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Effects of hydropeaking on the behaviour, fine-scale movements and habitat selection of an Iberian cyprinid fish

Ana Sofia Rato[1] | Carlos Manuel Alexandre[1] | Pedro Raposo de Almeida[1,2] | José Lino Costa[3,4] | Bernardo Ruivo Quintella[1,4]

[1]MARE–Centro de Ciências do Mar e do Ambiente, Universidade de Évora, Évora, Portugal

[2]Departamento de Biologia, Escola de Ciências e Tecnologias, Universidade de Évora, Évora, Portugal

[3]MARE–Centro de Ciências do Mar e do Ambiente, Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

[4]Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

Correspondence

Carlos Manuel Alexandre, MARE–Centro de Ciências do Mar e do Ambiente, Universidade de Évora, Évora, Portugal.
Email: cmea@uevora.pt

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Abstract

Hydropeaking is widely known for changing the quantity and quality of the available habitat downstream of hydroelectric facilities, thus affecting all stages of fish life cycles. Hydropeaking impacts on salmonids are widely studied, but knowledge of its effects on cyprinids, which are dominant in Mediterranean areas, is scarce. In this study, 11 Iberian barbel (*Luciobarbus bocagei*, Steindachner 1864) were tagged with radio transmitters equipped with ElectroMyoGram (EMG) sensors, aiming: to (a) assess the behaviour, fine-scale movements and habitat selection of the target species in response to periods of artificial and abrupt flow variations (i.e., hydropeaking); and (b) identify, which environmental variables and, in particular, flow components can influence the species behaviour. Results from the six barbel that provided analysable data indicate that fish were more active during the day and in periods of ecological flow. Moreover, during hydropeaking, especially during the increase in flow magnitude, fish activity decreased with the tagged fish showing a refuge-seeking behaviour. This information can be used to minimize the changes caused in the aquatic habitat and fish communities occurring downstream of hydroelectric dams.

KEYWORDS

ecohydrology, electromyogram telemetry, flow regulation, Iberian barbel, *Luciobarbus bocagei*, Mondego River

1 | INTRODUCTION

Artificial flow regimes are considered one of the most significant and persisting threats to the ecological sustainability of rivers and their flood plains (Arthington, 2012; Bunn & Arthington, 2002; Nilsson, Reidy, Dynesius, & Revenga, 2005). Around 77% of rivers in North America, Canada, Europe and the former Soviet Union are affected by dams operating for hydroelectric production and other water regulation schemes (Baras & Lucas, 2001; Dynesius & Nilsson, 1994). Large impoundments modify flow regimes (Dynesius & Nilsson, 1994), being responsible for direct and indirect consequences on communities' structure and composition, also changing the distribution and availability of habitats (Bunn & Arthington, 2002; Poff & Allan, 1995; Richter, Baumgartner, Braun, & Powell, 1998). Hydroelectric dams operate differently from other riverine infrastructures by discharging water in a discontinuous way. Flow fluctuations that should occur seasonally start happening daily or hourly (De Vocht & Baras, 2005) and with different magnitudes (Robertson, Pennell, Scruton, Robertson, & Brown, 2004), a phenomenon known as hydropeaking. This process involves the release of a massive amount of water from upstream impoundments in a short time, suddenly modifying the downstream water velocity, depth, turbidity, temperature, and other water physical–chemical characteristics (Bunt, Cooke, Katopodis, & McKinley, 1999). Most riverine species have adapted to the magnitude, frequency, and predictability of natural seasonal floods (De Vocht & Baras, 2005) but the occurrence of these high magnitude discharges in a short period makes the habitat downstream from dams highly unstable (Robertson et al., 2004). Effects of this phenomenon may be observed over all stages of fish life cycles inhabiting these highly regulated environments and at all spatial scales (Bunn & Arthington, 2002), causing significant bioecological impacts, such as the reduction in the abundance of migratory fish species (Arthington, 2012; De Vocht & Baras, 2005), decrease in quantity and quality of the available habitat (Bunn & Arthington, 2002), entrainment and drift of fish larvae (Baras & Lucas, 2001), favouring generalist species (Boavida, Santos, Ferreira, & Pinheiro, 2013) and fish stranding (Berland et al., 2004; Davey, Kelly, & Biggs, 2006). Therefore, assuming the increase in short-term habitat changes caused by this type of flow alteration, the probability of survival of affected organisms largely depends on their ability to find refuge, aggregation in deeper areas and/or ability to move to places of more stable flows (Davey et al., 2006).

