When "safe" dams kill: analyzing combination of impacts of overflow dams on the migration of silver eels

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Abstract

1. The drastic decline in European eel *Anguilla anguilla* stock is now widely recognized. However, while various causes for this decline have been identified, the relative importance of each cause remains unclear.
2. During the catadromous migration of silver eels, the negative impact of dams is frequently highlighted, but mainly for powered dams (with turbines) or where connectivity is completely ruptured. Mechanical impact due to turbine blades is often considered the most important cause of mortality of silver eels during downstream migration. Consequently, non-powered dams equipped with spillways are often considered safe for the passage of migrating silver eels.
3. We hypothesized that, to understand the negative impacts of dams, a much wider context must be considered than turbine mortality alone. Using an acoustic telemetry survey of silver eels, we demonstrated the negative effects of non-powered dams on downstream migration.
4. Five main impacts on eel populations were highlighted: (i) the attenuation or loss of triggering factors, leading to an absence of or delay in migration; (ii) extra delays and extra distances travelled when crossing the dam; (iii) extra energetic costs of the additional distance traveled as result of exploring the dam and the reservoir to find other escape passages; (iv) the selection of a more risky behavioral phenotype, i.e., bold eels; and (v) direct blocking once migration has started. Mortality was evaluated as a supplementary impact. Some of these effects (attenuation of triggers, extra delays to cross the dam) might be more important than the same effect from powered dams, probably due to the constant high water discharge required for turbines that facilitate the passage of eels.
5. As these "safe" dams are very widespread, they must be considered a potential threat to effective eel conservation.

Keywords. acoustic telemetry, silver eels, migration, mortality, non-powered dams, turbines drinking water intake

1. Introduction

Diadromous species are fishes that regularly migrate between freshwater and marine environments at a particular stage of their life cycle (McDowall, 1988). This breeding migration requires passing through narrow ecological pathways, called corridors, where anthropogenic (e.g., pollution and fishing) and ecological (e.g., predation) pressures may be strong. This complex life cycle leads to dramatic declines in most diadromous fishes, especially in areas in the North Atlantic ocean (Limburg & Waldman, 2009). The European eel *Anguilla anguilla* is no exception to this rule. Its estimated recruitment rate is currently lower than 10% of the maximum level recorded in the late 1970s (ICES, 2018), and the species is now far outside its safe biological limits. Therefore, the International Union for Conservation of Nature (IUCN) consider European eels as a critically endangered species (Jacoby & Gollock, 2014).

To protect the European eel, the European Commission has demanded that measures are taken to allow at least 40% escapement of reference silver eel biomass, relative to unexploited, unpolluted circumstances in unobstructed rivers (Dekker and Casselman, 2014; European Commission, 2007). The European Commission recommends actions focused on reducing commercial fishing, limiting recreational fishing, restocking measures, increasing watershed connectivity and quality, catching and transporting of silver eels, predator control, hydroelectrical turbine shutdowns, and aquaculture measures. These actions are targeted to reduce the effects of parameters contributing to major decline in eel stock. Unfortunately, the relative importance of each cause was not clearly established. Overfishing represents one of the primary causes of decline, followed by mortality as a result of turbines and dams (Feunteun, 2002). The impacts of hydroelectric complexes are well-known; specifically, they cause injuries (Bruijs and Durif, 2009), direct mortality (Winter, Jansen & Bruijs, 2006; Bruijs & Durif, 2009), delays to the timing of migration (Behrmann-Godel and Eckmann, 2003), and hinder downstream migration (Durif et al., 2003). Dams that are not equipped with turbines also impact the migration of silver eels, leading to, for instance, delays in migration (Larinier, 2000; Larinier and Travade, 2002).

Because the relative contribution of each cause of decline has not been clearly established, the mitigation measures recommended by European Commission might be not be appropriately targeted. For instance, overflow dams with spillways are often considered a safe passage for migration (e.g., Larinier, 2000; Larinier & Travade, 2002; Watene & Boubee, 2005; Boubée & Williams, 2006; Silva et al., 2016), with both scientists and environmental managers recommending that silver eels are guided towards spillways. Therefore, mitigation measures for spillways effects is not cited among the actions recommended by the European Commission. Although managing the passage of eels through spillways (rather than turbines) is highly commendable, when considering all of the difficulties encountered by diadromous species during migration, dams without turbines might negatively impact downstream migration. Indeed, recent studies have shown the different, and sometimes unexpected, effects of these simple dams. Expected impacts include delays to or the complete blockage of migration. The Frémur River is a small waterway in northwestern France, where Besson et al. (2016) showed that two major dams delay the migration of 75% silver eels, of which the passage of 65% was clearly stopped. However, other less expected effects also occur frequently. For example, in a highly important floodplain lake in France (Grand-Lieu), a small dam that was installed to regulate water level might contribute to the low escapement rate of silver eels (36%) by reducing their perception of environmental triggers and/or cues, and by disturbing them when gates are open at inappropriate times (Trancart et al., 2017). Furthermore, in the Rhine system in France, a dam was installed upstream of an old natural river (Vieux-Rhin) that might cause migration breaks and/or increased natural predation as a result of strongly reduced water flow in this section of the system, reducing motivation and orientation (Trancart et al., 2018).

The mitigation measures adopted to protect silver eels from the negative impacts of a dam should be considered over a wider context than just turbine mortality. The present study aimed to delineate all potential impacts of overflow dams on silver eels, including migration delay, migration stop, direct mortality, and loss of orientation. The behavior of eels was evaluated to highlight potential negative effects of spillway dams that have been less studied. To accomplish this objective, we surveyed silver eels using acoustic telemetry during the 2017–2018 downstream migration period in the Frémur River. This river is representative of many short coastal rivers and tributaries of main rivers in Europe, as it is strongly constrained by non-powered dams to supply freshwater for human consumption and/or irrigation.

2. Methods

2.1 Study site

This study was performed in the Frémur River in northwestern France. The Frémur River is a small coastal waterway (17 km long, 60 km^2 of watershed area) that supported a dense population of eels, which has shown a major decline over the last 18 years (80% decrease between 1995 and 2018; Acou et al., 2011; Charrier et al., 2018; Feunteun et al., 1998). The migration of eels along the Frémur River is severely impacted by six dams and weirs (Acou et al., 2008; Feunteun et al., 2000). This study focused on the main dam, which is considered to have the greatest impact on silver eel migration (Feunteun et al., 1998), and two smaller dams. Three minor works—a culvert under a road, a flow gauging device, and a sill (step) beneath a bridge—are present upstream, but were considered to not hinder silver eel migration and were excluded from the present study.

