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Fish pass use by shads (*Alosa alosa* L. and *Alosa fallax* [Lacépède, 1803]): Implications for monitoring and management

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Abstract

Fish pass monitoring is essential to ensure the device's effectiveness as a mitigation measure for river impoundment, guaranteeing the longitudinal continuity of rivers, which is particularly important for diadromous fish that depend on obligatory migrations to freshwater reproduction (anadromous) or feeding areas (catadromous) to complete their life cycle. The upstream migration of the anadromous allis (*Alosa alosa* L.) and twaite (*Alosa fallax* Lacépède, 1803) shad in the River Mondego, Central Portugal, is being monitored at the Coimbra Dam fish pass since 2013, using visual counts. Statistical models were used to evaluate shad passage and to identify the main environmental variables that seem to condition their behaviour. A total of 26,561 shad were recorded in this infrastructure during the study period (2013–2017), with 96.5% of the total counted fish being counted between April and June. Overall, water temperature and river flow are the environmental predictors that consistently influence the number of shad using the fish pass, although its individual contribution changed between years. The models (Boosted Regression Trees) obtained were robust with an average explained deviance of 0.79 (R^2), despite the poorer results associated with the 2015 spawning season, that were possibly related with the low number of adult fish observed that year. Results from this study contribute to better understand the dynamics associated with fish pass use by *Alosa* sp. and can help the conservation and management of these species through the improvement of fish pass attractiveness and, consequently, the overall efficiency of fish pass devices targeting shads.

KEYWORDS

allis shad, anadromous, twaite shad, upstream migration, vertical slot fishway, visual counts

1 | INTRODUCTION

River impoundment for flood control, irrigation, water abstraction and hydropower production has severe impacts on aquatic ecosystems and fish populations (McCartney, 2009). Dams and weirs are particularly detrimental for diadromous fish, since they constitute obstacles that prevent reproductive and trophic migrations, often resulting in loss of adequate habitat, fish mortality, population reduction and segregation or, in extreme cases, regional extinction (Freeman et al., 2003; Larinier, 2001). Although human populations have always used river systems, in the last century, the construction of hydraulic infrastructures that block rivers and considerably alter the flow patterns has increased (e.g., Baxter, 1977; Larinier, 2001; Nilsson et al., 2005).

Fish passes have been used worldwide as an attempt to mitigate habitat fragmentation impacts, enhancing passage for migratory fish and contributing to the restoration and sustainable management of impounded watersheds. These infrastructures facilitate the upstream and/or downstream migration of aquatic organisms over obstacles such as weirs and dams (e.g., FAO, 2002; Katopodis & Williams, 2012). There are several types of fish transposition systems, all designed to attract migrating fish to a specific location in the river, downstream/upstream of the obstruction, and then, either actively or passively, induce them to pass by providing an artificial open waterway, like pool-type fish passes, or by capturing them in traps and transfer them upstream, such as fish-lifts (Clay, 1994; Larinier & Marmulla, 2004).

The pool-type fish pass is the most used worldwide and one of the most ancient designs (Noonan et al., 2012). Within this type of structure, vertical slot fish passes are particularly efficient for fish migrating upstream ensuring high performances for species with different swimming capacities (Larinier & Travade, 2002; Romão et al., 2017). These are pool-type passes in which the cross-walls have vertical slots extending over the entire height of the cross-wall (Clay, 1994).

Although fish passes are vastly employed, their effectiveness, the ability of the fish pass to get the intended species through, and efficiency, the percentage of fish downstream that are able to overcome the obstacle, is at times far from ideal (Bunt et al., 2012; Noonan et al., 2012; Oldani & Baigún, 2002). Fish migration is dependent both on species morphology, behaviour, physiological capacity or motivation and also on a set of environmental variables responsible for inducing fish migratory behaviour, such as water temperature or streamflow, among others (Baras et al., 1994; Binder et al., 2011; Katopodis, 2005; Lucas & Baras, 2008). Fish pass use is determined by the ability to attract the fish to its entrance and once there ensure viable conditions for obstacle transposition. Location, design and hydraulic operation (e.g., flow discharge characteristics), condition fish pass attractiveness and use (Cooke & Hinch, 2013; Larinier, 2008). Since different target species have different requirements, the development of monitoring programs focused on fish pass effectiveness and efficiency is vital to recommend eventual modifications and guarantee upstream and/or downstream passage as intended (Larinier et al., 2006; Thiem et al., 2013).

The River Mondego is a highly regulated Portuguese watercourse, of great importance for threatened anadromous species such as allis (*Alosa alosa*, L.) and twaite (*Alosa fallax*, Lacépède 1803) shad, and sea lamprey (*Petromyzon marinus*, L.; Almeida et al., 2002). These species represent important fishing resources for riverine human communities and are considered a gastronomic delicacy with high commercial value, contributing to a significant increase in tourism in this region during the migratory season (Stratoudakis et al., 2016).

Allis shad abundance has been decreasing across its natural distribution area, raising concerns among academic and administration institutions responsible for the management of fisheries (e.g., Rougier et al., 2012; Stratoudakis et al., 2016). The collapse of its stocks across its geographic range has been attributed to overfishing, water pollution and habitat reduction due to river impoundment (Costa et al., 2001; Groot, 1990; Rougier et al., 2012). In this context, habitat rehabilitation through the construction of fish passes, which will allow access to upstream spawning grounds for adults and nursery areas for juveniles, is of great importance for the successful management and recovery of their populations.

In Portugal, allis shad still occurs in the main river basins, namely, Minho, Lima, Douro, Vouga, Mondego, Tagus and Guadiana (e.g., Cabral et al., 2006; Costa et al., 2001; Faria et al., 2012; ICES, 2015; Mota & Antunes, 2011). Its exploitation, a historically important source of food and revenue, is spread across the country, although with stronger presence in the north and central regions where the species is more abundant (Baldaque da Silva, 1892; Mota & Antunes, 2011).

Shad landings from River Minho decreased from over 100,000 individuals in 1914 to less than 10,000 in 2010 (Mota et al., 2016) trend similar to the one found in other Portuguese rivers. Presently, with the accentuated decline observed in the north, the most important river for shads in Portugal seems to be the River Mondego (Almeida et al., 2018; Stratoudakis et al., 2016).

Although this species is listed as Least Concern (LC) in the IUCN Red List Status (Freyhof & Kottelat, 2008), the observed drastic reduction in Portuguese landings granted the species the status of Endangered (EN), accordingly to the Portuguese Red List of Threatened Vertebrates (Cabral et al., 2006).