In the past decades, several studies have been conducted to understand the effects of hydropeaking on aquatic biota, especially fish fauna. However, even though there are several studies describing the effects of hydropeaking at the population (Poff & Allan, 1995), behaviour (Moreira, Costa, Valbuena-Castro, Pinheiro, & Boavida, 2020), physiological (Moreira et al., 2020; Taylor et al., 2014) and habitat and/or movement level (Alexandre et al., 2015; Boavida et al., 2013; Capra, Pella, & Ovidio, 2018; De Vocht & Baras, 2005), they often come to different conclusions on how this phenomenon affects the target species or river characteristics. There are only a few studies being conducted on southern European rivers, as most studies were developed on northern European or American rivers and using salmonids as their target species (Bunt et al., 1999; Korman & Campana, 2009; Pert & Erman, 1994; Robertson et al., 2004; Scruton et al., 2008). Moreover, until now, Taylor, Cook, Hasler, Schmidt, and Cooke (2012) and Taylor et al. (2014) were, to our knowledge, the only in situ studies, assessing the behaviour and physiological response, in terms of muscle activity rhythm, on salmonid species, in response to local sudden flow changes. Most of the extant studies about this impact and consequent behavioural responses are developed assessing other behavioural responses and often performed in a laboratory mesocosm (Costa, Boavida, Almeida, Cooke, & Pinheiro, 2018; Costa, Fuentes-Pérez, Boavida, Tuhtan, & Pinheiro, 2019; Moreira et al., 2020). Mesocosm studies, although providing valuable preliminary insights about these impacts and resultant biological responses, may have less applicability to real in situ scenarios of streamflow regulation. In the present study, an Iberian cyprinid fish (*Luciobarbus bocagei*, Steindachner, 1864) was used as the target species. Only recently cyprinids have been targeted in studies aiming to understand the impact of different types of flow regulation (e.g., Alexandre et al., 2015; Boavida et al., 2013; Costa et al., 2018). The few studies assessing hydropeaking effect on the Iberian barbel, often come to different conclusions regarding its physiological and behavioural response (Capra et al., 2017; Costa et al., 2018, 2019; Moreira et al., 2020). Costa et al. (2018) found that submitting this species to a prolonged peak flow was not beneficial, with individuals experiencing flow related stress due to excessive swimming (trying to hold their position). Moreira et al. (2020), found no physiological stress caused by increased discharges, reporting a refuge-seek behaviour during hydropeaking conditions. The Iberian barbel belongs to a cyprinid genus representing many species inhabiting European rivers (Kottelat & Freyhof, 2007). Using it as target species for this study was important to understand the consequences of anthropogenic action on Iberian and other southern European rivers, since this genus includes 35 species distributed through Europe (Fricke, Eschmeyer, & van der Laan, 2020).

This study aims to evaluate the effects of hydropeaking on freshwater fish at the individual behaviour level. A fine-scale biotelemetry technique such as the relative muscular effort can be used as a proxy for the activity of tagged fish. The specific objectives are: (a) study the behaviour, fine-scale movements, and habitat selection of Iberian barbel in response to hydropeaking; and (b) identify which environmental variables and flow components can predict the target species behaviour. The hypothesis under consideration is that the studied animals will react to habitat changes and increased flow, by increasing their physical effort expressed as muscle activity.

2 | METHODS

2.1 | Study area

This study was conducted in Central Portugal, in a stretch of Mondego River regulated for hydroelectric production (Figure 1). Mondego River is 258 km long and has a drainage area of approximately 6,658 km^2 (APA, 2012a). It has an average annual air temperature of 13.4°C, a mean annual precipitation of 1,073 mm, and an annual average discharge of 25 hm^3 (APA, 2012b).

The river stretch selected for this study is located between Raiva dam (upstream) and Palheiros weir (downstream). Raiva dam is part of the hydropower production scheme of Aguieira-Raiva-Fronhas dams, which started operating between 1981 and 1985. Raiva dam is a lower dam constructed for modelling flows released by the larger upper Aguieira dam, representing a reservoir with a maximum capacity of 24,000 dam^3. Although the hydrological characteristics of the river can generate a flood of ca. 3,500 m^3 s^{-1}, the dam's regulation is supposed to prevent discharge flows above 2,000 m^3 s^{-1} (APA, 1992). Mondego's flow regime is highly modified due to Aguieira-Raiva hydroelectric dams and the Fronhas dam (located in Alva River, one of the main tributaries of Mondego), which serves exclusively as a diversion reservoir to the Aguieira dam. Fronhas dam has a maximum discharge flow of 500 m^3 s^{-1} (APA, 1992). Environmental flow released by Aguieira-Raiva dams is ca. 4.8 m^3 s^{-1}, and from Fronhas dam is 2 m^3 s^{-1}, making a total of ca. 6.8 m^3 s^{-1} released in the river stretch selected as the study area. Since the Aguieira-Raiva system needs to meet the requirements of hydroelectric production, it produces electricity in a bi-daily regime (usually released once during the day, around 7 a.m., and another during the night, around 9 p.m.) (Figure 2). During operations, flow rapidly changes in a short period of time

