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Migration behaviour and escapement of European silver eels from a large lake and wetland system subject to water level management (Grand-Lieu Lake, France): New insights from regulated acoustic telemetry data

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Abstract

Current knowledge about the downstream migration of sexually mature European eels (*Anguilla anguilla*) remains incomplete, particularly in still water habitats such as lakes and wetlands subject to water level management. However, for the management of this endangered species, it is important to understand migration dynamics, and contribution to the breeding stock. This study aimed to assess the parameters that trigger and guide the migration of silver eels in the largest floodplain lake and associated wetlands in France (the sluice regulated Grand-Lieu Lake). A telemetry survey of 50 acoustic and PIT-tagged female silver eels was performed during the 2015–2016 migration period. We deployed a novel telemetric approach, using receivers to delimit several restricted virtual boxes to determine the instantaneous location of individuals and to transform simple discrete telemetric data into presence/absence data. The low numbers leaving the lake centre are probably explained by the lack of orienting water flows or other environmental clues, but whilst the fate of 34% (17/50) of the tagged eels is unknown, 18% (9/50) were caught by commercial fishermen. Modelling showed that detections were not clearly associated with environmental factors typically involved in riverine migrations (e.g. current velocity, atmospheric pressure and temperature) but they were particularly associated with higher and increasing water levels and, for eels exiting the lake, a sharp increase when sluice gates were opened to an effective gap of >75 cm. It is concluded that management of water levels and sluice gate opening during the migration period might aid escapement of silver eels.

KEYWORDS
Anguilla anguilla, cues, silver eel migration, triggers

1 | INTRODUCTION

European eels (*Anguilla anguilla*) exhibit one of the longest (2 × 5–10,000 km, depending on the growth stage site) animal migrations globally. This species begins life in the North Atlantic convergence zone as leptocephali larvae that are transported by the oceanic currents to the coast of Europe, from Norway to Morocco. Leptocephali undergo a first metamorphosis and migrate into fresh, brackish and coastal waters as sexually undifferentiated juveniles (glass eels). After 5–30 years in these habitats, where eel develop into elver and then yellow eel, sexual differentiation takes place and adult eel undergo a second metamorphosis (silver eel) enabling them to undertake a long (5–10,000 km) and slow (6–18 months) migration back to the spawning grounds (Feunteun, 2002; Righton et al., 2016).

The downstream migration of European silver eels is dependent on local environmental conditions that act at three different temporal scales. First, local conditions (e.g. temperature, photoperiod and food regime) influence the growth and maturation of yellow eel (Daverat et al., 2012). Second, the increase in temperature and photoperiod during spring stimulates the neuroendocrine system that promotes metamorphosis from yellow to silver eels (Dufour, 2003; van den Thillart, Dufour, & Rankin, 2009). Third, at the end of summer, silver eels are physiologically ready to migrate (Durif, Dufour, & Elie, 2006), with migratory behaviour being triggered and driven by environmental factors that generate stronger water discharge along rivers (rainfall, flood events, dam openings, and atmospheric depression) and low light conditions (increased turbidity and moon phases) (Winter, Jansen & Bruijs, 2006; Bultel et al., 2014). However, few studies have focused on downstream migration pattern in still water ecosystems like lakes, reservoirs and wetlands.

Throughout the complex mechanisms leading to downstream migration, the third phase is considered the most important, due to the unpredictability of triggering factors. Consequently, the absence, or the alteration, of the triggering factor is expected to have a major impact on population dynamics, delaying the timing of migration, or preventing it (Besson et al., 2016). Therefore, it is necessary to identify the factors that trigger downstream migration for the effective management of this endangered species. In rivers, silver eels appear to use floods to guide migration, as this phenomenon mechanically aids downstream movement (Lowe, 1952). The preference of migrating eels for areas with strong currents might help individuals to conserve energy, by reducing swimming activity, and to shorten the period required to reach the sea (Bruijs & Durif, 2009).

Still water ecosystems, like lakes, lagoons and reservoirs, are widespread (Vogt, Soille, & De jager, 2007) and are often productive and highly suitable for the development of eels (Grennan & Mccarthy, 2017; Kangur, Kangur, & Kangur, 2002; Matthews, Evans, McClintock, & Moriarty, 2002; Simon, 2007). These habitats are thought to support a large proportion of the spawning stock of European eels (see, for instance, Deelder, 1954; LaBar, Casal, & Delgado, 1987; Carss, Elston, Nelson, & Kruuk, 1999; Tesch, 2003; Allen, Rosell, & Evans, 2006; Westerberg & Sjöberg, 2015). In these habitats, currents are very slow to negligible, with most longitudinal physical and chemical gradients being absent; thus, the cues used by eels for orientation must differ to those used in running water. Even though several studies have been conducted on the migration of silver eels from lakes (e.g. Deelder, 1954, 1984; Todd, 1981), knowledge remains limited about the environmental triggers and drivers of downstream migration behaviour. Most of the still water ecosystems investigated thus far are regulated, managed and heavily impacted by human activities (Goudie, 2013), with all of these activities potentially altering or invalidating the triggers used for migration. For instance, in the highly regulated Fremur river, 75% of silver eels were delayed and up to 65% stopped downstream migration during a 9-month study (Besson et al., 2016). Therefore, knowledge about the factors that influence and/or control the migratory behaviour of European silver eels at the onset of their transatlantic breeding migration to the Sargasso Sea is needed.