The most upstream and important dam in this study is the "Bois-Joli Dam", which is 14 m-high with a 3.10^6 m^3 capacity reservoir to supply a drinking water treatment plant (Figure 1), hereafter called "Dam A". The downstream migration of silver eels is facilitated by an overflow crest and a pipe. This main pipe has two parts: a compensation pipe (0.04 $m^3.s^{-1}$ minimum flow) and a drinking water intake pipe (0.21 $m^3.s^{-1}$). The compensation pipe is designed to maintain a minimal instream flow within legal limits. The overflow crest is 28.20 m NGF (Niveau Général de la France; baseline mean sea level for France), and can be accessed by eels at the end of fall or the beginning of winter. A net was installed in front of the exit of the compensation pipe to prevent eel escapement. This net was frequently checked, and all eels that were caught alive were released downstream of the dam. A second net was installed at the exit of the drinking water intake pipe, and was checked in the same way as the first one. The entrance to the main pipe remains open year-round and is protected by a grid; however, this grid is not fully efficient, because eels were caught in the net.

The second dam ("Pont-es-Omnes", hereafter called "Dam B") is located 1 km downstream of dam A (Figure 1) and is smaller (3 m high and 50 m wide.) A 3 m-wide overflow crest facilitates eel escapement during overflow, and is equipped with a gutter to catch migrating eels, which are then channeled to a wolf trap. This trap was checked daily during the peak migration of silver eels. However, during the high-flow periods of the present study, the wolf trap might not have been fully effective because it overflowed. Any eels caught alive were released downstream of this second dam.

The third dam ("Pont-Avet", hereafter called "Dam C") is located 2.5 km downstream of dam B (Figure 1). It is similar in size to dam B (3 m high and 50 m wide), but the overflow crest spans the full width. This dam presents no obstacles to migration to the Frémur Estuary, which is 2 km downstream. However, compared to the other two dams, the depth (1–2 m) and width (3-4 m) of the final river section downstream of dam C is much narrower, generating small detection distances for telemetry surveys.

2.2 Collection and tagging of silver eels

Silver eels were captured with fyke nets during their migration period from September to October 2017. The nets were positioned upstream of the Frémur Reservoir, 2.5 km upstream of dam A (Figure 1), and were checked three times a week. Sixteen silver eels were selected using standard external characteristics of silvering (Acou et al., 2005). They were then anesthetized with benzocaine (150 mg/l), and tagged with acoustic tags (ID-LP9-69 kHz Thelmabiotel, 9 mm large, 4 g in air), following the 2% tag/body mass rule (Winter, 1996). Mean total length (TL) was 663 mm ± 127 (SD, range: 520–974 mm), and mean body weight (BW) was 566 g ± 358 (SD, range: 228–1515 g). All tagged eels were assumed to be female based on body length and sexually dimorphic features (Tesch, 2003). Their individual morphological characteristics are summarized in Table 1. The median lag between two successive acoustic transmissions was 60 s (uniform law from 30–90 s). Incisions were closed with absorbable sterile sutures (3-0 Ethicon Monocryl^{tm}, Ethicon Ltd, Livingston, UK) and disinfected with bactericidal antiseptic (0.05% chlorhexidine). After a recovery period, and when all anesthetic effects had dispersed (~1h), the fish were released 500 m below the fishing site (Figure 1) to prevent a second capture. Previous survival tests with eels tagged using the same method showed no death or injury (Trancart et al., 2017); thus, based on the endangered status of European eels, we chose not to perform a survival test for this experiment. We also assumed low natural mortality, as study site is free of potential predators of large silver eels, such as catfish (e.g., *Silurus glanis*), while grey herons (*Ardea cinerea*) are unlikely to consume eels of this size, and are limited to foraging along the banks of this river (Feunteun and Marion, 1994).

The collision of transmissions prevents receivers from detecting them. In this study, we were concerned that tagged eels would aggregate in front of the dams. Therefore, because of the size of the reservoirs, the power output of the acoustic tag, and acoustic receiver detection ranges. We restricted the number of tagged eels in the reservoir at any one time to

10 individuals. This allowed us to obtain precise and informative behavioral metrics. Consequently, the individual number of periods when a given eel was not detected in the receiver array was very low—below 10% of total time for all tagged eels. An increase in the number of tagged eels would have certainly reduced the quality of detection.

2.3 Acoustic design

The silver eels were tracked using an array of 36 acoustic receivers (Vemco, VR2W) from the release site to dam C (Figure 1) from September 2017 to January 2018. At dam A, receivers were positioned at 50–100 m intervals in the main passage of the river. Three small tributaries were monitored by three supplementary receivers. To detect eel escapement from dam A, two additional receivers were positioned 500 m downstream of it. Two other receivers were positioned immediately before dam B. To detect eel escapement from dam C, two supplementary receivers were positioned 500 m downstream of it. Dam C was monitored by two receivers in the reservoir positioned immediately before the dam and by two receivers in the section of the Frémur River downstream of the dam. Detection ranges of all receivers were tested, and were of high quality to 300 m. Certain conditions, such as low depth and width, caused the two final receivers (downstream of dam C) to have low detection ranges (~15 m), which prevented the optimal detection of tagged eels.

2.4 Environmental data

Environmental data were collected periodically for this study. Atmospheric pressure (hPa), wind direction (°, 0° = from North, 180° = from South), wind force (kn), pluviometry (mm/hour), and air temperature (°C) were measured every hour at the Pleurtuit Airport Weather Station, which was located 2 km from the study site. The data were provided by *Meteo France* for this study. Information on water level at the dam to the nearest centimeter was collected every 20 min using a HOBO 100-Foot Depth Fresh Water Level Data Logger. To remove errors in the log, this level was filtered using a 4 h moving average. Water temperature was continuously recorded (once an hour) by a thermic data logger placed in the river immediately before dam A. Water flow was estimated using three inclinometers (HOBO Pendant® G Data Logger) placed in the main stream of the river, immediately before dam A, in the middle of the study site, and at the release site. Lunar phase was also recorded.

