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Temporal patterns of the catadromous thinlip grey mullet migration in freshwater

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Abstract

The thinlip grey mullet (*Chelon ramada* Risso, 1827) is a catadromous fish that performs massive migrations to freshwater habitats for feeding purposes that can assume a structuring role on riverine ecology due to the biomass involved in these movements. Seasonal movements of thinlip grey mullet through a vertical slot fish pass located in River Mondego (Portugal) were continuously monitored between 2013 and 2017. The extent of trophic migration, population size structure, biomass and the environmental triggers of bi-directional species' migratory activity were analysed. Between March and November of 2013/2014, ~2 million and 1 million movements were respectively recorded. From a subsampling approach, the upstream movements between 2015 and 2017 were estimated. Annually, around five hundred thousand upstream movements can occur to provide species access to the upstream freshwater reaches. Movements are exclusively diurnal, and the population composed by young adults in their first year of maturity, yet juveniles and larger fish were present (TL range: 90–540 mm). Upstream movements increased with temperatures above 15°C, reaching a peak at around 20°C coupled with a photoperiod of 15 h. Downstream movements attained the higher rates when temperature dropped from 22°C to 20°C and photoperiod to 13 h. However, under wetter hydrological conditions (as in 2014), discharge flows have a higher influence.

These finding provide unique information regarding species migration to freshwater habitats in the Atlantic coast, namely the extended periods spent in such environments, overlapping with the spawning migration period. Additionally, highlights the importance of species' trophic migration both for its life cycle and riverine food-web.

KEYWORDS
catadromy, fish passage, habitat use, mugilidae, population structure, trophic migration

1 | INTRODUCTION

Grey mullets are among the most flexible and variable catadromous fish species, with complex life cycles that range from catadromous, to facultative marine wanderers, or entirely marine species (McDowall, 1997). The thinlip grey mullet *Chelon ramada* (Risso, 1827) is known to have one of the highest osmoregulatory competence (Khalil et al., 2012; Lasserre & Gallis, 1975; Rabeh et al., 2010) and it is the most abundant grey mullet species present in environments where salinity is below 13 (Almeida, 2003; Almeida et al., 1993; Cardona, 2006; Maitland & Herdson, 2009). Juveniles are considered, to some extent, euryhaline (Mires et al., 1974), yet they do not always occur on the same grounds as the adults, as osmoregulatory ability increases throughout development (Zydlewski & Wilkie, 2013). Preferentially, they remain in nursery areas of moderately brackish water (Cardona et al., 2008; Rochard & Elie, 1994; Torricelli et al., 1982; Trancart et al., 2012), where they can grow up to 120 mm during the first year (Almeida et al., 1995).

Along the European Atlantic coast, adults can display a wide variety of behaviours, and despite the high residence time in the upper estuary, there is a fraction of the population that seems to only occur in a marine environment (Daverat et al., 2011; Trancart et al., 2012) and another fraction that can perform one of the longest upstream trophic migration within the mugilidae family to freshwater habitats (Almeida et al., 1993; Costa et al., 1994; Hickling, 1970). Colonization of riverine habitats occurs in the spring and summer (Almeida, 1989; Guerra, 1976; Sauriau et al., 1994) when river flow is minimum. These habitats can be located 200–300 km up river as observed in Morocco (Rossignol, 1951), or even further than 650 km, as identified in historical records from River Tagus in the Iberian Peninsula (Almeida, 1989; Almeida et al., 1992), or River Loire in France (Sauriau et al., 1994; Trancard et al., 2011). However, there is a general lack of information regarding either the biological aspects of this catadromous migration to freshwater habitats or the prevalence in these habitats. Studies on thinlip grey mullet's life cycle, habitat use and movement dynamics were predominately conducted in estuarine environments and the available information regarding their permanence in freshwater is inferred base on their spatial–temporal absence from estuarine environment (Cardona, 2001; Glamuzina et al., 2007; Harrison & Whitfield, 2006). A few studies used otolith microchemistry (Chang et al., 2004; Chang & Lizuka, 2012; Daverat et al., 2011; Miles et al., 2018), mark-recapture with conventional tagging (Almeida, 1996a; Sauriau et al., 1993) and biotelemetry techniques (Almeida, 1996b; Funicelli et al., 1989; Le Pichon et al., 2017; Miles et al., 2018), yet applied to a very small sample size in estuaries. So far, the available knowledge fails to target all the possible migratory profiles displayed by this highly abundant species (Daverat et al., 2011) and to provide a clear support to our understanding of the population fraction at freshwater and its implications for the species and the environment.

Existing studies on thinlip grey mullet's presence and population composition at freshwater habitats, showed the existence of different spatial distributions among size-classes (Quignard & Farrugio, 1981; Sauriau et al., 1994) and Oliveira and Ferreira (1997) reported that in River Tagus, 170 km upstream from the estuary, adult thinlip grey mullets were present all year around, suggesting that a part of the population may not leave freshwater annually. More recently, fish pass monitoring programs have identified that, within fish communities where this species is included, it is the one that most abundantly and frequently uses these devices (Almeida et al., 2016; Aparicio et al., 2012; Cardona et al., 2008; Ordeix et al., 2011; Santos et al., 2005), being able to surpass and effectively colonize the upstream river stretches, emphasizing the importance of the freshwater environment for the species life cycle. On the other side, considering that they can become an important vector of marine-derived nutrients and by exploiting the first trophic level directly, their feeding activity and faecal production can promote an increase in the organic matter flux and energy at riverine ecosystems, it is expected that as observed in the estuaries (Almeida, 2003; Almeida et al., 1993; Brusle, 1981), they play an important role in freshwater trophic webs.

Monitoring programs can provide useful long-term data sets with the robustness needed to make population level inferences, but usually they target commercial and economically important species that display an earlier migration. Also, the seasonal and temporary character of the monitoring, or the absence of complementary data on species biomass at freshwater and population structure, makes it impossible to infer the biological aspects of the thinlip grey mullet migration, or the impact of river fragmentation on temporal patterns of migration and disruption of nutrient flow.

This study used a 5-year continuous monitoring data set obtained at a fish pass located in freshwater, at the first insurmountable obstacle to migration at River Mondego (Portugal) and aimed to (i) analyse thinlip grey mullet movements to freshwater in terms of seasonality and circadian activity; (ii) characterize the fraction of the population that uses freshwater habitats and estimate species biomass; and (iii) identify the environmental triggers of species' movements on both directions, up- and downstream.

2 | MATERIAL AND METHODS

2.1 | Study area

The thinlip grey mullet migration to freshwater habitats was studied in the Central West region of the Iberian Peninsula, more specifically in the River Mondego (Figure 1). With a drainage area of 6670 km^2, a total length of 234 km and an average annual run-off of 2457 hm^3, it runs entirely in Portugal, from its source in Serra da Estrela (1425 m altitude) to the mouth in the Atlantic Ocean at Figueira da Foz (NE–SW). Characterized by a Mediterranean type climate, it has strong inter-annual flow variation and accentuated seasonal events of flooding and drying over an annual cycle. The annual rainfall is high [mean (±S.D.) = 1196 ± 347 mm] and the average annual temperature low (12.6 ± 1.23°C), yet in the warmest part of the basin it reaches around 16ºC (lower Mondego region) (Graça et al., 2002). Precipitation is concentrated (70%) in the humid semester, from October to