Recent technological progress in acoustic telemetry has facilitated substantial advances in our understanding of the migratory ecology of eels (see for instance Amilhat et al., 2016; Béguer-Pon, Castonguay, Shan, Benchetrit, & Dodson, 2015; Righton et al., 2016). These studies provide information on escapement rates, activity periods, swim distances, speeds, and routes, and fisheries or hydropower-induced mortality (e.g. Aarestrup et al., 2010; Simon, Berends, Doerner, Jepsen, & Fladung, 2012; Winter, Jansen, & Bruijs, 2006) even if the detection efficiency never reaches 100%, precluding estimation of continuous real-time positions of all individuals. However, the intrinsic characteristics of telemetry data (discrete: one record, at a given time and a given space) limit the use of powerful models that are implemented in other scientific fields, such as fishery sciences or habitat modelling, as distribution models for instance.

This study was designed to (i) improve current knowledge on the migratory behaviour of silver eels in regulated lentic ecosystems, and (ii) to test a new methodological approach by transforming discrete acoustic telemetry data to continuous data (known position at regular time intervals). The latter was undertaken by dividing the study area into several restricted compartments (called boxes) so that the precise movements in time of the eels could be tracked. This approach allowed us to utilise a powerful distribution model, which helped identify the main factors that trigger the seaward migration of eels from a large floodplain lake.

2 | MATERIAL AND METHODS

2.1 | Study area

Grand Lieu Lake is a shallow (0.70–1.20 m in summer, 3.00–3.50 m in winter), turbid, eutrophic natural freshwater ecosystem located in western France (47° 05′ N; 1° 39′ W). The lake covers 3,900 ha in summer and around 6,500 ha in winter, due to the flooding of the surrounding peaty wet grasslands. Permanently flooded areas are restricted to extensive beds of floating-leaved plants (mainly nymphaeid patches, c.a. 10 km^2) and a central region of entirely open water (10 km^2). The open water portion is the main developmental habitat of eels. The lake periphery is composed of swampy or flood-zone areas and is drained by a network of manmade ditches facilitating water management. These areas are suitable for both migration and development of eels. Five main channels located to the north of this second habitat link the centre of the lake to the outlet. The lake system is fed directly by rainfall, land drainage and discharges from the Ognon and the Boulogne river basins (185 and 470 km^2) and drains via a large canal to sluice gates that control lake system water levels (Figure 1). Through this sluice gate, water moves downstream along the 22-km Acheneau River, and flows into the Canal de la Martinière. Then, the water flows into the Loire River and its estuary. Grand Lieu Lake is classified as a National Nature Reserve and is protected by the Ramsar Convention (1971) because it supports numerous bird colonies, including piscivorous species, such as ardeids and cormorants