Twaite shad is present in the same watersheds as allis shad and also in the southern rivers Mira and Sado, but it is commercially harvested only in the River Guadiana due to its smaller size, and also because the anadromous allis shad is rare in this river (Esteves & Andrade, 2008; Faria et al., 2012; ICES, 2015; Stratoudakis et al., 2016). Similar to allis, the twaite shad also experienced a considerable decline in abundance throughout its distribution range. For this species, the main reasons for decline are habitat loss and degradation due to human activities (Aprahamian et al., 2003; Maitland & Hatton-Ellis, 2003). This species is also classified as Least Concern (LC) by IUCN (Freyhof & Kottelat, 2008), although in Portugal, it is considered Vulnerable (VU) (Cabral et al., 2006). Both species are listed in Annexes II and V of the EU Habitats and Species Directive 92/43/EEC (Council of the European Communities, 1992) and Appendix III of the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, 1979).

The present study's main goal was to access the influence of environmental variables on the successful negotiation of a vertical slot fish pass, installed at the Coimbra Dam in the River Mondego, by allis and twaite shad.

With this purpose, an explanatory statistical model was used. The information gathered can contribute to the development of management measures directed to increase fish pass use by shads during the spawning migration.

2 | MATERIAL AND METHODS

2.1 | Study area

The present study was developed at the Coimbra dam fish pass located in the River Mondego (Figure 1), the largest river running entirely in Portuguese territory (234 km long, catchment area of 6,645 km^2). This system, despite heavily regulated, is one of the most important watersheds for diadromous fish in Portugal, making its rehabilitation essential for the conservation and sustainable management of these species (Almeida et al., 2018). Coimbra dam was built in 1981 mainly for flood control and irrigation purposes. This structure, located 45 km upstream from the river mouth, was, until 2011, the first unsurmountable obstacle for migratory fish, forcing anadromous species to reproduce in the highly modified 15 km freshwater river stretch available downstream of the dam. The Coimbra dam flow is essentially dependent on the daily operation of the larger dams located upstream (Almeida et al., 2002). Since its construction, this dam was equipped with a pool-and-weir fish pass that proved to be inadequate for its purpose. However, in 2011, a new vertical slot fish pass was built to provide access to suitable upstream habitat for anadromous fish, representing an increase of the available river stretch in the main stem of ~30 km and considering the two major tributaries, rivers Ceira and Alva (Figure 1), of an additional ~20 km (Almeida et al., 2016; Pereira et al., 2017).

The new fish pass constructed at this dam comprises a 125 m long channel with 2 m water depth, divided into 23 rectangular pools (4.5 × 3.0 m). Adjacent pools are connected by vertical slots (0.5 m width), and the water level difference between adjacent pools is 0.25 m. At the slots, water velocity is between 1 and 1.5 m s^{-1}, with dissipated power in the resting pools below 150 W m^{-3}. Flow discharged in the fish pass is kept permanently at 1.5 m^3 s^{-1} to attract the fish. These characteristics were particularly designed to ensure high passage effectiveness for *Alosa* sp. and sea lamprey (Pereira et al., 2019).

2.2 | Data collection

The vertical slot fish pass at Coimbra Dam includes a monitoring room equipped with a window (125 cm × 200 cm) and a video system that records all the fish that successfully negotiate it. These recordings represent a noninvasive and accurate method of observing and counting fish, without influencing their behaviour or movement patterns (Bowen et al., 2006; Haro & Kynard, 1997; McCormick et al., 2015).

The recording system includes a digital video recorder (Samsung SRD-470), a monitor (AgNeovo) for displaying images and a high-resolution camera equipped with an infrared LED system (Samsung SCO-2080R) to capture day and night images. Basic visualization software (Backup Viewer v1, Samsung Techwin Co., Ltd.), included in the recording system package, was used to analyse the images.

From 2013 to 2017, the number of shad using the fish pass, the direction of their movements (upstream/downstream) and any other peculiar behaviour was analysed by trained researchers through visual observation of the video-recordings.

Because the fish were not manipulated and due to the phenotypic similarities between allis and twaite shad, identification at the species level was not possible using visual counts. It was decided that hereinafter the generic term *Alosa* sp. should be used.

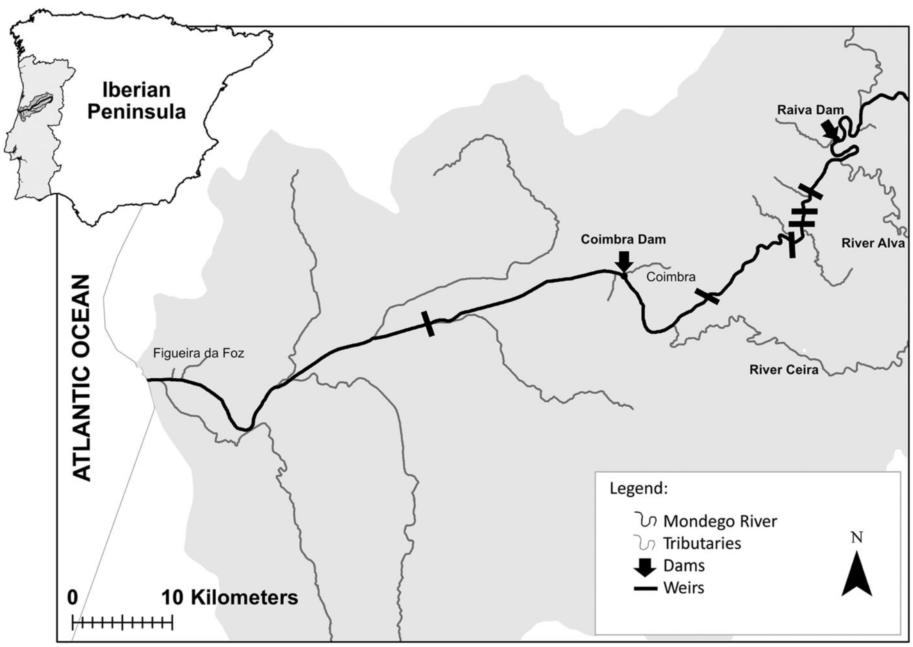

FIGURE 1 Map of the River Mondego, representing the main existent obstacles

2.3 | Data analysis

Seasonal and diel patterns of *Alosa* sp. fish pass use based on the number of individuals counted per hour of monitoring were analysed and plotted (R Development Core Team, 2017).

