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Proposals for optimizing sea lamprey passage through a vertical-slot fishway

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Abstract

Movement of sea lamprey through a vertical-slot fishway (built at the Coimbra dam, in central Portugal) was continuously monitored between 2013 and 2016 by a video recording system. Visual count data were used to quantify the overall successful movements and identify seasonal and circadian patterns of fishway use. Explicative models (Boosted Regression Trees) were used to study the relationship between frequency of successful movements during the species migration peak and environmental variables. The aim of the study was to identify predictors that may be related with successful sea lamprey upstream migration through the fishway. Collected information was used to support further management recommendations for optimizing the fishway performance. During the 4-year study, near 50,000 lampreys successfully negotiated the Coimbra dam fishway reaching the upper stretch of river Mondego. Migratory peak occurred between April and May with an increase in passages during the night period (between 11 p.m. and 6 a.m.). It was observed an increase in use frequency that was related with the combined effect of flow and temperature. Higher passages were achieved when Coimbra dam discharge flows are lower than 100 m^3/s and temperature between 15 and 19°C. Flow discharges higher than 150 m^3/s seemed to inhibit successful sea lamprey passage. In dry years, when flows are almost constantly lower than 50 m^3/s, temperature was the most important factor influencing fishway use.

KEYWORDS

anadromous fish, boosted regression trees, fish pass, Petromyzon *marinus*, visual counts

1 | INTRODUCTION

Construction of fishways has greatly increased in recent years in response to widespread river fragmentation by man-made structures (Larinier, 2001). However, the performance of such facilities has often been questioned (e.g. Bunt, Castro-Santos, & Haro, 2012; Cooke & Hinch, 2013; Roscoe & Hinch, 2010) together with their performance assessment methods (Bunt et al., 2012; Castro-Santos, Cotel, & Webb, 2009; Noonan, Grant, & Jackson, 2012), which led to the need of standardizing fishway terminology and urgent definition of a possible unifying framework to assess worldwide fishway performance (Bunt et al., 2012; Castro-Santos & Perry, 2012; Silva et al., 2018). Most of the research has been focusing on structural and hydraulic features of different fishway designs (e.g. Rodríguez, Agudo, Mosqueira, & González, 2006, Keefer et al., 2010, Fould & Lucas 2013) and whether these profiles were within the range of species swimming abilities or their relative influence on passage success (Branco, Santos, Katopodis, Pinheiro, & Ferreira, 2013; Castro-Santos, 2004; Haro, Castro-Santos, Noreika, & Odeh, 2004; Santos et al., 2012). However, it is known that important metrics of fishway performance, such as fish guidance and attraction, also depend on species behaviour, their migration timing, and motivation (Kemp, 2012), which in turn can be influenced by environment factors such as river discharge, water temperature, turbidity, light intensity, among others (e.g., Baek, Ku, & Do, 2015; Green, Lindmark, Lundstrom, & Gustavsson, 2011; Haro & Kynard, 1997; Larinier, 2008; Noonan et al., 2012). These variables can dramatically change, at different scales, near hydraulic infrastructures, diminishing or modifying abiotic cues (Hardisty, 1979), and the stimulus for the upstream migration of species. Yet, the influence of environmental factors on successful migration of species through fishways is still poorly documented (Bunt, Katopodis, & McKinley, 1999; Bunt, van Poorten, & Wong, 2001; Castro-Santos & Perry, 2012; Castro-Santos, Shi, & Haro, 2016). The delay and energetic costs associated with behavioural responses to inadequate environmental cues, such as irregular and artificial stream flows, can be crucial for fish survival and spawning success (Alexandre, Ferreira, & Almeida, 2014; Hatry, 2012; Hinch & Rand, 1998). Thus, identification of the abiotic factors that trigger fish upstream movement and successful passage through fishways are critical to determine the conditions that maximize fishway performance and support further management recommendations for optimizing these devices.

In central Portugal, more precisely in Mondego River basin, an important Iberian stronghold for anadromous species, efforts have been made to assess the performance of a vertical-slot fishway for sea lamprey (*Petromyzon marinus* L.). The sea lamprey is an anadromous and semelparous species with high economic value and cultural significance, which in Portugal starts its reproductive migration in December, with a peak between February and May (Almeida, Silva, & Quintella, 2000; Pereira et al., 2017). The loss of suitable habitat is one of the major threats to species survival (Mateus, Rodríguez-Muñoz, Quintella, Alves, & Almeida, 2012).

A previous telemetry study conducted at this vertical-slot fishway estimated that the percentage of overall passage efficiency for sea lamprey was 33% and observed that successful lampreys could experience a variable delay (on average between 1 and 2 weeks) downstream the dam (Pereira et al., 2017). However, due to the lack of information regarding the time of arrival, fishway entrance, and successful passage, this value of efficiency can be underestimated, and the delay observed overestimated (Castro-Santos & Haro, 2003). Moreover, it remains to identify the possible causes of overtime failure and understand how environmental variables constrain sea lamprey passages and fishway performance. Yet, it highlighted the importance of follow-up with fishway monitoring and the need to implement further management measures to maximize its performance.

Towards a more comprehensive understanding of sea lamprey movement though this vertical-slot fishway, here we used visual count data obtained between 2013 and 2016 to gather a robust data set aiming to (i) characterize sea lamprey seasonal upstream movements and circadian patterns of use, (ii) identify which are the conditions (abiotic factors) that seem to trigger successful sea lamprey passage, and (iii) define guidelines that maximize the general performance of the studied fishway targeting sea lamprey.

2 | MATERIAL AND METHODS

2.1 | Study area

Located 45 km from Mondego river's mouth (Central Portugal), the Coimbra dam, constructed in 1980, was until 2011 the first unsurmountable obstacle in this watercourse for anadromous fish migrating upstream. Built essentially for industrial and water supply, flood control, and irrigation purposes, this dam has a crest height of 6.20 m, nine tainter gates, and was equipped, since the beginning, with a pool-and-weir fishway with submerged orifices, that proved to be inefficient due to the lack of attractiveness and inadequate hydraulic conditions for target species (Santo, 2005).

In 2011, a new vertical-slot fishway, projected to specifically target anadromous clupeids (*allis shad Alosa alosa L. and twaite shad Alosa fallax Lacépède, 1800)* and sea lamprey, was built, in the left bank of the river, near the obsolete fishway. The new fishway is a 125-m-long channel with 2-m water depth, divided into 23 rectangular pools (4.5 × 3.0 m) connected by vertical slots (0.5-m width). The water level difference between adjacent pools is 0.25 m. The average velocity at the slots is approximately 1.1 m/s, with dissipated power in the resting pools below 150 W/m^3. Flow discharge at the fishway entrance is constantly maintained at 1.5 m^3/s.