2.5 Data analyses

<u>2.5.1 Dam A reservoir</u>

Mean position of individuals

Receiver density was highest in dam A reservoir, and the mean position of each silver eel at 20-min intervals was calculated as the mean position of receivers receiving signals from the eel during a given interval weighted by the number of detections from each receiver. Therefore, the calculated position did not reflect the exact position of the eel, rather the estimated short-term (20 min) centers of activity (Simpfendorfer, Heupel & Hueter, 2002). If the raw data had been used, the position would not have been that of the eel, but that of the receiver detecting the fish, which is less accurate. When no receivers recorded data at a given time interval, the position was estimated by linear regression between the last calculated position and the next calculated position using the R package "pastecs" (Grosjean and Ibanez, 2018) in R 3.3.1 (R Development Core Team, 2011).

Factors triggering migration

To highlight the factors triggering the downstream migration of silver eels, we considered migration to have started when eels reached dam A. The relationships between the environmental data (predictor variables) and the presence of silver eels in front of dam A were explored using Boosted Regression Trees (BRTs) (Elith et al., 2006; Elith, Leathwick & Hastie, 2008; Buston & Elith, 2011). Before implementing these models, all correlations between environmental descriptors were analyzed to remove variables, with a correlation level >50%. For modelling, we considered the environmental factors that occurred from the release time to the first detection in front of the dam. The analyses were fitted using the R "gbm" package (Ridgeway, 2006) and "dismo" supplement functions (Elith, Leathwick, & Hastie, 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). The ROC score ranged from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 indicates predictive discrimination that is no better than a random guess, and a score of < 0.5 indicates performance worse than random (Elith et al., 2006). The best model was chosen using the *gbm.simplify* function in "gbm" package, assessing the potential (changes in deviance and its standard error) to remove predictors using k-fold cross validation.

Escapement rate from dam A

At the end of the experiment, the rate of escapement (%) was defined as the number of individuals passing through dam A divided by the total number of tagged eels. The number of individuals passing through the dam was calculated as the number of eels caught in the nets after the compensation and drinking water intake pipes plus the number of eels recorded by the two first acoustic receivers located immediately downstream of this dam.

Effects of dam A on eel passage

To obtain a precise description of silver eel migration and behavior during migration, the following metrics were used for each eel: 1) daily swimming distance; 2) daily number of attempts to pass through the dam, i.e., the number of times an eel was detected in front of the dam (in cases with a long presence in this area, this value was incremented when the eel left the area and returned to it); 3) daily time spent attempting to pass the dam, i.e., the total time that an eel was detected in the area immediately in front of dam A compared to the number of tracked days.

The impact of the dam was studied using two variables. The first was the additive distance, which was defined as the distance travelled from initial detection in front of the dam to initial detection downstream of the dam, using the previously defined mean individual position. The second variable was additive time, which was defined as the time an eel spent from initial detection in front of the dam to initial detection downstream of the dam.

Individual efficiency to pass the dam A

Time to pass, which differs from additive duration, was defined as the time difference between initial detection of an individual in front of the dam when it overflowed and initial detection of the same individual downstream of the dam. Periods with dam overflow were exclusively used, because the time that an eel was present in front of the dam when it dam was not overflowing did not represent a real estimation of the efficiency of a given individual to pass. Time to pass was subsequently analyzed to detect possible correlations with the other behavioral metrics, such as the daily distance swam, the daily number of attempts, and the daily time to try to pass, using a principal component analysis (PCA, in "FactoMineR" package).

2.5.2 Dam B and dam C reservoirs

Because of the low density of receivers, the analyses at these two dams were performed differently to those in dam A reservoir.

Escapement rate and effects of dam B

Eel escapement rate for this dam was evaluated considering the ratio between the number of eels observed in the wolf trap and the number of eels detected by the last upstream receiver. However, considering the low efficacy of the wolf trap during high flow periods, eels observed at the first receiver downstream of the dam and not caught in the trap were added.

Because the stream immediately downstream of this dam was very small, and therefore not adequate for the acoustic telemetry survey, the downstream receivers were located at the mouth of dam C (500 m downstream of dam B), and were not relevant to evaluate the additional time to pass dam B. The impact of dam B was evaluated considering the additional time to pass it, which was defined as the time spent time from initial detection to final detection in front of the dam.

Escapement rate and effects of dam C

Considering the very low detection range of the receiver located downstream of dam C, eel escapement rate from this dam was only based on the final detection (number, time) of the last receiver located just upstream the dam, which was based on a number of assumptions. First, we expected escapement if the final detection occurred at night because silver eels are nocturnal species that avoid daylight, even though daily movement is possible. Thus, passage downstream of dam C is likely to occur if the final detection occurs very close to the final receiver. Therefore, we considered the mean lag between the final detections at the final receiver during the last 5-min of detection. A mean lag that was close to the theoretical mean lag given by the constructor (60 s) was assumed to indicate that an eel was located very close to the receiver. To improve readability, we used the ratio between the theoretical mean lag over the mean lag between the last detection, with a ratio close to 1 indicating eels were very close to the final receiver.

Thus, we considered that a silver eel successfully passed dam C when: (1) its final detection was at the receiver immediately in front of this dam; (2) the ratio observed/theoretical number of transmissions during the last 5-min was ~1; and (3) the time of the probable passages occurred at night. For eels that probably passed dam C, the additional time to pass the dam was defined as the spent time from initial detection in front of the dam to final detection in front of the dam, but only if the eel was never detected in front of the dam again.

2.5.3 Effects of eel size and weight on migration metrics

The relationships of individual migration metrics (probability to start migration, i.e., to reach dam A; escapement success from the three dams;, time to pass the three dams; additive distance to pass dam A) with eel biometry data (length and weight) were tested. For the probability to start migration and escapement success (binomial variables), the size of groups was unbalanced; thus, a Kruskal-Wallis test was used. For the other variables (quantitative variables, time to pass, and additive distance), linear regressions were implemented using R software.

3. Results

3.1 Factors triggering migration

Out of the 16 tagged eels, three did not migrate. These three eels were smaller and lighter than the migrant eels (Table 1), although Kruskal-Wallis rank sum test was non-significant ($p = 0.07$ for weight and $p = 0.12$ for length).