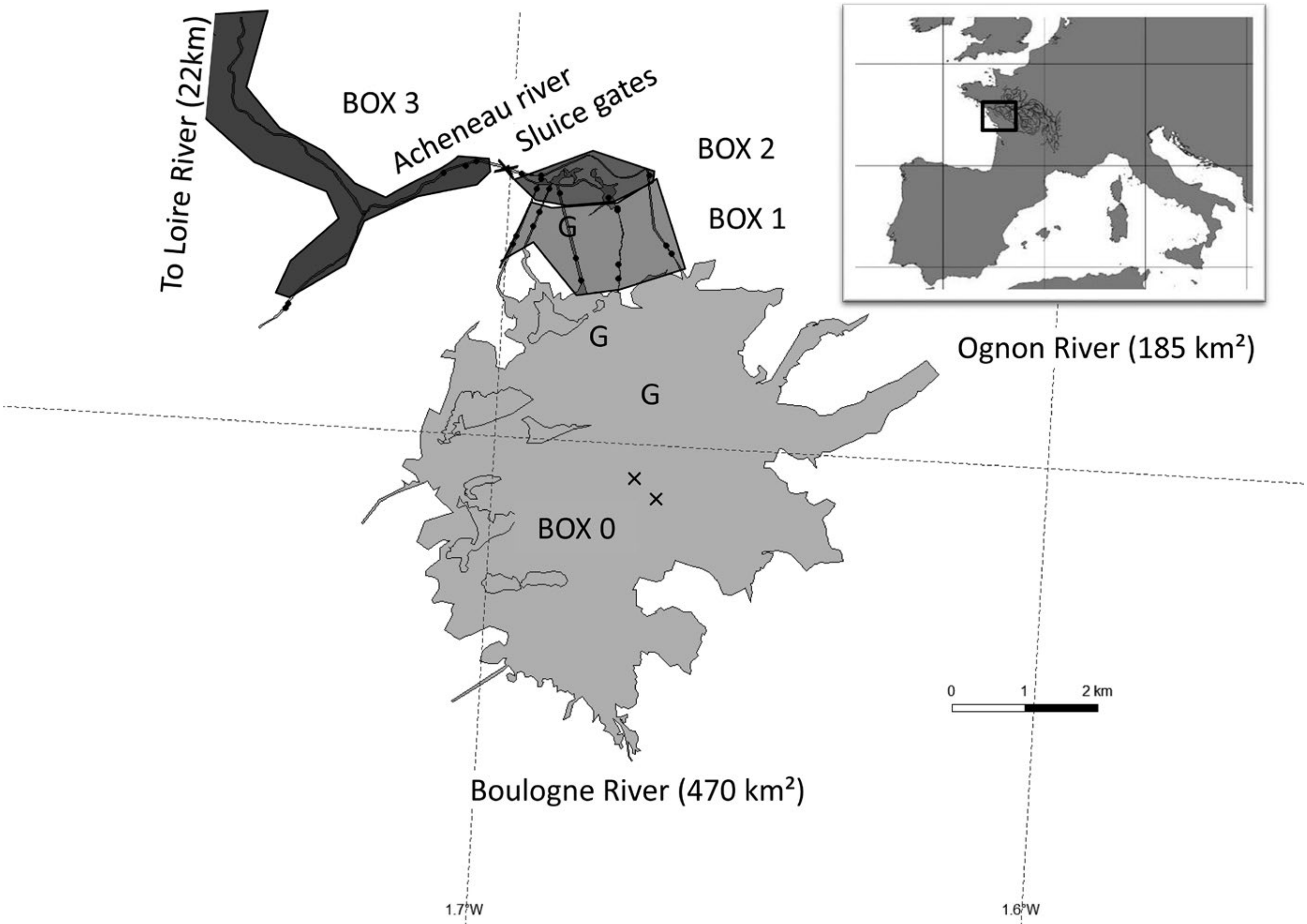

FIGURE 1 Positions of the acoustic receivers (black dots). The four boxes are indicated by different shades of grey; the release sites are marked with black crosses, and the accelerometers with G symbols

(Carpentier, Marion, Paillisson, Acou, & Feunteun, 2009). A traditional centuries-old fishery focusing on *A. anguilla* (Adam & Elie, 1994; Carpentier, 2003) is practiced in the lake. This fishery is currently represented by seven commercial fishermen who primarily capture silver eels from 1st October to 15th January each year.

2.2 | Collection and tagging method of silver eels

The silver eels assessed in this study (n = 50) were originally captured by the professional fishery using triple fyke nets in the fall 2015. Fish were housed in large tanks filled with lake water for 1 or 2 days until the tags were implanted. We first distinguished the silver eels from the other developmental stages based on classical external characteristics, for example eye size, dorsal and ventral colour surfaces and lateral-line differentiation (Acou, Boury, Laffaille, Crivelli, & Feunteun, 2005). 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. For transmitter implantation, fish were anaesthetised with benzocaine (150 mg/L). On reaching stage 4 of anaesthesia (total loss of swimming motion with weak opercular motion; Yoshikawa, Ishida, Ueno, & Mitsuda, 1988), the total length (TL, mm), body weight (BW, g), and average eye diameter (ED, mm) were measured for each silver eel to determine their stage of maturation, following Durif, Dufour, and Elie (2005). The silver eels were then strapped to a v-shaped support and aspirated with benzocaine (150 mg/L) to maintain full anaesthetisation. Acoustic transmitters (model V9-69 kHz, 3.7 g in air, 25 mm; Vemco®, Bedford, NS, Canada) were then implanted through a 2-cm mid-ventral incision. The 2% tag/body mass rule (Winter, 1996) was verified for all individuals. Passive-Integrated Transponder (PIT)-tags (model HDX12, 12 mm sterile PIT-tags; Biomark, Inc., Boise, ID, USA) were also inserted into the gastric cavity to detect marked individuals in the catches by professional fishermen. Incisions were closed with independent absorbable sterile sutures (3-0 ETHICON MONOCRYL™, Ethicon Ltd, Livingston, UK). During tag implementation, individuals were treated with sterile instruments and were disinfected with a bactericidal antiseptic (0.05% chlorhexidine) to prevent disease.

After closing the sutures, the eels were placed in a large tank and released to the lake 1–2 hr later after recovery. Each fisherman received PIT-tag readers (model HPR Plus™ reader; Biomark, Inc.) to identify tagged fish. An automatic detection system was also developed to analyse all trapped eels without human intervention. To avoid intentional release, the tagged eel fishing data were only available to scientist; the fishermen were unable to know if tagged eels were present in their catch.