To increase fish guidance to the left river bank where the fishway entrance is located, a modified dissipation basin was added immediately downstream the dam. Up to a river flow of 170 m^3/s, the operating gates are managed sequentially from left to right allowing to have the highest flow near the fishway entrance. In addition, an attraction channel of approximately 200 m was constructed immediately downstream to guide fish directly to this structure (Figure 1).

Because the upper river stretch is highly regulated for hydroelectricity production, through the operation of Aguieira dam (423 hm^3 of maximum storage capacity) and 10 other multiple-use dams, the flow discharge at Coimbra dam is highly dependent on the management of hydroelectric demand. Environmental flow is limited to 4.8 m^3/s, plus the discharge from Fronhas dam (2.0 m^3/s), located in the tributary Alva river, except when Raiva and Aguieira dams (447 hm^3 of combined maximum storage capacity) are hydropeaking, which normally happens twice a day, during which river flow can increase up to 150 m^3/s (Alexandre et al., 2015; Almeida, Quintella, & Dias, 2002).

2.2 | Visual counts

Visual counts data collected with the Coimbra fishway monitoring system during the spawning seasons of 2013–2016 were used to analyse sea lamprey migratory behaviour, particularly seasonal movements

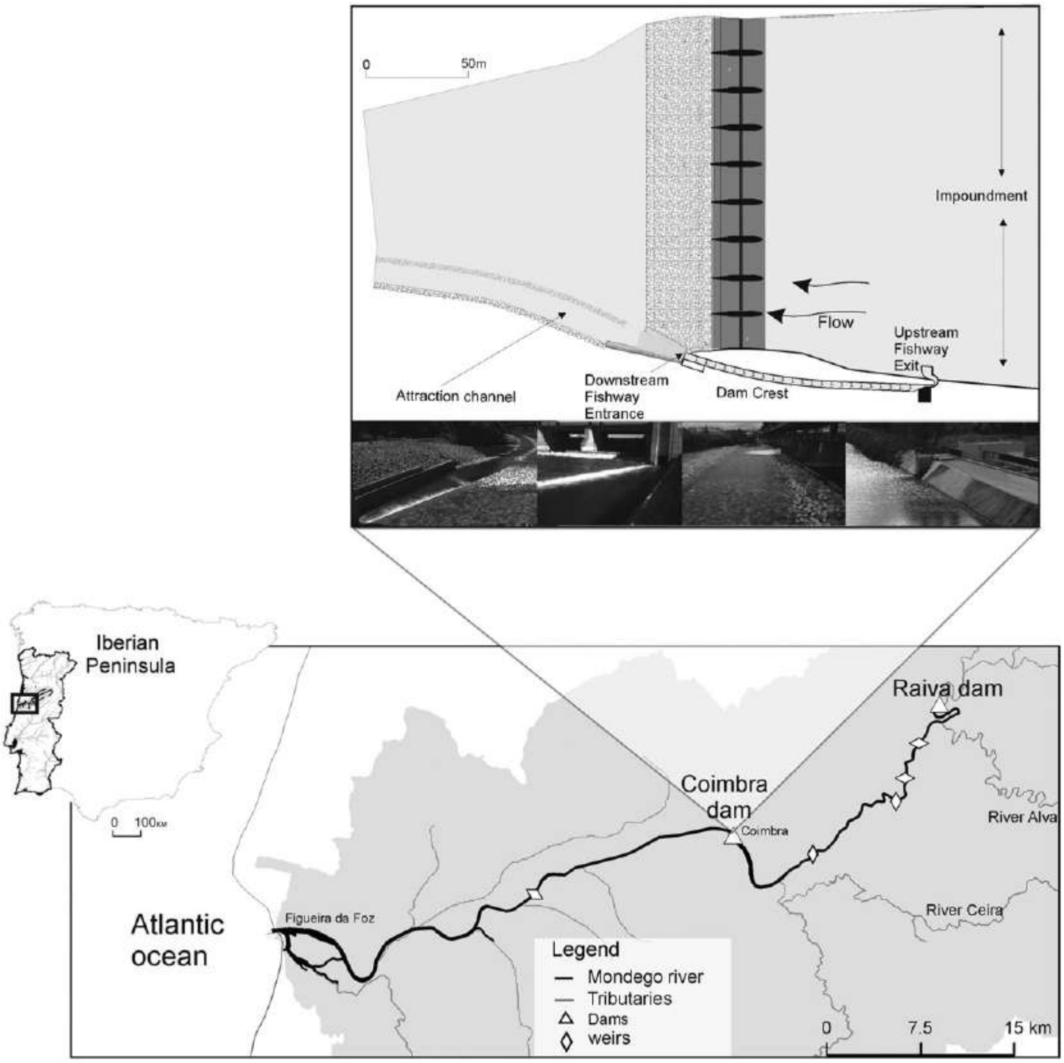

FIGURE 1 Map of the Mondego river basin showing details of the study area and schematic top view plan of Coimbra dam and fishway

and diel patterns. The fishway is equipped with a glass window located between the most-upstream pool (23rd) and upstream fishway exit, where a recording system composed by a digital video recorder (Model Samsung SRD-470) and a high-resolution camera equipped with infrared light-emitting diode lights (Model Samsung SCO-2080R) enable to obtain a 24/7 surveillance of fish movement. Continuous video records were obtained from the DVR installed at the monitoring window and were visually analysed using the software Backup Viewer v1 Samsung Techwin Co., Ltd. During video observations, sea lampreys and their movement direction (up or downstream) were identified. To reduce bias related with multiple counts from the same individual moving up and downstream, at the end of each day, the downstream movement counts were subtracted from the total upstream movements.

2.3 | Modelling fishway use and migratory behaviour

With the aim to develop an explanatory model for sea lamprey successful passages through the Coimbra fishway and thus have a glance on which environmental predictors could have a higher contribution to the observed passage frequency, sea lamprey visual counts obtained along the spawning migrations of 2013–2016 were statistically modelled.

Because the use of visual counts alone fails to provide information regarding the population size and variability downstream the dam, before proceeding with modelling, a proxy estimation of the expected fluctuation in sea lamprey's abundance at the downstream vicinity of the dam was first inferred from fishing mortality data (commercial fishermen surveys) and the information on species' migratory behaviour (telemetry studies). Based on sea lamprey catches from a continuously fishing commercial fyke-net located in the estuary (for 2016, two nets were considered), weekly variations of CPUE (catch/day) were estimated throughout the migratory season (corresponding to a proportion of animals entering the river), and considering that the total migration time needed for a sea lamprey with an average of 85 cm of total length to cover the distance from the river mouth to the Coimbra dam (where the fishway is located) is approximately 5 days (Almeida et al., 2000), time of expected arrival was estimated and sea lamprey abundance was corrected considering that 90% of the animals manage to reach this area (Pereira et al., 2017). The possible correlation between successful upstream passages (visual counts) and the relative abundance of animals downstream the dam was tested using Pearson correlation analysis.

