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Disrupted downstream migration behaviour of European silver eels (*Anguilla anguilla*, L.) in an obstructed river

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Abstract In the European eel (*Anguilla anguilla*, L.), the steep decline of reproductive silver eels is partly due to disorientation and mortality during their downstream migration, when facing turbines, but also reservoirs and dams. In the Frémur, an obstructed river in Brittany, which is representative of the western coastal hydrosystem of France, five hydrophones were used to study the downstream migration patterns of twenty acoustically-tagged silver eels. Using this acoustic telemetry design, we showed that, despite exceptionally favourable environmental conditions, silver eels experienced important issues to move downstream the river. Indeed, 75 % of eels were delayed and up to 65 % were definitively stopped in their downstream migration. The 14 m high Bois-Joli dam, located at 5 km from the estuary, and its reservoir were the major obstacles to downstream movements. Eels that managed to move downstream only passed over the dam crest, during the night, and under highly favourable environmental conditions: river flow >1.2 $m^3.s^{-1}$ and water level at the dam >28.26 mNGF (Niveau Général de la France; baseline mean sea level for France). Three different downstream migration behaviours were observed: "successful migrants", "uncertain migrants" and "unsuccessful migrants". None of them were related to biological traits, suggesting a behavioural plasticity of silver eels. This study provides useful information to manage eel populations in such water basins that are very likely to be applied to all water reservoirs and dams, which are widespread through the distribution range of European eels.

Keywords Migration delay · Acoustic telemetry · Fragmented river · Dam · European eel

Introduction

The European eel (*Anguilla anguilla*, L.) is a catadromous fish species with a complex life history including two migrations totalling over 10.000 km across the Atlantic Ocean (Tesch 2003). First, larvae migrate from the presumed Sargasso Sea spawning areas to the European coasts and rivers, then sexually pre-maturing eels, called silver eels, leave their rivers and catchments, join the sea and migrate back to the reproduction areas (Tesch 2003). This silvering process involves a series of morphological and physiological transformations such as an increase of the eye diameter, changes in integument structure and colour and differentiation of the

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lateral line, which are generally followed by the onset of migration behaviour and gonadal development (Pankhurst 1982; Acou et al. 2005; Durif et al. 2005). The downstream migration of silver eels occurs after three to more than 25 years spent to grow in European catchments. In natural environment, downstream migration peaks of European silver eels generally occurs in autumn and winter, and may last until spring (Feunteun et al. 2000; Acou et al. 2008b; Bruijs and Durif 2009). They follow short periods of favourable environmental conditions such as increases in water level and flow (Boubée et al. 2001; Tesch 2003; Acou et al. 2008b; Piper et al. 2013; Trancart et al. 2013), drops in water temperature (Boubée et al. 2001), and lunar phase (Tesch 2003).

The stock of European eels (*Anguilla anguilla*, L.) has severely dropped since the 1980s (ICES 2013). Their decline is not well understood yet, but it is likely due to a combination of factors that affect oceanic temperature, productivity and hydrology (Miller et al. 2009, 2016) together with inland mortality. The latter is the consequence of the physical degradation of habitats (Feunteun 2002), contamination by organic and metallic compounds (Robinet and Feunteun 2002) and overfishing (Feunteun 2002). Among inland factors, the river continuum, i.e. the accessibility to and from upstream habitats and the connectivity between them, has been strongly impeded by the construction of dams and weirs (ICES 2007), which are mainly used for hydroelectrical energy production or drinking water supply. Dams are physical barriers to fish migration that not only limit access of upstream habitats for young colonizing eels, but also can delay or prohibit downstream migration of silver eels, which ultimately impact survival and reproduction success (Bruijs and Durif 2009; ICES 2013).

The International Council for the Exploration of the Sea (ICES) / European Inland Fisheries and Aquaculture Advisory Commission (EIFAAC) Working Group on Eel (WGEEL) has noteworthy focused on the reduction of obstructions to migration and development of fish passes to restore passages at dams and weirs. In this context, first efforts were directed towards re-establishing the upstream migration of elvers (Miller et al. 2009) while downstream reproductive migration issues have not been considered in much detail until recently (Piper et al. 2013; Reckordt et al. 2013; Stein et al. 2015). France also adopted an eel management plan (Onema 2010), which clearly mentioned the necessity to restore the ecologic continuity of rivers by removing dams or setting up fish passage facilities on 1555 structures identified as obstacles to migration in France.

During their downstream migration, silver eels have to pass many types of dams such as large barrage, flood-control dams, flood gates, that are, in most cases, equipped with hydropower structures. Such hydropower stations impair silver eel escapement and affect the viability of escaped spawners by causing damages and inducing delayed or direct mortality, up to 100 % in some cases, while they pass through the dam's turbines (McCarthy et al. 2008; Calles et al. 2010). These structures are also known to interrupt downstream movements, with migrants getting lost in upstream reservoirs, therefore inducing delays in silver eel migration (Durif et al. 2002; Behrmann-Godel and Eckmann 2003; Piper et al. 2013). Such delays pool migrant fishes above the dams and therefore attract predators and increase the risk of diseases (Garcia de Leaniz 2008). Indeed, when facing such obstacles, which are known to buffer and highly reduce the perceived flow in reservoirs (Behrmann-Godel and Eckmann 2003), silver eels alter their migration dynamics, adopt circling behaviour or modify their route selection (Behrmann-Godel and Eckmann 2003; Jansen et al. 2007). This "searching" behaviour while eels are delayed could reduce the energy reserve silver eels had accumulated during their whole continental life-stage, and therefore their breeding success (Behrmann-Godel and Eckmann 2003; Brown et al. 2009).

