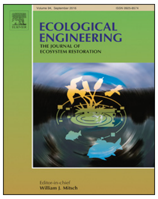
Ecological Engineering 123 (2018) 202–211

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng



Silver eel downstream migration in the River Rhine, route choice, and its impacts on escapement: A 6-year telemetry study in a highly anthropized system

Thomas Trancart[a,b,*], Stéphane Tétard[c], Anthony Acou[a,b,d], Eric Feunteun[a,b], Frédéric Schaeffer[e], Eric de Oliveira[c]

[a] *Museum National d'Histoire Naturelle, Centre de Recherche et d'Enseignement sur les Ecosystèmes Côtiers (CRESCO), 38 rue du port Blanc, 35800 Dinard, France*
[b] *UMR BOREA, MNHN, CNRS 7208, Sorbonne Université, IRD 207, UCN, UA, France*
[c] *EDF R&D LNHE - Laboratoire National d'Hydraulique et Environnement, 6 Quai Watier, 78401 Chatou Cedex, France*
[d] *UMS Patrimoine Naturel (Patrinat), AFB, MNHN, CNRS, CP41, 36 rue Geoffroy Saint-Hilaire, 75005 Paris, France*
[e] *Association Saumon Rhin, Route Départementale 228 – Lieu-dit « La Musau », 67203 Oberschaeffolsheim, France*

ARTICLE INFO

Keywords:
Escapement
Migration
Rhine river
Silver-eel
Telemetry
Path selection

ABSTRACT

Several routes are available for the downstream migration of silver eels in the river Rhine system. Very different effects on migration success can result from this choice, such as speed and migration duration or escapement rate. We studied the downstream migration of silver eels in a river section with two different routes. The first route is the initial and old riverbed, with two dams equipped with two rather small or medium sized hydropower plants (HPPs) located at the beginning and at the exit of the bypass stretch. Both HPPs have small bar spacing (10 mm and 20 mm, respectively) and the second HPP has two downstream bypasses. The second route is a power canal, supplying four major HPPs (maximum discharge capacity = 1400 $m^3 s^{-1}$) and a nuclear power plant with cooling water. Firstly, this study focused on highlighting the factors influencing route choice. Secondly, we focused on the consequences of this choice. We demonstrate that water current management in the old riverbed at the study site had a 40% higher negative effect on eel survival than that by a consecutive passage in four turbines.

1. Introduction

The European eel is a catadromous species widely distributed in Europe and northern Africa with an outstanding life cycle consisting of a single breeding in the Sargasso Sea, a first transatlantic migration as larvae, called leptocephali, which use oceanic currents that lead them from the spawning area to the continental shelf, and a growth stage in coastal and inland habitats where they remain and grow for 5–25 years (Tesch, 2003). Then, the silver eels swim downstream and undertake their breeding migration back to the Sargasso Sea, some 5000 km away from their growth habitats (Righton et al., 2016).

Because of the complexity of their life cycle, European eels are exposed to a number of threats, all caused by human activity (oceanographic regime shifts, river management, habitat destruction and related connectivity disruption, organic and metallic contaminants, fisheries, etc.) (Feunteun, 2002; Miller et al., 2016). Consequently, the recruitment of European eels is currently estimated below 10% of the maximum level recorded in the late seventies (ICES, 2018), and the species is now far outside its safe biological limits, and thereby considered by the IUCN as an endangered species (Jacoby and Gollock, 2014). In order to protect the European eel (Dekker and Casselman, 2014), the European Union has demanded that measures be taken to allow at least 40% escapement of reference silver eel biomass, relative to unexploited, unpolluted circumstances in unobstructed rivers (European Commission, 2007). A full understanding of the eel downstream migration biology and behavior are, thus, an absolute requirement to complete these objectives, and numerous studies have been conducted.

At the end of the growth stage, a complex hormonal activity enhances the silvering metamorphosis (Dufour, 2003; van den Thillart et al., 2009). The silver eels are then ready as potential migrants, but external cues are needed to trigger the downstream migration. In

---

[*] Corresponding author at: Museum National d'Histoire Naturelle, Centre de Recherche et d'Enseignement sur les Ecosystèmes Côtiers (CRESCO), 38 rue du port Blanc, 35800 Dinard, France.

E-mail address: thomas.trancart@mnhn.fr (T. Trancart).

https://doi.org/10.1016/j.ecoleng.2018.09.002
Received 25 June 2018; Received in revised form 30 August 2018; Accepted 3 September 2018

unobstructed European rivers, the main downstream migration peaks occur in November with great regional and interannual variations (David Righton et al., 2016). Numerous environmental parameters are known to trigger downstream migration of silver eels: rainfall, river flow, temperature, lunar phase, wind, atmospheric pressure, turbidity, and conductivity (see reviews in Haro, 2003; Bruijs and Durif, 2009; Trancart et al., 2013).

The impacts of hydroelectric complexes are well known: they can cause injuries (Bruijs and Durif, 2009), direct mortality (Winter et al., 2006; Bruijs and Durif, 2009), delay (Behrmann-Godel and Eckmann, 2003), or stop downstream migration (Durif et al., 2003). Navigation canals or bypassed stretches of rivers may also be used as routes during silver eel downstream migration (Klein Breteler et al., 2007; Verhelst et al., 2018). Heavily managed rivers are often transformed into complex networks of river sections regulated by dams that provide a wide range of routes for silver eels on their downstream migration to the sea. The consequences of route choice on migration success of silver eels has been poorly documented.

In the complex aquatic network of the lower Rhine, Klein Breteler et al. (2007) showed that numerous different routes were used by silver eels but with great temporal differences. In the same study site, Breukelaar et al. (2009) concluded that the route choice cannot simply be explained by the river water discharge. In a highly regulated river (river Stour, Southeast England), the gate position and the upstream water level had significant effects on the migration routes selected by eels (Piper et al., 2013).

The Rhine is one of the most important rivers in Northern Europe (1240 km long, 198,000 km^2 catchment area, 1053 $m^3 s^{-1}$ mean water flow at Rheinalle). For a long time, this high discharge has been used for hydropower and cooling water purposes: 28 hydropower plants (HPPs) (including 10 large plants in France) and 5 nuclear plants have been built along the river between 1898 and 2012. On the Rhine, the historical riverbed has been diverted to create navigation canals. Numerous pathways have become available for eel migration, and this route choice can have very important consequences. For example, in the case of the upstream part of the upper Rhine, where the river is diverted to the Grand Canal d'Alsace (GCA) in Kembs, a passage by GCA will induce turbine mortalities (8–27% depending on HPP (De Oliveira, 2012a)). On the other hand, a passage by the almost turbine-protected bypassed stretch, called the Vieux Rhin (two rather small or medium HPPs, both equipped with fish-friendly racks [10 and 20 mm] and with downstream bypasses for the second one), may probably induce higher survival probabilities rates.

A large and long telemetry experiment was conducted to study the migration behavior and success of silver eels on their downstream migration of one the largest hydropower complex of the Rhine River located in France. Silver eels could either choose the hydropower canal (the Grand Canal d'Alsace, hereafter called GCA) and the bypassed riverbed (Vieux Rhin, hereafter called VR). Our aim was to assess the consequences of route choice on the downstream migration of silver eels. In order to accomplish this, we specifically addressed the following objectives: 1) investigate the factors triggering the downstream silver eel migration; 2) to analyze the proportion of eels in each of the pathways (GCA and VR) and the factors controlling route choice; and 3) to investigate the migration characteristics (duration and speed) and the escapement rates in the two possible routes.