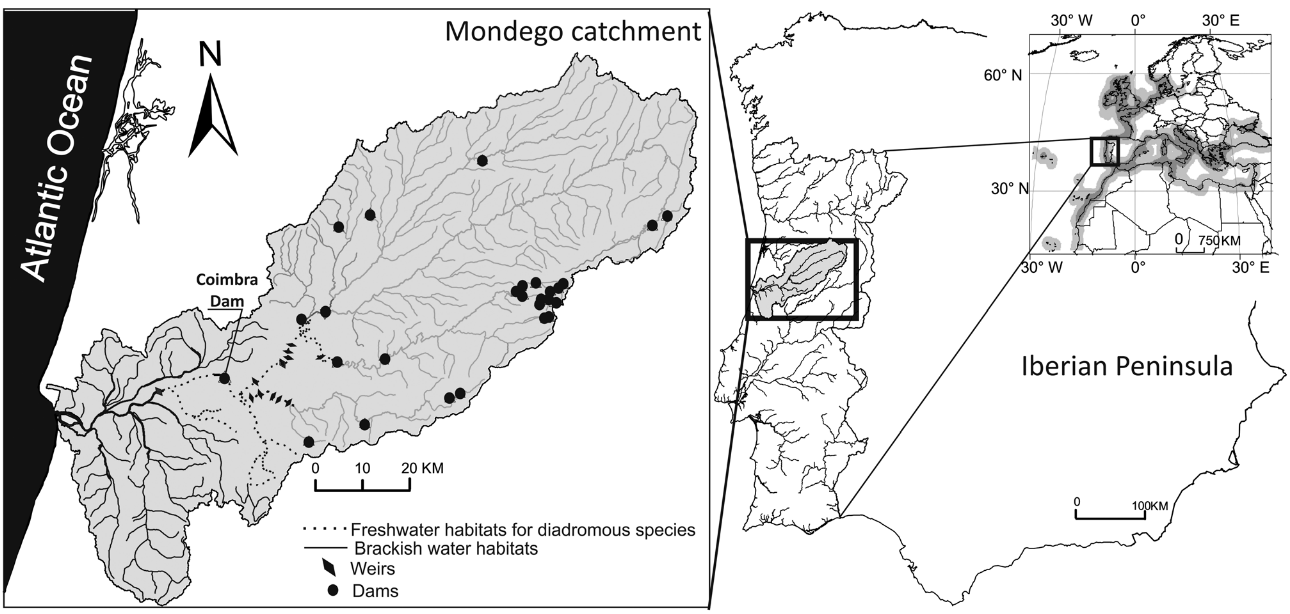

FIGURE 1 Location of the study area in relation to the global geographic distribution *of Chelon ramada*. Coimbra dam and major weirs and dams in the study area are also represented

March, with the coldest months of December and January reaching an average temperature of 6°C. The driest period occurs during the hottest months of July and August, where the average temperature is 19°C (monthly precipitation of 15 mm). River Mondego has a mean annual flow of approximately 86 m^3/s.

Hydro-morphologically, Mondego's catchment is divided in three regions: the lower, middle and upper section. Regarding the lower stretch, the estuary extends along 24 km, the salinity increase induced by tidal propagation can reach 18 km upstream from the mouth (salinity of 5) and the tidal effect is physically limited by a 3-m-high stone weir (RKM 32), the Formoselha weir, equipped with a fish ramp. This section includes the tributaries Arunca, Pranto and Foja rivers. The middle section of River Mondego, that runs along a narrow valley from the outskirts of Serra da Estrela mountain to Coimbra (including the outlets of the tributaries Dão, Alva and Ceira), is highly impounded by two large hydroelectric power dams (maximum storage capacity of 447 hm^3), Raiva (RKM 80) and Aguieira dams (near RKM 90), six multiple-use dams (1.6–89 hm^3) and several small weirs throughout its course. Major changes in the streamflow are related with the magnitude, variability, duration, and seasonality of low flow periods (Alexandre et al., 2015). Hydropower production and the associated hydropeaking conditions occur twice a day, flow discharge is highly irregular and river flow can increase up to 150 m^3/s (Alexandre et al., 2015; Almeida et al., 2002). 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 River Alva.

Habitat connectivity in the lower and middle sections of River Mondego is maintained through several nature-like fish passes in all existing weirs and through a vertical slot-fish pass at the Coimbra dam (Pereira et al., 2019). Upon its construction in 2011, this technical fish pass made available 50 km of upstream freshwater habitats for diadromous species to complete their life cycle in the catchment and was designed to target shads (allis shad *Alosa alosa* L. and twaite shad *Alosa fallax* Lacépède, 1803) and sea lamprey (*Petromyzon marinus* L.). It is a 125-m-long channel divided into 23 rectangular pools (4.5 × 3.0 m) with 2 m water depth, 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 ~1.1 m/s, with dissipated power in the resting pools below 150 W/m^3 and flow discharge at the fish pass entrance is constantly maintained at 1.5 m^3/s. Previous monitoring studies at this device have proven its effectiveness and efficiency for a wide range of species (Belo et al., 2021; Pereira, 2014; Pereira et al., 2017).

2.2 | Biological data

Thinlip grey mullet movements and contingent size structure were assessed at the Coimbra fish pass monitoring system (Pereira et al., 2019), namely through the daily analysis of the continuous video records (Samsung SCO- 2080R and SRD-470) collected during the entire period of 2013–2017.

In terms of species movement, between 2013 and 2014, the total number of thinlip grey mullet passages and their movement's direction (up- or downstream) were visually analysed, grouped at 15-min intervals and at the end of each interval, the total number of mullet's movements was obtained by the balance between up- and downstream counts. In the following years of 2015–2017, a weekly subsampling approach was adopted based on the results of a linear regression analysis that established the relationship between monthly movement counts from 2013 to 2014 and four distinct weekly subsampling scenarios.

Regarding contingent size structure, daily video images obtained at the fish pass monitoring system, from April to July and September to October of 2013–2017, were randomly sub-sampled on a weekly basis (for a total of 121 days) and within each day, for intervals of 1.5 h of video, the total length of the first 20 specimens was measured (a maximum of 320 specimens could be measured per day).

All further analyses were performed using the software R (R Development Core Team, 2020).

2.3 | Seasonal movements and diel patterns in freshwater

Frequency distribution of daily counts from 2013 to 2014 was used to study thinlip grey mullet's temporal patterns of movement and abundance reaching the freshwater stretch upstream the Coimbra dam (RKM 45). The period and extent of the up- and downstream migratory movements were then established based on the daily proportion of the movements in both directions and considering that for each period, more than 50% of the respective movement's direction remain consistently for at least a week. For each month and period of migration, it was analysed the balance of movements and obtained the total number of the species' movements.

A linear regression analysis was used to study the relationship between monthly movement counts obtained in each migratory period and four distinct weekly subsampling approaches that ranged from 1 to 4 days a week. To assess predictive performance, random sampling of the data set was undertaken with sample size set to the number of days counted per week. For each month, this process was repeated 100 times by selecting samples with replacement and for each replicate the sum of the monthly counts was computed. For each sampling size, the mean of the sampled monthly counts was obtained, and a linear regression model was built to fit the movements performed. Overall quality of the linear regression fit was assessed through R-squared (R^2) and residual standard errors (RSE) metrics. For the predictive performance and accuracy, a test data set extracted from the original data was used to identify the model with the lower prediction error RMSE (Root Mean Squared Error), the lower error rate and the narrower 95% confidence interval. The best regression model was then used to estimate thinlip grey mullet monthly movements during the following years (seasonal variation in species abundance) and provide a feasible way to infer species biomass in freshwater.

Regarding the diel patterns of activity, for each migration period, all the passage counts collected between 2013 and 2017, were grouped by hour, and frequency distribution of passages was used to infer species' circadian rhythm in freshwater.

2.4 | Freshwater contingent size structure

To characterize the fraction of the population that uses freshwater habitats, during the upstream migration, 83 days were sampled and a total of 13,498 specimens were measured. For downstream movement, 38 days were monitored, and 4803 specimens were measured during their downstream movement through the fish pass. Total length distribution (TL—mm) and spread across the years was visually analysed and monthly differences evaluated by nonparametric analysis of variance (Kruskal–Wallis test), followed by a Tukey-type multiple comparison test. To assess monthly length-frequency distribution, five length classes were established: [<130 mm]; [130–210 mm]; [210–290 mm]; [290–370 mm] and >370 mm. The present length classes correspond respectively to five age classes, namely, the age group lower than 1+, age group 2+ to 3+, age group 4+ to 6+, age group 7+ to 8+ and older fish (Almeida, 1989, 1996a). Additionally, to estimate the biomass of the freshwater contingent, for the uspstrem movements, it was obtained the proportion of individuals from each length class. From the relationship between the total length–standard length and eviscerated weight-standard length of thinlip mullet (Almeida, 1996a), we obtained the mean eviscerated weight of each length class and inferred species biomass associated with the total upstream movements of 2013–2014 and the estimated movement counts of 2015–2017.