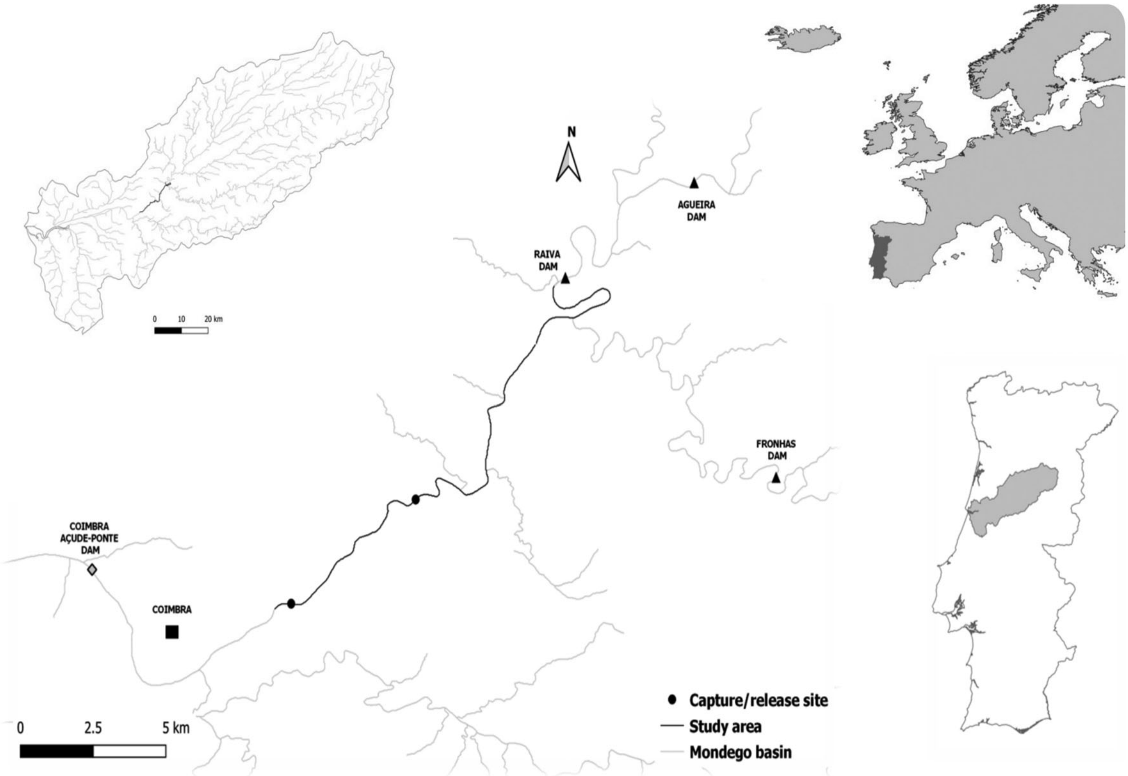

FIGURE 1 Location of the study area, including maps of Europe (a), Portugal (b), the Mondego river basin (c) and details on the river segment (d) were the Iberian barbels were captured and tracked

(normally between 1 and 2 hr), and an abrupt increase up to 150 m^3 s^{-1} may occur. During the wet season, the dam may release a larger number of discharges and/or for longer periods, in which case the flow rate far exceeds the usual values described above.

2.2 | Capture, tagging and tracking of target fish

Between August 2014 and July 2015, a total of 11 specimens of *L. bocagei* (see Data S1 for detailed information on tagged fish) of similar size (total length (TL): mean TL ± SD = 51.8 ± 2.8 cm, and total weight (TW): mean TW ± SD = 1,260 ± 218.12 g) were caught in the study area using an electrofishing gear (Hans Grassl, EL 62 generator, DC, 600 V). After capture, fish were maintained in a 600 L holding tank, equipped with a life support system (i.e., biological filter, aerator) and with a water temperature identical to the capture site. After a period of at least 12 hr of recovery, fish were tagged with implanted coded ElectroMyoGram (cEMG) radio transmitters (cEMG-R11-25, 12 g in air, 56 mm in length and 12 mm in diameter) manufactured by Lotek Wireless, Newmarket, Ontario. Transmitters weighted between 0.75% and 1.21% of tagged barbel body weight in the air.

The tagging procedure followed Thorstad, Økland, Koed, and McKinley (2000), Quintella, Andrade, Koed, and Almeida (2004) and Alexandre et al. (2013), with specimens being anaesthetized (aqueous solution of 2-phenoxyethanol of 0.4 ml/L). Fish were measured (TL), weighted (TW) and transferred to a V-shaped surgical table, ventral side up. The incision performed on the midventral line of the fish, posteriorly to the pelvic fins', was about 3 cm long. Transmitter antenna was placed in the left lateral wall of the peritoneal cavity, and the pair of gold-tipped electrodes positioned, around 1 cm apart, into the red axial musculature above the fish's lateral line. During the tagging procedure, fish were continuously supplied with the anaesthetic solution to maintain sedation and gills oxygenation. After surgery, fish were left to recover for 24 hr in a 600 L holding tank. During recovering, cEMG values were recorded and analysed to assess signal stability in relation to the tagged barbel swimming activity and to determine the resting cEMG value associated with motionless behaviour. Previous studies using the same species and same transmitters showed that the resting level may differ between individuals (Alexandre et al., 2013), hence the necessity to define this parameter individually for each tagged fish. After confirmation that the transmitters were sending a stable low cEMG signal (close to 0) during motionless periods and increasing with activity (up to a maximum of 50 cEMG), fish were released near the capture site.