Through the comparison of fish counts with several abiotic variables with potential to act as predictors of fish passage, we generated a model for each *Alosa* sp. spawning season to explain fish pass use. Considering the migration season described for the species at the present location, fish are more likely to be observed using the fish pass between January and June. For this period, fish counts were grouped in hourly intervals (Almeida et al., 2016). Hourly intervals with more fish moving downstream than upstream were removed from the data set. The respective peak of migration was identified, and of the total number of migrating fish observed in the window, the first and last 10% of all migrating fish were discarded to increase the resolution power during the peak of the spawning migration (i.e., 80% of total *Alosa* sp. movements), hence focusing the analysis on the variables influencing fish pass use for the majority of shad (Pereira et al., 2019).

Abiotic variables selected included temperature, turbidity, conductivity, discharged flow, lunar cycle, photoperiod and day period (Table 1). A multiparameter probe (EXO2 Water Quality Probe) equipped with sensors for turbidity, temperature and conductivity was deployed inside the first downstream pool of the fish pass and recorded these physical–chemical variables every 30 min. In addition, hourly records for total discharged flow from the Coimbra dam were obtained from the Portuguese Environmental Agency (APA). Other environmental data regarding lunar cycle, photoperiod and day period were obtained from the Astronomical Observatory of Lisbon (http://oal.ul.pt/; last time accessed in April 2017; Table 1).

TABLE 1 Environmental variables used as potential predictors to model *Alosa* sp. passage through the Coimbra dam fish pass

Variables (units)	Description
Temperature (°C)	River water mean hourly temperature, recorded in 30 min intervals.
Specific conductivity ($\mu S cm^{-1}$)	River water mean hourly specific conductivity, recorded in 30 min intervals.
Turbidity (FNU)	River water mean hourly turbidity, recorded in 30 min intervals.
Total discharged flow ($m^3 s^{-1}$)	Mean hourly discharged flow at Coimbra dam recorded every time one of the 9 gates position changes.
Photoperiod[a]	Day length in number of light hours
Lunar cycle	Moon phases. (Full Moon, FM; Last Quarter, LQ; New Moon, NM; first quarter, FQ)
Day period	Day stages according to twilights (night closed, NC; Sun rising, SR; Sun transit, ST; sunset, SS)

Abbreviations: DayPer, day period; Flow, total discharged flow; LunCyc, lunar cycle; PhoPer, photoperiod; SpeCond, specific xonductivity; Temp, temperature; Turb, turbidity.

[a]Variables removed due to correlation with other variables.

All environmental variables/predictors were submitted to a Spearman correlation test to check for redundancy among the set of selected environmental variables, and in case of high correlation ($r > 0.8$), one of them was removed from the data set to avoid the inclusion of redundant variables in the developed models (Ferreira et al., 2013; Snelder & Lamouroux, 2010).

In this case, photoperiod was removed from the analysis, since the statistical test applied showed high correlation from this variable with water temperature. Between the two variables, temperature was selected, since photoperiod variation is constant between sampling years; thus, temperature would more likely explain differences between migration seasons. Furthermore, temperature has been known to influence shad behaviour (e.g., Acolás et al., 2006; Aprahamian et al., 2003; Baglinière et al., 2003; ICES, 2015).

To analyse the effect of environmental predictors on shad passage, boosted regression trees (BRTs) were applied (Elith & Leathwick, 2017; Hastie et al., 2009; Leathwick et al., 2006, 2008; Segurado et al., 2015).

BRTs combine the regression trees' capacity to accommodate missing data, outliers and different types of predictor variables, with the improved model accuracy obtained by using a boosting algorithm (Elith et al., 2008). This flexible tool chooses relevant variables, produces accurate fit functions and identifies and models interactions, making them highly useful to analyse environmental data (Elith et al., 2008; Pereira et al., 2019).

In the BRT analyses, upstream movements of shads recorded at the monitoring window were considered as the response variable and the non-redundant abiotic variables as predictors. The fitting of the optimal models included the modification of model evaluation parameters such as tree complexity (tc) and learning rate (lr) until minimal predictive deviance was attained without overfitting. The tc represents the number of split points in each tree defining the maximum number of interactions adjusted, while lr, also known as shrinkage, determines the contribution of each tree to the growing model (Elith et al., 2008; Zhang et al., 2012).

To identify the optimal number of trees which should be used for each model and subsequently assess the model performance, tenfold cross-validation (cv) was applied. In 10-fold cv, the data set is partitioned into tenfolds or subsamples. Model calibration is performed using nine folds, while the left-out fold is used for comparison with the model created values. Model performance is assessed through the following parameters: (i) the smallest cv deviance (cv predictive deviance), (ii) percentage of explained deviance (R^2), ideally close to 1, in which case the model explains 100% of the observed variation, and (iii) the cv correlation, described as a measure of correlation between the observed data and set data, calculated from the Pearson correlation, that may have significant results (Elith et al., 2008). Model simplification was attained using a code developed by Elith et al. (2008), which removes non-informative variables by dropping the least important predictor and then resetting the model sequentially. Such simplification is most useful for small data sets where redundant predictors may reduce performance by increasing variance. This process is run with a cv procedure with 10 partitions that uses the average cv error to decide the number of predictors to be dropped while maximizing model performance (Elith et al., 2008). The contribution of each environmental variable in the model was determined using the 'gbm' package (Ridgeway, 2017). This relative influence is rescaled, so that the sum is 100, with greater values indicating higher influence on the response (Froeschke & Froeschke, 2011). Partial dependent and interaction plots were created for the most influential variables.

A total of five models were created and fitted; for each year, the best model was chosen based on their performance considering cv deviance, cv correlation and R^2. In addition, the contribution of each environmental variable was determined, to analyse which predictors were more frequently selected for division processes at the division nodes, during the construction of the model. The statistical analyses were conducted using R 3.4.1 (R Development Core Team, 2017) coupling 'gbm' library (Ridgeway, 2017) as well as code provided as supplementary information in Elith et al. (2008).

3 | RESULTS

From 2013 to 2017, a total of 26,561 shad successfully negotiated the Coimbra dam's fish pass (Table 2). Between 2013 and 2015, a regular decrease was observed in shad counts, with a minimum of 966 records in 2015. In 2016, a considerable increase in the number of shads counted in the fish pass was noted, and in 2017, a maximum record of 9,275 shads was observed (1.2× the 2013 results and 9.6× the minimum registered in 2015). These fluctuations are most likely due to the strength of each cohort.

During the five spawning migration seasons monitored, 96.5% of the fish, on average, were observed using the fish pass from April to June, generally peaking in May (Figure 2).