2.5 | Environmental triggers of migration

Following the previous studies developed at Coimbra fish pass (Belo et al., 2021; Pereira et al., 2019), Boosted Regression Trees (BRT) analysis was used (Elith et al., 2008) to assess the influence of environmental variables in the upstream and downstream movements performed at the fish pass during the trophic migration of 2013–2014. Independent models were obtained for each year and period of migratory movements. To increase the performance of the data analysis, for each migratory direction, the intervals associated with opposite movements were excluded and to limit the influence of extreme values a square root transformation was applied to the response variable, data counts.

The abiotic variables (independent variables) considered were the water temperature (°C; EXO2 Water Quality Probe), discharge flow at Coimbra dam (m^3/s; Portuguese Environmental Agency), photoperiod (day length in number of hours of light), day period (day stages according to twilights) and lunar cycle (Astronomical Observatory of Lisbon). Spearman rho coefficient was used to remove redundant variables (|rho| > 0.8).

BRT models were fitted in R package (R Development Core Team, 2020), 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 highest percentage of explained deviance (R^2) and (iii) the highest cv correlation. Following the BRT procedure, simplification of the obtained model was tested (removal of non-informative variables from the original model which can be discarded without affecting the model's 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 et al., 2010). For visualization of fitted functions, partial dependence 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 diel movement patterns

During 2013 and 2014, near 880,100 and 1,538,400 total upstream passage movements were respectively recorded, while downstream movements reached approximately 414,600 and 1,000,000, respectively (Figure 2). Downstream movements from 2013 were underestimated due to missing data from 10th to 31st October and 18th November to 2nd December (fish pass closed for maintenance). The presence of thinlip grey mullets at the fish pass started to be observed in March and continued until November.

Considering a threshold of the daily proportion of passage movements higher than 50% and its consistency for more than a week, the bulk of upstream movements occurred between April–August and more precisely between 12th April to 6th August in 2013 and 9th March to 20th August in 2014. On the other hand, downstream movements associated with the beginning of the supposedly spawning migration occurred from August to November (7th August to 10th October in 2013 and 21st August to 22nd November in 2014), with a peak of movements between September–November (Figure 3).

From the regression analysis applied to the collected data and the subsampling scenarios, it was observed that all the linear models were significant and showed a good fit between the sub-sampled monthly data and the predicted data, accounting for a high proportion of variation in the total counts ($R^2 > 0.9$, Table 1). In terms of sample size, for the upstream migration, the overall quality and accuracy was similar across the sample size tested, with low error rates (13%–15%). For the period of downstream migration, the prediction error varied greatly according to sample size and ranged between 3% and 38%. The highest error rates of nearly 38% and 36% were detected for a week sampling of one and 4 days; however, a weekly sampling of 2 days achieved an error rate lower than 5% (Table 1 and Figure 4). The bias and high error rate obtained through subsampling showed that it is not a suitable approach for estimating species movements during downstream migration.

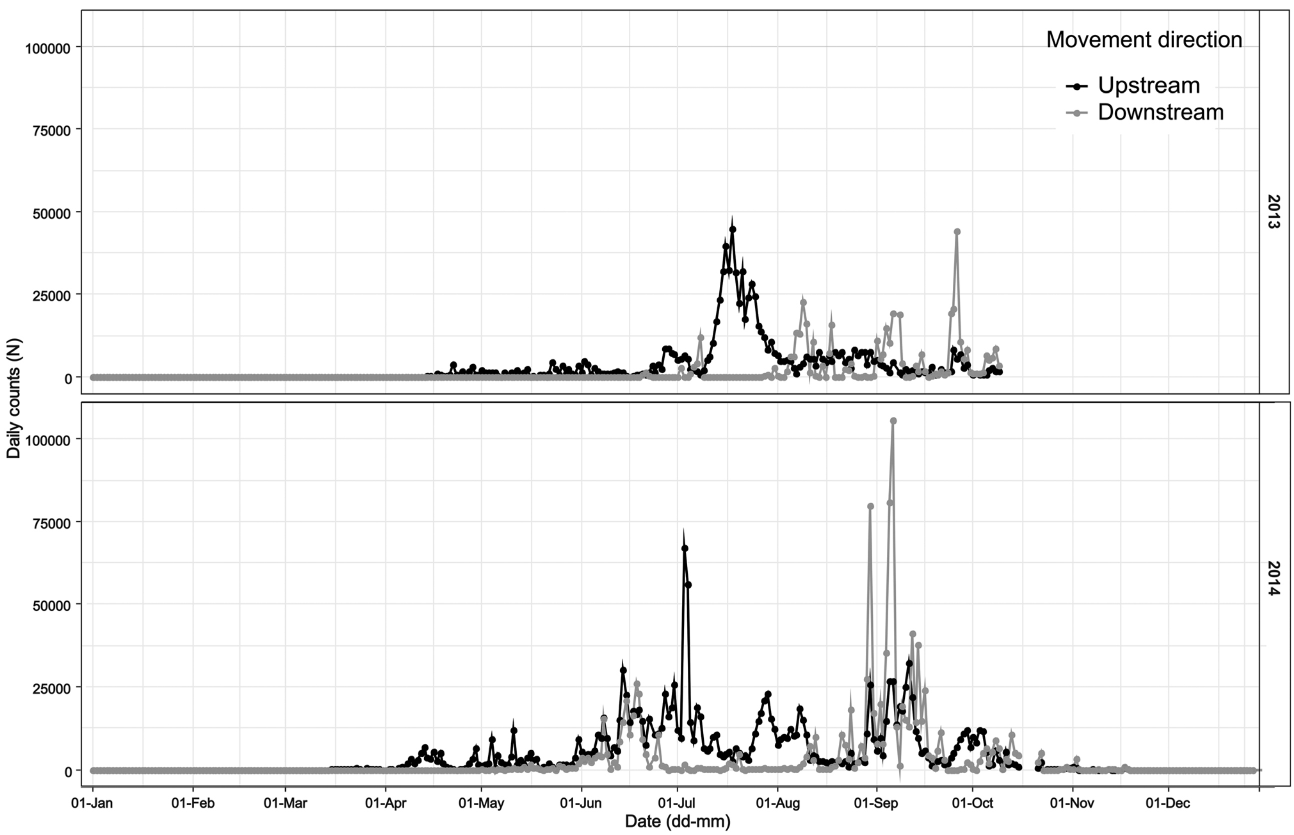

FIGURE 2 Daily counts of thinlip grey mullets' movement at Coimbra fish pass in 2013 and 2014. (—upstream movements; —downstream movements)

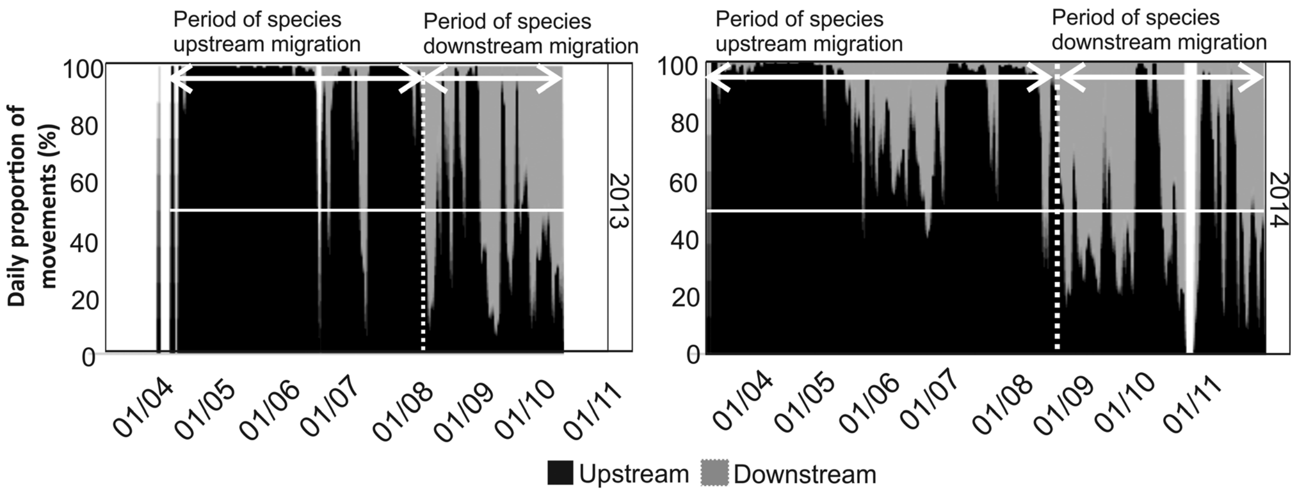

FIGURE 3 Daily proportion movements of thinlip grey mullet in both directions during 2013/2014 trophic migration. The 50% threshold of daily proportion of movements is set and the period of each migration period identified at the top