Only four variables were selected in the final model: water level, 12 h increase in water level, wind direction, and atmospheric pressure. This final model had a cross-validation explained deviance of 55.58% and an AUC of 0.95. Therefore, it was evaluated as excellent. The relative influence of water level, 12 h increase in water level, wind direction, and atmospheric pressure was 41.8%, 20.4%, 19.3%, and 18.5%, respectively (Figure 2). Water level had the strongest effect, with an abrupt threshold at around 25.7 m (Figure 2). Lower values indicated an absence of water in front of the dam, and that downstream migration was strongly suppressed. A 12 h increase in water level had a strong threshold of ~0.5 m/12 h, which favored silver eel migration (Figure 2). Wind direction had a positive effect when wind blew from 125° (east-southeast) to 170° (south-southwest). Finally, high atmospheric pressure enhanced migration (Figure 2).

3.2 Escapement rates

Out of the 16 tagged eels, three did not pass dam A. Two eels stayed at the release site and were detected by the receiver array for 8.8 and 118.6 days, and swam 9.44 and 62.9 km, respectively (Table 2). The first one, after this disappearance, was again observed in front of dam C the next year in another telemetry survey. The third eel was detected in front of the dam for 44.9 days and travelled 53.6 km; it failed to pass the dam after nine attempts during 560 minutes of activity near the dam (Table 2, Figure 3).

The eels that successfully passed dam A mainly travelled through spillways (81.2%, Table 3). Only three eels used the main pipe, but mortality was high, as two eels died (Table 3, Figure 3). No difference was observed in the length and weight of eels that successfully passed through spillways and those that successfully passed through the main pipe.

Out of the 13 eels that passed through dam A, two were found dead in the nets at the end of the main pipe; therefore, only 11 eels survived and were able to reach dam B. All of these eels passed through dam B (Figure 3). Seven eels were found in the wolf trap (of which three were not alive), and four were recorded by the receiver downstream of the dam, but were never found in the trap (Table 5, Figure 3).

Eight eels passed through dam B via the trap or over it, and were still alive afterwards. Two of these eels did not reach dam C and one did not pass it. Five other eels were recorded for the last time by the acoustic receiver near dam C. The ratio of mean theoretical lags between transmissions to the mean observed lags between transmissions at this receiver was ~1, except for eel 24. For eel 24 a final position very close to this receiver was indicated, and then very close to the dam (Table 6). Thus, these four eels likely passed through dam C (Figure 3). No difference was observed in the length and weight of eels that successfully passed through dam C and the eels that not passed (Kruskal-Wallis rank sum test, $p = 0.92$ for weight and $p = 0.93$

for length).

3.3 Effect of the dams on eel passage

The mean additive time to pass dam A was 21.3 ± 19.6 days, and ranged from 4.3 to 65.9 days. The mean additional distance to pass dam A was 39.7 ± 19.9 km, and ranged from 9.7 to 77.2 km (Table 4). The additive time to pass through dam B varied for each individual, ranging from 15 min to 7.25 days. The additive time to passed through dam C also varied, ranging from 2.4 days to 4.9 days (mean: 3.4 days). No relationship was observed for eel length/weight and additive time/distance (linear regression, R^2 = 7% for length and 14% for weight).

3.4 Efficiency of individuals to pass through dam A

The efficiency in passing through dam A varied among eels. Three eels passed through the main pipe of dam A before it overflowed. The group denominated as ‘fast’ was composed of eels that passed through the dam in less than four days after it overflowed. The group denominated as ‘slow’ was composed of eels that passed through the dam 14–21 days after it overflowed. The group denominated as ‘non-migrant’ was composed of eels that never crossed the dam. Therefore, after overflow started, two groups were observed (Figure 4).

The factorial analysis showed high segregation among the three delineated groups. The ‘non-migrant’ group was composed of three eels with the lowest values of daily time attempting to pass, daily distance swam, and daily number of attempts (Figure 5). The ‘fast’ group was formed of eight eels with a high number of attempts and a high daily distance swam, but with low daily time attempting to pass (Figure 5). The ‘slow’ group was composed of five individuals with the highest daily time attempting to pass, but with low daily number of attempts and daily swimming distance (Figure 5).

4. Discussion

4.1 Methodological limitations and the number of studied eels

Technological advances in acoustic telemetry have resulted in it becoming more widely used in recent years (Hussey et al., 2015). Some studies have used this technology to monitor thousands of animals simultaneously; however, the probability of signal collision increases, particularly when study sites are small or enclosed. Signal collision causes individuals (e.g., fish or eels) to become invisible to the receiver array, leading, for instance, to imprecise estimates of escapement. Second, telemetry data metrics might be misevaluated. Thus, these issues must be considered when designing telemetry surveys. A trade-off must be found between tagging as many individuals as possible and maintaining the quality of metrics for optimal evaluation and interpretation. In the current study, a number of behavioral metrics were used and refined. Tagging more eels in any one time period would certainly have hindered the quality of the studied metrics. In particular, cross validation between Capture Mark Recapture (CMR) and acoustic telemetry might provide the best compromise, but requires extensive time and technical effort.

4.2 Factors triggering migration

The factors triggering silver eel migration in river habitats have already been delineated (e.g., Trancart et al., 2013). Waterflow is the most frequently cited factor, presenting a strong positive effect (negative rheotaxis). The use of river flow to migrate represents selective stream transport, in which silver eels choose environmental conditions that limit effort and the consumption of fat reserves (Verhelst et al., 2018). In rivers that have dams, different factors appear to trigger migration. In our study, the main triggering factors were water level and a 12 h increase in water level. These triggers are similar to those described for lentic ecosystems (Trancart et al., 2018). In addition to hydrological factors, wind direction from south-south-east also had a strong positive effect on eel migration. This wind direction is the same as the direction of flow of the Frémur River; thus, wind might generate a surface water current that triggers migration by eels. Yet, locally prevailing winds are north-northwest associated with low atmospheric pressure. In comparison, winds from the south are associated with high atmospheric pressure, which is the fourth main triggering factor. Luminosity is considered a primary triggering factor for silver eel downstream migration, and was excluded from the final model. The very high turbidity (resulting in low light penetration) of the river during the migration period might explain the absence of this effect.