2. Material and methods

2.1. Study site

This study was conducted on the large and complex river Rhine system (1320 km long, 185000 km^2, across 6 countries, Fig. 1). This river is extensively used for freight transport and hydro-electrical production (10 large power plants ($>$ 100 MW) in France). The fish were released downstream Bâle (47.613°N, 7.578°E, Swiss, PK 170), 3–4 km upstream Kembs. Seven kilometers further downstream (Kembs, Kilometer Point 163), the Rhine river divides into 2 sections: the "Grand Canal d'Alsace" (GCA) and the "Vieux Rhin" (VR) (Fig. 1).

A dam is located at the beginning of VR in order to control the flow in the GCA (Kembs dam), which has a maximum discharge capacity of 1400 $m^3 s^{-1}$ and is 50 km long, from Kembs to Vogelgrun (Kilometer Point 120). There are four HPPs along the GCA: Kembs, Ottmarsheim, Fessenheim, and Vogelgrun, all managed by Electricité De France (EDF).

The second pathway for downstream migration is the VR section. This section is 50 km long and is the historical natural Rhine riverbed. The minimum flow in this stretch of the river changed during the course of this study due to relicensing of the Kembs hydroelectric complex. Before 2011, the minimum flow was set at 20 or 30 $m^3 s^{-1}$, depending on the period of the year: 20 between December and February; 30 the rest of the year. Since 2011, the minimum flow in the bypass stretch has been raised to 52 $m^3 s^{-1}$ in the winter period (November-March) and a maximum of 115 $m^3 s^{-1}$ in the summer period (June-August), with intermediate discharge thresholds in the periods in between. The first major dam of VR (Kembs' dam) located upstream is equipped with a small HPP ($Q_{max} = 27\ m^3 s^{-1}$) which used to deliver nearly all of the minimum flow in the bypass stretch (the complement being supplied by a fishway). The screen of this HPP has a small bar spacing (10 mm) which physically blocks the eels at this part of the river basin (Courret and Larinier, 2008). Since the raise of the minimum flow in 2011, this HPP continues to drive the turbine, although at a lower ratio of the minimum flow (from 23% to 52%). A second dam, built for agricultural purposes, is located at the end of the VR (Brisach dam). This dam is also equipped with an HPP ($Q_{max} = 60\ m^3 s^{-1}$) whose screen has a small bar spacing (20 mm) to prevent fish from entering turbines and which is also equipped with two fishways for upstream and downstream migration. The four gates (45 m wide each) of the Brisach dam (190 m wide) begin to open only when the HPP is at full capacity (60 $m^3 s^{-1}$). The VR river stretch remains relatively "pristine" compared to the GCA, despite the regulation of the water flow and the alteration of sediment transport. However, as mentioned above, minimum flow has been raised since 2011 and a major renaturation program has been conducted (sediments reinjections, habitats creations) (Garnier and Barillier, 2015). The canal and the river then reconnect just downstream of Vogelgrun (48.036°N, 7.568°E).

2.2. Tracking technology

The tracking technology used in the present study was Radio Frequency Identification (RFID), with the NEDAP Trail System (www.nedaptrail.com). This telemetry system consists of active transponders (including a battery), each with a unique code, implanted in the fish and a network of detection and recording stations. A detection station is composed of antenna cables stretched across the entire width of the river bed and the recording station. Preliminary tests showed a 10–20 m mean detection range in some NEDAP sites used in this study (Tétard, 2013). High non-detection rates are possible with this technology, as for instance 43% of fish were never detected in Breukelaar et al. (2009).

2.3. Location of the NEDAP sites

The tagged fish were recorded in the passage at several detection points distributed along the study site. The first NEDAP loop (called hereafter NEDAP 1) was located upstream from the diversion between the VR and the GCA (47.616°N, 7.573°E, Fig. 2). The second NEDAP loop (NEDAP 2, 47.627°N, 7.569°E) controlled the entry in the VR (located at about one hundred meters downstream of the Kembs dam). The entry in the GCA was controlled by two NEDAP loops (3 and 4, 47.652°N, 7.525°E) located downstream of the Kembs hydropower plant. The output of these two sections was controlled in the unified Rhine River, near Marckolsheim (NEDAP 5, 48.065°N, 7.573°E) (Fig. 2),

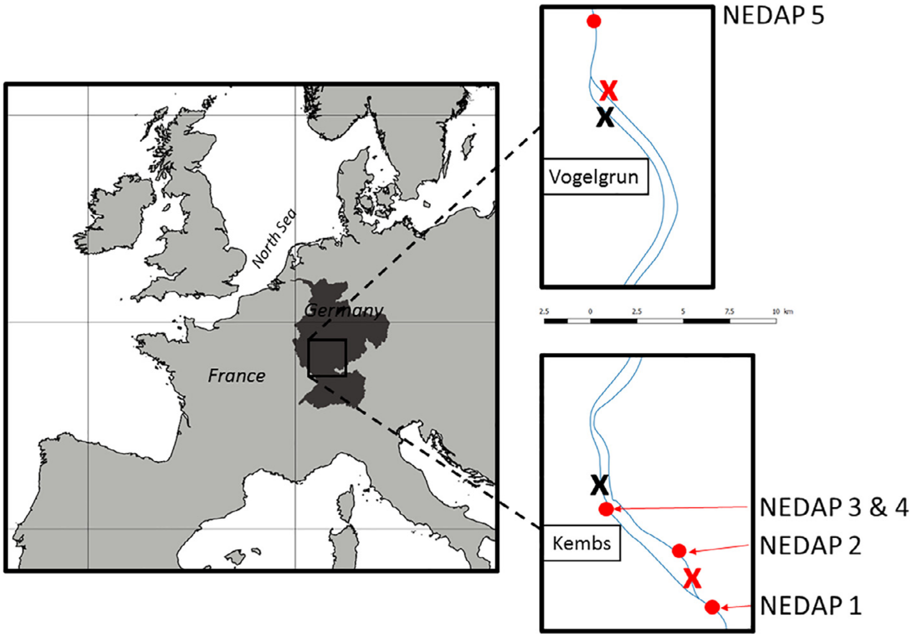


Fig. 1. Location of the study area in the Rhine river basin (in dark grey). The names of the main cities are in black frames. The red points indicate the location of the detection stations; black crosses indicate the location of the major hydropower plant with turbines, and red crosses indicate the location of the dam with small and protected turbines. The main release site was located 7 km upstream from Nedap 1 site. The second release site was 2 km downstream from Nedap 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

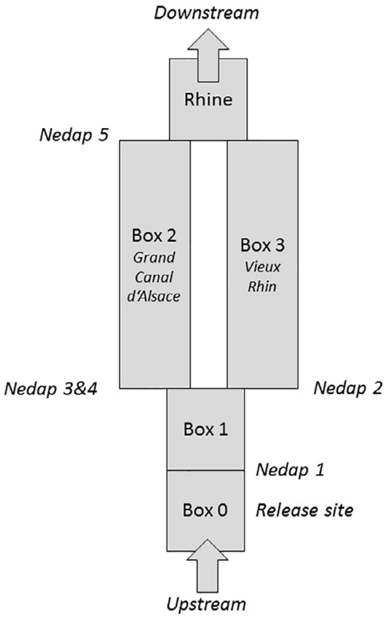


Fig. 2. Schematic graphic of the study site.

downstream the GCA and VR junction.

2.4. Fishing collection, tag implementation and eels release

One thousand and ninety-nine eels were collected at four sites located in two tributaries of Rhine (Ill and Moselle rivers, respectively, 101 and 254 eels), and at two different locations on the Rhine River (592 from the German location and 152 from the French locations). These four fishing sites show very different characteristics (Table 1).