TABLE 1 Summary of the linear model coefficients, significance and accuracy assessed through residual standard errors (RSE), R-squared (R^2)

Dataset	Sub-sample (days a week)	Intercept	Slope	*F* statistic	*P* value	R^2	RSE	RMSE	Error rate
Upstream migration (Apr-Aug)	1	−8837	6.90	318.6	9.945e−08	0.97	23,200	20,749	15%
	2	−6820	3.46	462.8	2.296e−08	0.98	19,320	17,281	13%
	3	−5441.8	2.33	367.8	5.664e−08	0.98	21,630	19,342	14%
	4	−7013.9	1.75	432.6	2.993e−08	0.98	19,970	17,862	13%
Downstream migration (Sep -Oct)	1	−553	9.18	19.1	0.04	0.91	49,430	36,381	36%
	2	2092	3.48	2399	4.166e−4	0.99	4635	3277	3%
	3	4645	2.80	90.84	0.01	0.98	23,570	16,664	17%
	4	1345	2.59	17.12	0.05	0.90	51,920	36,716	38%

Note: For model performance prediction error RMSE (root-mean-square error) and error rates are presented.

Thus, for 2015–2017 the subsampling approach was only applied to the period of upstream movements and a weekly subsample of 1 day was adopted. A proxy estimation of the monthly passages showed that in 2016, species migration followed similar timing as observed in 2013/2014, with the peak of movement at the fish pass occurring in July. In 2015 and 2017, despite following the same pattern, the peak of movements occurred earlier, between May/June (Figure 5).

The balance of the total monthly counts obtained between April and August of 2013 and 2014 points towards near 627,531 and 707,528 upstream movements, respectively, while the predicted number of movements in the following 3 years (for 2015–2017 counts between April and July) was 352,191, 476,023 and 430,912, respectively (Table 2).

In terms of the circadian rhythm of thinlip grey mullet's activity, movements occurred exclusively between sunrise and dusk (07 h to 19 h/20 h), in a window of 12 to 13 h of activity. Yet, it was observed that the peak of activity varied among the two periods of the species migration. During the upstream migration, thinlip grey mullet displayed a diurnal activity and passages increased along the day with 60% of the movements occurring between 12 and 19 h. On the other side, a predominant crepuscular activity was observed during the period of downstream migration, with most of the passages recorded in two distinct periods of the day, 08–10 h (30%) and 16–18 h (30%) (Figure 6).

3.2 | Size structure of the freshwater contingent

Between April and November of each year, from 2013 to 2017, a total of 18,301 thinlip grey mullets were measured. Specimens ranged from 90 to 546 mm of total length (TL), with a mean TL of 240 mm. Significant differences between the TL of the individuals that used the fish pass (Kruskal–Wallis test, $p < 0.05$) were identified along the months studied (Figure 7). Considering the monthly frequency distribution of the length classes throughout the migration period, the most abundant class was [210–290 mm], followed by [130–210 mm] and [290–370 mm] (Figure 8). A higher frequency of passages performed by larger specimens were observed to occur in April, May, and September, while smaller sizes were more frequent in June, July and

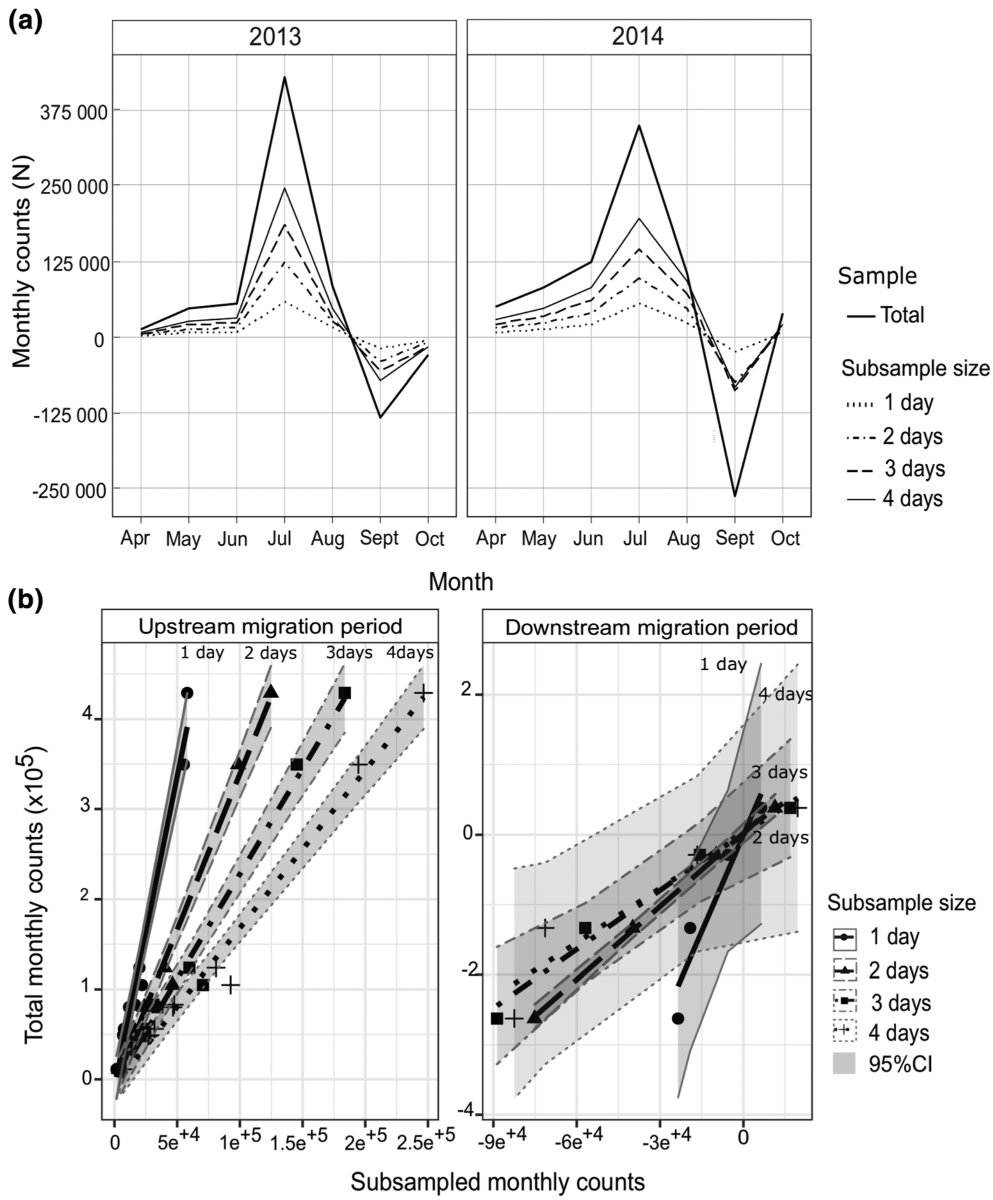

FIGURE 4 (a) Comparison between the sum of the total and sub-sampled monthly counts used to fit the regression line. (b) Linear regression models obtained for four weekly sampling approaches and species monthly counts at Coimbra fish pass between 2013 and 2014

October. Considering the proportion of individuals in each length class and the mean eviscerated weight (Table 3) the estimated biomass of the freshwater contingent during the upstream movement of 2013 and 2014 was 88.4 and 99.6 tons, respectively, while near 48.6, 67 and 61 tons in 2015, 2016 and 2017, respectively.