Downstream passage at non-powered dams (i.e. dams without turbine) was not considered to be a particularly important cause of damage for migrating silver eels as the passage is usually considered safer. Consequently, the impact of reservoirs and dams without turbines remains poorly documented (Legault et al. 2003), although their number is very high in some Europeans regions. For instance, the lack of ground water in Brittany (western France) leads to a high number of these reservoirs, required for human needs. In this region, there are 18 reservoirs used for drinking water supply (GIP Bretagne Environnement, pers. comm.) and in a context of global warming and intensive urbanisation, this number will be certainly increased in a close future. These 18 reservoirs are compounded by dams without turbines. In the most of cases, these dams are not adapted for downstream migration. The only way for eels to migrate toward sea is to wait the overflowing, during flood episodes. Unfortunately, very few studies were previously made on this subject. Acou et al. (2008b) highlighted the presence of a dam effect that could stop temporarily or permanently silver eels in the non-hydroelectrical reservoirs.

In the present study, we examined the movements and behaviours of twenty silver eels when facing two reservoirs and two dams, without turbines, during their downstream migration. For that, we used an acoustic telemetry design in an intensively studied river: the Frémur, a coastal river of northern Brittany, representative of the western coastal hydrosystem of France (Feunteun et al. 2000). Migration delays induced by reservoirs and dams, in relation to four environmental factors: water flow, temperature, atmospheric pressure (Okamura et al. 2002) and lunar cycle, were also studied. We discussed the impact of these obstacles and migration delays on the downstream migration successes of silver eels. These results were then compared to previous studies focused on dams with turbines. This study provides new insights on the effects of reservoirs and dams, without turbines, on the migration success and hence breeding success of silver eels. In turn, such information is necessary to improve the European eel's management plans and ways to mitigate silver eel mortality during migration.

Materials and methods

Study area

The Frémur is a small coastal river of northern Brittany (France) opening in the English Channel near Saint-Malo, with a main stream of 17 km long and a drainage area covering 60 km^2. The river's slope varies between 0.1 ‰ and 2 ‰ (average: 0.6 ‰; Acou et al. 2008a), and contains a variety of habitats ranging from man-made ponds and reservoirs to lowland still waters and high velocity trout zones. The total water surface covers 75 ha including 5 ha of running waters (streams) and 70 ha of still waters in the reservoirs (Acou et al. 2008b).

Among the six dams and weirs of the catchment, Dam-A (the *Bois-Joli* dam) (Fig. 1) is the most important barrier to migration. It is a 14 m high dam creating a 3.10^6 m^3 water supply reservoir (Reservoir-A, Fig. 1). Dam-A overflow crest is 28.20 m NGF (Niveau Général de la France; baseline mean sea level for France). A minimum flow of 0.04 m^3.s^{-1} is provided below the dam through a compensation flow pipe (located at 21 m NGF). This is the only flow available when water level in the reservoir is below 28.20 m NGF. The first eel lift in the world was designed and fixed on Dam-A in 1992 in order to restore upstream eel migration. However, downstream migration is only possible through the compensation flow pipe or over the crest of the dam during overflows (Legault et al. 2003). Previous studies indicated that silver eel migrations occurred mainly during these overflow time periods (Feunteun et al. 2000; Acou et al. 2008b). The Frémur is also equipped with a Wolf Trap, located at Dam-B (the *Pont es Omnes* dam) (Fig. 1), which is 1 km downstream Dam-A. When river flow is below 2 m^3.s^{-1}, water always overflows Dam-B and only through its Wolf Trap, which catches descending eel over 200 mm with an efficiency of 100 % (the trap was corrected after Feunteun et al. 2000). When river flow exceeds 2 m^3.s^{-1}, water overflows Dam-B over its entire crest and eel escapement from the Wolf Trap is plausible. However, such daily river flow values were observed in only 3 % of the present 228-days long study period.

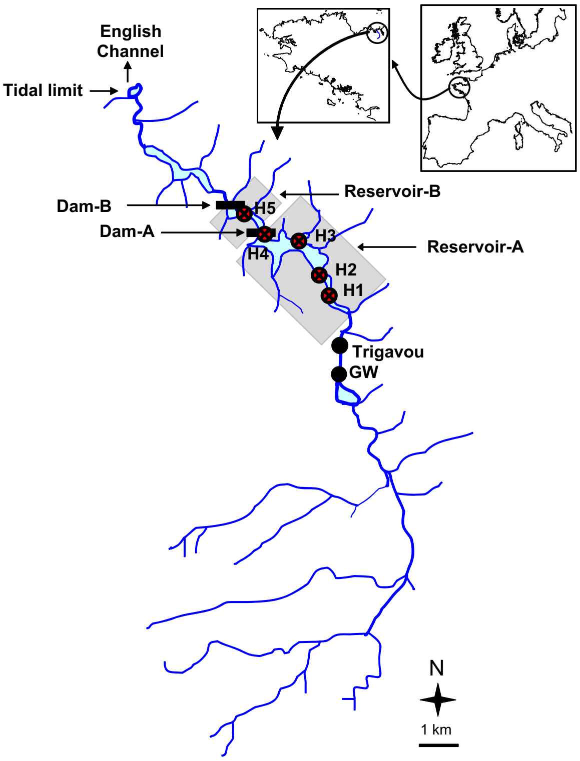

Fig. 1 The Frémur River, its dams, reservoirs and acoustic set of hydrophones. *Red circles* with *black crosses* indicate Vemco hydrophones (upstream to downstream: H1, H2, H3, H4, H5). BJ: Bois-Joli; PeO: Pont es Omnes; GW: Gauging Weir. *Grey boxes* indicate the two reservoirs that are generated by the dams

Acoustic telemetry design

Five hydrophones VR2W (VEMCO© radioacoustic positioning, Vemco Ltd., Shad Bay, Canada) were anchored on navigation buoys, facing downwards, 1 m under the water surface in order to obtain the most efficient detection array: at least 50 % detection efficiency at 50 m from the hydrophone (Le Pichon et al. 2014). These acoustic receivers were deployed from the upper part of Reservoir-A (the Bois-Joli reservoir, with H1 located at its entry, H3 in its middle area, and H4 at its end, near Dam-A) to Reservoir-B (the Pont es Omnes reservoir, between the two dams, where H5 is located) (Fig. 1), covering 3 km of the Frémur's stream: our detection area.