After approximately 5 days after release (for fish to recover and resume normal behaviour), we defined a maximum of six continuous monitoring periods for each barbel. These consist of four monitoring periods during daytime (ca. 8 hr/individual) and two during night (ca. 10 hr/individual) to obtain EMG data for the total circadian cycle (ca. 24 hr). Fish were continuously tracked from a boat during the previously define periods. The cEMG signal sent by the transmitter was detected and recorded by a portable combined receiver and data logger (SRX_400 from Lotek Wireless) through a coaxial Yagi antenna. Positions of tagged barbel were also determined and georeferenced at a 30-min sampling interval using a conventional GPS device (precision ca. 10 m^2). The planned monitoring periods for the tagged fish were not possible to obtain, mainly due to fish being recaptured by local anglers or due to their disappearance from the study area. However, for the tagged individuals, all data obtained prior to their disappearance/capture were used in the analysis. To guarantee larger independence of collected data for the day and night periods, monitoring for the same fish in these two periods was not conducted during consecutive periods. In addition, at each fish position recorded, we performed a micro and meso-habitat characterization, using the variables listed in Table 1.

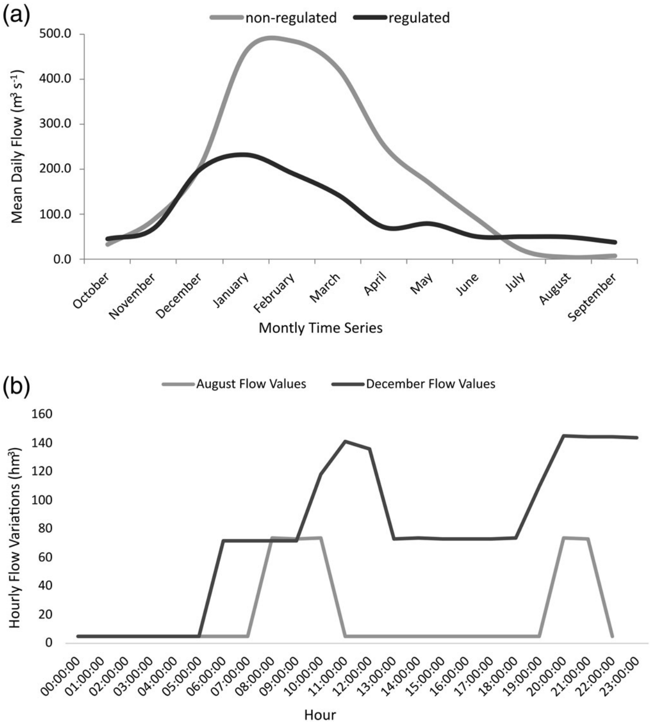

FIGURE 2 Hydrogram showing the flow variation in Mondego river: (a) mean monthly flow comparison before (1961–1980) and after (1993–2012) the construction of Raiva-Agueira-Fronhas hydropower systems, and (b) hourly flow variation in two different periods of 2014, during dry (August) and wet (December) seasons. Flow data was provided by the Portuguese Environmental Agency (APA/INAG) (SNIRH, 2012) and by EDP - Gestão da Produção de Energia S.A

2.3 | Data analysis

All recorded EMG values were considered by their monitoring period (i.e., day or night) and flow type (i.e., ecological flow or hydropeaking). In a previous study targeting the same species (Alexandre et al., 2013), it was possible to determine that similar values of EMG recorded by distinct transmitters in different individuals corresponded to different swimming activities. This result indicated that the same regression equation estimating swimming speed with cEMG records could not be applied, in a similar way, to all individuals in the study (Alexandre et al., 2013). Even though it is preferable to carry out an individual calibration of EMG values with swimming speed for each fish (e.g., Alexandre et al., 2013), we chose not to do this to avoid increased stress levels, resulting from additional transportation and further manipulation in the swim flume. Thus, to allow the comparison of activity values among all animals included in the study it was necessary to standardize the EMG records as previously performed by Quintella et al. (2004), dividing each recorded value by resting value (EMG_{rest}) determined for each individual during the 24-hr recovery period prior to fish release in the river, resulting in a relative index of muscular activity (EMG_{std}).

TABLE 1 Abiotic variables used for the characterization of meso and micro-habitat used by the Iberian barbels during the monitoring period

Variable	Measurement procedure (location with a precision of ~10 m^2)	Characterization classes	Variable values used in statistical analysis
Distance to riverbank	Georeference and SIG program	Distance evaluated in length classes in meters: [0]; [0–3]; [3–6]; [6–9]; [9–12]; [12–15]; [15–18]; [18–21]; [21–24]; [24–27]; [27–30]	Mean value of each class: 0; 1.5; 4.5; 7.5; 10.5; 13.5; 16.5; 19.5; 22.5; 25.5; 28.5
Substrate type	Visual observation[a]	Wentworth scale (particle size mm) classes: Silt (0–0.064); sand (0.064–2); pebble (2–64); cobble (64–256); Boulder (256–512)	Mean value of each class: 0.032; 1.032; 33; 160; 384
Depth	Graduated stick/rope (± 0.01 m)	Continuous variable	—
Flow velocity	Flowmeter, Hydro-Bios (± 0.01 m/s)	Continuous variable	—
Vegetation	Visual observation (% of occupancy)[a]	0–20%; 20–40%; 40–60; 60–80%; 80–100%	Ordinal codes assigned (by order): 0; 2; 4; 6; 8
Debris	Visual observation (% of occupancy)[a]	0–20%; 20–40%; 40–60; 60–80%; 80–100%	Ordinal codes assigned (by order): 0; 2; 4; 6; 8
Shade	Visual observation (% of occupancy)[a]	0–30%; 30–60%; >60%	Ordinal codes assigned (by order): 0; 2; 4

[a]During night tracking surveys, whenever necessary the measurement procedure was concluded on the following diurnal period.