3.3 | Environmental triggers of migrations

From the set of predictors initially considered, no variables were excluded to fit the BRT models (|rho| < 0.80, Spearman correlation). In terms of model's performance, explained variability (R^2) ranged between 0.88 and 0.82 for the upstream models of 2013/2014, and for the downstream migration models, 0.67 and 0.89, respectively (Table 4). Regarding the upstream movements performed during the peak of migration, the relative influence of each environmental variable varied for 2013 and 2014 (Figure 9). However, both BRT models show that temperature (26% and 35% in 2013 and 2014, respectively) and photoperiod (31% and 19% in 2013 and 2014, respectively) are among the most important variables. Also emphasized was the interaction between temperature and photoperiod and discharge flow with other factors, such as the day period (2013) and temperature (2014).

In general, it was observed that thinlip grey mullet upstream movements increased when temperatures rise above 15°C and achieve their highest around 20°C, when the number of hours of light is around 15 h and the discharge flows are lower than 160 m^3/s (Figure 10).

As for downstream movements, both models highlight the interaction between the day period-photoperiod, and the importance of the variable temperature. Higher number of movements occurred during the daylight hours, with a length of around 13 hours of light and when temperatures were from 20 to 22°C. Exceptionally in 2014, it was also observed an interaction between temperature and discharge

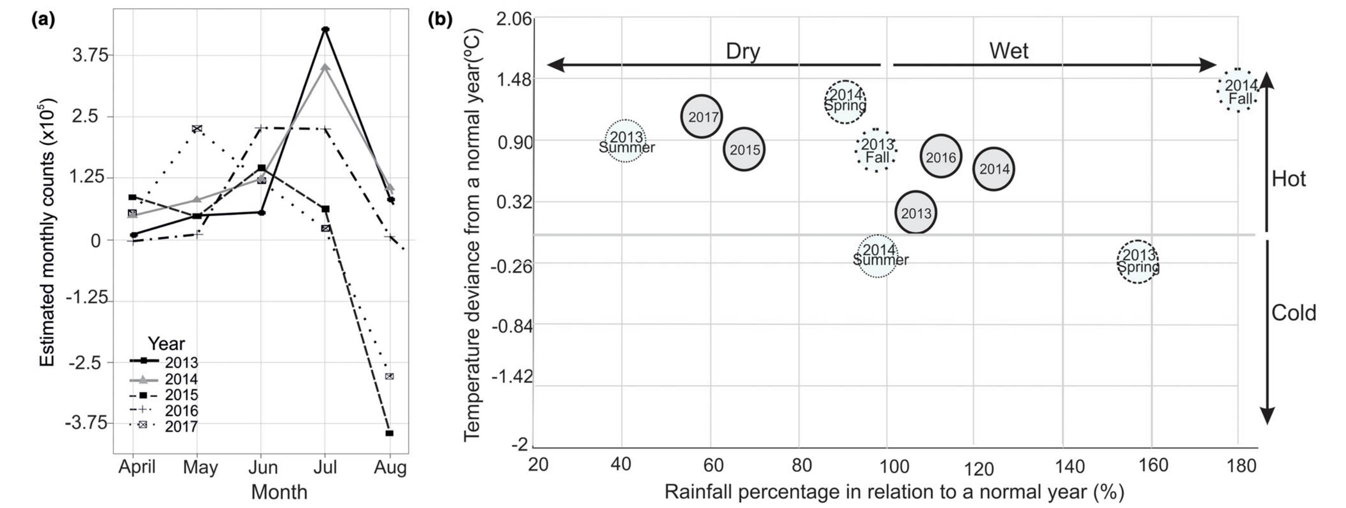

FIGURE 5 (a) Total monthly counts obtained in 2013–2014 and estimated monthly counts (predictive model) for the period between 2015 and 2017 based on the balance of movement counts obtained with a weekly subsample of 1 day per week. (b) Anomalies in the annual (2013/2014) and seasonal (2013/2014) mean temperature and percentage of rainfall in Portuguese mainland, during the studied period when compared to normal (1971–2000). Adapted from IPMA (2020)

TABLE 2 Species movement estimation according with the extend of upstream and downstream migration

	Sampled		Estimation (subsample 15%)		
	2013	2014	2015	2016	2017
Upstream	627,531	707,528	352,191	476,023	430,912
Downstream	162,038	224,304	—	—	—

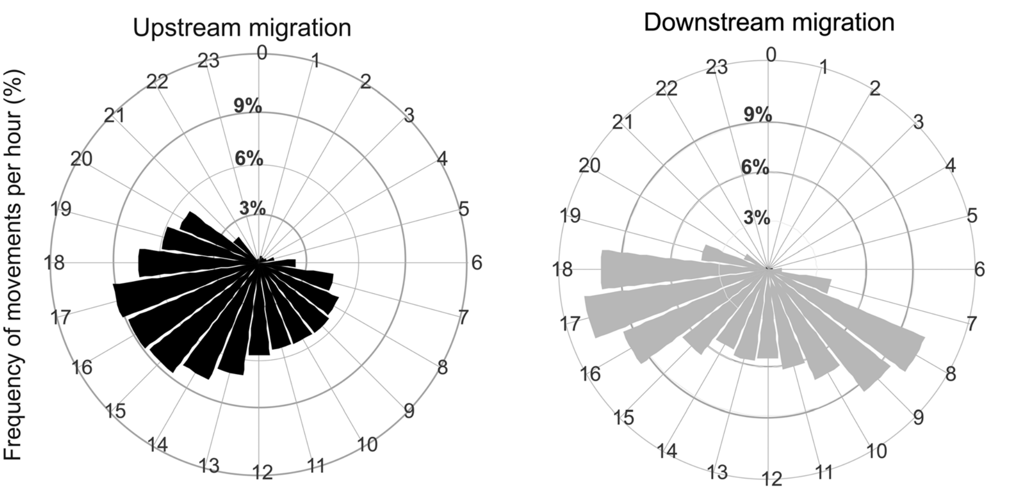

FIGURE 6 Circadian rhythm associated with the upstream and downstream freshwater migrations of thinlip grey mullet at Coimbra fish pass

flow (two of the most relevant factors), that point towards an increase of passages when discharge flows were around 20–40 m^3/s.

4 | DISCUSSION

Thinlip grey mullet trophic migration to freshwater began in March/April and their permanence in freshwater extends until October. The upstream and downstream migratory peaks occurred, respectively, in July and September/October. Very dry years seem to influence this timing, since in 2015 and 2017 the upstream migratory peak was anticipated by 1 month.

On average, ~500,000 thinlip grey mullet upstream movements may occur yearly to provide species access to the upstream reaches of the River Mondego, and it corresponds roughly to 70.4 tons of fish that use the main stem of the River Mondego upstream from Coimbra dam. Opposite to the upstream migration and due to the irregular behaviour pattern of the downstream migration, which is highlighted