The 50 silver eels were marked (acoustic and PIT-tags) over three tagging sessions (September 25: *n* = 18, October 16: *n* = 16, and November 20, 2015: *n* = 16). Eels were classified as potential migrants (FIII, *n* = 29), and migrants (FIV and FV, *n* = 21), based on previously established criteria (Durif et al., 2005). Mean TL was 727 mm ± 49 (*SD*) (range: 591–908 mm), and mean BW was 782 g ± 201 (range: 437–1,701 g). All tagged eels were assumed to be female based on body length and sexually dimorphic features (Tesch, 2003).

The first 8 days following transmitter implantation and release were excluded from analyses to avoid any effects of postoperative stress on movements (Le Pichon, Coustillas, & Rochard, 2015).

To test for mortality or tag loss, 10 additional silver eels were tagged with similar acoustic transmitters and were kept in captivity in a tank filled with water pumped from a similar watershed nearby. To reflect the field conditions, the tank water was aerated but not sterilised or filtered. To evaluate how the eels recovered from surgery, they were lightly anesthetised (benzocaine; 100 mg/L) for weekly examination over a 2-month period.

2.3 | Data regulation

This study was designed to transform data collected from classical telemetry surveys to regulated data, which is more appropriate for modelling. The data from classical telemetry surveys are discrete data, that is, one record corresponds to the position of one individual at one of the receivers at one precise time. The reception capacity of a receiver is mainly associated with the acoustic signal transmission power of the tag (the output signal) and the environment. Numerous factors influence signal transmission, including vegetation, bathymetry, substrate and human activity. In large ecosystems, it is technically and financially difficult to monitor the whole study site, leading to numerous periods with no detection. Between two successive detection events, the position of the eels is, unfortunately, not known. The improvement proposed here involves retrospectively determining estimated positions between two successive detections (Figure 2). This method is based on the assumption that the probability of downstream or upstream movement of individuals from a section of the watershed (hereafter termed box) to the next section without being detected is negligible.

2.4 | Delimitation of boxes

Based on the assumed possibility of eels escaping from the lake, and to improve our data analyses, four boxes were delimited using acoustic receivers to form detection barriers. Receivers were positioned to ensure that any tagged eels could not pass through barriers without being detected (Figure 1, and see details on the detection impermeability check below). The centre of the lake was labelled Box 0 (6 × 6 km wide, free water and 40% of surface covered by nymphaeid patches during summer only). Five channels (Box 1) linked the lake centre (30 m wide for the main, 10 m wide for the others) to the outlet closed by a sluice gate (Box 2, 1 km²). Through this sluice gate, water moves to the Acheneau River (Box 3, 22 km long) and then the Loire River. Twenty-three acoustic receivers (Vemco® VR2W) were deployed around the study area in to separate the four boxes virtually (see Figure 1 for experimental set-up).