Before any statistical procedure, all data were submitted to a preliminary analysis of parametric assumptions (e.g., normality and homogeneity of variances) through a Kolmogorov–Smirnov analysis and Levene test, using Statistica 12 package (Dell Software). As the data generally did not comply with those parametric assumptions, a non-parametric statistical test Mann–Whitney (*U*) was applied to assess the existence of differences in muscle activity (EMG_{std}) of tagged barbel between periods of ecological flow and hydropeaking. A boxplot was created to help in the data visualization; the box represents the interquartile range with the median bar, while the whiskers correspond to the non-outlier range and included possible outliers and extreme values. To further understand how EMG_{std} values of tagged fish changed during hydropeaking periods, a matrix was made consisting of 10-min intervals for each regular hydropeaking period (i.e., periods of 2–2.5 hr) for all tagged fish. A boxplot encompassing all fish and tracking hydropeaking periods considered was performed to assess the EMG_{std} variation within 10-min intervals and complemented with a Kruskal-Wallis test to identify significant differences between 10-min intervals within hydropeaking duration. To test for differences between groups, a pairwise comparison using the Dunn-Bonferroni test was performed to identify within which 10-min intervals those differences were obtained.

To identify which environmental factors were related to the observed variability of muscular activity in tagged barbel, a new data matrix was compiled, with a dependent variable and four predictors that were considered as most likely to be related to the expected variability in the muscular activity of the fish. The dependent variable corresponded to the average value of EMG_{std} for each 1-hr interval of the monitoring period of each tagged fish. Predictors were selected as variables related to the period of the day [*Time*: day (1) and night (0)] and environmental variations in terms of flow and temperature, more specifically, *Temp* (corresponding to mean water temperature for each 1-hr interval of monitoring period), *FlowM* (corresponding to the overall magnitude of flow discharge, expressed in $m^{-3}\ s^{-1}$, in each time period analysed), and *FlowV* (corresponding to the magnitude of flow discharge variation, expressed in $m^{-3}\ s^{-1}$, compared to the previous hour) (Table 2). The matrix also includes a column identifying each fish (i.e., “Barbel”) and a column called “Sessions” (corresponding to each monitoring period *per* individual). Temperature data were obtained through a continuous record (30 min. sampling rate) of data-loggers HOBO PRO Temp V2 placed along the study area and covering the entire monitoring period. Flow values recorded during monitoring periods correspond to the sum of the flow values discharged from Raiva-Agueira (river Mondego) and Fronhas (river Alva, located upstream the study area) systems and were provided by EDP - Gestão da Produção de Energia S.A. A Generalized Linear Mixed Model (GLMM) was applied using the SPSS software (IBM SPSS Software, Version 26, Chicago, IL) to identify the environmental variables related to the variation in relative muscle activity of studied individuals. This analysis was chosen because telemetry data usually present a high degree of autocorrelation and dependence observations and are usually the result of repeated measurements in the same individual (Cooke, Thorstad, & Hinch, 2004). To guarantee samples independence, the variable “Barbel” was considered the subject, and “Sessions” as our repeated measurement. The continuous predictors (*FlowM*, *FlowV* and *Temp*), the binominal predictor (*Time*), and the interaction between flow variables and Time (*FlowM* × *Time* and *FlowV* × *Time*) were added, considering the response variable (EMG_{std}), to identify which predictors were selected by the initial model as being significantly related with the dependent variable. The variable “Barbel” was added to the statistical analysis as random factor to understand the influence of individual variability on variation of EMG_{std} values. After the selection of the factors and interactions that were significantly related to EMG_{std} value, a new GLMM procedure was conducted, in which the significant predictors were hierarchically added to the model. To select the model that best explained the EMG_{std} variability, Akaike's Information Criterion (AIC) was used, considering the lowest AIC model as most appropriate (Symonds & Moussalli, 2011).

For the analysis related to habitat characterization at each detected barbel location, the discrete variables collected during fieldwork (i.e., distance to riverbank, substrate, vegetation, debris and shade), were transformed into ordinal variables (Table 1). Type of substrate was also qualitatively evaluated in the field, following an adaption of Wentworth scale estimated grain size, and the median of each class size was assigned as sample value (Table 1). The exact distance to riverbank of fish at the detection moment, was estimated as the distance (in meters) between the riverbank and the exact location, having midstream as maximum distance. After this procedure, and to account for a potential error in fish detection on the estimated distance to riverbank for each fish location, several distance/location classes were created with the median value of each class being used in the respective variable (Table 1).