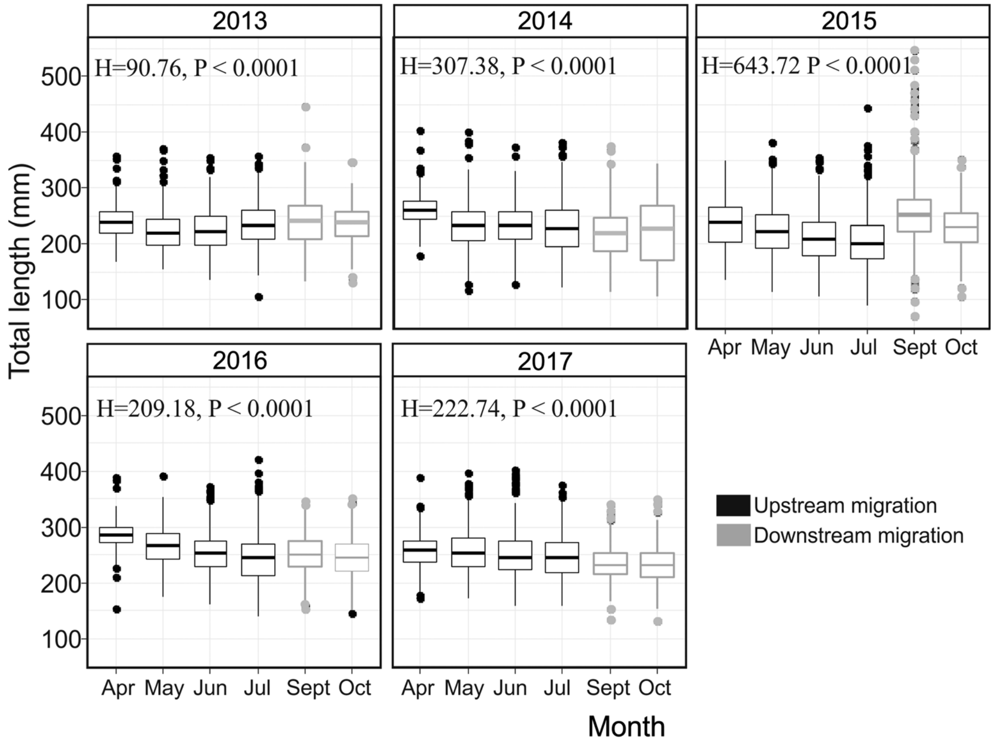

FIGURE 7 Boxplots showing the distribution of values for thinlip grey mullet's total length measured at Coimbra fish pass, across the month. Boxes indicate the 25th and 75th percentiles, with the median enclosed within. Whiskers indicate 1.5 the interquartile range beyond the box and outliers are displayed as separate circles (points that differ more than 1.5 and lower than 3 times the IQR from the respective quartiles). The results of the Kruskal–Wallis test are shown

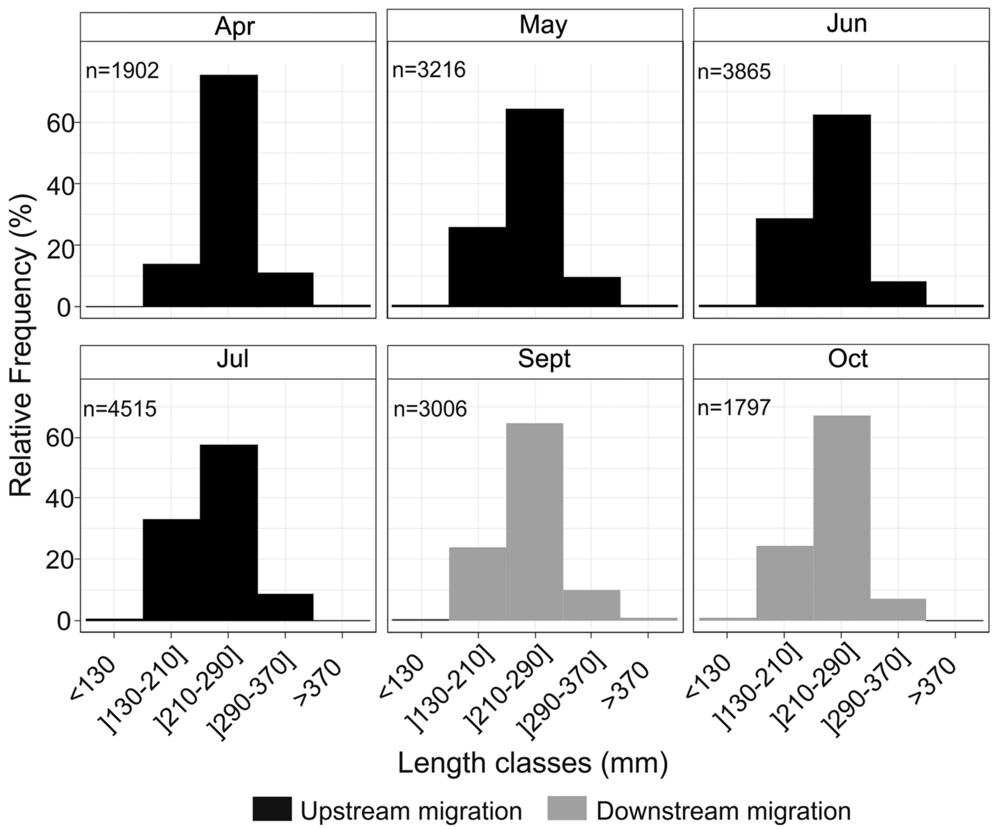

FIGURE 8 Monthly length-frequency distribution of thinlip grey mullets measured at the Coimbra fish pass. *n*—total number of specimens

by the existence of several events of high upstream fish passages, a subsampling approach was considered unsuitable, and it is required the assessment of the entire period. From the data collected in 2013 and 2014, downstream passages through the fish pass represented nearly 30% of the upstream passages. In this case it is important to note that despite our ability to reduce the bias associated with multiple daily passages through the fish pass, unpublished data (E. Pereira) point towards the possible existence of a population fraction that

TABLE 3 Proportion of individuals (%) in each length class (mm) and respective mean eviscerated weight (g)

		<130	[130–210]	[210–290]	[290–370]	>370
Upstream migration	%	0.4%	27.2%	63.1%	9.0%	0.3%
	Eviscerated weight	19.6	66.8	151.1	287.6	542.8

TABLE 4 Performance evaluation of BRT models for each study year

	Upstream		Downstream	
	2013	2014	2013	2014
Mean total deviance	12.73	13.33	24.7	23.30
Mean residual deviance	1.46	2.37	8.21	2.63
cv deviance	2.81 SE = 0.06	3.58 SE = 0.09	10.28 SE = 0.89	7.20 SE = 0.47
cv correlation	0.88 SE < 0.01	0.81 SE = 0.01	0.67 SE = 0.02	0.72 SE = 0.03
R	0.88	0.82	0.67	0.89

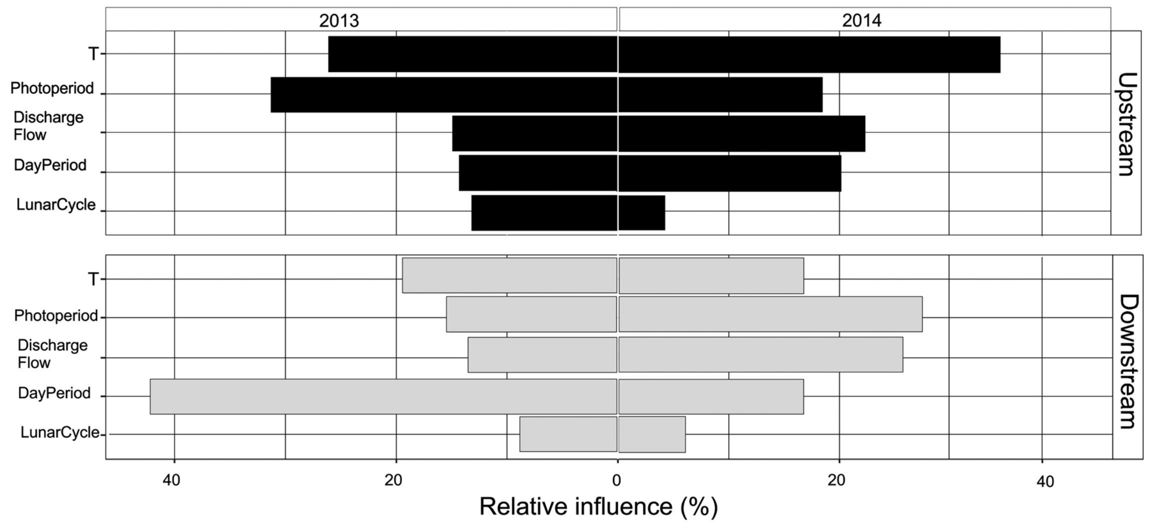

FIGURE 9 Relative influence of environmental predictors in the upstream and downstream movements performed at the Coimbra fish pass during 2013–2014 freshwater migration seasons

displays a pendular behaviour throughout the migration season, during which they can use the dam gates for downstream movements. In this sense, the counts obtained for the downstream movement can be underestimated, and the total upstream movements slightly overestimated. This may be the strongest explanation for the mismatch observed, as fishing pressure is absent, mortality associated with anoxic conditions or industrial pollution is rare, and predation mortality is reduced when compared with estuaries. In the study area only a few predators are identified, namely, some bird species (e.g., great cormorant *Phalacrocorax carbo* (L.), black-crowned night heron *Nycticorax nycticorax* (L.), grey heron *Ardea cinerea* (L.), the red kite *Milvus milvus* (L.)) and the European otter *Lutra lutra* (L.). Thus, to obtain the net balance between upstream/downstream movements it will be necessary to apply a correction factor that takes into consideration either the escapement rate through the dam gates or the population fraction that displays a pendular behaviour. An ongoing telemetry study will provide the information required to achieve a more accurate estimation of the freshwater contingent size.