Environmental data

Water level at Dam-A was measured every 2 days, on a limnimetric board located at the dam, and was used to define overflow periods. Daily mean water discharge (in $m^3.s^{-1}$) was calculated from hourly flow records obtained at a gauging weir (GW, Fig. 1). Daily river temperature (in °C) was recorded with a data logger set at 1 m deep near Dam-B Wolf Trap. Atmospheric pressures at the Dinard/Pleurtuit/Saint-Malo airport (2 km away from the Frémur) were kindly provided by MétéoFrance. Lunar phases data were kindly provided by the Calendar Calculation and Celestial Mechanics Institute (Institut de Mécanique Céleste et de Calcul des Ephémérides, IMCCE).

Biometric measures and tagging protocol

Twenty female silver eels (mean TL = 744 ± 95 mm, range: 599–979 mm; mean BW = 817 ± 395 g, range: 372–1912 g), evidenced by external characteristics such as length, large eyes, silvering body and differentiated lateral line (Acou et al. 2005; Durif et al. 2005; Tesch 2003), were captured at Dam-B Wolf Trap during their downstream migration, between the 7th and the 14th of December 2012. Before being measured and tagged, on the 18th of December, eels were anaesthetized using a 40 $mg.l^{-1}$ solution of Metomidate (Bultel et al. 2014). Then, total length (TL), body weight (BW) and girth were measured and ocular index (OI) and fin index (FI) were calculated using vertical (Dv) and horizontal (Dh) eyes diameter, length of the right (Lpr) and the left (Lpl) pectoral fin (Table 2), using the following formulas:

$$\mathrm{OI} = \frac{\pi}{TL} + \left(\frac{\mathrm{Dh} + \mathrm{Dv}}{4}\right)^2 * 100 \qquad (1)$$

$$\mathrm{FI} = \frac{100}{TL} + \left(\frac{\mathrm{Lpr} * \mathrm{Lpl}}{2}\right) \qquad (2)$$

These two criteria are used to determine the silvering stage of eels (Acou et al. 2005; Durif et al. 2005). Fat content (FC) was measured using a Distell FatMeter 992.

ADT9-LONG acoustic transmitters (ThelmaBiotel©, Trondheim, Norway), which weighted 6.8 g in air [<2.5 % of the eel weight, as classically recommended (Winter 1996)], 4.3 g in water and with 146 db water flow power, were then surgically implanted through a mid-ventral incision. They were programmed to emit a coded acoustic signal (69 kHz), individually recognizable, every 20 to 40 s. These acoustic tags were also able to provide an evaluation of the depth of the eels by a pressure measurement, and had a lifetime of approximately 1 year. Additionally, all eels were also tagged with a Trovan© Passive Integrated Transponder (PIT) tags (dimensions: 2.12 × 11.5 mm), in order to identify them if recaptured later (lifetime up to decades). Once the eels had recovered from surgery and regained an active swimming behaviour (stage 1) (Yoshikawa et al. 1988), they were individually placed in 70 l tank before release.

Releases and time parameters

Eels were released at Trigavou (Trig, Fig. 1), upstream the acoustic telemetry design. Release session occurred on the 18th of December 2012. The study period started at this release session and lasted until the 2nd of August 2013, which corresponds with the last detection of an eel in the study area. For each eel we calculated the minimal passed time in the study area (MPT, in days) that is the time between release and the last detection of the eel by the acoustic design.

Data analysis and statistical treatments

Data were collected by the five hydrophones and were then sorted and analyzed using the R-Cran project free software (http://www.rproject.org/). Multivariate analyses (MANOVA, Pillai test) were performed on biometric data in order to exhibit a potential role of morphological parameters (TL, BW, Girth and FC, Table 1) and particularly silvering stage (OI and FI, Table 1), on the migration behaviours of eels. Other parameter comparisons between groups were performed using Wilcoxon and Kruskal-Wallis tests.

For every eel, we analyzed all the detections at one hydrophone by subsetting these detections into passages, following this method: any detection which occurred at least 10 min after another detection belongs to another passage. We assumed here that this 10 min time window corresponds to an absence of the eel in the acoustic array of the hydrophone, meaning that the eel is not "passing" near the hydrophone. For each passage, mean duration (MT), mean depth, but also a coefficient of variation (CV) of depth were calculated. The latter was used to estimate if the silver eels, known to adopt a restlessness behaviour at the onset of their migration (Sudo and Tsukamoto 2015), were either moving through an important range of depth: "searching behaviour" ($CV > 1$) or close to the surface: "surface behaviour" ($CV < 1$ and mean depth of the passage inferior to 3 m). Downstream migration speeds of eels between hydrophones were calculated with the times of the first arrivals at each hydrophone.

Table 1 Biometric data. LT: total length (in mm); BW: body weight (in g); OI: ocular index; FI: fin index; Girth data are in mm; FC: fat content (in %); MS: morphological stage, assessed using Durif et al. 2005

Eel	LT	BW	OI	FI	Girth	FC	MS
1	715	629	10.25	5.07	130	20.2	FV
2	803	1201	11.56	5.51	168	19.4	FIV
3	837	1250	10.73	5.01	168	15.8	FIV
4	836	1100	11.06	4.79	148	19.5	FIV
5	663	477	8.97	5.14	118	13.4	FV
6	872	1286	10.12	4.36	173	19.1	FIV
7	979	1912	11.36	5.38	195	15.9	FIV
8	751	823	11.10	5.29	152	18.2	FV
9	641	479	10.15	5.62	120	20.8	FV
10	612	410	9.60	5.24	114	23.9	FV
11	778	1038	11.24	5.69	155	19.7	FIV
12	692	590	11.81	5.88	128	22.2	FV
13	759	938	10.35	4.89	150	18.7	FIV
14	783	891	10.13	5.40	146	17.6	FV
15	662	480	9.82	5.07	115	21.9	FV
16	702	646	8.27	5.64	134	19.6	FV
17	649	464	11.98	5.45	118	23.1	FV
18	760	870	10.44	5.70	144	20.8	FV
19	599	372	13.78	5.78	109	23.0	FV
20	778	479	9.89	5.07	109	19.0	FV

