, the TND close to the dam was similar for both groups (Table 3; Figure 7).

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

	Test transmitter #1	Test transmitter #2
Number of estimated locations	2,355	1,058
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

3.4 | Behaviours during escape attempts

3.4.1 | Behavioural differences between eels passing through the spillways and eels passing through the compensation pipe

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

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

In contrast, the areas close to the compensation pipe were not explored more than other areas by eels that passed through the spillways. Most detections were recorded the right side, close to the bottom. No clear difference was observed between the periods before (Figure 9, upper slide) and during overflow (Figure 9 lower slide). During overflow, the range of explored areas seemed to be higher than before overflow. However, this phenomenon was just an artefact linked to the number of detections during both periods (1,880 and 3,347 detections for periods before and during overflowing respectively).

4 | DISCUSSION

This study demonstrates the behaviour of endangered silver European eel attempting to cross a dam using high accuracy 3D acoustic telemetry based on TDOA analysis. This method is described in the annex so it may be reproduced without the need for

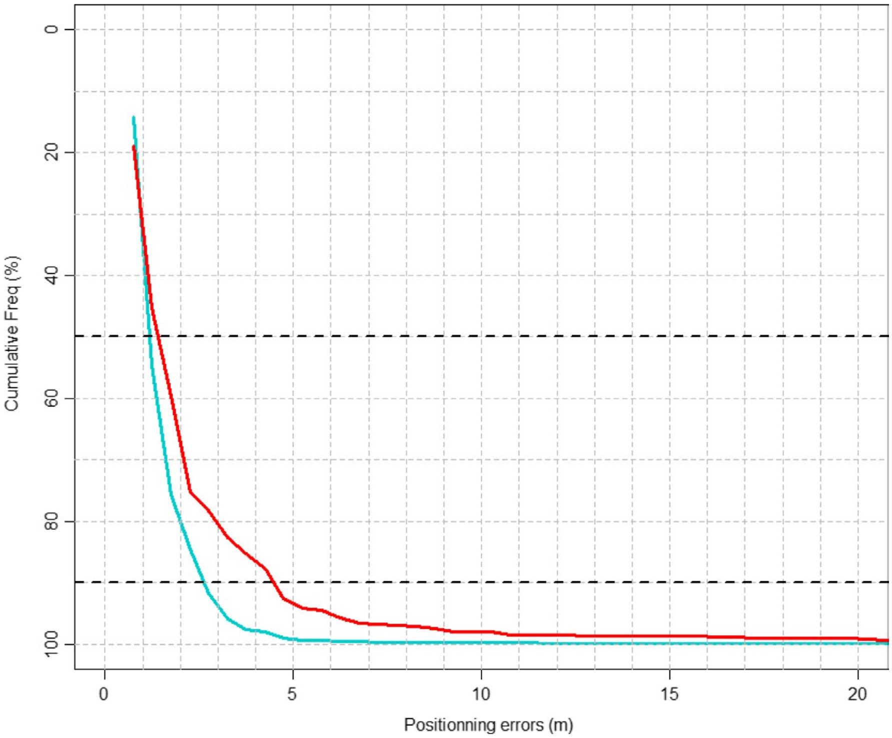

FIGURE 4 Cumulative quantile of error location distribution for test transmitter #1 (blue line) and test transmitter #2 (red line). The two dashed lines represent the 50% and 90% quantiles