The importance of this species' trophic migration and the access to freshwater habitats in fragmented rivers have been emphasized in other fish pass assessments where thinlip grey mullet abundance is high (Benites, 2019; Bochechas, 1996; Lemonnier, 2019; Ordeix et al., 2011). Despite the proximity to the river mouth, in the channelized River Vilaine, west of France, Lemonnier (2019) estimated that between March and October of 2013–2019, nearly 2.3 million thinlip grey mullets successfully negotiated the d'Arzal dam through the fish pass. Considering that this fraction of the population was mainly constituted by specimens older than 5 years (5–11 years), this can

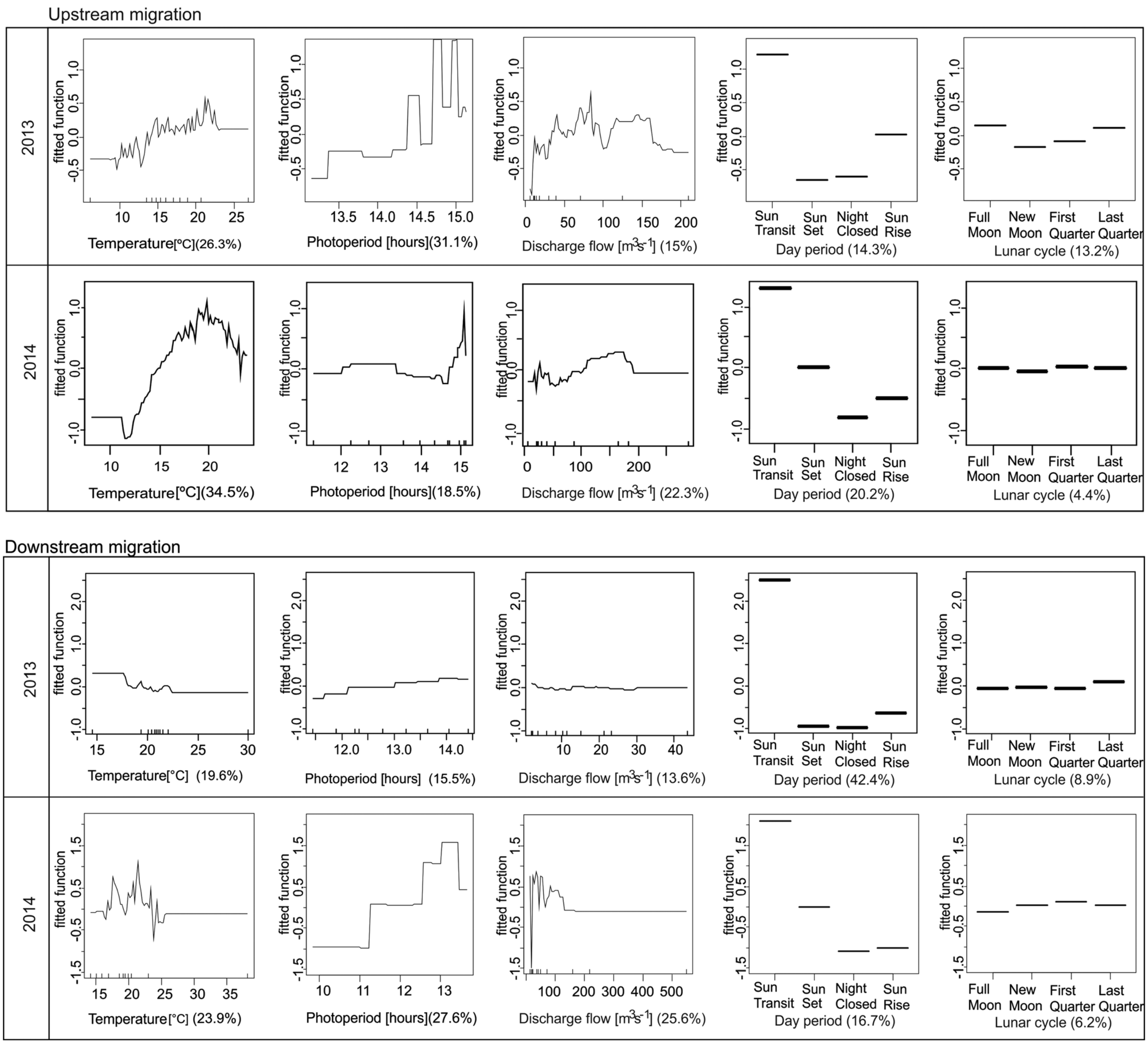

FIGURE 10 Partial dependence plots presenting the fitted functions for the influential predictors in the Boosted Regression Trees models. For each plot, the vertical axis is on the logit scale and centred to have zero mean over the data distribution

represent around 200 tons of biomass. Moreover, due to the presence of navigation locks that are mainly used during summer, precisely during the peak of migration, it is expected that video counts at the fish pass represent a small proportion of the real migratory population that reach the freshwater stretch. In the Portuguese part of River Douro, a highly impounded river by several dams with a system of navigation locks that enable the navigation in the river main stem, thinlip grey mullet was one of the few species able to use the Borland fish lock at the first dam, Crestuma-Lever, located 20 km from the river mouth (Bochechas, 1996). In recent reports from a 13-month monitoring where more than 1200 fish lock operations were analysed, the passage of approximately 61,000 mugilids were reported, representing 49% of the total fish (Benites, 2019). Similarly, in River Tagus, Oliveira and Ferreira (1997) reported the occurrence of large accumulations of thinlip grey mullets downstream of the Belver dam, 170 km upstream from the river mouth.

In terms of seasonal migration, along the European Atlantic Coast and NW Mediterranean the main migration to freshwater occurs in the spring (Sauriau et al., 1994), starting between March/Abril as it was also observed in the lower Guadalquivir, Spain (Fernández-Delgado et al., 2000), in River Tagus, Portugal (Almeida, 1989), in rivers of Catalonia such as Lower Ter and Low Tordera rivers (Ordeix et al., 2011), or River Ebro (Aparicio et al., 2012; López et al., 2015; Sostoa et al., 1990), with a peak in July/August (Almeida, 1989; Aparicio et al., 2012), which is in accordance with our results.

Regarding the period spent in freshwater and timing of the downstream migration, this is not consensual across the existing studies. However, and despite some intraspecific variation that can be attributed to different methodological approaches, studies on gonad maturity stages and gonadosomatic index (GSI) from thinlip grey mullet captured at the estuaries along its geographic distribution, allow to infer if the period of downstream migration reported here is in accordance with the species spawning season. In the Cantabrian Sea (Farrugio, 1975) and River Tagus (Almeida, 1989; Guerra, 1976), the spawning season is reported to occur between August/September and November/December, respectively. In the Mediterranean Coast, the highest GSI are reported in October/November (González-Castro & Minos, 2015), and spawning season may extend until December/January (Farrugio, 1975; Modrusan et al., 1991; Salem & Mohammad, 1983). Almeida (1996a) reported that in River Mira, South-Western Coast of Portugal, spawning migration can extend from November to February. This variability may reflect the existence of a wide range of different life tactics regarding habitat use and migratory behaviour (Daverat et al., 2011; Trancart et al., 2012).