The daily searching activity (S) of each silver eel in Reservoir-A was estimated using the formula (3):

$$S = \sum_{i=1}^{4} \frac{NPH(i)}{TSH(i)} * CVDH(i) \tag{3}$$

where NPH(i) is the number of passages made by the eel at the hydrophone number i (a high NPH indicates that the eel was active, since detected at many different times of the day); TSH(i) indicates the total time spent at the hydrophone i (a high TSH highlights a rest behaviour) and CVDH(i) is the depth coefficient of variation at the hydrophone i (calculated on all depths of all detections at the hydrophone). Therefore a high CVDH implies a great searching activity and no resting, as constant depth swimming is poorly conceivable in this river area.

Generalized linear models (GLM) (McCullagh and Nelder 1989) were applied in order to estimate the role of environmental factors on the activity of eels within Reservoir-A and the percentage of new eels detected each day at H5 (Gaussian model). A delta GLM was used to cope with the numerous zeros in the data set of eel in H5 and to extract significant factors influencing the "presence" (recorded detection) at H5 (Acou et al. 2011). Two models were then created, the first to understand the impact of environmental factors on the presence/absence data of eels at H5 (Binomial model) and the second to understand the role of these factors on the variability of "presence" at H5 (Gamma model). All possible combinations of the four environmental parameters were tested, including moving averages (simple average over a defined number of days, indicated by m.a. (mean average), in order to analyze potential long-term trends) and interactions when biologically relevant. The model that best fitted the observed data was chosen according to its parsimony, which was evaluated through the Akaike Information Criterion (AIC; Akaike 1974). Its significance was then tested with an ANOVA.

Results

Detection efficiency and survival rate after tagging

All the 20 eels were acoustically detected by the four hydrophones (H1, H2, H3 and H4, Fig. 1) located upstream Dam-A, 0.62 to 96.69 days after release (Table 2). So 100 % of the eels were detected upstream Dam-A (Fig. 1). After Dam-A, this rate depended on both the detection efficiency and the passing success and was therefore more complex to interpret. Eels stayed from 1.12 to 226 days (MPT, Table 2) in the detection area (H1 to H5, Fig. 1). Individuals who exhibited a short MPT (<30 days, Table 2) were eels who left the detection area after passing over both Dam-A and Dam-B, and being recaptured at the Dam-B Wolf Trap, except for eel number 9. The latter spent only 2.4 days in the detection area but was not recaptured at Dam-B Wolf Trap (Table 2). Therefore the survival rate after surgery and tagging was at least 95 %, as eel 9 could have died from surgery and tagging but could also have escaped Dam-B Wolf Trap or died from passing Dam-A.

Table 2 Temporal data. All times are expressed in day, with the release time of the eel as the origin. MPT: Minimal passed time (in the detection area), it corresponds to the time between the first and the last detection in the acoustic array. Hi indicates the time before the first detection at the hydrophone i. Recapture indicates the time between release and the recapture at Dam-B Wolf Trap

Eel	MPT	Time before first detection at					Recapture
		H1	H2	H3	H4	H5	
Group 1: "A - Successful Migrants"							
1	2.75	1.63	1.71	1.84	2.4	2.71	2.89
2	3.83	1.38	1.37	2.7	2.75	3.81	5.91
3	84.65	49.41	49.47	51.44	51.52	84.64	85.89
5	54.43	2.37	2.38	2.42	2.55	53.81	NO
8	83.44	1.31	1.33	1.36	1.41	83.43	NO
9	2.4	0.36	0.35	0.38	0.62	2.39	NO
11	5.68	1.34	1.32	1.36	4.27	4.28	5.85
13	88.41	83.29	87.38	87.5	87.65	88.31	NO
14	54.68	1.49	1.49	1.56	50.7	54.67	NO
16	4.64	1.49	1.64	1.81	3.31	4.34	5.83
17	88.49	0.56	1.29	55.29	55.4	87.47	89.83
18	86.38	4.36	1.58	58.47	58.56	86.36	NO
20	49.28	2.27	2.5	2.57	2.73	46.43	51.82
Group 2: "Unsuccessful Migrants"							
4	106.55	1.37	1.57	1.6	1.7	NO	NO
6	80.78	55.41	55.44	55.49	55.65	NO	NO
7	84.52	4.36	4.48	4.52	19.37	NO	NO
10	227.43	1.43	2.33	2.76	55.39	NO	NO
12	169.45	4.64	4.65	4.82	96.69	NO	NO
15	160.69	0.37	0.36	0.48	0.78	NO	NO
19	170.65	0.44	0.46	2.23	2.77	NO	NO

Migration patterns

Upstream movements were noticed for eels 6, 7, 8, 10, 12, 14 and 20, either upstream Dam-A, with consecutive detections at H1 a few hours or days directly after another detection at this same hydrophone, with no detection at H2 in between, and/or within Reservoir-A, with detections at H1 or H2 a few hours or days directly after another detection at respectively H2 or H3. However, once eels entered our acoustic array and passed Dam-A or Dam-B, none of them moved upstream these dams through the fish passage facilities located there.