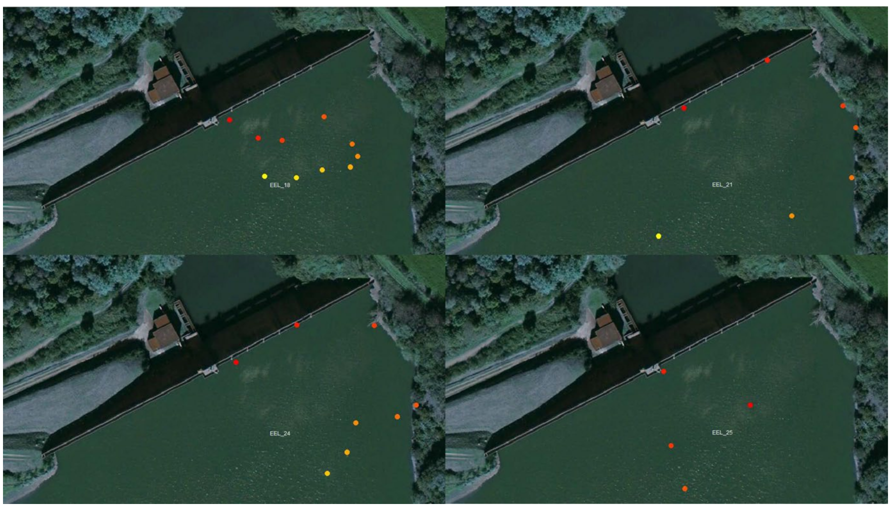

FIGURE 5 Example of the 10 last estimated locations (~10 min) of four silver eels that swam through the first spillway. These individuals were representative of all eels that swam through the spillways. The colour of the dots represents the temporal evolution (yellow for the first, red for the last).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

payment of software and services. The method developed here produced sufficiently accurate location (<2 m), allowing the precise description of eel behaviour. Eels used two escape routes, with some behavioural differences being detected between these two groups.

4.1 | Accuracy of the location determination method

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

The accuracy in the present study was better than, or equivalent to, that reported in comparable studies using commercial positioning systems. For example, Espinoza, Farrugia, Webber, et al. (2011) showed that the mean positional accuracy of VEMCO Positioning System (VPS) estimates from a stationary transmitter deployed at several locations within the receiver array was 2.64 ± 2.32 m. In comparison, Guzzo et al. (2018) found that the accuracy estimates of HR-VPS positions for all stationary trials was 5.6 m. Biesinger et al. (2013) demonstrated a positional accuracy of approximately 2 m. This improved accuracy

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

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

could be explained by (a) the positioning of the receiver to the nearest centimetre using a theodolite for x and y coordinates, and using a decametre for z, and (b) the real-time measurement of water temperature to continuously correct the speed of sound in water at the exact moment of acoustic signal reception. This was possible using the intern thermic sensor included in Thelma Biotel receivers.

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

4.2 | A paradox in the choice of escape routes

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

Seventy-seven per cent of individuals used spillways to successfully cross the *Bois Joli* dam. When both routes were available at the same time (i.e. during the overflow period), no eel passed through the compensation pipe. Although spillways were the principal route used, it is still not clear if it is a beneficial one. For

TABLE 3 Statistics of migration efficiency for the 13 silver migrating eels that passed the Bois Joli Dam *via spillways (SW) or the compensation pipe (CP)*

	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

Note: The negative number in the second column indicates passage before the overflow was operational.

instance, the downstream movement of eels predominantly occurs close to the river bed (Brown & Castro-Santos, 2009; Gosset, Travade, Durif, Rives, & Elie, 2005); therefore, eels may prefer bottom fishways over surface ones. However, the compensation pipe might induce strong rejection, resulting in most eels using a surface route (spillway). The limited diameter of the intake pipe is highly restrictive, accelerating flow (Legault et al., 2003), which might also deter eels. Finally, Piper et al. (2015) observed that eels tend to move rapidly back upstream when exposed to high velocity gradients downstream. Although the grid covering the compensation pipe was not fully effective at preventing eels from entering, visual inspection is required to evaluate its impact on eel migration.