Highly significant fishing-site dependent differences in eel biometry were observed for total length ($p < 0.005$) and total weight ($p < 0.005$). Post-hoc analysis (Tukey test) showed that the largest and heaviest eels were those in Ill river and in the French part of Rhine river, with no difference between the two sites ($p = 0.88$ for length and $p = 0.92$ for weight). The smallest eels were caught in Moselle and in the German Rhine, without significant difference in eels for length ($p = 0.99$) or weight ($p = 0.96$).

Table 1
Characteristics of the fishing sites.

	Ill	Moselle	Rhin (France)	Rhin (Germany)
Size of the watershed (km^2)	4760	11400	185 000	
Total length (km)	216	560	1233	
Mean discharge (m^3 s^{-1})	60	290	1053	
Fishing method	Traps	Fyke nets	Fyke nets/Electrofishing	

Fishing and tagging were performed from 2010 to 2015. Approximately 200–220 fish were released each year, except in 2010 (~30), with several different sessions by year, mainly (96%) during the downstream migration period in this area (October to January). The site of release is located 7 km upstream from Nedap 1. Some sporadic releases were made in June (n = 7 eels) and August (n = 32 eels) at the same site. Supplementary releases have been made directly in VR, just downstream from the Kembs dam, to study the escapement from this route during the winter in 2011 and 2012 (n = 95). The mean size of the tagged eels was 855 mm (sd = 58 mm, Table 2) and the mean weight was 1256 g (sd = 277 g, Table 3), and their stage of silvering were III (16.5%), IV (15.7%) and V (67.8%), according to the Durif classification (Durif et al., 2005).

The tag weight in air was 25 g, implicating a ratio tag/body mass slightly above the 2% rule of thumb (Winter, 1996). However, this value is often objected to (Jepsen et al., 2003) and, given the large size

Table 2
Total length (mm) of tagged eels according to migration stages (Durif classification) and fishing sites.

	Ill	Rhin (FRA)	Moselle	Rhin (GER)
St III	846 ± 15	847 ± 16	831 ± 18	844 ± 16
St IV	807 ± 14	799 ± 19	812 ± 15	812 ± 15
St V	888 ± 6	891 ± 8	867 ± 8	859 ± 7
TOTAL	877 ± 5 (a)	872 ± 7 (a)	850 ± 7 (b)	849 ± 6 (b)
Number of tagged eels	101	152	254	592

Different letters denote factor categories that were different ($P < 0.05$) using Tukey's multiple comparisons tests.

Table 3
Total weights (g) for tagged eels according to migration stages (Durif classification) and fishing sites.

	Ill	Rhin (FRA)	Moselle	Rhin (GER)
St III	1140 ± 66	1165 ± 72	1102 ± 79	1121 ± 69
St IV	987 ± 48	1049 ± 63	1055 ± 51	1040 ± 50
St V	1462 ± 29	1499 ± 40	1285 ± 36	1288 ± 32
TOTAL	1394(a)	1373(a)	1211(b)	1221(b)
Number of tagged eels	101	152	254	592

Different letters denote factor categories that were different ($P < 0.05$) using Tukey's multiple comparisons tests.

of eels studied here, we assumed that the mass of the tag was not disadvantageous. Moreover, absolutely no difference was statistically highlighted in the pre-downstream behavior (i.e., duration of pre-migrating period) according the class of length, a finding which reinforced the assumption that the mass of the tag was not disadvantageous.

2.5. *Data treatment and modeling*

This experimental protocol provided location information from 12/23/2010 to 06/26/2016.

2.5.1. *Factors triggering the downstream silver eel migration*

Firstly, to identify the environmental conditions that favored downstream migration, we used the presence/absence model. The relationships between the environmental data (predictor variables) and eel presence/absence in the different river sections were explored using Boosted Regression Trees (BRTs) (Elith et al., 2006; Elith et al., 2008; Buston and Elith, 2011). This technique is considered to be a powerful modeling technique to assess fish distribution (França and Cabral, 2015). In the present models, we considered the presence/absence data in two different boxes: box 0 was the release site upstream from the first Nedap loop; while, box 1 was the river section just before the diversion of the Kembs dam (Fig. 2).

Data were regulated to obtain daily presence/absence data, following Trancart et al. (2017). An eel is supposed to be present in a given box until its detection in another box. In case of a "box drop," i.e., when a fish was recorded in a *n* box without be recorded in the *n-1* box, the data from this fish were removed from analysis. In these models, environmental factors have been collected close to the NEDAP stations. The following parameters were collected on a daily basis: rainfall (in mm), mean water temperature (°C), atmospheric pressure (hPa), turbidity (FNU), luminosity (lx), and water flow ($m^3 s^{-1}$). The daily mean has been used for all these data. For water flow, three different measures were available: total Rhine flow measured upstream of the GCA (Rheinalle), and one value of flow in each pathway (GCA and VR).

We considered the environmental factors that occurred between the first detection in box 0 and the first detection in box 1; while, environmental factors that occurred after the movement from box 0 to box 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 deviation explained, cross-validated correlation between model prediction and observed data, and the area under the Receiver Operating Characteristic (ROC) curve, after recent reports (e.g., Amorim et al., 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).

2.5.2. *Route choice and factors explaining this distribution*

We used Ivlev's electivity index, (Ivlev, 1961) for route choice. This index is commonly used to describe predator preference for prey. We used it to investigate route choice according to the intensity of water flow, since migration pathways to the migration runs are thought to depend upon water discharge (Legault et al., 2003). Ivlev's index was scaled from −1 to 1; where −1 indicates total avoidance of a route; 0 indicates that a route is taken in proportion to water flow, and 1 indicates total preference for a route. This index is used to determine if the route choice is voluntary (some factors attract or repulse) or involuntary (water discharge proportional).

After this, when route choice was voluntary, we investigated what factors could cause this choice. For this, to identify the environmental conditions favoring the passage by a given pathway (VR or GCA), we used the same methodology as for the first point, i.e., presence/absence model. The relationships between environmental data (predictor variables) and eel presence/absence in the two pathways were explored using BRTs. In the present models, we considered presence/absence data in three different boxes: box 0 was the release site, box 2 was GCA and box 3 was VR (Fig. 2). Each box (except for the first) was located within two NEDAP stations.

2.5.3. *Migration pattern and escapement*

For the third part of this study, we compared the characteristics of the migration along the two routes using classical metrics: speed, transit time and escapement rate.

3. Results

3.1. *Biometrical and stage effects on silver eel migration*

There were no significant differences in length or weight between migrant and non-migrant eels (ANOVA Gaussian GLM, $p = 0.46$ and $p = 0.20$ respectively). The proportion of each migration stage (III, IV and V) were also similar between migrant and non-migrant eels.

3.2. *Factors triggering downstream silver-eel migration*

The final model describing eel movements from Box 0 to Box 1 showed a large predominance of a unique factor: the number of days after release, with a huge peak during the first seven days (Fig. 3). Great differences between the four fishing sites were observed for this factor. Eels collected from Ill river (60 $m^3 s^{-1}$ mean water flow) and introduced in the Rhine river exhibited a great downstream migrating behavior, since 61% migrated downstream the first day after release, and 90% during the first week (Fig. 4). Eels from Moselle (290 $m^3 s^{-1}$ mean water flow) exhibited this same behavior, although to a lesser extent (40 and 66%, respectively, for the first day and the first week after release). Finally, a few eels from the Rhine (1053 $m^3 s^{-1}$ mean water flow) migrated just after release (23 and 13% the day after for German and French Rhine, and 53 and 38% in the first week for the same sites, respectively).