Two groups of eels were identified accordingly to their downstream migration pattern and success to migrate through Reservoir-A and to pass over Dam-A. Thirteen eels (eels 1, 2, 3, 5, 8, 9, 11, 13, 14, 16, 17, 18 and 20, Table 2) were detected at H5, located in Dam-B reservoir (Reservoir-B, Fig. 1), and therefore succeeded to migrate through Reservoir-A and to pass Dam-A (Group 1: "A - Successful Migrants", as they succeeded in moving downstream Reservoir-A and Dam-A obstacles). The remaining seven eels (eels 4, 6, 7, 10, 12, 15 and 19, Table 2) managed to migrate through Reservoir-A but didn't pass Dam-A (detected at H4, but neither detected at H5 nor recaptured at Dam-B Wolf Trap) (Group 2: "Unsuccessful Migrants", as they did not pass Dam-A or failed to find a way out Reservoir-A and Dam-A). Among "A - Successful Migrants", seven eels were recaptured at Dam-B Wolf Trap (eels 1, 2, 3, 11, 16, 17 and 20, Table 2), confirming their successful downstream migration. There was no relationship between the time spent in housing before the release and the two migrating groups (Wilcoxon, $W = 26$, $p > 0.05$), as well as between these two groups and any of the biometric data presented in Table 2 (MANOVA, Pillai test, $F = 2.3227$, $p > 0.05$).

Downstream migration speeds and delays

Sixty-two percent of "A - Successful Migrants" and all "Unsuccessful Migrants" were at least delayed once during the study, either (i) before entering Reservoir-

A, (ii) within Reservoir-A and/or (iii) at Dam-A (see speed values inferior at 0.1 km.day^{-1} in Table 3). In "A - Successful Migrants", 15 % of eels were delayed before entering Reservoir-A, 23 % within Reservoir-A and 46 % by Dam-A (some eels were delayed multiple times). In "Unsuccessful Migrants", 14 % of eels were delayed before entering Reservoir-A and 29 % were delayed within Reservoir-A. Overall, 20 % of eels migrated in less than 5 days from the release point to Dam-B Wolf Trap (Table 2) whereas the other 80 % were delayed in their downstream migrations. Two main delays were observed in passing Dam-A and Dam-B: around 50 days and 85 days after release (Fig. 2a, b). Downstream migration speed varied a lot (0.01 to 64.64 km.day-1, Table 3), reflecting these multiple delays. No significant difference in downstream migration speeds was observed within (between each area) and between "A - Successful Migrants" and "Unsuccessful Migrants" (Kruskal-Wallis test, $\chi^2 = 7.7482$, df = 5, $p > 0.05$).

Table 3 Downstream migration speeds. Speeds are expressed in km.day^{-1}. Downstream migration speeds were estimated between the release point and the entry of the detection area (Trig-H1), within Reservoir-A (H1-H4), above Dam-A (H4-H5) and within Reservoir-B (H5-Dam-B)

Eel	Speed			
	Trig-H1	H1-H4	H4-H5	H5-Dam-B
Group 1: "A - Successful Migrants"				
1	0.87	3.21	2.09	2.24
2	1.03	1.80	0.61	0.19
3	0.03	1.17	0.02	0.32
5	0.60	13.72	0.01	NA
8	1.08	24.69	0.01	NA
9	3.93	9.50	0.37	NA
11	1.06	0.84	64.64	0.26
13	0.02	0.57	0.98	NA
14	0.95	0.05	0.16	NA
16	0.95	1.36	0.63	0.27
17	2.53	0.05	0.02	0.17
18	0.32	0.05	0.02	NA
20	0.62	5.37	0.01	0.07
Group 2: "Unsuccessful Migrants"				
4	1.03	7.48	NA	NA
6	0.03	10.29	NA	NA
7	0.32	0.16	NA	NA
10	0.99	0.05	NA	NA
12	0.30	0.03	NA	NA
15	3.82	6.02	NA	NA
19	3.22	1.06	NA	NA

Downstream movements, environmental factors and searching activity

Downstream migration peaks matched with peaks of water flow and water level at Dam-A (Fig. 2c, d). During 137 days, from the release to the 3rd of May, water always overflowed Dam-A (water level > 28.20 m NGF). Downstream movements over Dam-A only occurred during the night and during this temporal window (at the opposite, the few upstream movements only occurred during "non-peak" water flow period).

The percentage of new eels detected at H5 and the days of presence/absence of eels at H5, which indicate the preponderant factors for passing Dam-A, were linked to peaks of water flow (Table 4A, B). When the water flow was superior to 1.2 m^3.s^{-1}, and the water level at Dam-A overflew crest (superior to 28.26 m NGF), the presence of eels at H5 was significantly higher (Table 4C, D). Eel's searching activity, within Reservoir-A, is also higher during rise of water flow (Table 4E).

Behaviours at Dam-A

Eels performed between 1 and 228 passages at H4, immediately upstream Dam-A (Table 5). Mean duration (MT) of each passage lasted from 9 min to around 4 h and their mean depth varied from 0.7 to 11.1 m (Table 5). Eels preferentially faced Dam-A near the surface rather than exploring an important range of depth in both "A - Successful Migrants" and "Unsuccesful Migrants" (respectively 69 % and 71 % of eels showed a higher %Surf value than %Search value, Table 5). These swimming behaviours are neither linked to downstream migration success (Kruskal-Wallis tests, $p > 0.05$) nor to the eel's biometric factors measured in the study (MANOVAs, $p > 0.05$). However, eels that were not delayed at Dam-A, i.e. that passed Dam-A in less than 10 days after release (Fig. 2a, Table 1), had much shallower depth ranges than those that were delayed (Wilcoxon test on Mean depth value from Table 5, W = 4, $p < 0.05$). Finally, all "A - Successful Migrants" last detections upstream Dam-A were shallow [mean depth of the last passage (LPD): 0.1 to 1.7 m, Table 5], and final depth recorded always inferior to 3 m suggesting that all "A - Successful