The triggers commonly found in rivers were attenuated in the Frémur River, due to the presence of dams. This phenomenon might have a major impact on this endangered eel species, delaying or entirely stopping downstream migration. Moreover, the triggering factors described in the Frémur River were only documented in January, whereas classical migration in non-obstructed rivers of the same geographic area normally occur between September and November.

4.3 Escapement rate from dam A

The presence of dam A likely prevented two eels from initiating downstream migration due to their failing to interpret/detect the triggers. Both eels exhibited significant movement after release; thus, post-surgery death was not a reason. One eel (number 20) was observed for a short period (8.8 days) before disappearing. However, this eel was observed 12 months later in another study in front of dam C; thus, it moved to the most upstream part of the river, where no acoustic receivers were present. A third eel (number 32) attempted to pass through the dam nine times over a cumulative 9.3 h period, but then migrated upstream. At the end of the tracking period, this eel was again detected at the release site. These eels were smaller and lighter than the other eels, even if the low size of the group blocked to reach a significant difference between the two groups.

4.4 Effect of dam A on eel passage

Only three eels crossed dam A through the compensation pipe and the drinking water input pipe, but two of these individuals were found dead in the nets at the end of the pipes. High water pressure and the 90° angle of the main pipe likely explains this mortality. Yet, the third eel successfully passed through the pipe and was recorded crossing the third and most downstream dam (dam C), demonstrating that it was not injured and still able to migrate. The grid blocking the pipe does not seem to be effective at preventing eels from entering, with management measures being required to address this problem. We suggest that the design of the grid is improved to block any fish from passing through.

The dam adds time to the migration of eels, by delaying their passage. This was demonstrated through the measurement of additive time, which is the accurate measurement of the difference between the first detection of eels in front of the dam and the first detection of the same eels downstream of the dam. The measurement of additive distance of migration induced by the dam was based on the mean longitudinal position of animals at 20-min intervals. Thus, this measurement is actually a minimal estimate, because potential lateral movements cannot be measured. Additive distance was very low compared with the total distance eels normally migrate to their reproduction areas (6,000 km from Frémur River). However, while this distance was minimal for a single barrage, this value must be multiplied by the number of dams in a given river (70,000 dams in French Rivers). Considering that this long migration occurs without food intake, this additive energetic cost might have significant effects on reproductive success. Moreover, this additive time might negatively impact eel migration by increasing the risk of predation (natural and anthropic).

4.5 Efficiency of individuals to pass through dam A

Two different behaviors were observed in eels that succeeded in crossing the dam. The fastest eels exhibited exploratory behavior, moving extensively and searching for alternative escape passages. The slowest eels exhibited sedentary behavior, and did not fully explore the reservoir, but attempted to pass through the dam after a long time (~20 days). The dam overflowed for a long period during our study (from December to the end of the study), which potentially facilitated the successful passage of both fast and slow eels. If the dam overflows for only a short period, which is a potential scenario under global climate change, only eels from the ‘fast’ group would be able to pass through the dam. This phenomenon might lead to the indirect selection of the ‘fast’ phenotype, i.e., animals with bold behavior. Caudill et al. (2007) showed that slow passage across dams by adult salmon is associated with unsuccessful anadromous migration; thus, fast eels exhibiting bold behavior have a greater chance of exiting from their growth watershed and reaching the site for reproduction. In comparison, Andersen, Marty & Arlinghaus (2018) showed that fishing has a greater negative effect on fish exhibiting bold behaviors than timid fish.

4.6 Impact of dam B

All eels recorded in dam B reservoir passed through dam B (the second dam), which was probably related to the low distance between the first and the second dam (i.e., there is a lower probability of eels becoming lost in a small area) and the small size of the second dam (i.e., higher probability of finding the exit passage). However, almost half of the eels (3 of 7) were found dead in the wolf trap. This mortality rate was higher than that usually observed in this trap (e.g., 17.7% in 2016–2017) even though high mortality events have been documented (Charrier et al., 2018). The cause of death remains unclear, but might have occurred during the upstream passage of eels to dam A by spillways or the main pipe. For instance, two of the three dead eels found in the trap had the lowest transit times between dams A and B; thus, they might have died before entering the trap, and were carried by water flow into the traps. Alternatively, excessively high water discharge at dam B might induce trauma or mortality. Of note, some of the eels were able to pass over the wolf trap; thus, this trap is not completely efficient for measuring the passage of eels during migration when overflow is high, as observed in this study. These observations led to the formulation of important recommendations for managing the Frémur River, especially dams A and B. We strongly recommend adding soft coats to the spillways, and adding a larger reception area at the foot of dam A. For dam B, we strongly recommend extending the size of the trap and revising the design of the entrance to the trap. These actions would reduce the amount of trauma and mortality to eels. These recommendations have already been taken into consideration.

4.7 Impact of dam C

Eight eels escaped from dam B, after which they encountered dam C. The condition (presence of injuries) of the four eels that crossed dam B over the wolf trap was not known; however, all four individuals that were caught and released from the wolf trap appeared healthy, but with cutaneous erosion. Therefore, the reason why two of the eels stopped migration between these two last dams, which are only 2.5 km apart, was not known. Similar to that documented between dam A and B, the very low water flow these two dams might explain this migration break.

Out of the six eels detected in the reservoir of dam C, only one returned to the upper part of the reservoir. Because the detection of eels downstream of this final dam was not very efficient, only an estimate of successful passage was obtained. The final record of the five remaining eels was obtained by the last acoustic receiver immediately upstream the dam (four of the five eels were very close to it), and at night. These five individuals likely passed through the third dam; however, one of these eels was detected farther upstream and in daylight, so it is not clear whether it eventually passed the dam or not. Therefore, the escapement rate of eels from dam C was considered to be 4/6.

4.8 Cumulative effect of the three dams

Out of the 16 eels that were tagged in the reservoir upstream of the first dam, only four (25%) successfully reached the estuary. Considering the small size of the Frémur River and the type of the dams (one with spillways and two with overflow crests), which are usually regarded as safe, this rate was unexpectedly low.