To study the relationship between visual counts and environmental variables, for each spawning season, sea lamprey counts were grouped by hour (dependent variable) and a subsample period that corresponded to 80% of the accumulated counts was selected for following analyses, ensuring that only the species migration peak was considered in the model. Abiotic data (independent variables) were selected by their potential relevance to sea lamprey migratory behaviour (Table 1). Variables related with water turbidity and temperature were obtained from the multiparametric probe (EXO2 Water Quality Probe, records at each 30 min) installed inside the Coimbra Dam fishway. Discharge flow downstream the Coimbra dam was obtained from the Portuguese Environmental Agency. Data related with photoperiod (day length in number of hours of luminosity), day period (day stages according to twilights), and lunar cycle (Moon phases) were obtained at Astronomical Observatory of Lisbon (http://oal.ul.pt/; accessed in January 2017). Lunar cycle was determined by dividing the lunar cycle into four phases, according to the percentage of illuminated area of the moon disc based on the ephemeris. Redundancy between potential abiotic predictors was tested with Pearson's correlation, and for correlations higher than 0.8 (e.g. Snelder & Lamouroux, 2010), only one of the redundant variables was maintained in the analyses.

To statistically model these data, Boosted Regression Trees (BRT) analysis was used (Elith, Leathwick, & Hastie, 2008; Leathwick, Elith, Chadderton, Rowe, & Hastie, 2008). BRT is a flexible additive regression modelling technique that combines regression trees and boosting to fit multiple simple trees in an adaptative process (forward stagewise instead of the common stepwise). By considering stochasticity (random or probabilistic component) it reduces the variance of the final model and improves the predictive performance. Beside the advantage of dealing with different types of data, missing values, and no need of prior transformations nor elimination of outliers, they select relevant variables, fit accurate functions, and automatically identify and model interactions (Elith et al., 2008). BRT models were fitted in R package (R Development Core Team, 2006), using the *gbm* library (Ridgeway, 2017). Optimal models were obtained by optimizing the number of trees, tree complexity, and learning rate that produced the lowest predictive deviance without overfitting. Tenfold cross validation (cv) was used to identify the optimal number of trees to use for each model and subsequently assess the model performance. For each migratory season, the chosen model has (i) the smallest cv deviance, (ii) the higher percentage of explained deviance (R^2), and (iii) the highest cv correlation (described as a measure of correlation between the observed data and set data, calculated from the Pearson correlation). Following with BRT procedure, simplification of the obtained models were tested (removal of noninformative variables from the original model without affecting the model performance), interactions between predictors were analysed (relationship between the model predictions and all possible pair-wise combinations of predictors), and relative influence (%) of each environmental variable in the model was determined. This relative influence is rescaled, so that the sum is 100, with higher values indicating greater influence on the response (Froeschke, Stunz, & Wildhaber, 2010). For visualization of fitted functions, partial dependent plots, that show the effect of a variable on the response after accounting for the average effects of all other variables in the model, were created and fitted values were analysed.

3 | RESULTS

3.1 | Seasonal and daily patterns of migration

Between 2013 and 2016 a total of 49,490 sea lampreys successfully used the Coimbra fishway during their upstream migration. Considering annual counts, 2013 had the lowest number of passages, with a total of 7,821 lampreys, and the highest value was recorded in 2014, with a total of 21,979 animals. In the two following years, 2015 and 2016, a similar number of animals were recorded, reaching near 10,000 per year.

Throughout the 4-year study, sea lamprey passage occurred mainly between March and May, with the peak of migration occurring in April for all monitored spawning seasons (Figure 2). Exceptions to these results were identified in 2014 when sea lamprey passages were more distributed throughout the season, and in 2016, when a high number of lamprey movements was also observed during June (Figure 2).

TABLE 1 Environmental variables selected and respective range of values for each species migration peak considered for BRT models (80% of passages) between 2013 and 2016

			Range			
Predictor	**Code**	**Units**	**2013**	**2014**	**2015**	**2016**
Temperature	Temp	°C	[7.98–16.55]	[11.24–20.01]	[15.59–22.91]	[8.37–19.13]
Specific Conductivity	SpeCond	µS/cm	[46.50–119.00]	[52.00–157.00]	[72.00–166.00]	[44.00–140.00]
Turbidity	Turb	FNU	[4.15–168.65]	[7.35–8450.95]	[11.4–3137.35]	[2.05–143.15]
Discharge flow	Flow	m^3/s	[6.58–853.47]	[7.85–362.74]	[2.29–57.54]	[11.78–399.24]
Photoperiod	PhoPer	hours	[9.20–15.13]			
Lunar cycle	LunCyc		Full Moon (FM); Last Quarter (LQ); New Moon (NM); First Quarter (FQ)			
Day period	DayPer		Night closed (NC); Sun Rising (SR); Sun Transit (ST); Sun Set (SS)			

Note. BRT: Boosted Regression Trees.

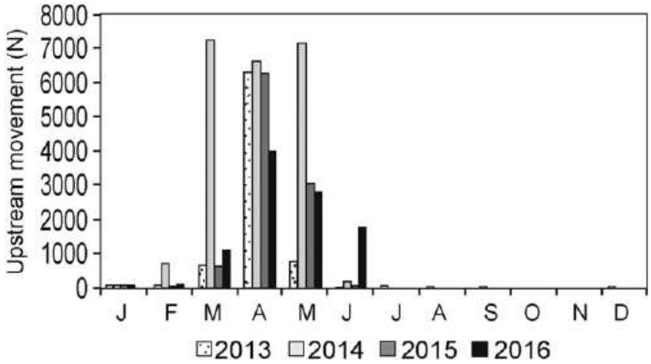

FIGURE 2 Monthly sea lamprey upstream movement obtained through visual counts at the Coimbra fishway monitoring window between 2013 and 2016