Some variability was perceived among years in the period of the day chosen by shad to negotiate the fish pass, but some constancy in preferring daylight hours from 12 to 20 h was detected (Figure 3). However, while most individuals used the fish pass during the afternoon period (preferred hours: 2013 from 12h00 to 16h00; 2014 from 13h to 19h00; 2016 from 12h00 to19h00; 2017 from 14h00 to 17h00), in some years, a slight increase in passages was observed between 02h00 and 04h00, and in 2015, they were mostly recorded using the fish pass at night (00h00 to 06h00). Although shad seemed to prefer a particular time of day each year, especially for the first 2 years of sampling, when the observations for the five migration seasons were analysed together, no specific diel preferences were identified (Figure 3).

In 2013, 2014 and 2017, we observed events of 'peak passage' when more than 500 animals used the fish pass in the same day, whereas these were not recorded in 2015 nor 2016 (Figure 4). For the first 2 years of study (i.e., 2013 and 2014), when a more prolonged fishing season was still in place, peaks of passage seemed to occur during or immediately after the intermediate fishing closure set at the end of April and 80% of the fish got through in less than 30 days (average of 24 days). Whereas in later years (i.e., 2015–2017), during which a distinct (earlier and shorter) fishing season was implemented, fish passage seemed to be less concentrated in time taking at least 40 days for 80% of the fish to cross (average of 44 days).

Five models were chosen based on their performance (Table 3). The adjusted models performed well resulting in R^2 values of 0.79 on average (R^2_{2013} = 0.92; R^2_{2014} = 0.99; R^2_{2015} = 0.53; R^2_{2016} = 0.76; R^2_{2017} = 0.75). When 2015 is set aside, a year with a very low count of shad on the fish pass (966 individuals; Table 2), the average R^2 increased from 0.79 to 0.86 (Table 3).

In 2013, the lunar cycle was the most important factor (42.7%), followed by discharged flow (20.8%), whereas in 2014, discharged flow assumed higher percentage of explanation (70.2%), followed by water temperature (24.4%). In 2015, specific conductivity (22.7%) and discharged flow (22.7%) showed the highest percentage values and in 2016 and 2017 water temperature (26.6% and 37.5%, respectively),

TABLE 2 Total number of *Alosa* sp. identified using the fish pass between 2013 and 2017

	2013	2014	2015	2016	2017	Total	Average
Number of shad using the fish pass	7,503	3,427	966	5,390	9,275	26,561	5,312
Percentage of shad using the fish pass from April to June	98.24	95.30	100.00	99.26	89.68	-	96.50

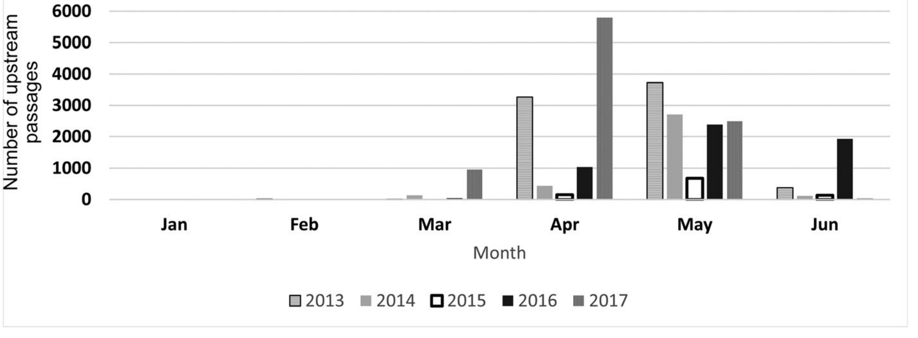

FIGURE 2 Monthly records of *Alosa* sp. using the fish pass at the Coimbra dam from 2013 to 2017