The additive time to pass these successive dams (21.3 ± 19.6 days, 20.1 ± 51.8 h, and 83.72 ± 27.52 h for dam A, dam B and dam C, respectively, reaching 25.62 days in total) might be problematic for reaching the breeding sites in time to ensure reproduction. As expected, the time to pass through a dam was inversely related to the size of the dam and its respective upstream reservoir. Nevertheless, a difference was documented between dam B and C; thus, the location of the overflow crest might affect the time required to pass. For instance, at dam B, the overflow crest points in the direction of the river. In comparison, at dam C, the overflow crest points to the side of the river. Another difference was the width of the spillways. For instance, the spillway at dam B was very small (3 m), while the one at dam C was very large (50 m). Consequently, the velocity of the water current passing over the crest of dam C was very low. We strongly recommended that the managers of dam C reduce the width of the spillway and lower the threshold. These actions would make the total surface of the opening similar to dam B, but the water current would be greater, possibly favoring the passage of silver eels.

Other possible assumption to explain the difference in the observed escapement rates might be some heterogeneity in water quality between the three reservoirs. This has been observed in different sites from a lined river section, where Gomes and Wai (2019) showed that water quality could influence the species distribution. One can assume that these differences could be also induce variations in behavioural responses and then escapement rate difference. For example, a low oxygen rate could be penalizing for eels during their exploration phase to find the exit. Unfortunately, there was no monitoring for these data in the three dams from this study. Nevertheless, this phenomenon could potentially be verified by comparing the representative population fraction of eels from each reservoir in the biological dataset.

Because the density of acoustic receivers was low in dam B and C, it was not possible to obtain an accurate estimate of the additive distance covered by eels across the three dams. Based on the total additive time of presence (i.e., 25.62 days) and the mean daily distances swam by eels in dam A (1.86 $km.d^{-1}$), the additive distance for the three dams was estimated as 47.65 km. Travelling this additive distance has extra energetic costs, likely contributing to the various factors impairing the reproductive migration route of European eels in this highly disturbed river.

4.9 Individual variation

Although our sample size was small, no relationship was observed between the morphological characteristics of eels and their efficiency in passing through the three dams. For instance, longer and heavier individuals were not the fastest to pass. Moreover, there was no difference in the morphological traits of eels between the two ways available to pass dam A (spillways versus main pipe). Thus, the efficiency of individuals in migration did not appear to be linked to morphology, but to differences in behavior.

4.10 Comparing the impacts of dams with mechanical elements

In comparison to our estimate of 25.62 days for eels to pass three dams without turbines, Behrmann-Godel and Eckmann (2003) showed that silver eels required 0 to 8 days to cross a hydroelectrical power dam in the Meuse River (Germany). Carr and Whoriskey (2008) showed that the median time for eels to pass dam turbines in the USA was just 1 min at night and 8 min during the day, and 46.5 min for eels passing by bypass. In a small river in France, Travade et al. (2010) detected five different behaviors with very different time to pass a small hydroelectrical dam, with a maximum delay of 30 h to pass the dam. Longfin (*Anguilla dieffenbachia*) and shortfin eels (*A. australis*), (Brown et al., 2007) in New Zealand required

0.93 h (55.9 min; range 1 min to 9.96 h) and 0.23 h (13.9 min; range 1 min to 4.92 h) to pass a hydroelectric dam, respectively. Time to pass seems to a major issue for non-hydroelectrical dams, maybe because energy production requires a constant high flow of water, which contrasts with dams created to generate reservoirs for water supply, which retain the main part of water discharge.

5. Conclusions

This study clearly showed that dams without turbines that are equipped with large spillways or overflow crests have a strong negative impact on the migration of silver eels. First, the triggering of migration might be delayed or entirely halted by the masking or attenuation of the effect of environmental triggers that have been previously identified, such as water flow. This delay might extend several months, with serious implications on the timing of arrival of eels at supposed reproduction sites (Sargasso Sea) after the mean peak of arrival, which is estimated to be in February (Righton et al., 2016). Second, the presence of successive dams has clear negative and additive impacts, increasing the time and distance required by eels to exit the river. This increase, added to the that caused by the attenuation of triggering factors, further increases the final time of arrival at the reproduction site. This increase in distance also impacts fitness, as it reduces the energy that eels are able to allocate to reproduction. Third, part of the population might never find a passage through the dam, contributing to the loss of the reproductive potential of this species. Fourth, a possible evolutionary effect might appear, leading to the possible selection of the fast/bold phenotype. Yet, this phenotype is very sensitive to human pressure caused by fishing. Finally, the rate of direct mortality caused by the successive dams strongly affects the silver eel population and impairs the 40% of escapement, reducing the abundance of the pristine stock required to sustain the population.

Based on these observations, strong recommendations have been made by the National Museum of Natural History, which have already been taken into consideration. Although the present study was limited to a single study site, global recommendations could be made for natural sites where eels are present. Indeed, many important rivers supporting eel populations have similar dams in some parts of their watersheds. These dams, considered as safe to date, must be revised as they actually represent an important potential threat to the persistence of eel populations.

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Tables

Table 1. Morphological characteristics and silvering stage of tagged European eels

Eel number	Total Length	Total Weight	Sex
17	794	788	f
18	644	383	f
19	629	360	f
20	530	228	f
21	640	506	f
22	520	261	f
23	660	597	f
24	537	304	f
25	561	320	f
26	605	466	f
27	776	689	f
28	853	1247	f
29	974	1515	f
30	680	621	f
31	635	441	f
32	572	338	f

Table 2. Activity descriptors for the three silver eels that did not pass dam A.

Eel number	Number of tracked days	Total swimming distance (km)	Daily swimming distance (km)	Number of attempts to pass dam	Time to attempts to pass dam (min)
19	118.6	62.9	0.5	0	0
20	8.8	9.4	1.1	0	0
32	44.9	53.6	1.2	9	560

Table 3. Summary of European eel escapement, passing strategies, and survival rates at dam A. “SW” = spill way; “MP” = main pipe; “-” = unknown. Survival rate was only evaluated for fish caught in nets close to the main pipe.

Eel number	Passing strategy	Survival
17	SW	-
18	SW	-
21	SW	-
22	MP	Alive
23	MP	Dead
24	SW	-
25	SW	-
26	SW	-
27	MP	Dead
28	SW	-
29	SW	-
30	SW	-
31	SW	-
Total	76.9 % by SW	

Table 4. Impact of dam A on the migration of silver eels

Eel number	Additive time (days)	Additive distance (km)
17	65.9	71.4
18	57.1	30.4
21	21.2	32.6
22	9.1	9.7
23	4.7	33.9
24	24.8	77.2
25	15.5	53.2
26	30.7	39.4
27	11.2	21.8
28	10.7	47.3
29	5.1	38.9
30	16.2	46.8
31	4.3	14.2
Mean	21.3	39.7
Standard deviation	19.6	19.9

Table 5: Fate and behavior of the European eels that reached dam B. Survival was only evaluated for eels caught in the wolf trap. "Y" = yes; "N" = no; "-" = unknown.