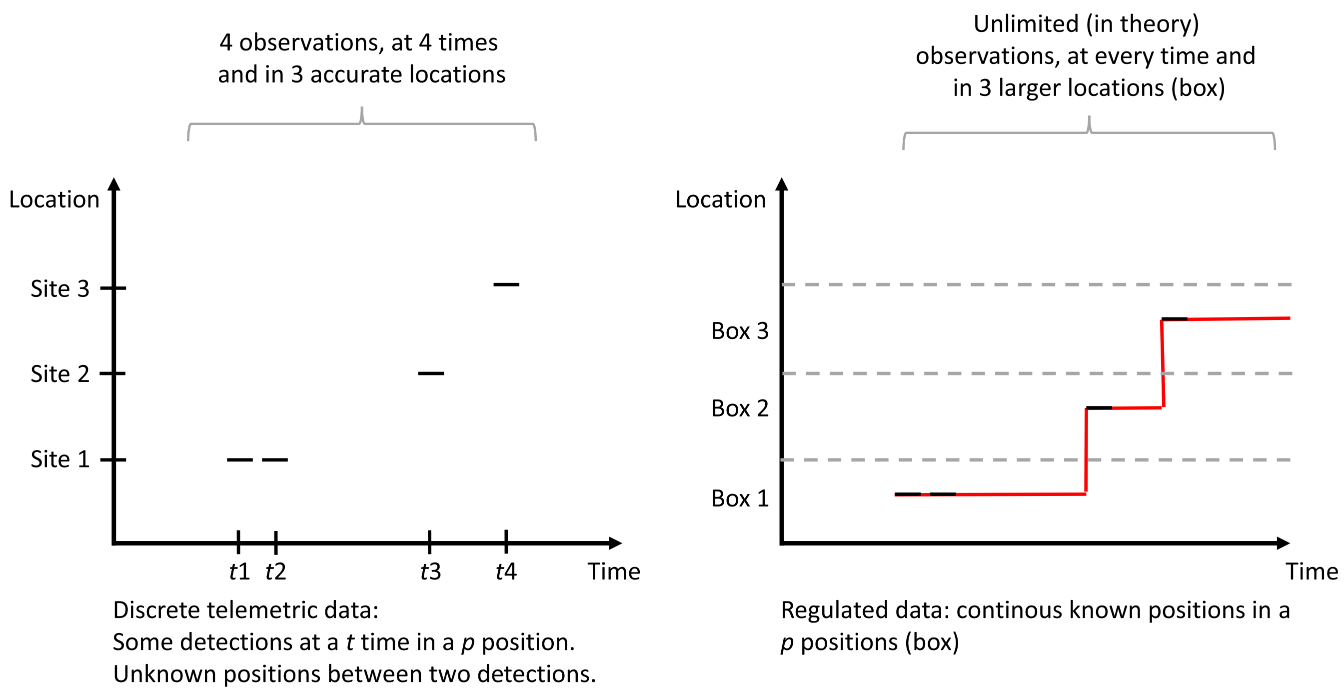

FIGURE 2 Principle of the regulation of discrete data using virtual restricted boxes. (a) Represents actual data and (b) represents regulated data

The most important prerequisite for this method was to assess eel presence or absence correctly in a given box. The detection performance of acoustic signals was, therefore, tested for each receiver, using bagged test tags at 1 m water depth, spaced 50 m apart along a 500 m stretch from the receiver. The ratio of detection counts per location to detection count at 0 m was calculated to obtain the detection probability for that specific distance. In each barrier between two boxes, a second receiver (and a third if required) was added to ensure 90% overlap of the detection buffers (Figure 3). The minimum diameter of this detection buffer was always greater than 500 m. Given this minimum distance and the maximum delay between two acoustic emissions (90 s for the selected tags), it was statistically unlikely for the largest eel in our study (90 cm), swimming at maximum speed (1 body length per second), to avoid detection while moving between two boxes. This prerequisite was checked a posteriori at the end of the experiments, and the results confirmed that no eels were recorded at a given receiver array without be detected by the previous upstream receiver array. Data from the receiver array were collected once a month after the first eel was released on 25th September in 2015, until 1st June in 2016, when migration ceased.

2.5 | Environmental data

The main objective of this telemetry deployment was to identify the factors that trigger the downstream migration of eels. Consequently, because existing studies have shown the importance of running water as a trigger (Sudo 2013; Trancart, Acou, De Oliveira, & Feunteun, 2013), we obtained information from the weather station (Meteo France) at Nantes International Airport (5 km from the lake) on rainfall, air temperature, atmospheric pressure, wind speed, wind direction and nebulosity (1 record/hr throughout the entire experiment). Water temperature was measured with data loggers that were placed in the main canal of the lake (1 record/hr). A proxy of water flow in the main canal (Fig. 1) was recorded hourly with an accelerometer (Hobo Pendant Event Data Logger; range: ± 3 g; accuracy: ± 0.075 g) in the same canal. The accelerometer had a g-value of −0.05 g during periods without flow. Two other accelerometers were installed in the lake, but no flow was recorded. Therefore, we only measured currents in the main outlet canal of the lake. Lake water level (1 record/day) and sluice gates opening period and duration were provided by SAH Sud Loire (Syndicat d'Aménagement Hydraulique). The management of the sluice gates is very complex and is mainly adjusted to the water level according to the period of the year (i.e. a target water level is previously defined for each month). During the study period, the sluice gates were closed at the beginning of the study, slightly opened (50 cm) on 1st November 2015 and finally fully opened to 300 cm after 11th January 2016. The sluice gates were finally closed on June 2016, after the last eel detection. The moon phase (percentage: 100% = full moon, 0% = new moon) was also recorded as a possible influence on migration. Daily means were used in models for all variables. For relevant variables, deltas were also used in models by subtracting the daily means from the daily means of the previous day.

2.6 | Data analysis

Once the discrete raw data were regulated according to the principle described in the previous section, the effects of environmental and anthropogenic variables on migration behaviour were analysed according to modelled eel movements between the three boxes: from Box 0 to 1, then from Box 1 to 2 (where the sluice gate blocked the lake exit), and, finally, from the lake (Box 2) to the Acheneau River (Box 3). The relationships between the environmental data (predictor variables) and these successive downstream migration steps were explored using Boosted Regression Trees (BRTs) (Buston & Elith, 2011; Elith, Leathwick, & Hastie, 2008; Elith et al., 2006). This technique is considered to be a powerful modelling technique for assessing fish distribution (França & Cabral, 2015). In the BRTs, downstream migration steps were considered as the presence/absence data in each box (response variable). Specifically, the response variable was the presence/absence data in box $z + 1$ (i.e. from first presence in box z until first presence in box $z + 1$). For modelling, we considered the environmental factors that occurred between the first detection in box z and the first detection in box $z + 1$; environmental factors that occurred after the movement from box z to box $z + 1$ were not considered.