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

Eels that passed through the compensation pipe exhibited a long final period of exploration (time spent within 10 m of the dam), slow movements before passing, nocturnal activity and narrow exploration areas located close to the compensation pipe, at around 6–7 m depth (i.e. depth of the pipe mouth). In comparison, eels that passed

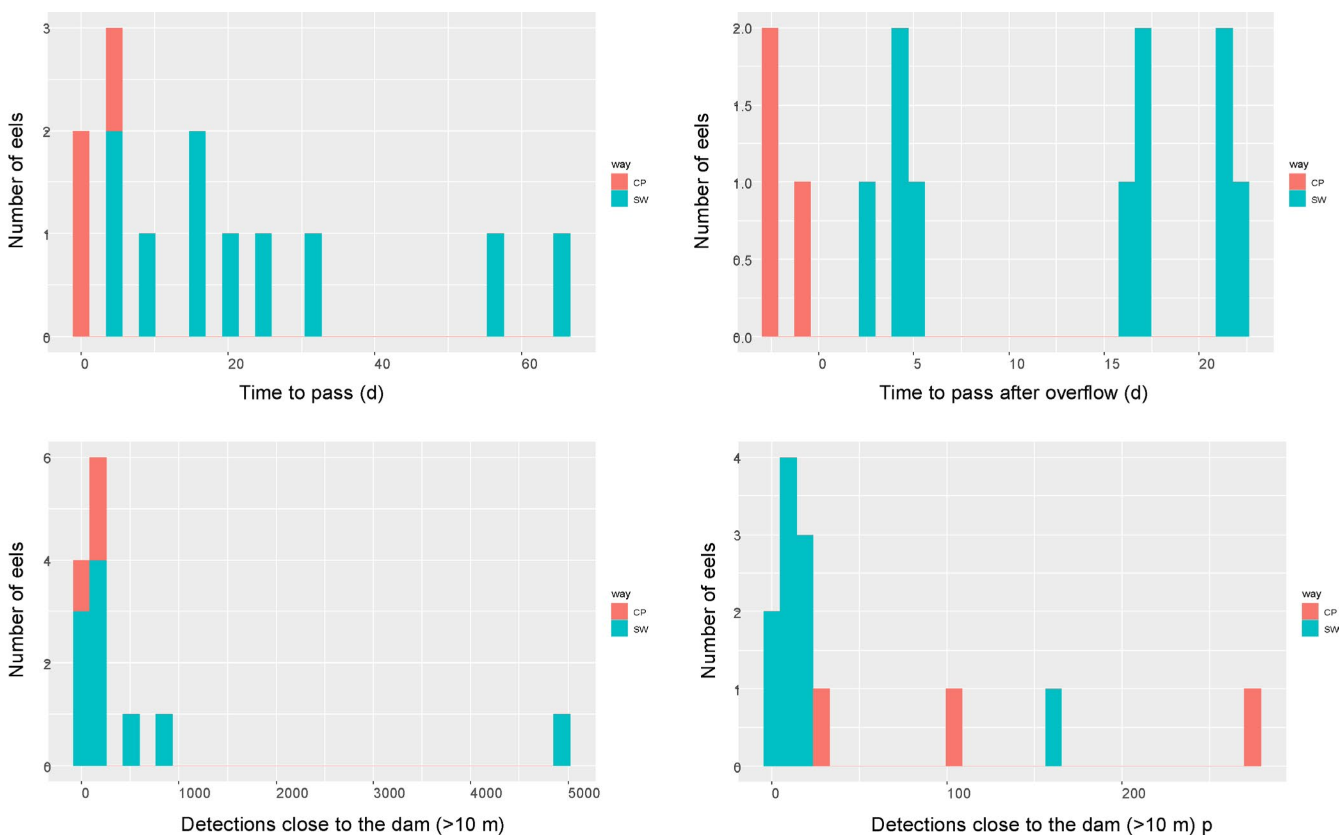

FIGURE 7 Efficiency at passing through the dam evaluated via four metrics: time to pass, time to pass after overflow, number of detections close to the dam (<10 m), number of detections close to the dam (<10 m) per day, according the final route. CP: compensation pipe in orange, SW: spillways in green