In order to avoid behavioral bias related to the impact of the fishing site, all movements that occurred less than seven days after release (348/616) were considered as false bias movement and not real downstream migration. For that reason, they were removed from the analysis of movements, as suggested by previously studies (e.g., Le Pichon et al., 2015).

Without these data, the final model describing eel movements from Box 0 to Box 1 highlighted four main factors triggering downstream movement (68.6% of total deviation accounted for) (Fig. 5). The first of these factors is phenology, which showed two main periods during migration: one peak during the fall (October-December) and a second peak during the spring (April-June). The second factor is river flow, with an abrupt threshold at about 1400 $m^3 s^{-1}$. The third factor is temperature, with an 8 °C threshold. Finally, the last factor triggering

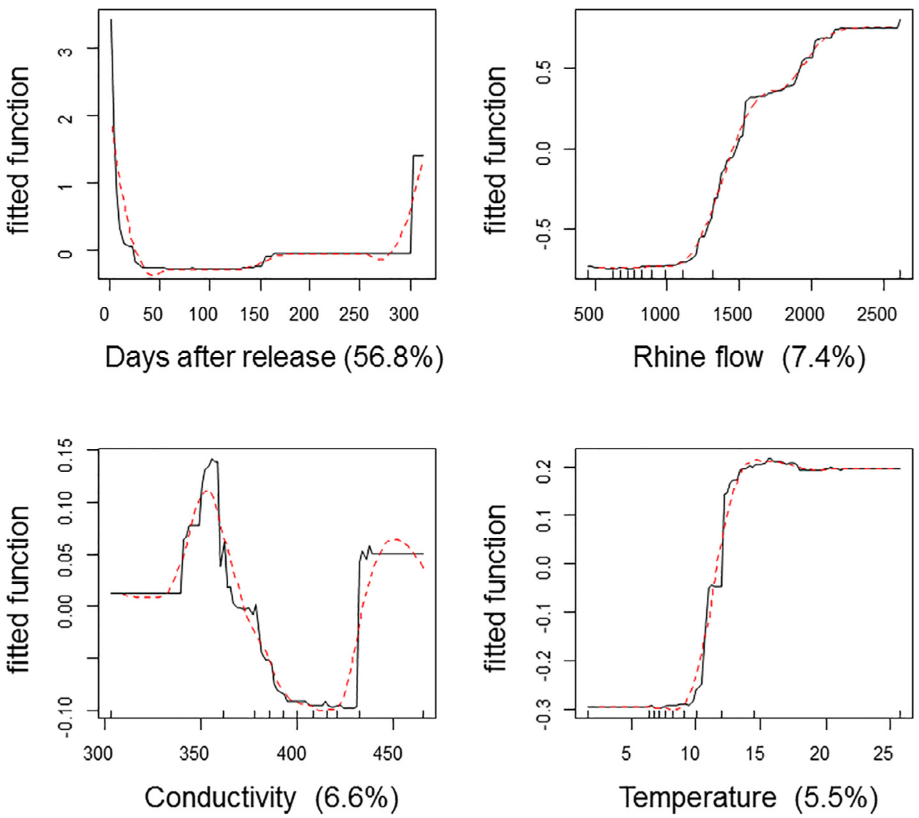


Fig. 3. Partial plots of the functions fitted for the final Boosted Regression Trees (BRT) models describing movement from Box 0 to Box 1 (n = 616). The relative contribution to explain the variance of each descriptor is shown in parentheses (black lines are raw data and red lines are smoothed data). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

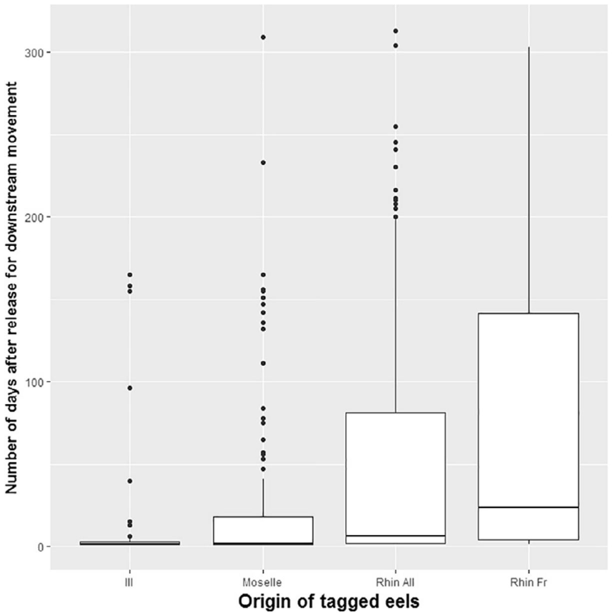


Fig. 4. Influence of fishing site on the first movement between box 0 and box 1 after release.

migration is rainfall, with a low threshold at about 0.2 mm day^{-1}.

3.3. Route choice and factors explaining this distribution

The analysis of water flow distribution showed that 85% of the days in the study period had a water flow ranging from 448 to 1440 m^3 s^{-1} (Fig. 6), which is the low limit for opening of the VR floodgates. Days with higher values were scarce (Fig. 6).

The proportion of eels migrating through VR and CGA was not proportional to the flow distribution between the two routes (Fig. 7). At low water flow values in the Rhine (500–1000 m^3 s^{-1}), the percentage of water flow discharged in VR accounted for approximately 10% of the River Rhine flow, and the percentage of eels migrating through VR was twice as small. After 1000 m^3 s^{-1}, the percentage of eels choosing VR increased strongly. At 1400 m^3 s^{-1} in GCA, corresponding with 1700–1750 m^3 s^{-1} in the Rhine, the water capacity in GCA was full and the floodgates in VR were largely opened, and then the proportion of eels choosing VR increased more markedly again. For instance, at 2500 m^3 s^{-1}, the proportion of eels choosing VR was twice the proportion of water in VR. The electivity index showed a non-stable evolution (Fig. 8), with negative values below 1200 m^3 s^{-1}, suggesting a rejection of the VR route during low flow. On the other hand, this index became positive above 1200 m^3 s^{-1}, suggesting a slightly but significant attraction for the VR route. However, results from high water flow have to be considered carefully, because of the low number of fish migrating during these high-water flow regimes.

The four main factors influencing the passage (74.4%) by the GCA were: phenology (two peaks, as in the previous model), flow in GCA with a 1200 m^3 s^{-1} threshold, turbidity, and luminosity (Fig. 9). The movement by GCA was totally repressed by low turbidity and high luminosity.

The four main factors (77.1%) influencing the passage by VR were: water flow in GCA with a 1400 m^3 s^{-1} threshold, water flow in VR with a 200 m^3 s^{-1} threshold, month with a unique peak in the fall, and temperature, with a highly significant decrease below 10 °C (Fig. 10).