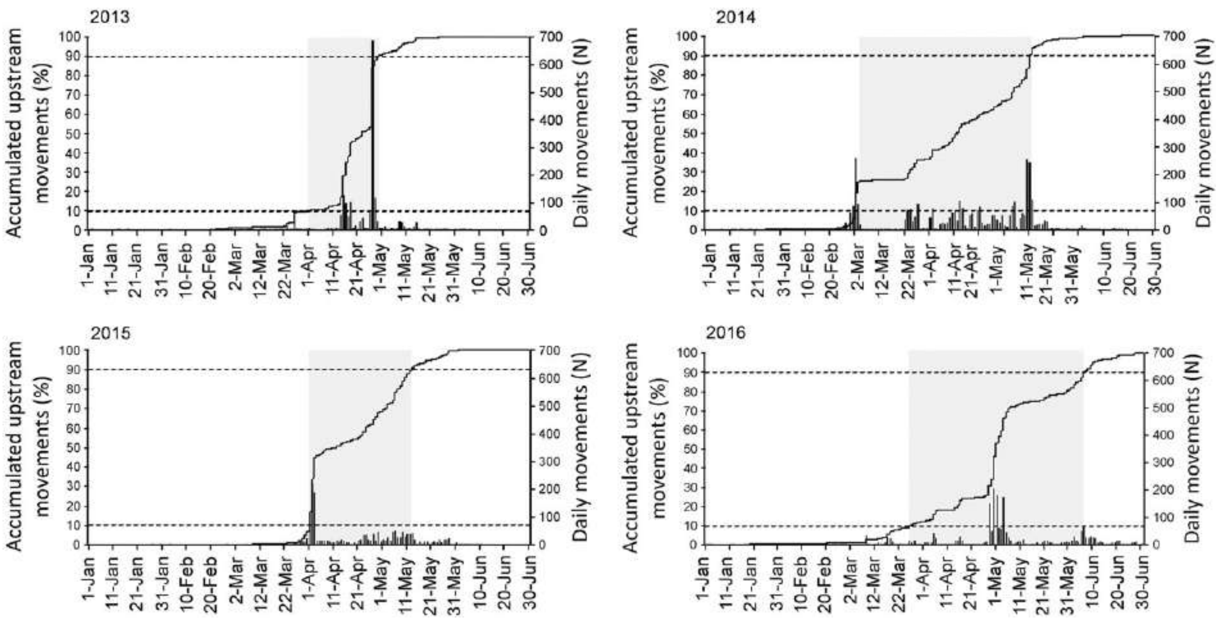

FIGURE 3 Frequency distribution of daily sea lamprey successful passages at Coimbra fishway for each of the study years and the respective accumulated counts (black line). The dashed lines indicate the 10th and 90th percentiles, and the grey bars identify 80% of sea lamprey passages

Analysis of daily movements and accumulated counts (Figure 3) emphasizes these exceptions, since in 2013 and 2015 the bulk of upstream migration through the fishway, considered as the range between the 10th and 90th percentiles of the recorded movements, was concentrated in a period of 29 and 42 days, respectively, while in 2014 and 2016, the bulk of movements was reached later within 69 and 72 consecutive days, respectively.

Along the study period, sea lamprey movements occurred largely between dusk (7 pm) and dawn (6 am), comprising 54% of the movements in 2013, 67% in 2014, 68% in 2015, and 74% in 2016 (Figure 4).

3.2 | Environmental triggers influencing sea lamprey upstream migration through Coimbra fishway

In terms of sea lamprey's relative abundance and availability downstream the dam, some fluctuations along the migratory season were observed taking in consideration the data collected during the surveys to commercial fisheries. Nevertheless, a pool of animals is always available to potentially use the fishway (Figure 5). Pearson correlation showed no correlation ($P < 0.05$) with the number of sea lampreys using the fishway during upstream migration.

From the set of variables initially considered, a high correlation ($r > 80$, Pearson's correlation) was found between photoperiod-water temperature; thus, photoperiod was dropped from following analyses. BRT model was run with annual data sets subsampled to cover the species migratory peak, including 80% of the movement (i.e., lamprey counts), which differ among study years (Figure 3). In terms of model's performance, explained variability (R^2) ranged between 0.83 and 0.93 (Table 2). Boosted regression tree models developed for each year identified the same main predictor variables; nevertheless, their relative contribution (%) varied, reflecting interannual variability. For 2013, frequency of successful upstream movements was strongly influenced by flow but also by conductivity and temperature (relative

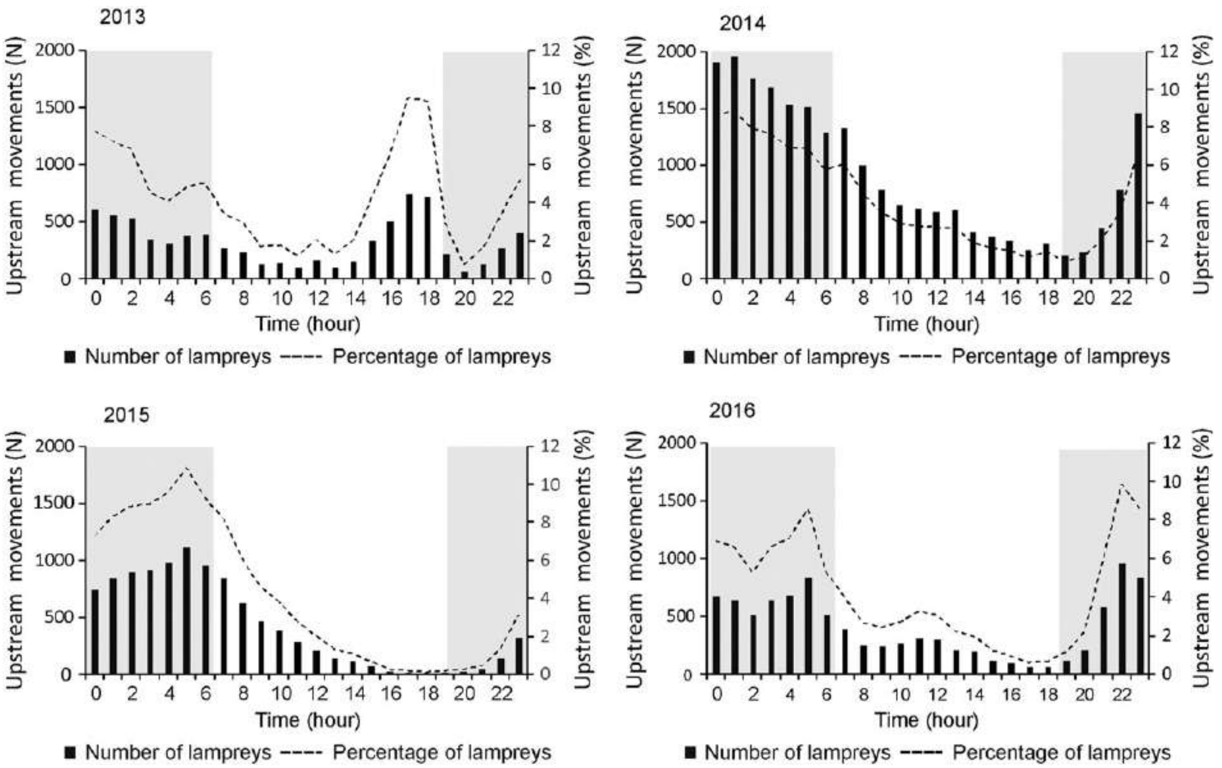

FIGURE 4 Circadian rhythm of sea lamprey upstream movements through the Coimbra dam fishway in 2013–2016. The grey areas indicate night periods according to approximated local sunrise and sunset times