To test for the existence of significant differences in relation to habitat characteristics of monitored fish between periods of ecological flow and hydropeaking (a fixed factor FLOW, with two levels), a unifactorial PERMANOVA (Permutational multivariate analysis of variance) was used. A SIMPER (dissimilarity percentages) analysis was performed to identify which habitat variables contributed the most to the existing differences between the two periods of flow relative to

TABLE 2 Description of the environmental variables included in the generalized linear mixed model (GLMM) analyses, as potential predictors of fish activity and behaviour

Variables	Description
Time	Relative to the monitoring period [Day (1), Night (0)]
FlowM	Overall magnitude of flow discharge ($m^3\ s^{-1}$) operated by both hydroelectric systems (Raiva-Aguieira and Fronhas)
FlowV	Magnitude of the flow discharge variation ($m^3\ s^{-1}$) compared to the previous hour period FlowV = (magnitude of the flow discharge at time h) – (magnitude of the flow discharge at time h − 1) Positive values are related to a flow increase and negative values are related to a flow decrease
Temp	°C, mean value for each hour considered in the analysis

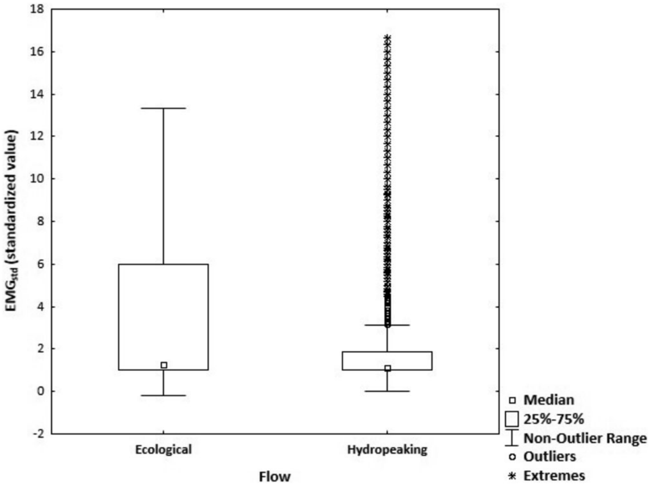

FIGURE 3 Boxplot representing the differences in EMG$_{std}$ values between the two different flow periods (ecological vs. hydropeaking)

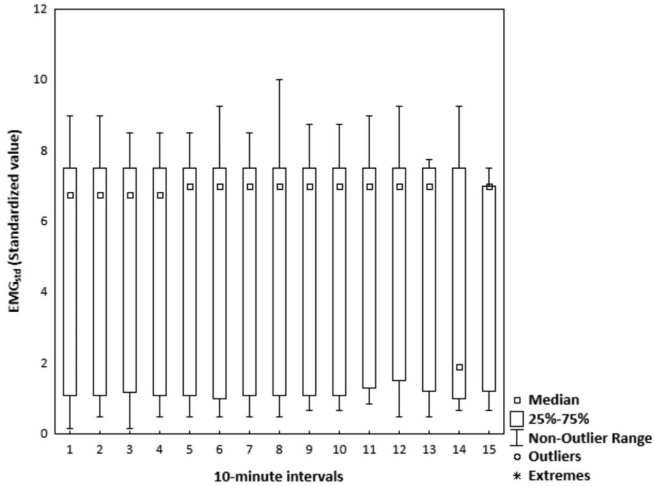

FIGURE 4 Boxplot representing EMG$_{std}$ variation within regular hydropeaking periods (for each 10-min intervals)

the location occupied by the tagged fish. Both analyses were conducted using PRIMER+v6.0, and its add-on PERMANOVA.

3 | RESULTS

3.1 | Impact of hydropeaking on fish behaviour

From the total of 11 barbel tagged with EMG transmitters in the study, six (B1, B4, B6, B8, B9 and B10) were included in the following data analyses (see Data S2 for average EMG data for each barbel in each monitoring period). The remaining five fish were excluded from analysis, due to their rapid disappearance from study area or capture by local anglers. The six analysed barbel provided a total of 205,793 EMG records, with an average of 34,298 records per fish (B1-30776 EMG records; B4-7738; B6-16251; B8-60279; B9-55942; B10-34807) and a total of ca. 195 monitoring hours.

A Mann–Whitney (*U*) analysis showed significant differences ($U = 4.80$; $p = .000$) of EMG$_{std}$ between both flow types, with tagged barbel displaying higher values during ecological flow periods (median EMG$_{std}$ ± *SD* $= 1.29 \pm 2.75$) compared to hydropeaking values (median EMG$_{std}$ ± *SD* $= 1.14 \pm 2.08$). A boxplot diagram (Figure 3) helps to visualize these differences on EMG$_{std}$ values, with values from the ecological flow period having a larger variation (min. $= 0.17$; max. $= 13.33$) in comparison to the values obtained during hydropeaking (min. $= 0$; max. $= 3.14$, excluding outliers). During short-term artificial flow discharges, higher muscular activity from tagged barbel was only recorded occasionally, with these higher values being considered outliers or extreme values by the boxplot analysis (Figure 3). Regarding the analysis of EMG variation within hydropeaking periods, the Kruskal-Wallis test identified significant differences of average EMG (EMG: Chi-square $= 166.39$; $p < .000$) values between the different 10-min intervals (Figure 4). From the 100 different possible multiple comparisons, the post-hoc test revealed significant differences ($p < .05$) in 39 of them, but without a clear temporal variation pattern. Although significantly variable within hydropeaking periods, EMG$_{std}$ of the tested fish did not appear to be dependent of any specific hydropeaking period, neither of the duration of this phenomenon.