3.4. Migration pattern (duration and speed) and escapement rate

Ninety-nine hundred and thirty-nine eels were marked and released at site A during the 5 years of this study. A great majority of them went through the GCA route (598 eels), whereas only 45 went through the VR. The others (296 eels) were never recorded or never observed beyond NEDAP1. An analysis of variance showed no difference (p = 0.48) in the total length of eels taking the GCA route and then taking the VR

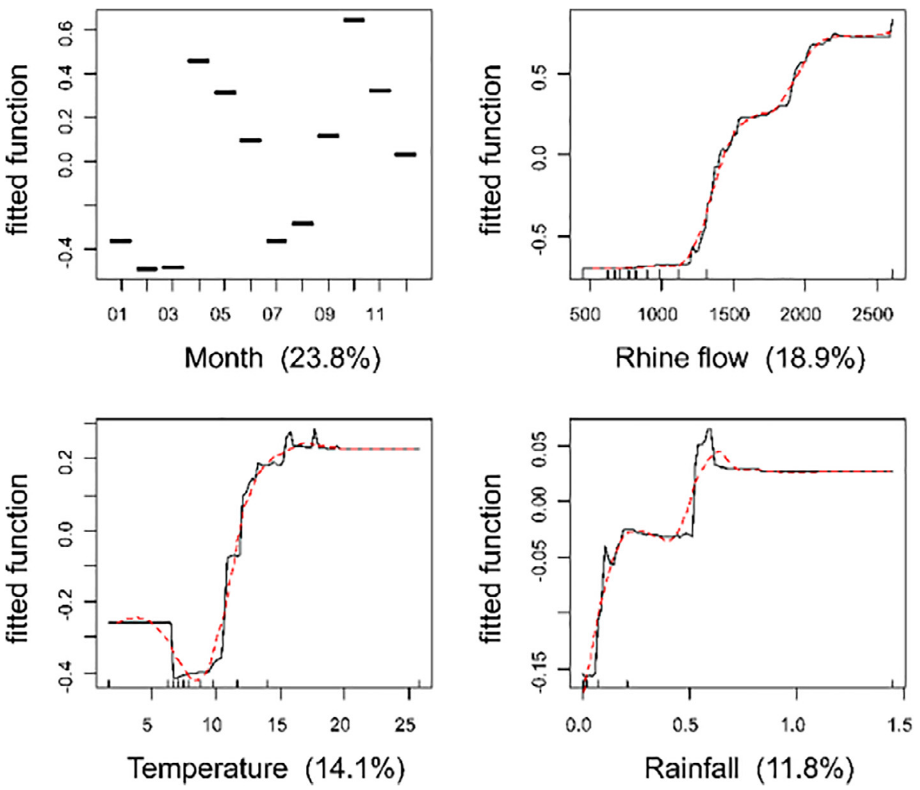


Fig. 5. Partial plots of the functions fitted for the final Boosted Regression Trees (BRT) models describing movement from Box 0 to Box 1 without fish moving less than 7 days after the release (n = 268). The relative contribution of each descriptor is shown in parentheses (black lines are raw data and red lines are smoothed data). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

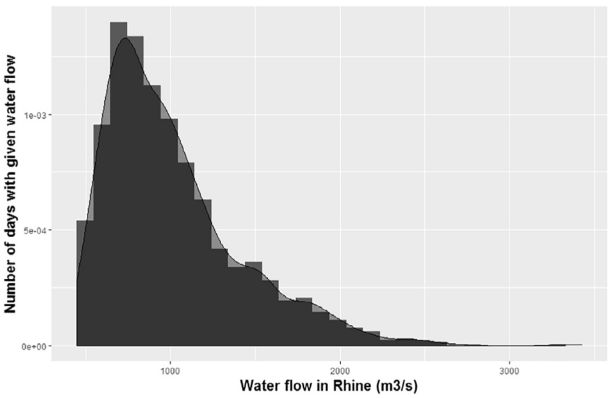


Fig. 6. Distribution of days with a given water flow during the 6-year study period.

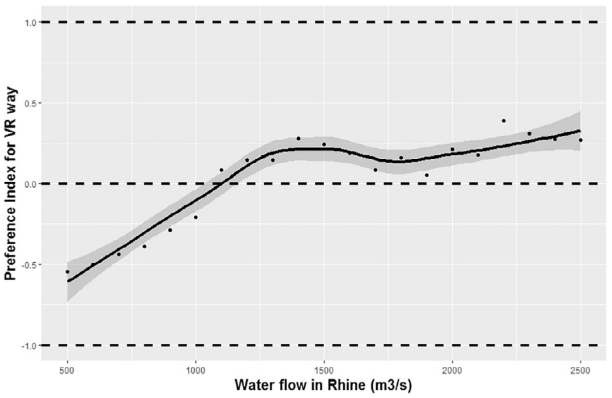


Fig. 8. Electivity index for route choice.

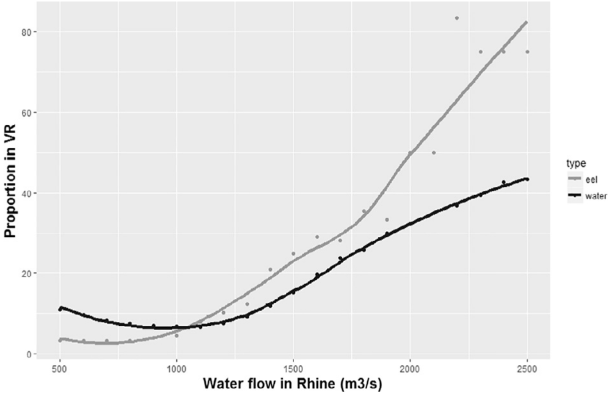


Fig. 7. Comparison between water flow in VR/water flow in GCA and between the number of eels crossing via VR/number of eels crossing via GCA.

route, nor any difference in total weight (p = 0.48).

A total of 95 eels were released in the VR immediately downstream of the dam of Kembs to better understand the migration behavior in this section of the Rhine. From all the fish observed at the mouth of VR (95 + 45), only 30.7% were detected again, at the exit. The two escapement rates from VR for eels released at the first site (and observed crossing the dam) and at the second site were equal (31.1% and 30.5%, respectively).

Out of the 598 eels observed at the beginning of the GCA, only 301 were detected at the exit (i.e., at station Nedap 5), indicating that only 50.3% of the eels escaped from the GCA, which is a larger percentage of eels than the proportion escaping from the VR section.

The median time for travelling the VR route was 15.25 days, but with a large variability. The fastest individual travelled this route in 0.26 day, and the slowest in 308.43 days. The median duration for travelling the GCA route was 5.75 day, with a large variability (range = 0.32 day/209.88 day).

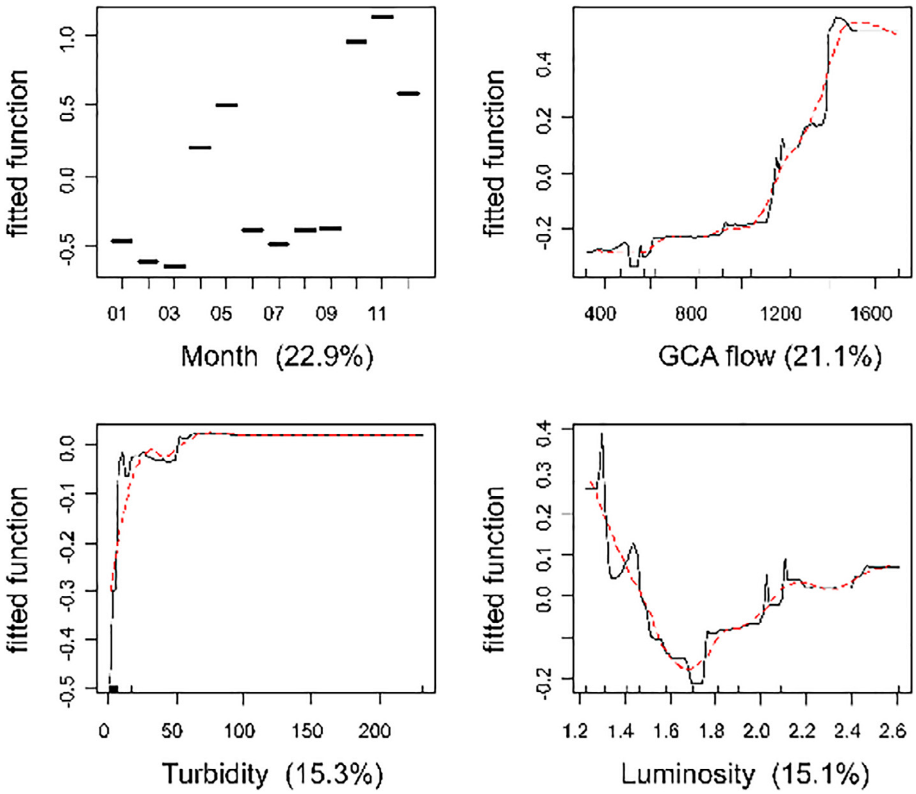


Fig. 9. Factors influencing the selection of the pathways trough GCA (n = 289 eels).