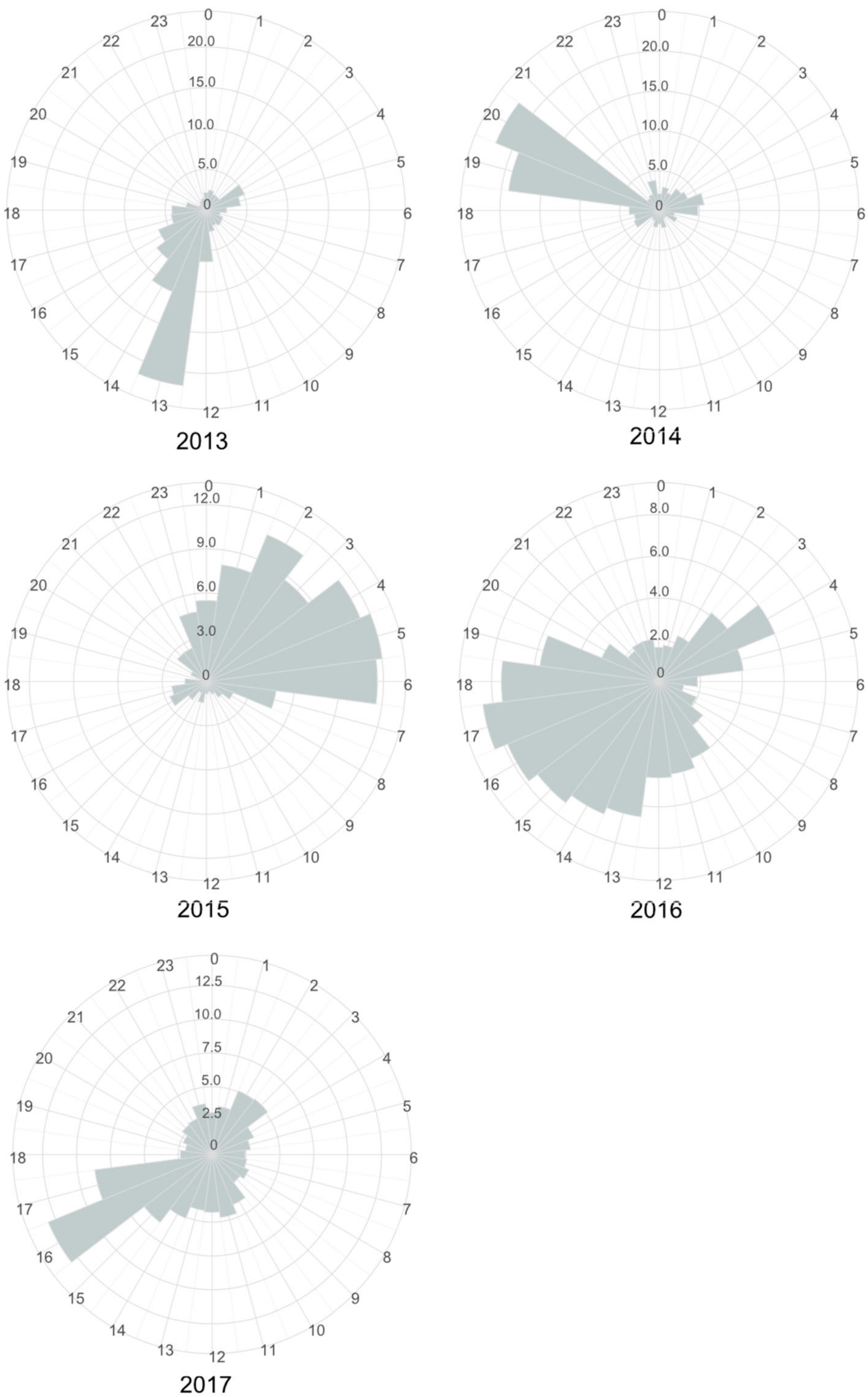

FIGURE 3 Circular plots representing percentage of upstream *Alosa* sp. movements per hour for each of the studied migration seasons and for the combination of the 5 years of the study

followed by flow (22.5% and 33.9%, respectively), were responsible for most of the variation. Although the factors with greater explanatory power varied across sampling years, river flow and temperature were consistently within the first three most important variables in all BRT models (Figure 5).

The partial functions which model each predictor effect on the response variable are plotted in Figure 6. Across the five spawning seasons monitored in this study, discharged flow had a percentage of explanation always above 20%, associated with decrease in fish pass use whenever river flow exceeded ~35–50 $m^3\ s^{-1}$. In 2015, this limit was as low as 25 $m^3\ s^{-1}$, and in 2016, although a reduction in shad counts at flows over 50$m^3\ s^{-1}$ was observed, fish passages seemed to increase again maintaining stable between 100 and 180 $m^3\ s^{-1}$, only to drop drastically once more at 300 $m^3\ s^{-1}$. In all datasets, optimal water temperature for shad successful negotiation of the fish pass was higher than 14°C, peaking at between 17°C and 19°C.

Lunar cycle, turbidity, specific conductivity and the day period accounted for a reduced percentage of variation in most years,

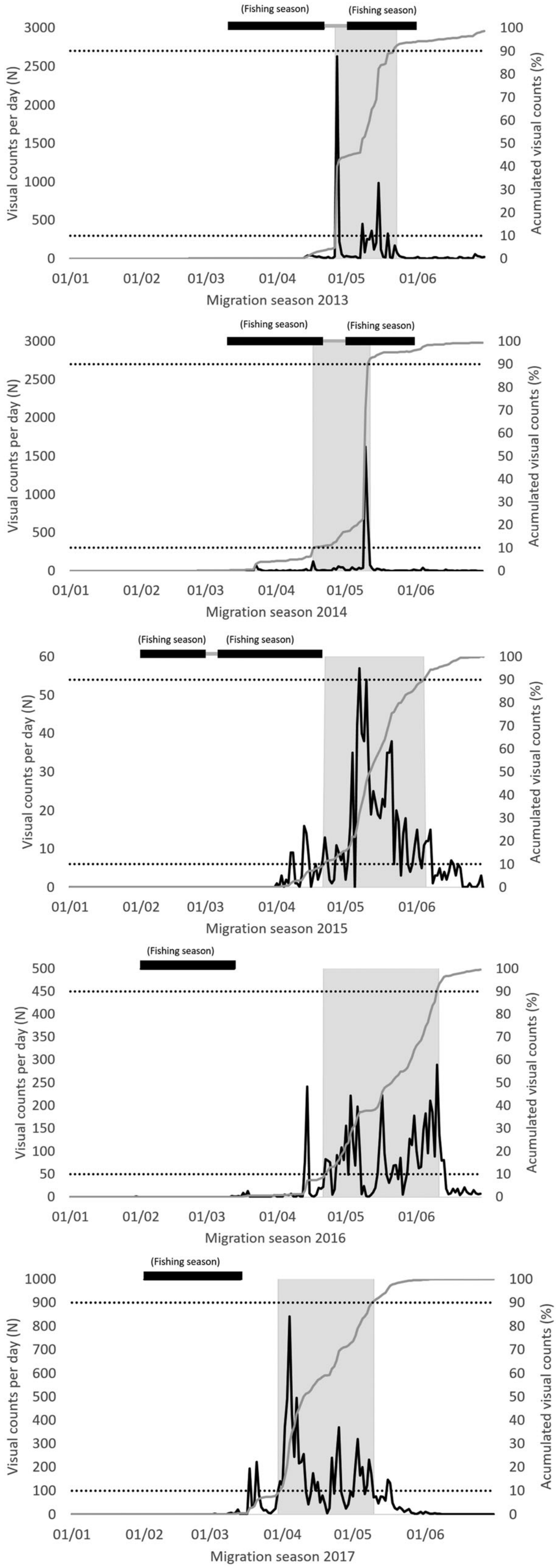

FIGURE 4 Dimensioning of sample data according to the cumulative visual counts 10–90%. Shadow area represents the portion of data used to build the models; the black line indicates the daily *Alosa* sp. counts; the grey line stands for the accumulated visual counts; the dashed horizontal lines limit the 10% and 90% thresholds

notwithstanding some exceptions as we can perceive by the 42% of variation explained by the lunar cycle in 2013.

Shad seemed to prefer full moon conditions during 2013 and 2014, new moon in 2015, first quarter and new moon in 2016, although there is not a clear preference associated to lunar cycle in this year, and Last Quarter and Full moon in 2017. For turbidity and specific conductivity, no clear influence patterns were found (Figures 5 and 6).

As perceived from Figure 6, the day period has a small contribution for the explanation of the variation observed. Both the fitted function plots (Figure 6) and the rose diagrams (Figure 3) indicate that diel patterns are considerable different in-between migration seasons as stated above (Figures 5 and 6).

Interactions between variables were accessed and plotted for river flow and water temperature (Figure 7), in all migration seasons studied except 2015 because no interaction between these two predictors was found in this year. These plots show as well that the best conditions for using the fish pass were met in general when flow was under 35–50 $m^3 s^{-1}$ and water temperature above 14°C. In addition, a second peak of fish pass use was found at 50 $m^3 s^{-1}$ in 2014 and 2016, and a third peak was observed in 2016 with flows around 100 $m^3 s^{-1}$ (Figure 7).