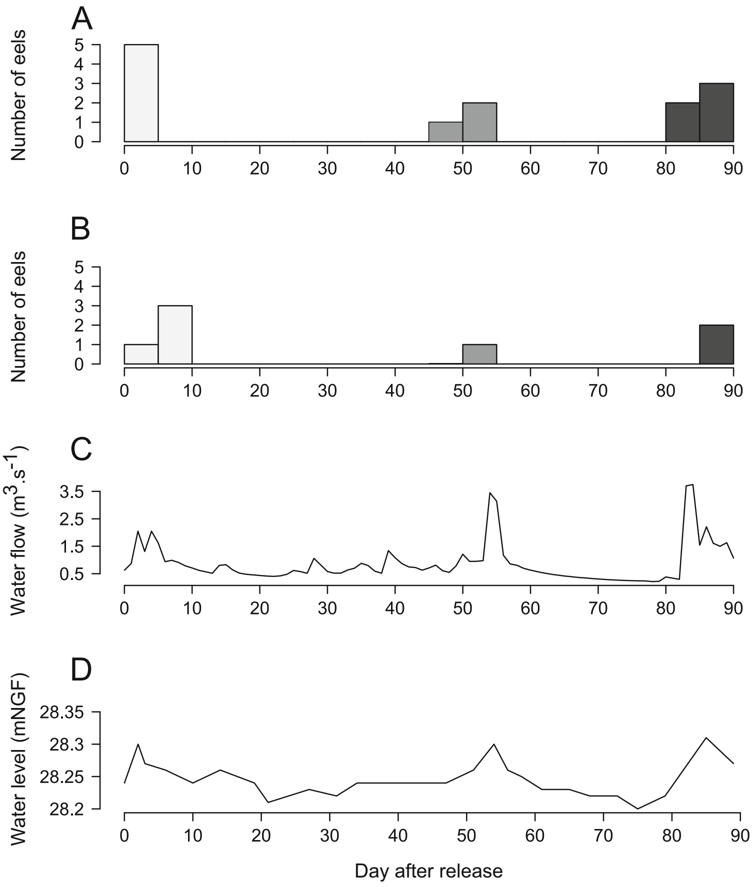

Fig. 2 Downstream migration delays and environmental conditions. On abscissa, the temporal data has for origin the release day (18th of December 2012). **a**: Passing Dam-A; **b**: Passing Dam-B (**a** and **b**: *shaded histograms* indicate the three main downstream migration events); **c**: Daily Frémur water flow; **d**: Water level at Dam-A

Table 4 GLM analyses of the activity of eels within Reservoir-A, the percentage of new eels detected and the presence/absence data of eels at H5, in relationship with environmental factors. Parameters indicate the biologically significant environmental parameters that were selected using AIC; *: *p*-value < 0.05; **: *p*-value < 0.01; ***: *p*-value < 0.001

A - Percentage of new eels detected at H5 (Gaussian GLM)						
Parameter	Effect	t-value	Df	F	p-value	Variance explained (%)
Water flow	+ (***)	8.379	1	70.202	***	35
B - Presence/absence of eels at H5 (Binomial GLM)						
Parameter	Effect	z-value	Df	Deviance	p-value	Variance explained (%)
Water flow (3d. m.a.)	+ (***)	4.626	1	54.234	***	42
C - Threshold effect of the water flow on the presence/absence of eels at H5 (Binomial GLM)						
Parameter	Effect	z-value	Df	Deviance	p-value	Variance explained (%)
Water flow >1.2 m^3.s^{-1}	+ (***)	2.627	1	52.86	***	44
D - Threshold effect of the water level at Dam-A on the presence/absence of eels at H5 (Binomial GLM)						
Parameter	Effect	z-value	Df	Deviance	p-value	Variance explained (%)
NGF > 28.26 m	+ (**)	4.626	1	65.227	***	31
E - Eels' searching activity in Reservoir-A (Gaussian GLM)						
Parameters	Effect	t-value	Df	F	p-value	Variance explained (%)
Water flow	+ (*)	2.591	1	32.3703	***	18
Temperature	+ (***)	4.431	1	16.7477	***	9

Table 5 Eel behaviours at Dam-A. NB: Number of passages; MT: mean time spent at H4 for all these passages; %Search. and %Surf. indicate respectively the percentage of passages with "searching" and "surface" behaviours, defined in Materials and Methods. Mean depth represents the mean of all the depth measured at H4 when the eel was detected (from all its passages). LPD indicates the mean depth of the last passage of the eel at H4

EEL	NB	MT (min)	%Search.	%Surf.	Mean depth (m)	LPD (m)
Group 1: "A - Successful Migrants"						
1	4	39	25	75	0.9 (±0.9)	0.8 (±0.5)
2	5	30	20	40	2.4 (±2.4)	1.3 (±0.6)
3	12	29	17	50	3.0 (±3.6)	1.7 (±0.7)
5	213	123	6	6	10.7 (±3.9)	1.2 (±1.3)
8	17	25	24	29	3.9 (±3.9)	1.5 (±0.9)
9	7	21	14	71	1.5 (±1.6)	1.4 (±0.5)
11	1	19	0	100	0.7 (±0.4)	0.5 (±0.4)
13	2	33	50	0	3.1 (±3.8)	0.4 (±0.6)
14	2	58	50	0	3.7 (±3.8)	1.6 (±0.6)
16	3	74	67	33	2.4 (±2.4)	0.5 (±0.4)
17	22	224	9	41	10.9 (±4.6)	0.1 (±0.3)
18	19	131	21	26	6.1 (±4.2)	1.2 (±0.9)
20	26	105	12	27	6.3 (±4.0)	1.3 (±0.5)
Group 2: "Unsuccessful Migrants"						
4	54	62	9	35	7.1 (±5.3)	1.0 (±0.0)
6	4	35	50	25	0.8 (±1.0)	0.7 (±1.0)
7	9	52	22	33	8.0 (±5.6)	10.0 (±5.2)
10	36	9	3	64	1.4 (±0.9)	1.7 (±0.3)
12	61	57	5	0	11.1 (±4.1)	7.9 (±0.4)
15	228	48	7	33	6.9 (±5.3)	0.6 (±0.2)
19	52	72	0	8	9.9 (±4.8)	10.9 (±4.4)

Migrants" passed Dam-A over its crest rather than through its compensation pipe (located at least at more than 7 m deep).