4. Discussion

4.1. Post-surgery and location of fishing site

Our results clearly supported our allegation that the location of the fishing site had highly significant consequences on post-release eel behavior. With all the data, the main factor triggering the onset of the downstream movement from the release site was the number of days after release, with a very high contributive effect (56.8%, and only 7.4% for the second effect). Moreover, a very high peak was observed

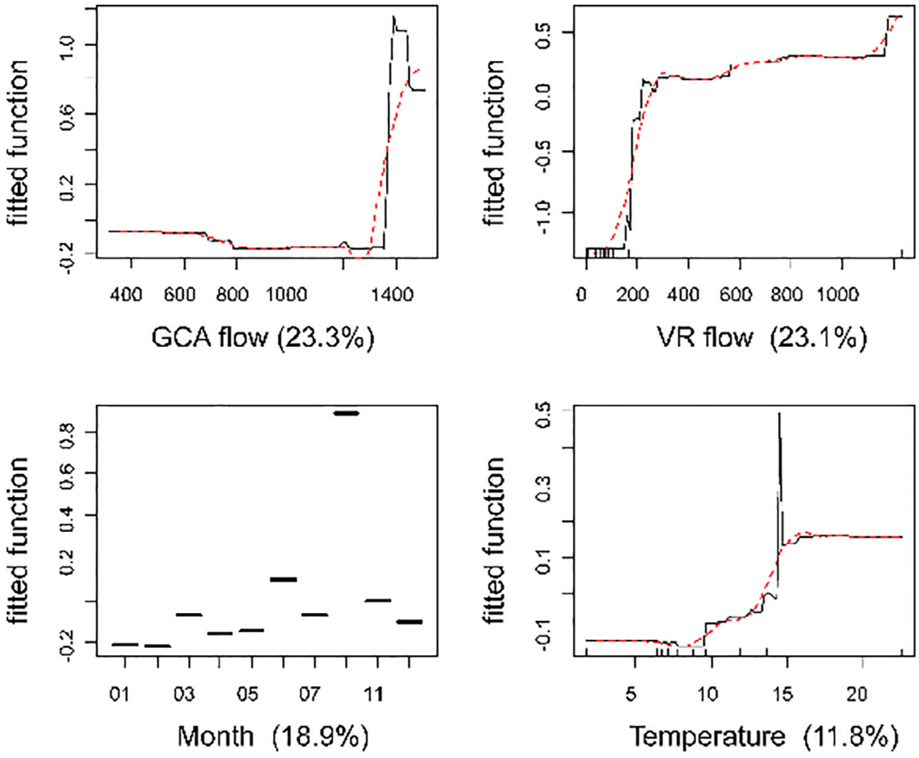


Fig. 10. Factors influencing the selection of the pathways trough VR (n = 40 eels).

for the smallest values (less than seven days), suggesting a very fast beginning of the migration after release. This phenomenon is usually observed in telemetry studies (e.g., Bultel et al., 2014).

Fish from Ill and Moselle rivers started migrating mainly the first week after release (90 and 66%, respectively). A lower proportion of eels collected from the two sites in the river Rhine started migrating the first week after release (53 and 38%, respectively). The size of the watershed and the mean water flow is directly linked with the proportion of eels that started migrating during the first week after release (60 $m^3 s^{-1}$ mean discharge for river Ill, 290 $m^3 s^{-1}$ for river Moselle and 1053 $m^3 s^{-1}$ for river Rhine). Eel growth may last several years during which individuals may imprint hydrological regimes, and abrupt change of water flow regimes from one river system to another may lead to over-sensibility of water conditions. Whatever the causes, this result highlights the importance of the fishing site origin in telemetry studies, and strongly suggests favoring fishing sites with similar hydrodynamic characteristics.

4.2. Double period of migration

In the present study, the movement probabilities were clearly time dependent, with two main periods of maximal activity. The first one during autumn and early winter is typically observed for silver eels (Vollestad et al., 1986; Poole and Reynolds, 1990; Cullen and McCarthy, 2003; David Righton et al., 2016). The second period, which takes place during spring (April–May–June) is more rare but has already been observed (Westin, 1998; Tesch, 2003; Aarestrup et al., 2008; Stein et al., 2016). The main assumption for this late migration in the Baltic is the low water flow in early autumn (Westin, 1998). In Danish rivers, no environmental cues apparently explained the springtime runs (Aarestrup et al., 2008). In a recent study, two peaks were also observed in silver eel migration in the Elbe River (Germany), and the triggering factors were different: spring migration seems to be triggered solely by water temperature (Stein et al., 2016) and water flow. In the current study, high water flow periods were observed during spring and autumn. It is likely that the spring river floods are caused by snow melting, which triggered the migration of the remaining silver eels from the previous season or precocious migrants.

4.3. Triggering factors

The migration of silver eels on the Rhine was also triggered by water flow, temperature and rainfall, which confirmed the current knowledge on European silver eel migration (Feunteun, 2002; Bruijs and Durif, 2009; Trancart et al., 2013). The main benefit of the employed method is to precisely highlight threshold values in the factors structuring the eel presence/absence. For instance, below 1300 $m^3 s^{-1}$, silver eel migration is totally repressed. On the other hand, over 2000 $m^3 s^{-1}$, a plateau is observed: the probability of presence will not increase anymore, indicating migration behavior is stabilized at this value.

4.4. Route selection

Our study depicted the pathways chosen by silver eels on their downstream migration: the hydropower canal (GCA) or the natural Rhine River (VR). The dominant way was clearly the GCA (598 vs 45 for VR), as a result of the water management in this river section. Indeed, floodgates divert most of the river flow to the GCA and limit the discharge towards the VR most of the time to 20–100 $m^3 s^{-1}$ in order to maintain legal minimum water flow, representing an average of 10% of the total water flow in Rhine (during the study). The floodgates are widely open only when water flow in GCA exceeds 1400 $m^3 s^{-1}$. During low flow conditions (i.e., $< 1200\, m^3 s^{-1}$), the electivity index for VR way is negative, suggesting that silver eels did not voluntary select VR and then actively select the GCA. On the other hand, in our study, when the water flow was higher than 1200 $m^3 s^{-1}$, the electivity index was positive, suggesting a preference for VR way once the floodgates are opened. A clear route choice in silver eels migrating downstream, which cannot be fully explained by different discharge ratios between two possible routes, was previously observed in the lower Rhine (Breukelaar et al., 2009). However, on some sites, escapement rates via spillways (compared to passages through powerplants) were closer to discharge ratios (Bau et al., 2013). This reveals that downstream migration of silver eel may not only be a passive drift with flow and that route selection may highly depend on the behavior of fish and on the geometry of sites (e.g., orientation of intakes, orientation of dams, orientation of main stream before obstruction). The cause of this selection is still unclear, and data provided are not relevant to conclude.