The analyses were fitted with the "gbm" package (Ridgeway, 2006) and "dismo" supplement functions (Elith et al., 2008) in R 3.3.1 (R Development Core Team, 2008). Two important parameters were adjusted in the BRTs (learning rate and tree complexity) following Elith et al. (2008). Model performance was assessed via the amount of cross-validated deviance explained, cross-validated correlation between model prediction and observed data, and the area under the Receiver Operating Characteristic (ROC) curve, following recent publications (e.g. Amorim, Ramos, Elliott, & Bordalo, 2016). The ROC score ranged from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 implies predictive discrimination that is no better than a random guess, and values <0.5 indicate performance worse than random (Elith et al., 2006).

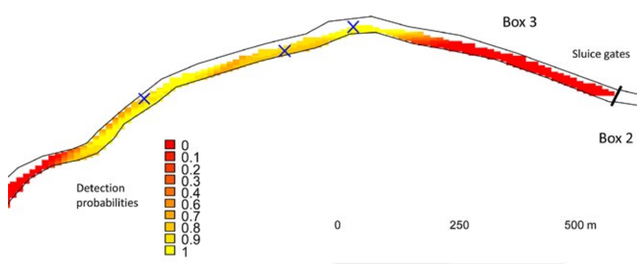

FIGURE 3 Example of the probability of overlap in the detection buffer for the first three receivers in Box 3. Blue crosses represent the location of the acoustic receivers. The size of the 90% detection buffer always exceeded 500 m

	Movement from Box 0 to Box 1	Movement from Box 1 to Box 2	Movement from Box 2 to Box 3
Number of eels	24	23	18
Number of trees	850	4,200	4,450
Explained variance (%)	22.4	59.6	72.9
Cross-validation correlation	0.145; *SEM* = 0.065	0.578; *SEM* = 0.095	0.770; *SEM* = 0.048
ROC	0.743	0.91	0.945

TABLE 1 Predictive performance of the final boosted regression tree (BRT) model developed to describe eel movement along the three downstream migration steps

3 | RESULTS

3.1 | Postsurgery monitoring

No mortality was observed for the 10 eels monitored during the postsurgery experiments, and all eels exhibited full recovery. Nine of 10 of surgical incisions fully healed within 6 weeks of surgery, with no visible scar remaining.

3.2 | Eels with uncertain fate

Less than half of the tagged silver eels (48%, 24/50) had moved out of Box 0 and been detected in Box 1 by the end of the study (June 2016). Of the remaining 26 eels (52%), 9 (18%) were caught by fishermen in the lake, the fate of the other (34%) is unknown.

3.3 | Models of eel movement and factors triggering downstream migration

The factors that triggered migration for each of the three downstream migration steps (between the four virtual boxes) were analysed separately. Preliminary test showed no difference in the migration behaviour between the different maturation stages: the ratio FIII/FIV&FV of tagged eels was 1.38, and the same ratio for migrant eels (i.e. observed just upstream of the dam) was 1.2. Data for all (24) eels detected have therefore been kept in the models.

The data used in the first model were the presence/absence of eels in Box 1 (n = 24), from 8 days post-tagging until their initial detection. The model performance was very low (ROC = 0.743, Table 1); thus, this model was rejected.

The second model (movement from Boxes 1 to 2), involving 23 eels, was a better predictor than the first model. The explained variance of the second model was close to 60%, and the ROC score was 0.910. Four factors primarily explained movement: water level, Δ daily variation in water level, Δ water flow (acceleration), and Δ moon phase (Figure 4). Increasing water level and its daily variation were the strongest contributors, explaining 28.9% and 24.3% of total deviance respectively (Figure 4). Except for one individual at a water level of 4 m, the partial plot of the functions fitted for the final model showed that migration was inhibited when the water level was below a threshold of 4.3 m. A strong threshold occurred also for the Δ water level, with variation greater than +0.08 m per day strongly favouring migration (Figure 4). Similarly, a strong threshold was observed for the Δ water flow (acceleration), with variation greater than +0.08 g per day strongly favouring migration (Figure 4). Moon phase also positively affected migration, but only when it was waning after the last quarter (Figure 4).

The third model (eel movement between Boxes 2 to 3), involving 18 eels, was the most efficient (Table 1), explaining 72.9% of deviance and with an ROC score of 0.945 ROC. Sluice gates opening and Δ water level were the two main contributors to variance in eel movement (Figure 5), explaining 66.5 and 11.4% of deviance respectively. Movement from Box 2 into Box 3 was favoured by increases in water level of >0.05 m per day and, especially, when sluice gates were opened by >75 cm.

4 | DISCUSSION

The present study reports the continuous, long-term (9 months) acoustic tracking of 50 tagged silver eels that were possibly ready to migrate downstream from a lowland lake and associated wetlands. The novel acoustic telemetric method and modelling employed here allowed us to characterise the factors that might trigger and guide downstream migration of eels from the lake to the estuary.