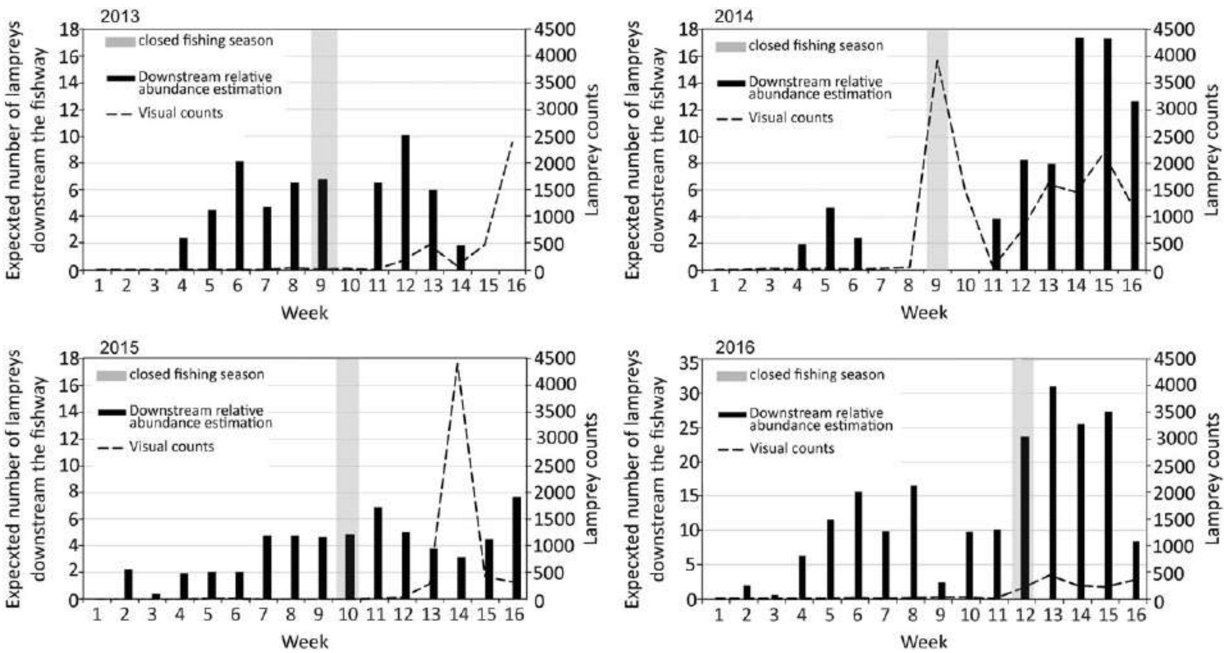

FIGURE 5 Weekly distribution of estimated relative abundance of sea lampreys downstream the Coimbra dam (dark bars) and successful passages (- - -). Period of intermediate closed fishing season is identified in grey (distinct scales on the vertical axis)

contribution of 46%, 23%, and 19%, respectively). In 2014 and 2016 the main predictors were flow (30%, 22%, respectively), temperature (28%, 23%), and turbidity (17%, 21%). In 2015 a distinct pattern in predictor's contribution was observed, with the highest relative contributions associated with temperature, turbidity, and conductivity (31%, 28%, and 20%, respectively). Overall, flow and temperature were identified as the two main variables associated with sea lamprey movements through the fishway. Box and whisker plots of these

TABLE 2 Performance evaluation of BRT models for each study year

Model evaluation	2013	2014	2015	2016
Mean total deviance deviance	40.11	29.08	23.51	14.43
cv deviance	18.21; se = 7.5	9.55; se = 0.9	7.99; se = 0.47	5.56; se = 0.44
cv correlation	0.60; se = 0.09	0.74; se = 0.04	0.83; se = 0.02	0.66; se = 0.36
R^2	0.91	0.88	0.85	0.83

Note. BRT: Boosted Regression Trees.

variables show the interannual variation observed during the study period emphasizing the distinct characteristics associated with the 2015 spawning season in terms of temperature and flow regimes (Figure 6).

Fitted functions for each predictor in BRT models (Figure 7), relating sea lamprey upstream movements with the explanatory environmental variables, indicate that successful passages of sea lamprey at Coimbra fishway increase with discharge flows lower than 100 m^3/s (70% of the total lamprey counts used in the BRT model) and highest for flows lower than 50 m^3/s (55% of the total counts used in the BRT model). This threshold is emphasized by the result obtained in the model developed for 2015, where in the absence of discharge flows higher than 57 m^3/s, temperature is the dominant variable explaining the frequency of passages. Regarding temperature, sea lamprey movements through fishway occurred mainly at 15–16°C. However, in 2014, part of sea lamprey passages also occurred at lower temperatures (11–12°C), and the interaction with the flow (Figure 8) shows that these passages are associated with higher discharge periods (>200 m^3/s) during the month of March.

Most successful passages occurred when specific conductivity fluctuated between 80 and 120 μS/cm, values reinforced by the interactions observed with flow and temperature for 2013 and 2015 when this range was identified as the optimal conductivity conditions for lamprey passage (Figure 8).

A great variability was observed for turbidity; however, for the years where this predictor had a higher contribution, sea lamprey passage increased with an increase in turbidity. Regarding the remaining abiotic predictors, their contribution was relatively low, and without a clear pattern. In the case of the day period, migration occurs particularly throughout night and sunrise, but a distinct pattern was observed in 2013 where a peak of passages was observed between 16 and 18 hr (Figure 4). The interaction identified between temperature and day period in 2016 model demonstrates a higher passage when temperature reached 16–18°C during the night period (Figure 8).

4 | DISCUSSION

The optimization of fishways requires not only the information regarding seasonal movements and diel patterns of target species during migration through the device but also the identification of the main abiotic triggers and threshold values that potentiate the number of animals that successfully negotiate a fishway.