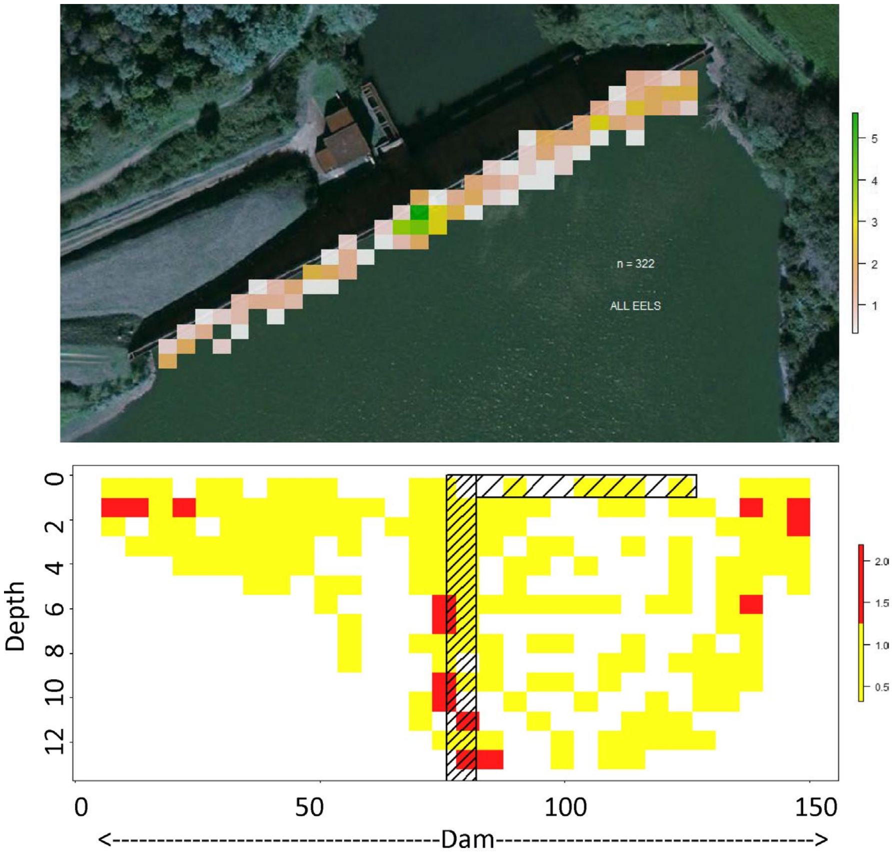

FIGURE 8 Detections close to the dam (<10 m) for eels that passed through the compensation pipe, viewed from above (left) and in front (right). In the frontal view, the tower of the compensation pipe and spillways are depicted by vertical and horizontal black dashed rectangles respectively