4.1 | Factors triggering and guiding silver eel migration

Tagged eels were released in Box 0, which was located close to the lake centre. The environmental variables tested in this study did not explain movement from Box 0 to Box 1. Several possible explanations exist for this outcome. First, a potentially important environmental factor might have been omitted in the study, but this seems unlikely, given our inclusion of all cues that are known to influence the downstream migration of silver eels (e.g. Trancart et al., 2013). Another possibility is that Box 0-to-1 movement was Brownian, random or exploratory, although generalised activity could be enhanced by environmental cues (Adam, 1997; Adam, 2000). The lack of proprioceptive cues (current, temperature and chemical gradients) likely prevented eels from orientating, despite their strong olfactory senses (Barbin, 1998; Barbin, Parker, & McCleave, 1998; Silver, 1982). Instead, eels might have attempted to navigate using internal cues, which are seasonally determined (Trancart et al., 2013). Because the lake is large compared to its narrow exits, silver eels might simply settle in the lake or in undetectable backwaters if they fail to find the outlet in time.

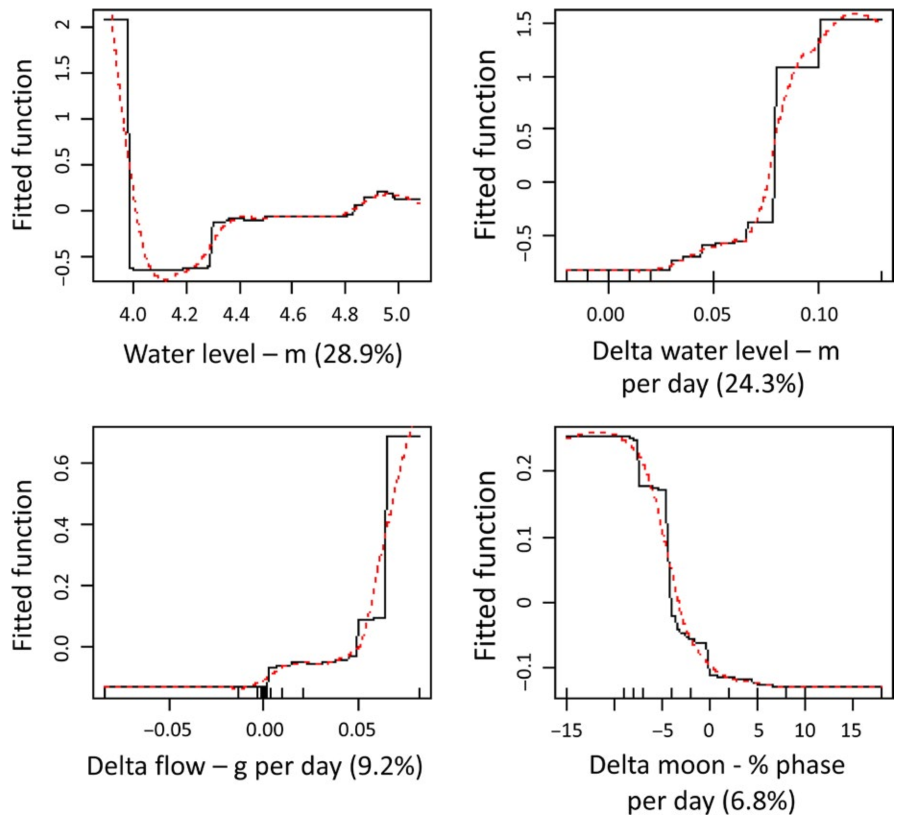

FIGURE 4 Partial plots of the functions fitted for the final Boosted Regression Trees (BRT) models describing movement from Box 1 to Box 2 (n = 23). The relative contribution of each descriptor is presented in parentheses (black lines are raw data and red lines are smooth data)

Although this hypothesis requires further investigation, it provides a plausible explanation for why such a high proportion (34%) of silver eels were never observed in Box 1 and other downstream reaches of the system. According to Westin (2003) migration failure in silver eels in a lake could be imputed to the restocking, suggesting that stocked eels have no opportunity to imprint the directional clues necessary to migrate successfully (Westin, 2003). To our knowledge, the last restocking operation in the study site ended in 1994 (Adam, 1997), which precludes this hypothesis.

For eels close to the lake exit (Box 1), their downstream migration (Box 1 to Box 2 movements) was mainly triggered by two hydrological variables: water level and variation in water level. Except for one eel that passed the sluice gates immediately after the onset of monitoring (when the opening was only 5 cm and the water level was extremely low), migration was generally encouraged by higher and increasing water levels. In running rivers, rainfall is the primary trigger of the downstream migration of silver eels, followed by river flow (see for review Bruijs & Durif, 2009a,b). However, rainfall was not identified as a trigger for downstream migration in Grand-lieu Lake by the current study. Thus, rainfall might not be a trigger in lotic systems, but is, instead, a confounding variable of river flow. In contrast, water flow might only be a minor trigger of eel migration from closed systems. An extensive review by Bruijs and Durif (2009a,b)) found that the effect of lunar phase and atmospheric pressure are often cited as influencing the behaviour of eels where no flow is perceptible, such as in captivity, lakes or closed water bodies. However, even though our study tested these two factors in the proposed model, both parameters seemed to be minor triggers of downstream migration by eels in Grand Lieu Lake. Only moon phase was one of the four main factors triggering migration, but with a small relative contribution (6.8%). Our model showed that migration peaked during the waning moon in Grand Lieu Lake, confirming a classical observation of light avoidance (Hadderingh, Van Aerssen, De Beijer, & Van der Velde, 1999; Lowe, 1952; Pankhurst & Lythgoe, 1983).