4 | DISCUSSION

The monitoring approach employed in this study revealed crucial information regarding shad upstream migration, and this was accomplished without manipulating individuals and with no associated mortality or impact in behaviour, proving itself adequate to fulfil the goals established. It also confirmed that relatively large numbers of shad use the vertical slot fish pass at Coimbra dam, proving this structure built in 2011 can also be considered a successful habitat rehabilitation measure for shads as well as for sea lamprey (Pereira et al., 2017, 2019). During the study period (2013–2017), over 26,000 *Alosa* sp. successfully negotiated this fish pass, possibly reaching high quality habitat for reproduction in the upstream river stretches.

The selected set of abiotic variables allowed the development of four, out of a possible five, robust models with high performances (average R^2 = 0.79). Many insightful studies have been developed on fish pass efficiency (e.g., Cooke & Hinch, 2013; Noonan et al., 2012; Pereira et al., 2017; Santos et al., 2012), migratory behaviour of *Alosa* sp. (e.g., Acolás et al., 2004, 2006) and ecological modelling of spatial distribution (e.g., Nachón et al., 2016; Taverny et al., 2012; Trancart et al., 2014). BRTs have proven to be useful and to produce better results than other modelling techniques in the understanding and prediction of spatial distribution of fish (e.g., Bangley et al., 2020; Ferreira et al., 2013; Segurado et al., 2015); however, their application in the study of temporal distribution is less frequent (Escalle et al., 2016; França & Cabral, 2015; Pereira et al., 2019; Pittman & Brown, 2011). Furthermore, to our knowledge, the use of BRTs to model fish pass use and the environmental factors

TABLE 3 Performance evaluation of the developed BRT models and parameters chosen

	2013	2014	2015	2016	2017
tc	3	5	4	5	4
lr	0.01	0.01	0.01	0.01	0.01
nt	3,600	6,700	1,300	4,050	3,500
cv deviance	24.923; se = 14.918	7.097; se = 3.731	1.722; se = 0.142	4.242; se = 0.26	9.723; se = 1.604
cv correlation	0.604; se = 0.071	0.791; se = 0.091	0.441; se = 0.033	0.555; se = 0.031	0.539; se = 0.061
R^2	0.92	0.99	0.53	0.76	0.75

Abbreviations: cv correlation, cross-validation correlation; cv deviance, cross-validation predictive deviance; lr, learning rate; nt, number of trees; tc, tree complexity; R^2, percentage of explained deviance.

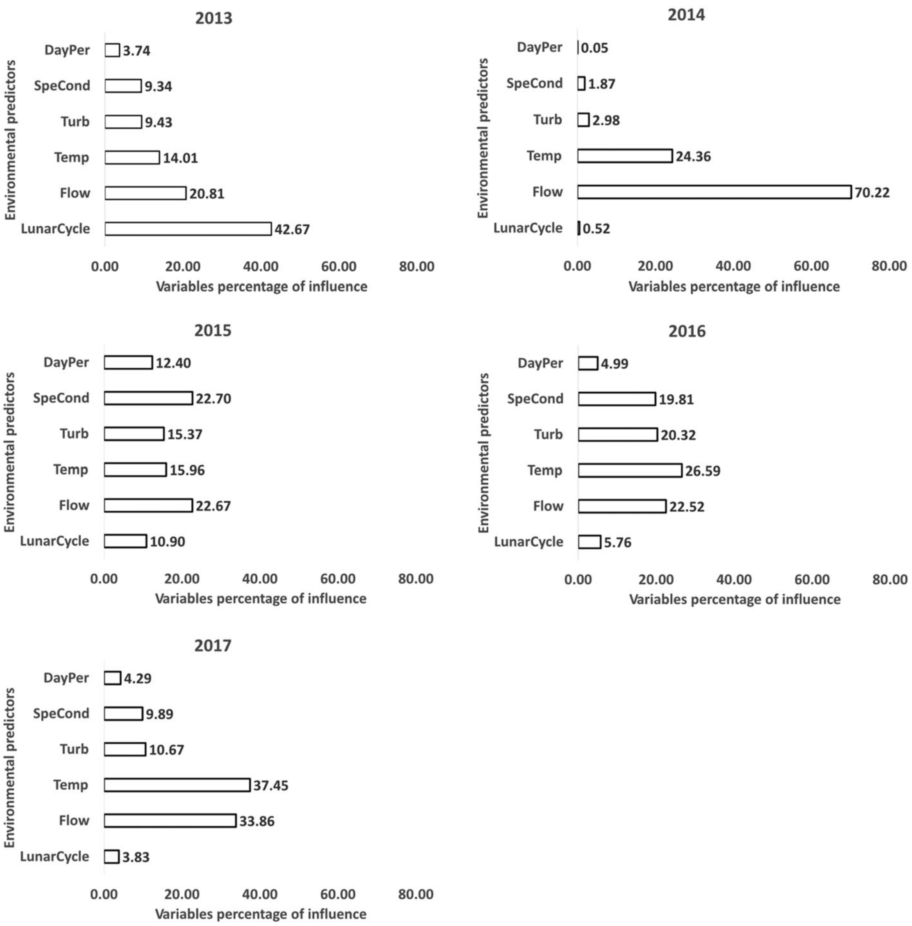

FIGURE 5 Percentage of contribution of each of the environmental factors considered, per year. SpeCond (specific conductivity, μScm^{-1}); Turb (turbidity, FNU); Temp (temperature, °C), Flow (total effluent flow, m^3 s^{-1}); LunarCycle (lunar cycle); DayPer (period of the day)

influencing its successful negotiation is a recent approach to these problems and may bring new insights on the matter (Pereira et al., 2019), especially due to its capacity to deal with missing data, outliers, different types of variables and non-linear relationship between response and explanatory variables, which render the use of other statistical tools inadequate (Elith et al., 2008; Escalle et al., 2016).

For all sampling seasons, the bulk of fish pass usage took place from April to June, in accordance with seasonal migration patterns described for these species in other rivers (e.g., River Minho in Portugal; Mota & Antunes, 2011). Massive fish passage events (>500 fish in 24 h) were observed in 2013, 2014 and 2017, which might reflect migration peaks described in literature that can occur once or twice per season usually in April/May (Mennesson-Boisneau et al., 2000; Mota et al., 2015). On the other hand, these events may be related with a temporary reduction of the attractiveness of the transposition device that leads to shad accumulation downstream, with most fish entering at the same time, when passage conditions become optimal (Larinier & Travade, 2002). A similar situation was observed for lampreys at the same location, with unfavourable flow conditions causing fish accumulation downstream and a posterior peak of passage (Pereira et al., 2019).