Discussion

All eels were initially successful migrants, since they were caught, during the first downstream migration peak of the season (Charrier et al. 2013), in Dam-B Wolf Trap (i.e. they had already passed both reservoirs and both dams before the study), and were all clearly classified as silver migrating eels (FIV and FV silvering stages, Table 1) (Durif et al. 2005). With water continuously overflowing both dams (water flow >1.2 m^3.s^{-1} and water level > 28.26 mNGF), from the release to the 3rd of May (137 days), environmental conditions for downstream movements were highly favourable. This enabled the highest emigration of silver eels in the Frémur River since 2000 (Feunteun et al. 2000; Acou et al. 2008b; Charrier et al. 2013) and confirms this exceptional temporal window for eel downstream migration. Despite all these facts, we detected, as in other studies, delays between release and migration (Trancart et al. 2012; Béguer-pon et al. 2014; Bultel et al. 2014), but also and above all interruptions and failures in silver eel downstream migration.

Downstream movements are delayed and/or interrupted by Reservoir-A and Dam-A

After release, three eels did not reach Reservoir-A immediately. Even if a proportion of silver eels are known to interrupt their migration, such a behaviour could also have been influenced by handling and tagging (Durif et al. 2002; Bultel et al. 2014). After entering Reservoir-A, eels swam downstream towards Dam-A at a mean speed of 0.097 ± 0.146 km.day^{-1}. It is much slower compared to global estuary speeds (GES) of eels in the Loire (non obstructed) river in 2012/2013 (GES = 1.91 ± 1.550 km.day^{-1}, unpubl. data, T-test, $t = -7.1305$, df = 38.326, $p < 0.001$) or other years (Bultel et al. 2014). These slow speeds might be caused by bidirectional movements and settling behaviours inside the reservoirs. Such settling behaviours in still waters contrast with the restlessness behaviour that silver eels usually exhibit at the onset of their downstream migration (Sudo and Tsukamoto 2015), and have been associated with delayed downstream passages over the dams (Brown et al. 2009). Indeed, whatever their final success in migrating downstream the study area, 75 % of eels (62 % of "A - Successful Migrants" and all "Unsuccessful Migrants") were affected by delays in Reservoir-A, at Dam-A or right after passing Dam-A (Table 2), but also seemed to have adopted settling behaviours near Dam-A (low CV of depth at H4 and passages with long durations; Table 5). "Unsuccessful Migrants" definitively stopped their downstream migration in Reservoir-A and/or at Dam-A (last detection was not at H1 and none of them was recaptured the following years according to the PIT tag routine monitoring performed at Dam-B Wolf Trap, data not shown).

Only 35 to 50 % of eels succeeded to move downstream both reservoirs and dams

Only 7 eels (35 %) from the 13 "A- Successful Migrants", were recaptured at Dam-B Wolf Trap. This low percentage of eel caught at Dam-B Wolf Trap could be interpreted in different ways:

(i) Not only Dam-A, but also Dam-B is difficult for eels to pass over and some "A - Successful Migrants" may have settled or be lost within Reservoir-B. However, in a previous study on the Frémur River, 80 % of the PIT tagged silver eels which were located inside Reservoir-A, reached Dam-B Wolf trap in 3.5 days (on average) once the spilling at Dam-A started (Legault et al. 2003). It suggests that after passing Dam-A, eels usually do not adopt a settling behaviour within Reservoir-B. Among the seven eels that were recaptured at Dam-B Wolf Trap after being detected at H5, none of them was delayed within Reservoir-B or at Dam-B (number of passages <10 in the H5 acoustic array and total detection time at H5 inferior to 3 days). Delays after passing Dam-A were only observed in the other six eels that passed Dam-A but were not recaptured at Dam-B Wolf Trap. They were also not captured the following years (PIT tag routine monitoring, data not shown). Finally, since water always overflow Dam-B because of the water flow regulation exerted by Dam-A compensation pipe, conditions are always highly favourable for eels to pass over Dam-B, confirming that Reservoir-B (much shorter and shallower than Reservoir-A) and Dam-B have little influence on silver eels migration dynamics compared to the Reservoir-A and Dam-A (Legault et al. 2003).

(ii) Eels were predated (dams are known to delay downstream migration and therefore to pool downstream migrants above dams, which attract predators; Enders 2012) or caught by fishermen. Nevertheless, the fishing pressure is low in the Frémur, since there is no professional fishery while anglers mainly focus on other fish species. Moreover predation mortality remains low or null because only few cormorants or herons are found at the Frémur River (Feunteun, pers. comm.).

(iii) Passing Dam-A induced physical or behavioural inabilities (e.g., injuries and disorientation; Behrmann-Godel and Eckmann 2003) preventing eels to continue their downstream migration. This is particularly relevant since eels 3, 17 and 1B were found in Dam-B Wolf Trap with scars and injuries on their body (not shown). Also, the six eels that were not recaptured at Dam-B Wolf Trap experienced delays that were recorded between Dam-A and H5 (middle of Reservoir-B) but not between H5 and Dam-B Wolf Trap (Table 2), suggesting that passing Dam-A was more stressful than finding a way through Reservoir-B.

(iv) Some eels may have successfully passed Dam-B but escaped Dam-B Wolf Trap. Consequently to Feunteun et al. (2000) study, Dam-B Wolf Trap was improved and escapement reduced to 0 % under 2 $m^3.s^{-1}$ water flow condition. When the river flow exceeds 2 $m^3.s^{-1}$, water overflows the entire crest of Dam-B, not only at the Wolf Trap. So there is a probability that eels 5, 8, 9, 13, 14 and 18 may have escaped Dam-B Wolf Trap under such conditions. These conditions occurred between 52 and 55 and 80–86 days after the release, which excludes eels 9, 13 and 18, who passed over Dam-A and were detected at H5 at different times. Moreover eels 9, 13 and 18 were detected for short period (less than 2 h), and only at the surface (constant of depth of 0 m, as if they were resting or floating dead). These observations argue that eels 9, 13 and 18 may have been injured or killed while passing Dam-A. Therefore, it is likely that Dam-A could induce direct or delayed mortality as for hydropower plants (Calles et al. 2010). At the opposite, eels 5, 8 and 14 may have migrate downstream Dam-A and through Reservoir-B under these exceptional flow conditions with water overflowing the entire crest of Dam-B. Indeed, these three eels passed from Dam-A to reservoir-B during the night (usual time window for downstream migration) and by scanning a whole range of depth (e.g. not resting or floating dead).