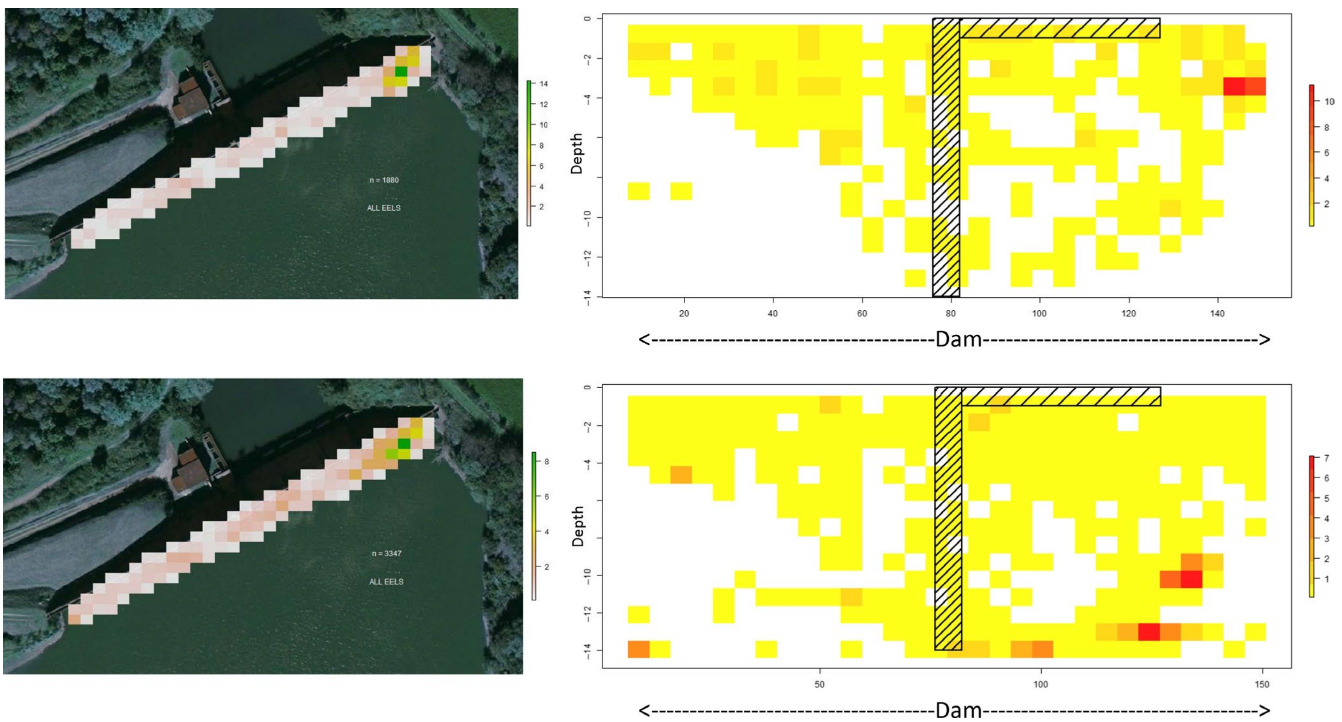

FIGURE 9 Detection of eels located close to the dam (<10 m) after passing through the spillways, from above (left) and in front (right), for the period before (upper slide) and during (lower slide) overflow. In the frontal view, the compensation pipe and spillways are depicted by the vertical and horizontal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

through the spillways showed a short final period of exploration, fast movement before passing, were active both day and night, and explored large areas.

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

4.3 | Behaviour during escape attempts

Very few studies have analysed the behaviour of eels in front of dams. Comparative studies have mostly been conducted at hydroelectric project intakes, not reservoirs, as in the present study. For instance, Brown et al. (2007) conducted a 3D-telemetry experiment to track 21 silver eels that encountered a hydroelectric power station during the downstream migration. Brown et al. (2007) showed that longfin eels (*A. dieffenbachia*) and shortfin eels (*A. australis*) primarily migrated at night and that most eels entered the reservoir in the mid-channel section. Residence time in the reservoir ranged from several minutes to 10 hr. Several eels swam back upstream before returning and continuing to search for a route through. The only downstream passage outlets in the reservoir were the turbine intakes. Two types of behavioural responses were observed when eels encountered the power station intake trash racks, with these responses being species-specific. Eels either passed directly through the trash racks or intakes on their first encounter, or they immediately rejected entrainment and began searching for an alternative passage route in the forebay or upstream of the detection zone. Shortfin eels were the only species that exhibited this behaviour. Longfin eels made a significantly greater number of attempts to pass downstream via the turbines, which corresponded with significantly longer residence times in the reservoir than shortfin eels, possibly searching for alternate passage locations.

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

In another study, nine European eels were tagged using acoustic transmitters (Sonotronics©) in the Mosel River (Germany; Behrmann-Godel & Eckmann, 2003). When migrating eels arrived at the dam, they either immediately passed through the turbines or remained upstream of the powerhouse for up to 8 d. During this period, they exhibited a repeated behaviour: approaching the trash rack, sprinting upstream and finally passing through the turbines. This phenomenon was also clearly present in our study. The lag between two successive transmissions was approximately 60 s, suggesting that the number of detections close to the dam could be used as a proxy of the time spent in the area closest to the dam (<10 m). The strong difference between the time spent close to the dam and the total TTP suggests repeated entry to the area in close proximity to the dam. Moreover, the detailed analysis of eel trajectories before passing indicated repeated movement from the mouth to the reservoir, and following the right-hand shore of the basin, until they finally escaped via the spillways.