Visual counts reflect both fish pass use and fish migratory behaviour inherent to the species biology. This way, exploring the

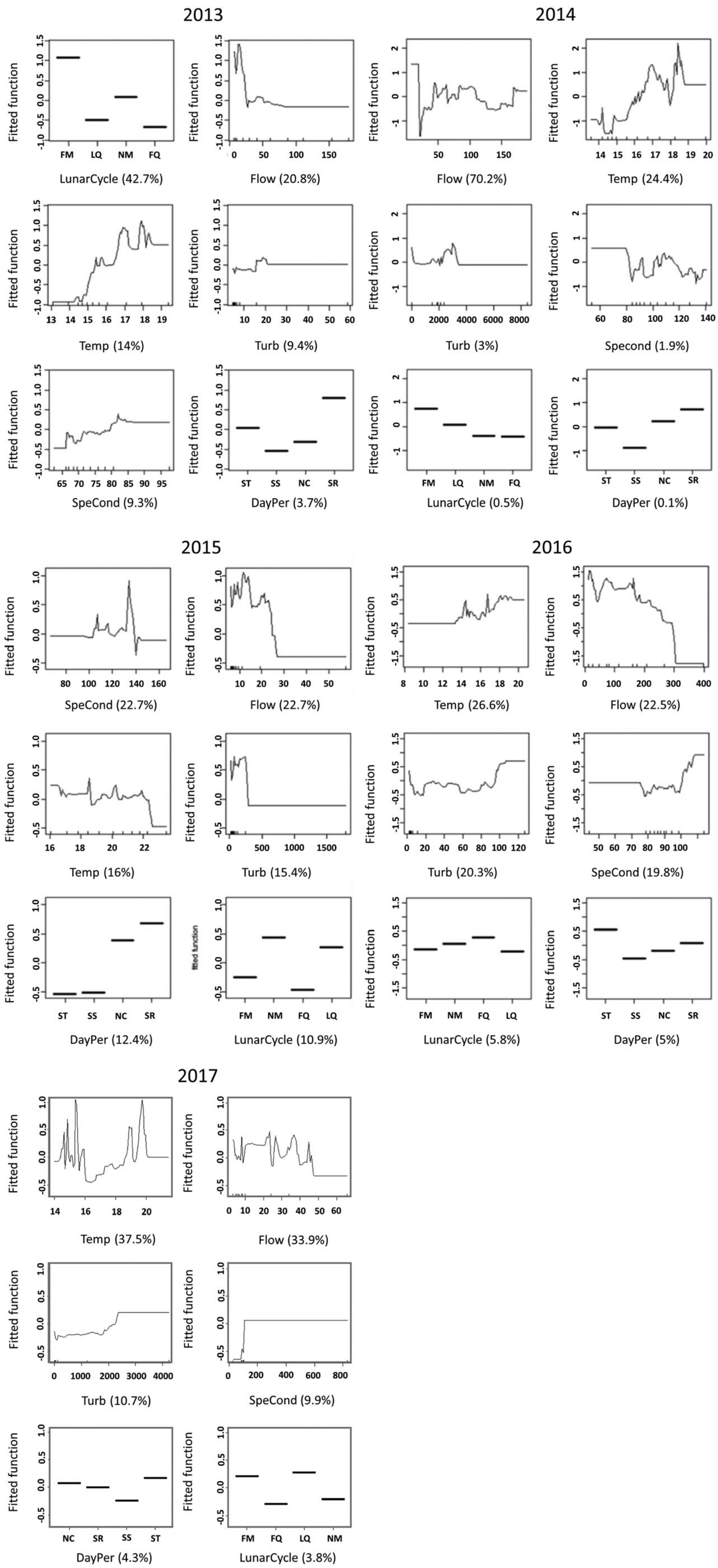

FIGURE 6 Fitted functions for the most influential predictors per sampling year organized in descending order of contribution. The vertical axis observed in each of the presented plots is based on the logit scale and centred to have zero mean over the data distribution. SpeCond (specific conductivity, μScm^{-1}); Turb (turbidity, FNU); temp (temperature, $^{\circ}C$), flow (total effluent flow, $m^3 s^{-1}$); LunarCycle (lunar cycle); DayPer (period of the day). Axes are presented with different scales