The initial Generalized Linear Mixed Model (GLMM) identified five out of six variables considered in the analysis (FlowM, FlowV, Temp, Time and FlowV × Time) as significantly influencing EMG$_{std}$ as a measure of fish activity (Table 3). The factor "Barbel" was not identified as a significant factor, indicating that the obtained results are not individual dependent. The second GLMM analysis conducted to identify the best model explaining the variation of EMG$_{std}$ values, showed that the best solution was the one that only includes the variable corresponding to Magnitude of Flow Discharge (FlowM), with an AIC of -19.789, the smallest value of the tested models (Table 4). The GLMM analysis revealed that when FlowM increased (variable coefficient $= -0.001$) the EMG$_{std}$ decreased.

3.2 | Habitat selection

Regarding habitat use by tagged fish, the PERMANOVA performed on the abiotic variables related to barbel locations identified significant differences between ecological flow and hydropeaking periods (FLOW: $F_{1:173} = 7.25$; $p < .001$). Through SIMPER analysis, it was possible to identify the variables Debris, Distance to Riverbank, Vegetation and Shade, respectively, as the four habitat characteristics that contribute the most to the differences in habitat selection in each flow period (Table 5). According to the results, during hydropeaking fish tend to occupy more shaded habitats closer to the riverbank, with a higher accumulation of Debris and Vegetation. During ecological flow periods, fish are more frequently located away from riverbanks, in habitats with less refuge value.

TABLE 3 Summary of the initial GLMM analysis applied to identify the predictors that significantly influence barbel activity (EMG_{std})

Factor	F	*df*1	*df*2	Significance	Coefficient
Intercept	10,784.342	6	205	0.000[a]	0.220
FlowM	283.844	1	205	0.000[a]	−0.001
FlowV	5.801	1	205	0.017[a]	0.000
Temp	48.212	1	205	0.000[a]	0.012
Time	152.806	1	205	0.000[a]	0.115
FlowM*time	2.313	1	205	0.130	0.000
FlowV*time	16.469	1	205	0.000[a]	−0.001

Note: In this analysis FlowM, FlowV, Temp, Time and the interactions FlowM × Time, FlowV × Time were considered our fixed factors, whilst the factor Barbel was considered our ID plus our random effect.
[a]Significant at $p \leq .05$.

TABLE 4 Summary of the GLMM hierarchical addition previously identified as significantly influencing the Iberian barbell activity

Variable	F	*df*1	*df*2	Sig.	AIC
FlowM	6.747	1	211	.010	−19.789
FlowM + FlowV*time	3.349	3	209	.020	6.668
FlowV + FlowV*time	4.234	2	210	.016	−8.634
FlowM + FlowV	3.852	2	210	.023	−3.978
FlowM + FlowV + temp	5.399	3	209	.001	1.800
FlowM + FlowV + temp + time	1,695.002	5	207	.000	−13.898
FlowM + FlowV + temp + time + FlowV*time	8,196.894	6	206	.000	−2.149

Abbreviations: AIC, Akaike's Information Criterion; *df*: degrees of freedom; *F*, test statistics; Sig, *p*-value.

TABLE 5 Results of the SIMPER analysis based on the characteristics of the habitat used by the Iberian barbel during periods of hydropeaking and ecological flow

	Mean value			
Variables	Ecological flow	Hydropeaking	% of contribution	% of cumulative contribution
Debris	−0.42	0.35	15.72	15.72
Distance to riverbank	0.20	−0.16	14.37	30.08
Vegetation	−0.13	0.11	14.31	44.40
Shade	−0.22	0.18	14.30	58.70

4 | DISCUSSION

4.1 | Influence of environmental predictors

The magnitude of flow discharge (FlowM) was the variable that best explained variability in terms of activity, with fish exhibiting lower activity when flow magnitude was higher (i.e., hydropeaking events). A study conducted by Costa et al. (2018) in an indoor experimental flume demonstrated that the behaviour of Iberian barbel was also significantly affected by flow magnitude and hydropeaking event duration, with the fish showing a refuge-seek behaviour under hydropeaking conditions to conserve and recover energy. According to Taylor et al. (2014), bull trout respond with a lower muscle activity to rapid increases of flow discharge, also supporting the results obtained in this study, where Iberian barbel reduced their activity with flow increase, probably associated with refuge-seeking behaviour. Marchetti and Moyle (2001) and Belmar, Bruno, Martínez-Capel, Barquín, and Velasco (2013) had already identified flow magnitude released by hydropower facilities as the major determinant of river habitats, riparian conditions, and consequently, of the local fish composition and functional associations, with some recent studies, in an indoor experimental flume (e.g., Costa et al., 2019) and in situ (e.g., Taylor et al., 2014), strengthening those results. However, in the present study, an in situ experiment was performed in an attempt to understand the impact of the flow magnitude component on the behaviour of a freshwater fish species at the individual level. The information was obtained at finer spatial and temporal scales since the fish were manually tracked, and the tag sensor implanted on the fish allowed to assess the muscular activity of a cyprinid species through its physiological response. This is one of the most representative families of fish assemblages in Iberian rivers (Magalhães, 1992), providing important information about the behaviour and habitat selection in hydropeaking scenarios.