The proposed scenario is that eel migration is favored when the Rhine River flow exceeds 1200 $m^3 s^{-1}$. When they reach the bifurcation between the hydropower canal (GCA) and the old Rhine River (VR), they follow the main current stem because the flow drives them there. When the river flow is $> 1400\, m^3 s^{-1}$, the floodgates are more largely opened (according the Rhine flow) and eels seemingly prefer to pass the floodgates and travel by the natural Rhine River. However, this route is more dangerous, because only 30% silver eels are detected 54 km farther, downstream the junction between GCA and VR, whereas, "only" 50% seem to survive to the travel through the Grand Canal d'Alsace. In other words, the water discharge regulation seems to be problematic for silver eel migration.

4.5. Increasing the number of migrating eels via VR and escapement

When VR is open (i.e., water flow in GCA $> 1400\, m^3 s^{-1}$), a minimal additional 200 $m^3 s^{-1}$ is required to increase the probability of presence in VR; and, although a higher water flow in VR does not seem to significantly increase the probability of presence, this may be an artefact due to detection failure. For management purposes, this result suggests that a water flow of 200–300 $m^3 s^{-1}$ in VR is enough to favor passage by VR and then without turbine passages. However, other results showed that escapement was much lower in VR than in GCA (30.7% vs 50.3%), while four dams with turbines and one nuclear powerplant cooling system are located on GCA. The passage by the dam at the beginning of the VR cannot explain this lower escapement, because there is no difference in escapement rate between eels that have experienced the passage by this dam (i.e., released in the first site) and eels that have not experienced this passage (i.e., released directly in VR, downstream from this dam). This lower escapement success came as a surprise. Due to low intake capacities of hydro power plant Brisach ($Q_{max} = 60\, m^3 s^{-1}$), high passage rate from spillways were expected and then a low mortality.

We hypothesize that it could be a consequence of the artificial low water flow regulation maintained in VR, which prevented eels from getting environmental stimuli from their environment. Eels do not usually display a uniform migratory behavior (Stein et al., 2016), making stops when environmental cues decrease or disappear, but in the case of a highly regulated system, this phenomenon could be exacerbated. Under such conditions, eels are exposed to increased hazards as predation by fish or avifaunae. Indeed, catfish *Silurus glanis* is abundant in river Rhine with a population statistically increased during the last decades (Pawlowski et al., 2012), and could take advantage of corridors with low water flow. Another possible explanation could be a loss of orientation cues caused by low water flow. The decrease or the loss of these cues, very important for downstream migration in the river (Acou et al., 2008; Trancart et al., 2013), could cause a stop in the migration, as observed in front of dams (Durif et al., 2003). Indeed, the selection of the VR pathway implies exposure to a loss of river flow gradient in a very short time. For instance, an eel can experience a drastic reduction in water flow from 1600 $m^3 s^{-1}$ before selection (in the Rhine), to and average flow no greater than 200 $m^3 s^{-1}$ once in VR. Although habitat and river morphology, are strikingly different in the two river sections, this strong difference in water flow is bound to have a strong impact on eel behavior.

Finally, we can also hypothesize that the low escapement rate from VR could be a consequence of blockage of the final dam (Brisach) by natural, industrial and domestic wastes, as frequently reported by Brisach dam managers. Nevertheless, the low intake capacities of this HPP suggest a main passage by spillways, and then rejects this assumption.

Mortality tests made by the power company EDF (Electricité De France) highlighted a 21.6% mortality rate for the Ottmarsheim powerplant and a 7.4% mortality rate for the Fessenheim powerplant (De Oliveira, 2012). For the two other dams with turbines, considering the type of the turbines, the authors estimate the mortality at equal rates, i.e., around 20% for the Kembs dam and around 7% for the Vogelgrun dam. Thus, a realistic estimation of cumulative turbine mortality for GCA is around 50%, which nearly corresponds to the remaining escapement rate (50.3%) measured by this telemetry study. This suggests that no other cause for mortality was at play in this section of the river. On the other hand, this study showed that, once silver eels have managed to migrate through the floodgates leading to the VR, this migration route may prove up to 40% more dangerous than migrating through four hydropower plants.

5. Conclusion

Overall, our study unequivocally demonstrates that, besides direct mortality caused by turbines, which is already well-known, the regulation of water flow in very long bypass stretches of the river, or waterways obstructed in any way, must be properly managed, in order to increase silver eel escapement and survival success.

Acknowledgements

The authors want sincerely thank Electricité De France Unité de Production EST for logistic and funding, Saumon Rhin Association for tagging and monitoring, the natural reserve Petite Camargue Alsacienne for technical help and the fishermen providing the eels.

References

Aarestrup, K., Thorstad, E.B., Koed, A., Jepsen, N., Svendsen, J.C., Pedersen, M.I., Skov, C., Økland, F., 2008. Survival and behaviour of European silver eel in late freshwater and early marine phase during spring migration. Fish. Manage. Ecol. 15, 435–440.

Acou, A., Laffaille, P., Legault, A., Feunteun, E., 2008. Migration pattern of silver eel (*Anguilla anguilla*, L.) in an obstructed river system. Ecol. Freshw. Fish 17, 432–442.

Amorim, E., Ramos, S., Elliott, M., Bordalo, A.A., 2016. Immigration and early life stages recruitment of the European flounder (*Platichthys flesus*) to an estuarine nursery: the influence of environmental factors. J. Sea Res. 107, 56–66.

Bau, F., Gomes, P., Baran, P., Drouineau, H., Larinier, M., Alric, A., Travade, F., De Oliveira, E., 2013. Suivi par radiopistage de la dévalaison de l'anguille argentée sur le Gave de Pau au niveau des ouvrages hydroélectriques d'Artix, Biron, Castetarbe, Baigts et Puyoo (2007-2010).

Behrmann-Godel, J., Eckmann, R., 2003. A preliminary telemetry study of the migration of silver European eel (*Anguilla anguilla* L.) in the River Mosel, Germany. Ecol. Freshw. Fish 12, 196–202.

Breukelaar, A.W., Ingendahl, D., Vriese, F.T., De Laak, G., Staas, S., Klein Breteler, J.G.P., 2009. Route choices, migration speeds and daily migration activity of European silver eels *Anguilla anguilla* in the River Rhine, north-west Europe. J. Fish Biol. 74, 2139–2157.

Bruijs, M.C.M., Durif, C.M.F., 2009. Silver eel migration and behaviour. In: Spawning Migration of the European Eel: Reproduction Index, A Useful Tool for Conservation Management. Springer, pp. 75–95.

Bultel, E., Lasne, E., Acou, A., Guillaudeau, J., Bertier, C., Feunteun, E., 2014. Migration behaviour of silver eels (*Anguilla anguilla*) in a large estuary of Western Europe inferred from acoustic telemetry. Estuar. Coast. Shelf Sci. 137, 23–31.

Buston, P.M., Elith, J., 2011. Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. J. Anim. Ecol. 80, 528–538.

Courret, D., Larinier, M., 2008. Guide pour la conception de prises d'eau « ichtyo-compatibles » pour les petites centrales hydroélectriques.

Cullen, P., McCarthy, T.K., 2003. Hydrometric and meteorological factors affecting the seaward migration of silver eels (*Anguilla anguilla*, L.) in the lower River Shannon. Environ. Biol. Fishes 67, 349–357.

De Oliveira, E., 2012a. Estimation de l'échappement des anguilles argentées lors de la dévalaison sur le Rhin. 6 quai Watier – 78401 CHATOU CEDEX.