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

4.4 | Proposed management under global change

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

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AUTHORS' CONTRIBUTION

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

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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ANNEX 1

STEP 1: DATABASE SYNCHRONISATION AND REMOVAL OF DRIFT

Before the analysis, it was necessary to synchronise the data from each receiver to the nearest millisecond and to correct the mechanical drift in the internal clock (this phenomenon is systematically observed for each receiver). These two biases were corrected using synchronisation transmitters located in the centre of the reservoir (Figure 2), at a position 5 cm below a receiver (hereafter, referred to as the reference receiver (RR). This transmitter was set up to emit to the nearest millisecond, every 600.000 s. Each synchronisation acoustic signal was separately identified (# of the sync signal; Figure S1). These two elements provided the theoretical emission time (TET, in milliseconds) (Figure S1). Given that sound velocity in water is temperature-dependent, temperature recorded by the RR for each TET was used to correct the sound velocity in real-time.

Distances between the ST and each acoustic receiver were calculated to the nearest centimetre, as shown in the distance between ST and receiver (DSR) table presented in Figure S1.

From the TET and DSR tables, the theoretical reception time (TRT) was calculated for each synchronisation signal and each receiver (Figure S1). The TRT was defined as follows:

$$\mathrm{TRT} = \mathrm{TET} + t\left(\mathrm{RR} - \mathrm{receiver}\right)_{\mathrm{Temp}} \quad (1)$$

where *t*(RR-receiver) Temp is the time taken for a signal to travel from the RR to a given receiver at a particular water temperature. The time taken for the signal to travel to the given receiver was calculated as follows:

$$t\left(\mathrm{RR} - \mathrm{receiver}\right)_{\mathrm{Temp}} = \frac{d\left(\mathrm{RR} - \mathrm{receiver}\right)}{v_{\mathrm{Temp}}} \quad (2)$$

where *d*(RR- receiver) is the distance between the RR and a given receiver, and *v* is the sound velocity in water. The velocity of the sound in water was calculated as follows:

$$\begin{aligned} v_{\mathrm{Temp}} = {} & 1449.2 + 4.6 \times \mathrm{Temp} - 0.055 \times \mathrm{Temp}^2 + 0.00029 \times \mathrm{Temp}^3 \\ & + \left(1.34 - 0.010 \times \mathrm{Temp}\right) \times \left(S - 35\right) + 0.016 \times z \end{aligned} \quad (3)$$

where *z* is the depth and Temp is the temperature. *Z* is the mean value between the depth of the RR and the depth of each receiver for each synchronisation signal. Temp is the mean between the temperature close to the RR and the temperature close to each receiver for each synchronisation signal. For each synchronisation signal (identified based on the consistency between # of the sync. signal in the TRT Table and # of the sync. signal in the ORT Table), the difference between TRT and the observed reception time (ORT) (i.e. the recording downloaded from receivers) was calculated (Figure S1). This value was the correction factor (only for sync. signals).

For all acoustic detection values in the ORT Table, it was necessary to interpolate the correction factors. The correction for the actual signals (that is not a synchronisation signal) was calculated based on a linear regression using the correction factors corresponding to the two closest synchronisation signals. The reception time was modified according to these correction factors to yield the real reception time, without drift and with perfect synchronisation (Figure S1).

STEP 2: MULTILATERATION

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

$$\mu\mathrm{TDOA}\left(\mathrm{Hn}, \mathrm{Hm}, t(i)\right) = \frac{\left(\left(x_{\mathrm{Hn}} - x(t(i))\right)^2 + \left(y_{\mathrm{Hn}} - y(t(i))\right)^2\right)^{0.5} - \left(\left(x_{\mathrm{Hm}} - x(t(i))\right)^2 + \left(y_{\mathrm{Hm}} - y(t(i))\right)^2\right)^{0.5}}{v} \quad (4)$$

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

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

STEP 3: FILTERING

Having determined the locations, all estimations that were not located in the study site were removed.