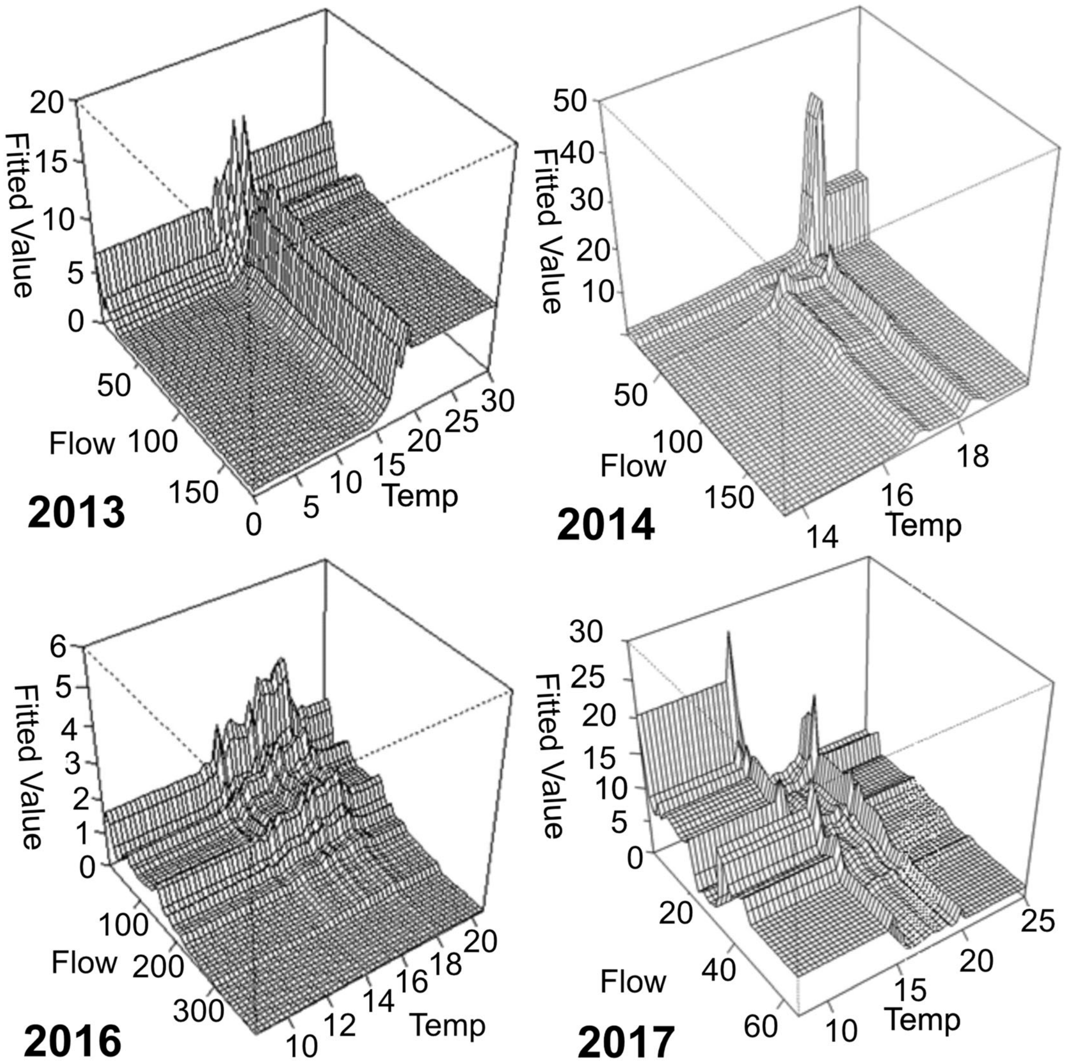

FIGURE 7 Fitted function for the interaction between water temperature and river flow observed during 2013, 2014, 2016 and 2017 spawning migration seasons. Axes are presented with different scales

environmental factors that influence fish passage, reveals both insight information on device use and migration stimulus. Several factors interacting at different scales are likely to determine periods of use and the number of fish using the fish pass (Katopodis, 1992; Pavlov, 1989).

River flow conditions are known to influence fish pass attractiveness, since high water levels may turn the attraction flow inefficient and mask the fish pass entrance (Larinier & Marmulla, 2004; Larinier & Travade, 2002). In the present study scenario, river flows above ~35–50 m^3 s^{-1} drastically reduced fish pass usage by the target species even if some occasional passages were recorded for higher flows. Similar results were obtained by Pereira et al. (2017, 2019) for sea lamprey in the same fish pass covering the same period of time.

Our findings suggest that temperatures under 14°C limit the fish passages, reflecting the typical migration patterns observed in other studies where temperature thresholds limit migratory behaviour (Acolás et al., 2004). Water temperature is believed to play a decisive role in shad migration with optimal conditions usually being met between 12°C and 20°C and little evidence of migratory behaviour with temperatures under 12°C (Acolás et al., 2006; Aprahamian et al., 2003; Baglinière et al., 2003).

No significant and concordant diel patterns were observed across migration seasons, although in most years, shad preferred to use the fish pass during daylight hours. Other studies also found an increase in shad migration behaviour during the day period (Baglinière et al., 2003; Pavlov, 1989). This diurnal behaviour may have been partially suppressed due to the influence of variable interaction on the fish pass attractiveness. Also, the run with most recordings during the night (00h00 to 06h00) was 2015, considering the exceedingly low number of fish registered, we could be observing a less common behaviour that would be otherwise less significant if a higher number of fish for a longer period of time had used the fish pass.

We found some inter-annual variation in the most influential predictors of fish passages, probably resulting from environmental factor interaction or from natural causes related either to individual plasticity and/or context-dependent responses (Binder et al., 2011; Keefer et al., 2013; McDowall, 1997).

Moreover, environmental fluctuations were observed between migration seasons. River discharge was much lower during the 2015 season than in the previous and following years, and in 2016, season high flows were recorded later in the season. Additionally, average water temperature was higher in 2015 and lower in 2016 than in 2013 and 2014 (see Supporting Information i and ii). This intra- and inter-annual variation in discharge and water temperature patterns could also be responsible for the differences found with the models used, considering these variables influence on these species' migration.

The fact that passage data were obtained from visual census, and the impossibility to distinguish between the two species of the genus *Alosa* (*A. alosa* and *A. fallax*) through this method, might be responsible for some of the detected variation. Although these species are very similar and can produce viable hybrids (Alexandrino, 1996a, 1996b; Faria et al., 2012), their behavioural responses might be slightly different and the proportion of individuals from each species may influence the results.

Shad numbers at the fish pass may also be affected by downstream commercial fisheries and poaching activities. These species have high market value and are under substantial fishing effort. Hence, a break in these activities might increase the number of animals reaching the upstream stretches (Costa et al., 2001; Stratoudakis et al., 2016). Our results suggest that the adjustments to the fishing season (i.e., reduction of the fishing period and adjustment in the timing to avoid fishing activities during the peak of migration) may have promoted a more even use of the fish pass by the target species throughout the season. In this context, careful monitoring of fishing activities and associated impact is advised.

5 | CONCLUSIONS

The study area, the River Mondego, is highly regulated by the presence of several dams. Hence, dams' operation could be used to minimize the negative effects of obstruction, from an eco-regulation perspective, by bringing flow to the ideal conditions, identified in the present study for this system, during migration season once or twice a week, for example. In this manner, the influence of flow conditions and their manipulation at the dams could be used to ensure intervals of increased successful negotiation of the fish pass during the migration season.

Moreover, our findings clearly isolate a short window of time, when fish pass use/migration behaviour is at its maximum for these species. Therefore, we suggest for example that flow discharged from the dam should be kept between $\sim$35 and 50 $m^3 s^{-1}$, for at least 3 h twice a week, in between 12 and 22 h, so that accumulating schools might find the fish pass entrance. This measure would be particularly beneficial between March and June, after water temperature reached 14°C, ensuring better conditions for the usual migratory peak and during warmer years. Due to the importance of this period for shads, additional control by the authorities should also be focused during these months.

The information obtained with this work is an important contribution for management and monitoring purposes, since it can reduce the time and resources necessary to monitor this fish pass, highlighting when shads are more vulnerable in this stretch of the river and thus when protection measures are more necessary and efficient. In this case, a minimum cost approach would focus monitoring efforts from March to June.

Furthermore, to deepen our understanding of shad reproductive migration in the River Mondego, the use of other monitoring methods, such as biotelemetry (radio and PIT), could enhance the knowledge available on this matter, regarding passage efficiency for these species (Acolás et al., 2004; Breine et al., 2017; Pereira et al., 2017).

Several factors are at play regarding successful negotiation of fish passes by target species. The methods used in this study and the information collected on shads' migratory behaviour in the River Mondego and respective fish pass effectiveness can be used to improve current management and conservation measures directed to these species, not only in the River Mondego but also in other similar systems, as well as to elaborate efficient monitoring protocols focused on the migration of other diadromous and/or potamodromous species.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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