Eel number	Escapement (Y/N)	Passing strategy	Survival	Additive time (hours)
17	Y	Trap	Dead	29.3
18	Y	Trap	Alive	14.4
21	Y	Over the trap	-	0.4
22	Y	Over the trap	-	174.1
24	Y	Trap	Alive	0.4
25	Y	Trap	Dead	0.2
26	Y	Trap	Alive	1.5
28	Y	Trap	Dead	0.2
29	Y	Trap	Alive	0.3
30	Y	Over the trap	-	0.4
31	Y	Over the trap	-	0.3
Total / Mean	100 %	64 % trap	43 % dead, 57 % alive	20.1 ± 51.9

Table 6. European eels escapement from dam C and additive migration time. "Y" = yes; "N" = no; "-" = unknown.

Eel number	Attempts to pass the dam (Y/N)	Last detection location	Theoretical lag / last observed lag	Time of last detection	Escapement (Y/N)	Additive time (hours)
18	N	Downstream dam B	-		N	-
21	Y	Last receiver upstream dam C	1.06	05:00 AM	Y	58.6
22	Y	Last receiver upstream dam C	1.37	07:00 AM	Y	118.8
24	Y	Last receiver upstream dam C	3.85	02:00 PM	N	-
26	N	Downstream dam B	-	-	N	-
29	Y	Last receiver upstream dam C	0.86	11:00 PM	Y	92.2
30	Y	Downstream dam B	-	-	N	-
31	Y	Last receiver upstream dam C	1.69	10:00 PM	Y	65.3
Total / Mean	75% attempted				50% escaped	83.72 ± 27.52

Figure captions

Figure 1. Map indicating the positions of the acoustic receivers (red circles) in the Frémur River, northwestern France, and the A, B, and C dams.

Figure 2. Partial plots of the functions fitted for the final Boosted Regression Trees model describing the triggering of downstream movement. The relative contribution that explains the variance of each descriptor is shown in parentheses. Black lines represent raw data and red lines represent smoothed data.

Figure 3. Overview of the fates of tagged European eels for each dam.

Figure 4. Number of European eels and the time required to pass dam A. Time to pass is defined as the time difference between an individual first being detected in front of the dam, when the dam overflowed, and when the same individual was first detected downstream of the dam. Negative time to pass values indicate passage before overflowing, i.e., via the main pipe.

Figure 5. Factorial map of the efficiency of individual European eels to pass through dam A based on behavioral metrics (indicated by arrows). Each eel is represented by a group symbol and a number, with a barycenter for each group.