In the present study, visual count data encompassing four spawning migration seasons allowed to study the migratory activity and the identification of the main environmental conditions related with successful upstream movements of sea lamprey through a vertical-slot fishway. However, it is important to note that by using this approach, and despite our effort to gather some quantitative estimations of the variability in the size of the population attempting to negotiate the fishway, the interpretation of the results must be done with some cautions and having in mind that visual counts alone fail

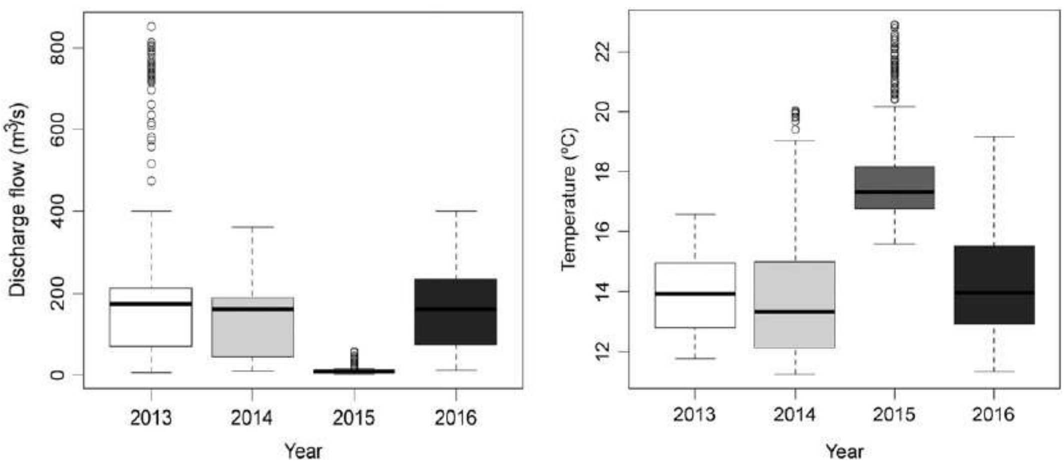

FIGURE 6 Box plots with the mean (horizontal lines), interquartile ranges (boxes), ranges (vertical lines) and outliers (open circles) of discharge flow and temperature at Coimbra fishway for the period comprising 80% of lamprey passages between 2013 and 2016

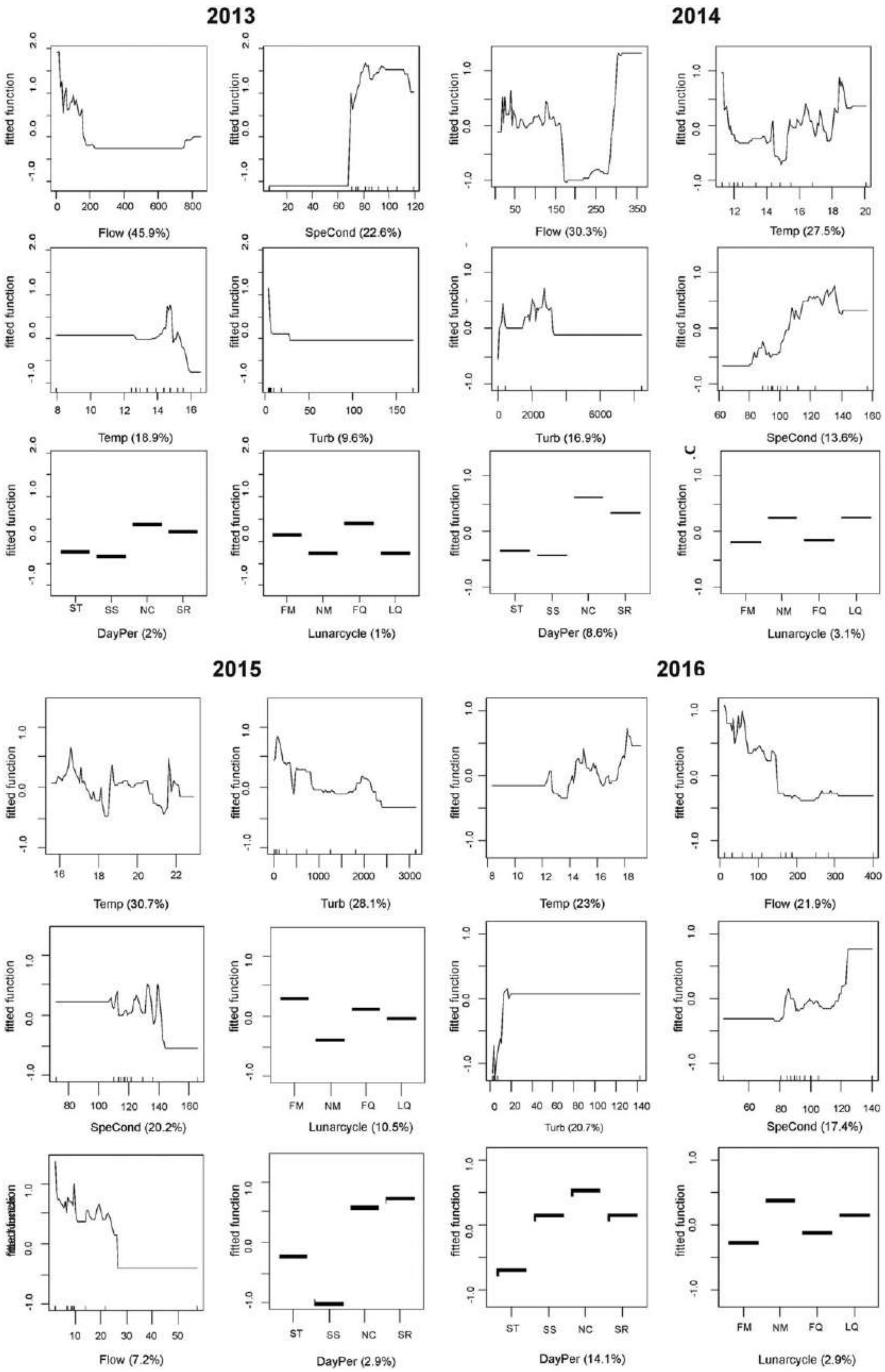

FIGURE 7 Fitted functions for the influential predictors in the Boosted Regression Trees models relating sea lamprey successful upstream movements (visual counts) with explanatory environmental variables in each of the study years (2013–2016). For each plot, vertical axis is on the logit scale and centred to have zero mean over the data distribution