De Oliveira, E., 2012b. Estimation des taux de survie et de blessures pour des anguilles européennes (*Anguilla anguilla*) franchissant une turbine Kaplan. Chatou.

Dekker, W., Casselman, J.M., 2014. The 2003 Quebec declaration of concern about eel declines-11 years later: are eels climbing back up the slippery slope? Fisheries 39, 613–614.

Dufour, S. 2003. Reproductive endocrinology of the European eel, *Anguilla anguilla*. In: Eel biology. pp. 373–383.

Durif, C., Dufour, S., Elie, P., 2005. The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. J. Fish Biol. 66, 1–19.

Durif, C., Elie, P., Gosset, C., Rives, J., Travade, F., 2003. Behavioral study of downstream migrating eels by radio-telemetry at a small hydroelectric power plant. In: D. DA, ed. Biology, Management, and Protection of Catadromous Eels (Vol. 33). Bethesda, Maryland: American Fisheries Society Symposium.

Elith, J.H., Graham, C.P., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., Hijmans, J.R., Huettmann, F.R., Leathwick, J., Lehmann, A., Li, J.G., Lohmann, L.A., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC, M., Overton, J., Townsend Peterson, A.J., Phillips, S., Richardson, K., Scachetti-Pereira, R.E., Schapire, R., Soberón, J., Williams, S.S., Wisz, M., Zimmermann, N., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813.

European Commission, 2007. Council Regulation (EC) No 1100/2007 of 18 September 2007. Establishing measures for the recovery of the stock of European eel. Official Journal of the European Union.

Feunteun, E., 2002. Management and restoration of European eel population (*Anguilla anguilla*): an impossible bargain. Ecol. Eng. 18, 575–591.

França, S., Cabral, H.N., 2015. Predicting fish species richness in estuaries: which modelling technique to use? Environ. Modell. Software 66, 17–26.

Garnier, A., Barillier, A., 2015. The Kembs project: environmental integration of a large existing hydropower scheme. La Houille Blanche 21–28.

Haro, A., 2003. Downstream migration of silver-phase anguillid eels. In: K. Aida, K. Tsukamoto, & K. Yamauchi, Eds., Eel Biology. US Geol Survey, SO Conte Anadromous Fish Res Lab, Biol Resources Div, Turners Fall, MA USA. Haro, A (reprint author), US Geol Survey, SO Conte Anadromous Fish Res Lab, Biol Resources Div, POB 796, Turners Fall, MA USA: Springer-Verlag Tokyo.

ICES. 2018. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL). Kavala, Greece.

Ivlev, V.S., 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, Connecticut.

Jacoby, D., Gollock, M. 2014. Anguilla anguilla. The IUCN Red List of Threatened Species.

Jepsen, N., Schreck, C., Clements, S., Thorstad, E. B. 2003. A brief discussion on the 2% tag/bodymass rule of thumb. In: M. T. Spedicato, G. Lembo, & G. Marmulla, Eds., Aquatic telemetry: advances and applications. Rome, pp. 255–259.

Klein Breteler, J., Vriese, T., Borcheding, J., Breukelaar, A., Jörgensen, L., Staas, S., de Laak, G., Ingendahl, D., 2007. Assessment of population size and migration routes of silver eel in the River Rhine based on a 2-year combined mark-recapture and telemetry study. ICES J. Mar. Sci. 64, 1–7.

Le Pichon, C., Coustillas, J., Rochard, E., 2015. Using a multi-criteria approach to assess post-release recovery periods in behavioural studies: study of a fish telemetry project in the Seine Estuary. Anim. Biotelem. 3, 30.

Legault, A., Acou, A., Guillouët, J., Feunteun, E., 2003. Suivi de la migration d'avalaison des anguilles par une conduite de débit réservé. Bull. Fr. Pêche Piscic. 43–54.

Miller, M.J., Feunteun, E., Tsukamoto, K., 2016. Did a "perfect storm" of oceanic changes and continental anthropogenic impacts cause northern hemisphere anguillid recruitment reductions? ICES J. Mar. Sci. 73, 43–56.

Pawlowski, S., Jatzek, J., Brauer, T., Hempel, K., Maisch, R., 2012. 34 years of investigation in the Rhine River at Ludwigshafen, Germany – trends in Rhine fish populations. Environ. Sci. Eur. 24, 28.

Piper, A.T., Wright, R.M., Walker, A.M., Kemp, P.S., 2013. Escapement, route choice, barrier passage and entrainment of seaward migrating European eel, *Anguilla anguilla*, within a highly regulated lowland river. Ecol. Eng. 57, 88–96.

Poole, W.R., Reynolds, J.D., 1990. Observations on the silver eel runs of the Burrishoole River System, Ireland, 1959 to 1988. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 75, 807–815.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Ridgeway, G., 2006. Generalized Boosted Regression models. Documentation on the R package "gbm." (http://www.i-pensieri.com/gregr/gbm.shtml, Ed.).

Righton, D., Westerberg, H., Feunteun, E., Økland, F., Gargan, P., Amilhat, E., Metcalfe, J., Lobon-Cervia, J., Sjöberg, N., Simon, J., Acou, A., Vedor, M., Walker, A., Trancart, T., Brämick, U., Aarestrup, K., 2016. Empirical observations of the spawning migration of European eels: the long and dangerous road to the Sargasso Sea. Sci. Adv. 2.

Stein, F., Doering-Arjes, P., Fladung, E., Braemick, U., Bendall, B., Schroeder, B., 2016. Downstream migration of the European eel (*Anguilla anguilla*) in the Elbe River, Germany: movement patterns and the potential impact of environmental factors. River Res. Appl. 32, 666–676.

Tesch, F.W., 2003. The Eel. Biology and Management of Anguillid Eels. Chapman & Hall, London.

Tétard, S., 2013. Test de détection des antennes NEDAP.

Trancart, T., Acou, A., De Oliveira, E., Feunteun, E., 2013. Forecasting animal migration using SARIMAX: an efficient means of reducing silver eel mortality caused by turbines. Endangered Species Res. 21, 181–190.

Trancart, T., Feunteun, E., Danet, V., Carpentier, A., Mazel, V., Charrier, F., Druet, M., Acou, A., 2017. 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. Ecol. Freshw. Fish 1–10.

van den Thillart, G., Dufour, S., Rankin, J.C., 2009. Spawning Migration of the European Eel. Springer, Netherlands.

Verhelst, P., Buysse, D., Reubens, J., Pauwels, I., Aelterman, B., Van Hoey, S., Goethals, P., Coeck, J., Moens, T., Mouton, A., 2018. Downstream migration of European eel (*Anguilla anguilla L.*) in an anthropogenically regulated freshwater system: implications for management. Fish. Res. 199, 252–262.

Vollestad, L.A., Jonsson, B., Hvidsten, N.A., Naesje, T.F., Haraldstad, O., Ruud-Hansen, J., 1986. Environmental factors regulating the seaward migration of European silver eels (*Anguilla anguilla*). Can. J. Fish. Aquat. Sci. 43, 1909–1916.

Westin, L., 1998. The spawning migration of European silver eel (*Anguilla anguilla* L.) with particular reference to stocked eel in the Baltic. Fish. Res. 38, 257–270.

Winter, J.D., 1996. Underwater biotelemetry. In: D.L.J.L.A. Nielsen, Ed. Fisheries Techniques. American fisheries Society: Bethesda, MD, pp. 555–590.

Winter, H.V., Jansen, H.M., Bruijs, M.C.M., 2006. Assessing the impact of hydropower and fisheries on downstream migrating silver eel, *Anguilla anguilla*, by telemetry in the River Meuse. Ecol. Freshw. Fish 15, 221–228.