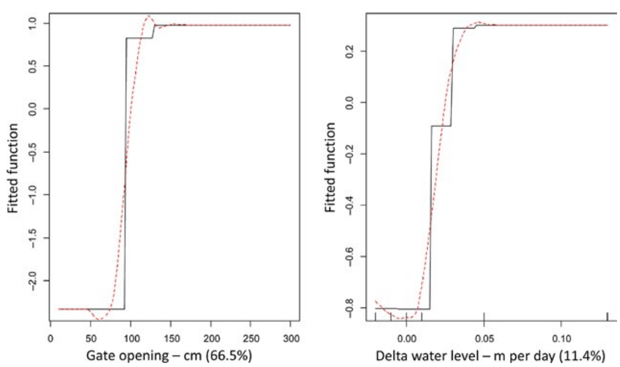

FIGURE 5 Partial plots of the functions fitted for the final Boosted Regression Trees (BRT) models describing eel movement from Box 2 to Box 3 (n = 18). The relative contribution of each descriptor is presented in parentheses (black lines are raw data and red lines are smooth data)

Water level and its daily variation primarily contributed to eel movement in our study. However, the effects of these two parameters varied strongly and abruptly. A sharp threshold was present for both parameters; specifically, under +8 cm per day for Δ water level and around +8 cm for water level. Changes in distal migration triggers of water quality might be associated with variation in water level, including increases in oxygen, suspended matter and turbidity.

In an unmanaged-water system, migration to the Loire River would probably have been continuous. The dam at Grand-Lieu Lake has, effectively, stopped the migration of silver eels other than via the sluice gates. Consequently, we also studied a third step: the passage through the sluice gates (i.e. from Box 2 to Box 3). In the final model, sluice gates opening was logically the main factor triggering eel movement, with a very high rate of explained deviance (72.9%) and ROC (0.945). These results might seem trivial; however, the analysis of the partial plots of the function fitted for the final models showed a strong and abrupt threshold at a high value (75 cm). Thus, passage from Box 2 into 3 was low until the cumulative sluice gate opening exceeded 75 cm. This observation indicates the need for a larger exit. One possible explanation is that noise and current speed increase as the opening narrows, which might deter the silver eels (Bruijs & Durif, 2009a,b).

By the end of the study, 26 (52%) of the silver eels tagged had not been detected outside Box 0 in the centre of the lake, these included nine (18%) caught by fishermen and the fate of the other 17 (34%) is unknown. The lake's stillness and low chemical gradient probably limit the ability of eels to orientate and navigate downstream (Barbin et al., 1998; Hain, 1975). Our results suggest few silver eels migrate out of the lake in any one year and that prolonged residence periods increase their vulnerability to fishing mortality. The fishing mortality value is difficult to address as the study was not designed to evaluate it. Nevertheless, this value is in the range of mortality measured in the Loire river (10%–20%; Acou, A; unpublished data), even if the is more prolonged residence period in Grand-Lieu relative to the Loire, leading to a potential higher cumulative mortality.

We also examined the possibility that the 17 eels finally died, due to surgery. However, our postsurgery experiment suggested that tag implantation did not cause mortality.

Mortality from predators represents another possibility, due to the abundant piscivorous bird community (e.g. cormorants, herons) on the Lake. However, the large eels that were tagged (591 to 908 mm, mean = 727 mm, *SD* = 49 mm) were out of the range of the prey size range for cormorants (120 to 520 mm, mean = 316 mm, *SD* = 11 mm) (Carpentier et al., 2009) and for herons. Furthermore, herons mainly forage on the banks of the lake or in proximate marshes, rather than the centre, which is where eels are found (Feunteun & Marion, 1994). Thus avian predation can be considered as negligible for this study.

Therefore, we suggest that only half the eels found the lake exit, most likely because environmental gradients were too subtle for orientation. The very low migration efficiency found in our study corroborates previous research of strongly managed habitats with manmade obstructions that modify fish movement (Besson et al., 2016; Feunteun, Acou, Laffaille, & Legault, 2000).

4.2 | The monitoring method

The monitoring method used in this study permitted the use of a powerful model requiring continuous data. In classical telemetry surveys, data are rarely continuous. With this method, continuous data were available. However, spatial precision was reduced because the actual position of eels was simplified to that of presence/absence in a given box. Nevertheless, we demonstrated the utility of this method to identify the factors that trigger the downstream migration of silver eels in nonrunning systems (i.e. no water flow). We suggest that the proposed method could be used for numerous other applications, including predictive habitat models.

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