Therefore, after Dam-A, "A - Successful Migrants" turned into "Successful Migrants" (eels 1, 2, 3, 11, 16, 17, 20, which succeeded to move downstream the whole study area) (35 % of the studies eels) or "Uncertain migrants" (eels 5, 8, 9, 13, 14 and 18), which may have died (half of them, 15 % of all eels) or escaped the study area (the other half, raising overall downstream migration success to 50 %) after passing Dam-A. All the three downstream migration behaviours are summarized in Fig. 3.

Water flow rules eel activity and downstream movements differentially in "A - Successful Migrants" and "Unsuccessful migrants"

We confirmed here the importance of the water flow in the departure of downstream migration of silver eels (Durif et al. 2002; Acou et al. 2008b; Carr and Whoriskey 2008; Piper et al. 2013; Trancart et al. 2013; Bultel et al. 2014), since all downstream movements occurred during rises and peaks of water flow (Fig. 2, Table 4). It confirms that silver eels adjust their behaviour to environmental factors that are likely to reduce cost of transport and facilitate orientation seaward. "A - Successful Migrants" were more reactive to rise of water flow (ANOVA, F = 38.196, df = 1, $p < 0.001$ and 31 % of the Searching Activity variance explained by changes in the daily water flow) than "Unsuccessful Migrants" (less reactive, and only to long-term rises, ANOVA, F = 7.2757, df = 1, $p < 0.01$ and only 5 % of the searching activity variance explained by 5 days mean average changes in water flow). These results suggest that "A - Successful Migrants" and "Unsuccessful migrants" adopted distinct searching behaviour toward the same environmental cue. Even if it is still not clear, it gives a first indication why "Unsuccessful migrants" failed to carry on the downstream migration under similar environmental conditions. No effect of atmospheric pressure nor lunar cycle as observed.

Reservoir-dams affect silver eel downstream migration similarly to dams with turbines

Our study suggests that assessment of obstacles impacting on downstream migration should not be limited to quantifying mortality at hydroelectric facilities, but should also consider the delays and interruptions induced by reservoir dams. Indeed, despite highly favourable hydrological conditions, the Frémur River, theoretically safe to descend (no turbines), and known to present an important stock of eels (Acou et al. 2011),

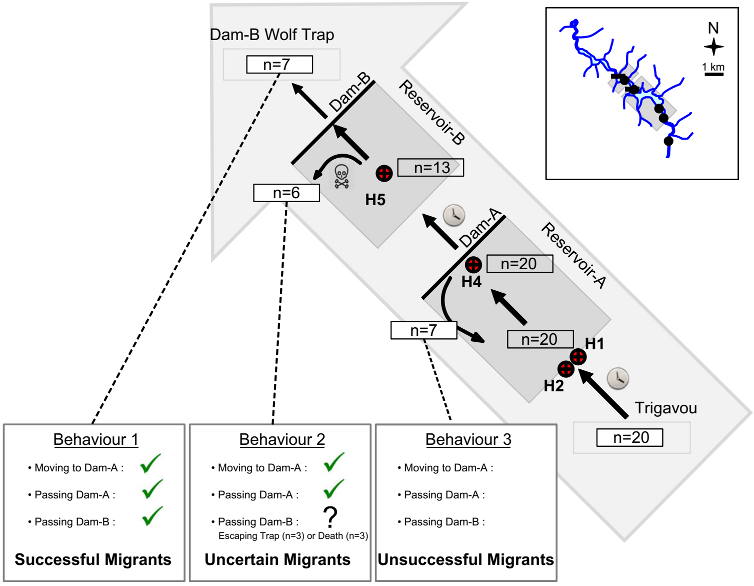

Fig. 3 Migration behaviours of eels in the Frémur's system. The Frémur River has been resumed as a "two reservoirs" (Reservoir-A and Reservoir-B) and "two dams" (Dam-A and Dam-B) system. For a precise location of these barriers on the Frémur River, see the box on the top right. Eels were released at Trigavou; *black crossed red circles* indicate hydrophone locations; *black arrows* indicate eel movements or, in the case of "uncertain migrants", eel's plausible fate: death; clock logos indicate delays in downstream migrations. n = X indicates the number of eels which were detected in this area (among the 20 released eels)

appears to be a fatal trap for silver eels because of its dams and reservoirs. Indeed 50 to 65 % failed to move downstream (with none of these "trapped eels" captured the following years during the migration season) with potentially 15 % of eels killed because of passing over Dam-A. It raises the comparison with turbine-equipped rivers, where 11 to 100 % mortality are observed (Carr and Whoriskey 2008; McCarthy et al. 2008; Brown et al. 2009; Calles et al. 2010). Further studies should be undertaken with a higher number of individuals and hydrophones (especially in Reservoir-B and downstream Dam-B) to determine the fate of these "Uncertain Migrants" so that the full impact of reservoirs on European eels can be better quantified.

We emphasized here why water reservoirs and dams may constitute a major threat for European eels as they are widespread through the distribution range of this endangered species and as most efforts we directed towards upstream migrations and turbines escapement. Apart from the unrealistic removal of the Bois-Joli dam, because of county's growing water need, management options that would allow silver eels to safely escape from the Frémur catchment are: (i) "Trap and transport", which is an efficient and practical strategy, only at short and medium-term, for increasing silver eel escapement from a variety of obstructed water bodies (McCarthy et al. 2008) and (ii) "Surface bypasses", which is a non-intrusive mitigation measure showing promising results in New Zealand (Boubée and Williams 2006) and which sound logical in the Frémur case with eels never moving through the deep compensation pipe of Dam-A. It would be valuable to determine if this technique can be used to pass European eels through dams, weirs and others obstructed catchments.

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