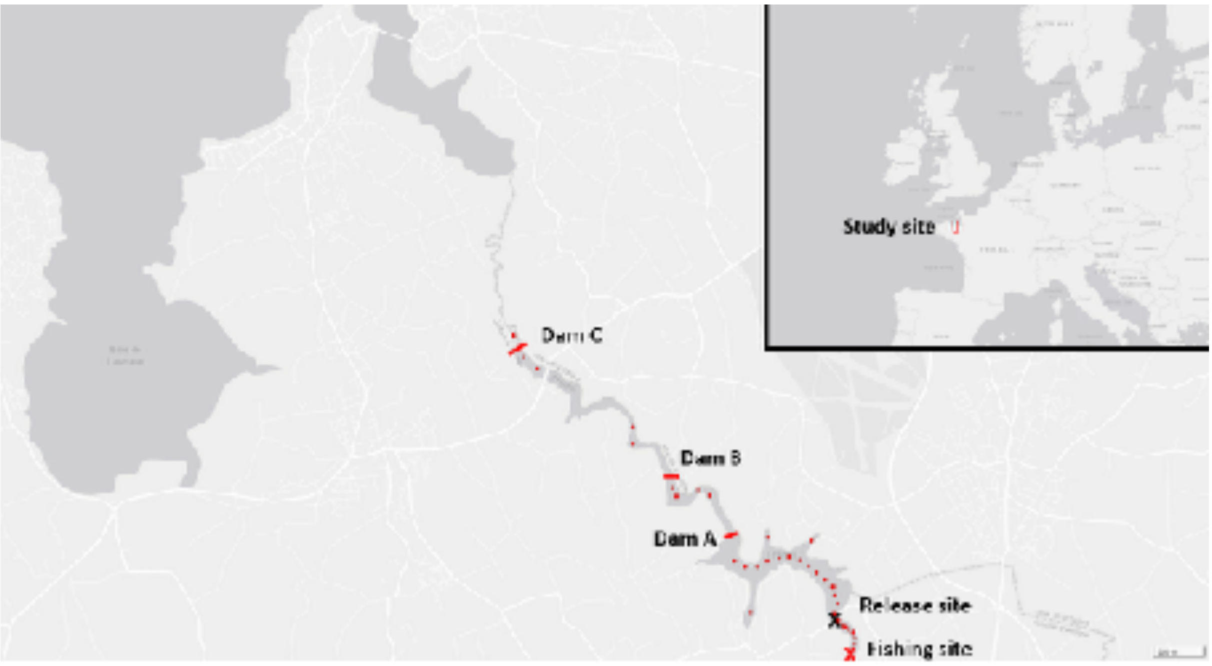

Figure 1

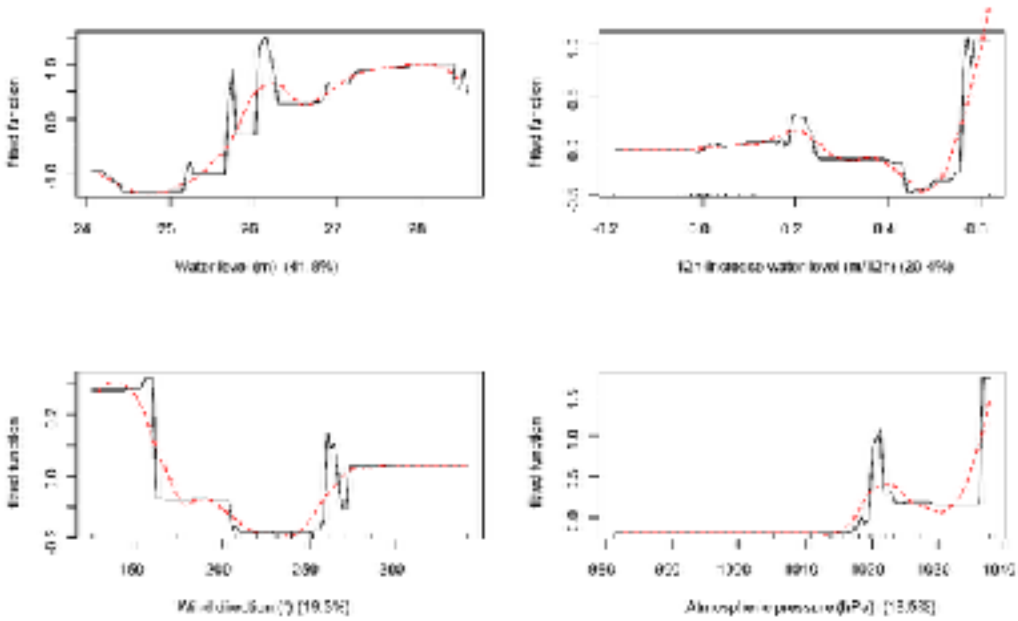

Figure 2

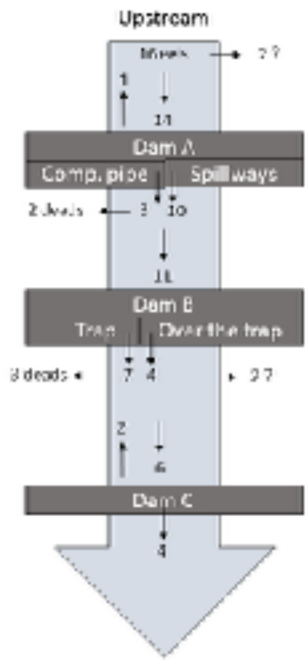

Figure 3

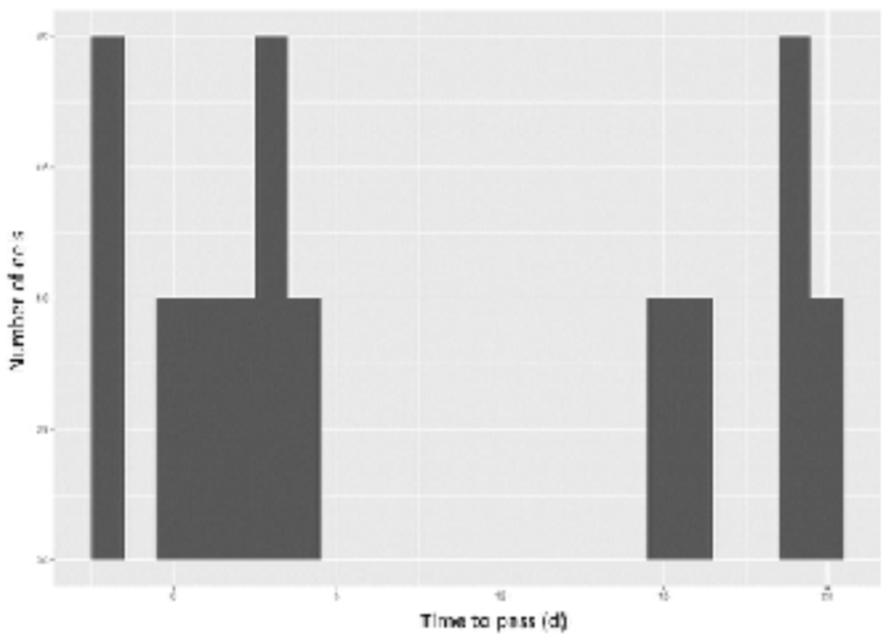

Figure 4

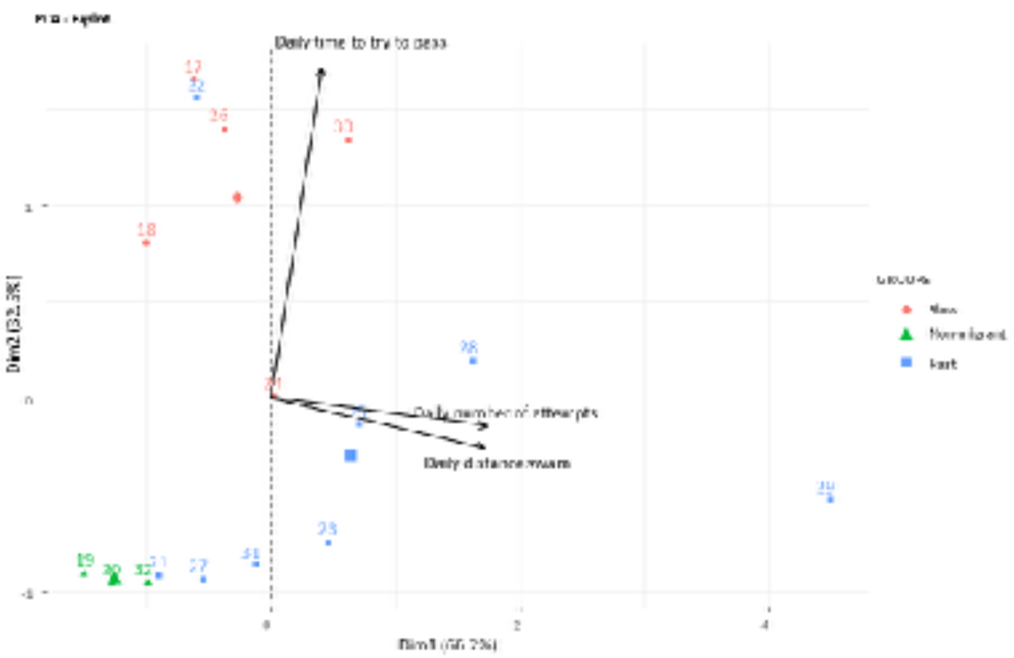
Daily time to try to pass
Daily number of attempts
Daily distance swum
Slow
Fast

Figure 5