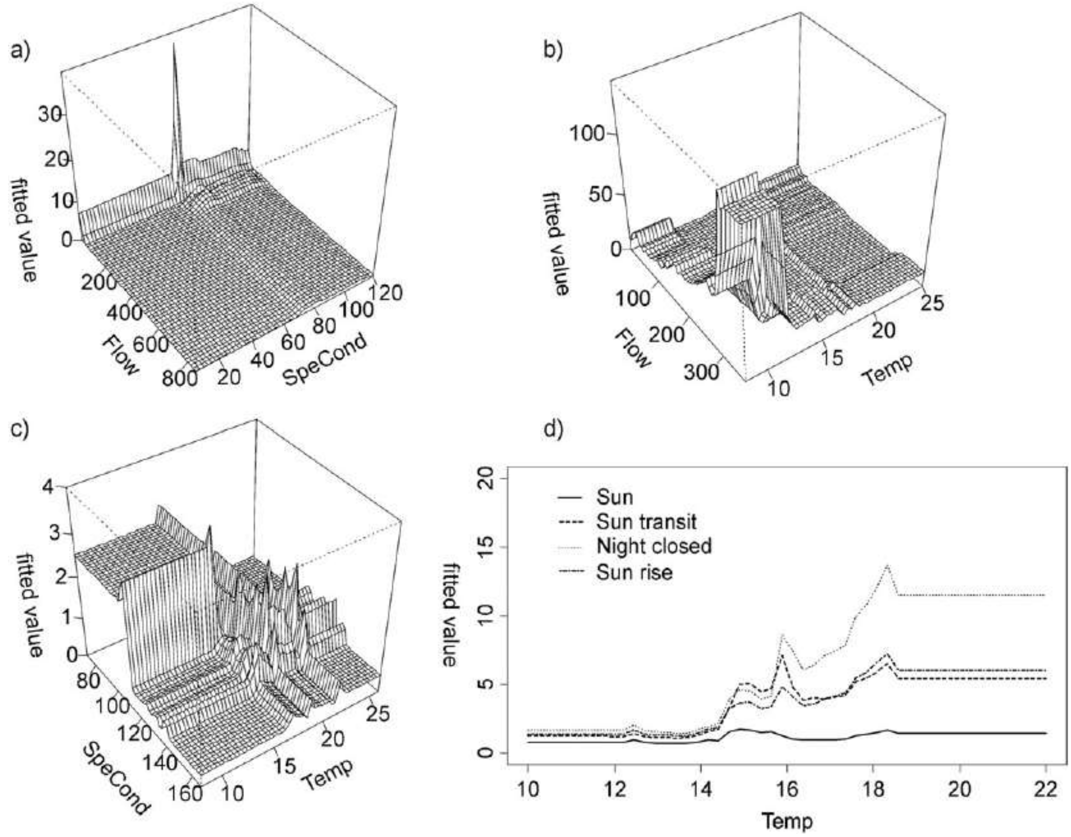

FIGURE 8 Three-dimensional partial dependence plots for the strongest interaction between influential explanatory variables in the Boosted Regression Trees models developed with the data collected in (a) 2013, (b) 2014, (c) 2015, and (d) 2016 sea lamprey spawning seasons

to provide important information such as rates of fishway entrance approach, entry and successful passages, rates of failure, and associated delay or transit times. These are important metrics that aid to clarify the precise influence of environment variables in the behaviour of migrating fish in the vicinity of fishways. Taking this in consideration, the main focus of this discussion is to propose guidelines that can potential increase the overall frequency of successful sea lamprey passages and as well as to suggest related future work perspectives.

4.1 | Seasonal and daily patterns

The timing of spawning migration in anadromous sea lamprey exhibits great variability across the species distribution range, with the occurrence of a latitudinal gradient, where lower latitudes are associated with earlier migration (Almeida & Quintella, 2013; Beamish, 1980). In Portuguese rivers, and particularly in Mondego, data from commercial fishing catches in estuarine environment indicate that sea lamprey spawning migration begins in middle December with a migration peak between February and April. Although spawning occurs during May/June depending on the climacteric conditions (Almeida et al., 2000; Quintella, Andrade, Koed, & Almeida, 2004).

Data gathered at Coimbra fishway (located 45 km from the river mouth) allowed to identify that the first animals start to appear at the upstream fishway exit in January/February and the peak of migration in this river stretch occurs between April and May. Despite the presence of an 11-km man-made stretch of 10 riffle areas of submerged blockstone weirs (turbulent flow patterns and relatively high current speeds [0.8–2.9 m/s]) that extend downstream from Coimbra fishway to Formoselha weirs (limit of freshwater zone), Almeida et al. (2000) estimated that the total migration time needed to cover this distance is approximately 5 days (Almeida et al., 2000). Yet because we are unable to identify and separate the time between arrival, fishway approach, entrance, and passage, the accurate delay and the 67% of failures (33% of passage efficiency according to Pereira et al., 2017) are not completely clear.

Throughout the study period (2013–2016), interannual differences were observed in terms of the numbers of sea lamprey spawners and the period comprising the bulk (80%) of the passages. As emphasized by the output of BRT models, it can be attributed to the identified differences in hydrological and meteorological conditions between studied years (Figure 6). The attractiveness of a river for sea lamprey is thought to increase with higher discharge flows at the beginning of the migration season (Almeida et al., 2000), and in the present study, it was observed that the lower number of animals entering in Mondego river and successfully used the fishway also occurred in the most dry and hot year (Instituto Português do Mar e da Atmosfera, 2015).

Regarding circadian rhythms, sea lampreys are negatively phototaxic and it is recognized that during upstream migration, spawners exhibit strong diel patterns of migratory activity, being more active during dusk and darker hours (Stier & Kynard, 1986, Almeida et al., 2002, 2000, Quintella et al., 2004). This strong diel pattern was also confirmed in the present study; however, 34% of the total sea lamprey upstream movements at the fishway occurred during daylight (7 a.m. to 7 p.m.). Similar findings were observed by Castro-Santos et al. (2016), where the authors identified that due to the rate of movement through the fishways, even though sea lampreys entered mostly by night, passage events occurred during daylight hours. Thus, these daylight movements can be the result of animals with higher transit times or a late fishway entrance (i.e. during the night period) and consequently its progression, due to the absence of light refuges inside the fishway. Data from two CEMG-tagged lampreys that negotiated Coimbra fishway have suggested a transit time of approximately 3 hr (Pereira et al., 2017), but it may be longer depending on environmental conditions faced by the lampreys.

4.2 | Environmental triggers

Fish migration depends on several factors, such as fish morphology, species behaviour, physiological capability, motivation, but also on environmental variables that act as triggers or cues for this ecological process (Cooke & Hinch, 2013; Jonsson, 1991; McDowall, 1997). Shifts in activity tend to occur over relatively small spatial and temporal scales, highlighting the substantial behavioural plasticity of anadromous species (Binder, McLaughlin, & McDonald, 2010; Keefer, Caudill, Peery, & Moser, 2012; McDowall, 1997). Although the environmental triggers of sea lamprey migration are relatively well known (Moser, Almeida, Kemp, & Sorenson, 2015), that is, discharge flow and temperature among the most important (Almeida & Quintella, 2013; Applegate, 1950; Beamish, 1980; Hardisty & Potter, 1971), there is little information regarding the external factors and the threshold that optimize the fishway performance for lampreys.

In the present study, by complementing visual counts with a relative estimation of animal's abundance downstream the dam, we addressed indirectly the uncertainty related to the variability in the size of the population attempting to negotiate the fishway and reduce the potential bias associated with it, but keeping in mind that it may constrain the precision of the information that was collected. The number of sea lampreys using the fishway was independent from the estimated number of available fish downstream the dam, whereby we considered that is reasonable to accept that observed frequency of successful passages is being modulated by fishway operation and related environmental variables.