In our study the highest number of downstream movements was performed in September/beginning of October, being associated with the movement of larger animals, yet almost half of the females captured at the Coimbra dam fish pass in September had their gonads on an early stage of maturation (E. Pereira unpublished data), anticipating that further gonad development would occur in the estuary or at sea (Almeida, 1996a; Almeida et al., 1992; Cambrony, 1983; Ibáñez & Gutierrez-Benitez, 2004). Moreover, since the species was present in freshwater during October and beyond, and it is likely that the spawning migration will occur in large schools with previous aggregation in the estuary before exiting to the sea, this can indicate a longer migration period. Thus, the escape to sea may occur later in the year, as observed in the River Mira (Almeida, 1996a). Oliveira and Ferreira (1997) also described a longer migration period in River Tagus, with captures of thinlip grey mullet all year round, suggesting that part of the population does not perform the annual downstream movements, staying in freshwater habitats instead. Our observations from River Mondego also support the hypothesis that not all the population occurring in freshwater will spawn. In fact, the underdeveloped gonads observed in some of the specimens in October (E. Pereira, unpublished data) and the presence of juveniles later in the season support this hypothesis. Hence, population dynamic and migration to freshwater may not be exclusively related with gonad maturation as also suggested in Oliveira and Ferreira (1997). However, from December on, when temperatures drop below 13° C which may constrain species growth (Cardona, 1999), very few thinlip mullet movements are recorded at the Coimbra dam fish pass.

Diel movements occurred exclusively during the daylight hours, showing a marked circadian rhythm. This can be attributed to their feeding activity (Albertini-Berhaut, 1979; Almeida, 2003) and synchronization with photosynthetic production and food availability (Torricelli et al., 1982). Similar species preference for diurnal activity is reported in other studies (e.g., Oliveira & Ferreira, 1997; Ordeix, 2016; Ordeix et al., 2011; Torricelli et al., 1982; Trancard et al., 2011). Yet, under tidal influence, thinlip mullet movements may be performed with no preference for a particular time of day (Almeida, 1996b).

In River Mondego, the thinlip grey mullet that migrate to freshwater belong, mostly, to younger age classes (i.e., 4+ to 6+), with the predominance of specimens in their first year of gonad maturation (Almeida et al., 1989; 1996a) and young mature adults (Aparicio et al., 2012; Trancart et al., 2011). In the present study it is described one of the smallest thinlip grey mullets reported at freshwater habitats and a fish pass user (i.e., juveniles with a total length ~90 mm). Lemonnier (2019) reported the presence of juveniles 0+ with less than 100 mm at the fish pass in d'Arzal dam, yet this is an estuarine dam located in Vilaine. In other locations, as in river Ebre, in Xerta weir located 56 km from the river mouth, the smallest specimens observed had a furcal length of 150 mm and in River Tagus, at the Belver dam, the smallest were 220 mm (TL). On the other hand, it is also confirmed that a fraction of older animals reaching up to 13 years (E. Pereira unpublished data; Lemonnier, 2019) continue to exploit the freshwater habits.

During the trophic season, there is some evidence of a temporal segregation in migration timing between different size classes. Larger specimens (TL > 370 mm) displayed an earlier migration (i.e., upstream migration in April–May and downstream migration in September) while the upstream movement of younger specimens increased later during the summer and the downstream migration occurred in the beginning of autumn. A similar pattern was reported in the Atlantic Coast and NW Mediterranean, either at estuaries during spawning migration (Almeida, 1996a) or migration through fish passes (Lemonnier, 2019; Ordeix et al., 2011).

In terms of the environmental triggers behind species migratory movements, temperature, photoperiod, and day period were consistently identified as the most relevant triggers for both migratory directions, with upstream movements increasing with temperatures from 15°C to 20°C, and a photoperiod of 15 h. Higher downstream movements occurred for a photoperiod around 13 hours and a temperature drop from 22 to 20°C. Both variables are known to act at the central nervous system and regulate grey mullet movement, feeding behaviour (Ibáñez & Gutierrez-Benitez, 2004) and gonad development (Ibáñez & Gutierrez-Benitez, 2004; Kuo et al., 1974). In *Chelon aurata* (Risso, 1810) juveniles, swimming capacity and feeding events increased with warmer water, namely when temperatures raised from 10°C to 20°C (Como et al., 2013), and at freshwater the species occurrence is also associated with temperatures above 13°C, increasing considerably at temperatures around 21°C (Oliveira & Ferreira, 1997; Ordeix et al., 2011). On the other hand, a decrease in photoperiod from 15 h to 13 h and a drop of temperature to ~20°C are in accordance with the range of values previously reported and identified as being responsible for stimulate gonad development (Ibáñez & Gutierrez-Benitez, 2004; Sagi et al., 1983), namely, vitellogenesis, that starts 2 months before the spawning season (Mousa et al., 2018). These results emphasize that the downstream migration peak between August/September may be linked with gonad development of the freshwater fraction of annual spawners.

Regarding discharge flow, since the peak of upstream migration occurs particularly during periods of low flow (summer), and the water velocity inside the fish pass is constant and lower than the velocity observed to limit the ability of smaller thinlip grey mullet specimens to overcome obstacles, that is, 2 m/s (Ordeix, 2016), this predictor only gains a higher relevance when discharge flows are higher than what is expected in habitual flow values. Under hydrological conditions associated with high precipitation and instream flow, thinlip upstream movements through the fish pass were constrained by dam discharges higher than 160 m^3/s. This threshold is significantly higher than the one observed for sea lamprey (Pereira et al., 2019) and shads (Belo et al., 2021) at the same fish pass device (i.e., 100 m^3/s). Yet high flow discharges are known to promote confounding turbulence and a shift of the main flow towards the middle gates, lowering fish pass attractiveness (Pereira et al., 2017).

On the other side, during downstream migration, a higher relevance of discharge flows lower than 100 m^3/s, associated with a temperature drop to around 22°C was identified during season characterized by higher temperatures and precipitation (i.e., +1.4°C from the normal value [17.6°C] and 449.5 mm of precipitation, that correspond to 180% of the normal). So, our results indicate that under a hot and rainy season, as observed in the fall of 2014, that was considered the second hottest and rainiest year since 2000 (IPMA, 2020), the bulk of the movements were preferentially performed in the beginning of the rainy season when dams were still storing, and discharge flow was still low. This is in accordance with fishermen reports from the estuary, that identify the occurrence of large thinlip grey mullet schools associated with the first significant rainfalls taking place in the early fall. However, we must bear in mind that downstream movement can also occur through the dam's gates, and under high flows released from the upstream hydroelectric dams this passage route may be used in detriment of the fish pass.

5 | CONCLUSION

The extensive analysis of thinlip grey mullet movements to freshwater provides unique information regarding the biological aspects of their catadromous migration to freshwater habitats in the Atlantic coast, namely, the extended periods that this species spends in such environments, overlapping with the spawning migration period.

Despite the construction of dams and increasing river fragmentation, our data support that thinlip grey mullet continues to perform a massive trophic migration to freshwater habitats. This fraction of the population comprises specimens with a huge amplitude of sizes, with ages ranging from 0 + to near 13 years, and confirms their ability to use with efficacy a vertical slot fish pass built for sea lamprey and shads (Pereira et al., 2017, 2019, Belo et al., 2021). This emphasizes the importance of freshwater habitats to thinlip grey mullet life cycle and the urge to ensure and maintain the access to the upper freshwater stretches between the period of March/April and October/November, especially in fragmented rivers, through suitable water management policies, the installation of fish pass devices and monitoring programs.

Considering the length classes observed, the presence of immature specimens and a later downstream migration in November, leads to the hypothesis that freshwater migration may not be exclusively linked to gonad maturation and spawning. On the other hand, older specimens that have lower predation rates or competition in estuarine environments, continue to perform this trophic migration towards freshwater. As so, it is necessary to further understand the mechanism that drives the migration and its respective benefits.

The large numbers involved in this trophic migration contribute to some provisioning and regulating services in the riverine ecosystem, since they consume large quantities of microalgae that could be responsible for eutrophication scenarios. Further studies are needed to evaluate the impacts of this massive biomass migration to freshwater in terms of the nutrient fluxes and structure and functioning of freshwater food webs.

Monitoring data from fish pass devices with proven efficacy and known efficiency, can provide important information about the catadromous thinlip grey mullet movement dynamics in freshwater, demographic parameters and the abiotic factors triggering the migratory movements that are detrimental to assess the questions raised above. Yet, some limitations must be considered, namely the possible existence of size selective passages and the presence of alternative migratory routes such as the dam's gates, turbines, or water uptakes. Under these conditions, it will be necessary to complete the available information with complementary methodologies such as biotelemetry, to obtain a correction factor.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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