Our data show some interannual fluctuation in the contribution of each predictor to sea lamprey passage, that we considered to be the reflection of the environmental variability observed along the studied years. Nonetheless, the most important predictors that constrained sea lamprey successful upstream movements through the fishway were consistently identified along the years, and threshold values identified. The frequency of movements was mainly influenced by a combined effect of flow and temperature, which is in accordance with the described triggers for upstream migration (Almeida & Quintella, 2013; Applegate, 1950; Hardisty & Potter, 1971; Keefer, Moser, Boggs, Daigle, & Peery, 2009; Moser et al., 2015) and also identified as important factors in the observed fishway entry rates of sea lamprey at two dams on the Connecticut River, USA (Castro-Santos et al., 2016).

The explanatory power of the predictors that were tested varied across years, being observed some evidences that in dry years, flow discharge loses importance and temperature assumes more relevance in triggering sea lamprey migration through the fishway. Differences in the magnitude of the predictors role associated with different hydrological years are not so well documented, but our results present some preliminary evidences of these relationships. However, to characterize these behavioural patterns with higher accuracy future telemetry studies should be developed.

Moser, Zabel, Burke, Stuehrenberg, and Bjornn (2005) identified that the delay in Pacific lamprey, Entosphenus tridentatus (Gairdner) migration at hydropower dams in Columbia River basin varied as a function of time and temperature, observing a decrease in migration delay as the season progressed and with an increase in water temperature. Variables associated with dam operation, as flow or spill, were not relevant. However, it is important to highlight that migratory peak of this species is in summer, after maximum discharges occurred and both species present pronounced species-specific differences in terms of swimming and passage abilities, particularly regarding kinematic of climbing, as Pacific lamprey shows strong vertical climbing abilities (Moser et al., 2015). Also, the studied fishways and dam's vicinity are quite distinct, presenting different velocities and turbulence conditions.

Regarding fishway negotiation, successful movements were reduced with flow discharges higher than 150 m^3/s, and frequency enhanced with discharge flows lower than 100 m^3/s. Similar results were observed by Pereira et al. (2017) during the assessment of the Coimbra dam fishway efficiency, where all the PIT tagged lampreys negotiated the fishway during discharge flows lower than 100 m^3/s and 88% near 50 m^3/s. When swimming in a free river stretch, Almeida et al. (2002) also identified that sea lamprey migration in Mondego river was stimulated (increase in ground speed) with a rise in flow discharge during the night periods, but only until water flow reaches approximately 70 m^3/s, above which can hinder lamprey's progression (Almeida et al., 2002). Findings from Castro-Santos et al. (2016) show that for sea lampreys exposed to low-moderate flows, increasing flows had higher entry rates, highlighting the importance of discharge in motivation and orientation of these animals.

In the presence of higher flows, conditions near the dams change as a result of higher turbulence and confounding flows, being expected to alter the movements of sea lamprey (strong rheophilic behaviour) and act as impediment of fishways' use. The assessment of migratory behaviour and muscle activity downstream the Coimbra dam through conventional and EMG radio tracking and PIT telemetry showed that under higher flows (above 100 m^3/s), lampreys are diverted from the fishway attraction flow and entrance, remaining in the central gates of the dam where they continue to develop a very high level of activity (Pereira et al., 2017) and consequently a reduction on the overall performance of the fishway was observed. In these circumstances, sea lampreys are regularly observed jumping out of the water by performing extremely intense swimming movements trying to overcome the obstacle through the gates. However, due to the absence of a continuous monitoring and a spatially detailed array of telemetry receivers downstream the dam, we could not quantify the causes of failure and precise time of delay.

Temperature was also considered in this study as one of the major predictors affecting the activity of movements assessed through the Coimbra fishway monitoring window. The bulk of passages occurred when temperatures reached values between 15 and 19°C; however, migratory activity was detected along a higher range of temperature from 11 up to 22°C. The interaction between temperature and flow in 2014 emphasizes that the passages at lower temperatures were related with the higher flows when present in the beginning of the migratory peak in March. Previous studies on sea lamprey migration identified that this process occurred when temperature reached values between 10 and 18°C (Applegate, 1950; Beamish, 1980) with the peak at approximately 15°C (Binder, McLaughlin, & McDonald, 2010) corroborating the data collected with the present study. In the absence of high flows, temperature plays a key role in triggering migratory activity and, on regular hydrological years, both predictors interact. In dry years, as described for landlocked sea lamprey (Binder, McLaughlin, & McDonald, 2010), migration seem to rely more heavily on thermal triggers than on flow variation.

4.3 | Fishway optimization

It is consensual that visual counts alone only allow to enumerate the total number of animals that use a device, regardless overtime information on population size downstream the dam, the rates of failure, the transit times, or even their fate afterwards. Being a time frame, it unable to fully understand continuous processes such as route's selection and the intricated effects of covariables that are constantly changing overtime (see Castro-Santos & Perry, 2012). The information collected in the present study is hampered by that constrain. Nevertheless, because a robust dataset was used (four migratory seasons associated with about 49,490 lamprey upstream movements through the fishway), we were able to statistically identify relations that when complemented with additional collected data, such as mortality by commercial fisheries (as a proxy for the relative abundance of spawners downstream the fishway) and overall fishway efficiencies (Pereira et al., 20017), can be used to identify with some confidence the environmental variables thresholds that explain higher passages for sea lamprey in Coimbra fishway. This allowed us to draft some management proposals and guidelines for future study designs.

As mentioned, hydrological conditions will determine the contribution of the major factors influencing the passage performance, so attention must be given when considering dry and normal/wet years.

Overall, management should privilege the implementation of discharge flows centred in periods of the spawning migration that meet the abiotic conditions identified as preferential. In normal/wet years, when temperature rise above 15°C, the maintenance of discharge flows below 100 m^3/s seems to be associated with a higher passage frequency, and considering the species' diel pattern, night periods (11 p.m. and 5 a.m.) should be prioritized. Because during the migration peak an intermediate closed fishing period is implemented in the Mondego basin (March–April), it is important to take advantage of the reduced fishing pressure over the resource and ensure the highest successful passages at this device with the lowest delay. On the other hand, in dry years, a suitable alternative compatible with water demand and management could rely in synchronizing the hydropeaking (i.e., regulated increased river discharge) with the migratory period that comprise the peak of migration (i.e., April) and meet the identified range of temperatures. These results can contribute to optimize the overall passage performance and reduced the high mortality of this species that often occurs in dam's vicinity, mainly caused by poaching (Mateus et al., 2012).

For future studies, a deeper understanding of route selection, rates of movement, and failure overtime in the vicinity of the fishway are important information that we did not manage to collect during this or previous studies. This can be achieved by adding to the already installed PIT antenna in the upstream section of the fishway, additional PIT antennas deployed in strategic places, such as the vicinity of Coimbra dam tailrace and gates, the fishway entrance, and the forebay or with an extensive radio telemetry receiving array (multiple antennas).

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