When facing a decrease in water temperature and sudden increase flows, fish may reduce their activity considering their energy expenses (Baras, 1995; Liao, 2007; Murchie et al., 2008; Bartolini, Butail, & Porfiri, 2014), and although their activity is related to a preferential time of day, this may change in response to specific events, such as daily feeding, reproduction or other components of seasonal variability (Reebs, 2002; Sánchez-Vázquez, Madrid, Zamora, Ilgo, & Tabata, 1996). That being said, and while flow magnitude was the environmental variable, flow-related, best explaining the activity rhythm and muscular effort of target species, the other three variables (i.e., magnitude of flow variations, water temperature, time of day) as well as the interaction between the magnitude of flow variation and time of the day, were also significantly related to the fish activity.

4.2 | Behaviour and habitat selection

During hydropeaking events, there is a sudden increase in river flow and current velocity (De Vocht & Baras, 2005; Jones, 2013; Vehanen, Jurvelius, & Lahti, 2005). The initial hypothesis of this study assumed that the target fish would react to this abrupt hydraulic alteration through increased effort shown by an increase in their swimming activity recorded by cEMG transmitters. The results obtained contradict this initial hypothesis, since the target barbel showed higher and more variable levels of muscular activity during the ecological flow period and lower and less variable values during hydropeaking events. This result can be associated with a behaviour related to the management of energy expenditure by target fish during both flow periods (Korman & Campana, 2009; Taylor et al., 2014). Besides showing a higher muscular activity during periods of ecological flow, the studied individuals also showed a greater variation in this parameter during the same period, whereas during hydropeaking they display the opposite behaviour, with lower muscular activity and less variation in the recorded values. These results seem to indicate that the studied individuals tend to maintain a low and constant rate of muscle activity during hydropeaking events, which is most likely associated with a refuge behaviour while facing abrupt flow increases (Krause, Loader, Kirkman, & Ruxton, 1999; Taylor et al., 2014). However, outlier values (high cEMG values associated with higher activity levels) detected during barbel tracking surveys covering hydropeaking periods can be indicative of behavioural stress when fish face an abrupt increase in current velocity in the habitats that they normally occupy during ecological flow periods. These high-level activity periods can be associated with short movements between refuges to avoid higher flow velocities and harsh hydraulic conditions during hydropeaking due to their propensity to move to preferential habitats during high flow periods (Costa et al., 2018). This hypothesis seems to be confirmed by the PERMANOVA and SIMPER analyses based on the habitat variables collected at fish locations. Results show that during hydropeaking periods fish tend to occupy habitats with higher refuge value, that is, habitats closer to riverbanks, with greater amounts of debris, vegetation and shade. During ecological flow periods, the preferred habitat characteristics of fish can be found at a larger scale on the river. Differential results obtained during hydropeaking periods seem to suggest that the optimal and preferential habitat of fish tend to be reduced, resulting in a search for habitats with less demanding characteristics energetically, as showed by several authors (Baras & Lucas, 2001; De Vocht & Baras, 2005; Taylor et al., 2014). High variability in flow rates, quality and presence of a diverse and heterogeneous habitat, not only determines communities in a river but also allows fish to search for temporary refuges (Boavida, Santos, Ferreira, & Pinheiro, 2015; Britton & Pegg, 2011; De Vocht & Baras, 2005; Schwartz & Herricks, 2005). Since fish survival depends on the complexity of physical habitat available for use (Schwartz & Herricks, 2005), the refuge mechanism allows species to persist both in natural streamflow fluctuations but also during sudden changes caused by anthropogenic activities such as hydroelectric dams (Parkos III, Ruetz III, & Trexler, 2011).

The existing specialized literature often describes hydraulics parameters such as current velocity and water depth as highlight influential on habitat selection by fish species (Bunt et al., 1999; Flodmark, Forseth, L'Abée-Lund, & Vøllestad, 2006), and since these are some of the variables in riverine environments that vary the most during hydropeaking phenomena (Costa et al., 2019; Moreira et al., 2020), fish habitat preferences in relation to these variables may also vary with increasing or decreasing flow magnitude caused by dam operation. This was not the case in our study, as these two variables were not the ones that contributed most to the differences in the habitat occupied by the target species between hydropeaking and ecological flow periods. During hydropeaking periods, fish mostly occupied marginal habitat, with high cover and refuge value, independently of their depth, whereas during ecological flow, habitat occupied by target fish were much more variable in terms of depth and current velocity, as they were swimming between different habitats and occupying both high and low depth and velocity sites, thus reducing the importance of these variables in the habitat selection between hydropeaking and ecological flow.

Although a total of 11 barbel were tagged in this study, it was only possible to analyse data from six of them, which can be considered a small number, when compared to what is used in other biotelemetry studies to increase results representativeness and decrease the effects of individual variability of fish behaviour (Cooke et al., 2004; Hay & Nebel, 2012). However, the data collected from the six fish represents a total of 195 hr of behavioural monitoring, resulting in a total of 205,793 EMG records, and an average of 34,298 EMG records per fish, a considerably large and robust dataset that is representative of fish behaviour within aforementioned environmental conditions.

4.3 | Hydropeaking mitigation

To minimize the impacts of hydropeaking operations on freshwater fish, it is necessary to design and apply suitable mitigation measures (e.g., restoration, compensation, operational) focusing on an in-stream perspective (Charmasson & Zinke, 2011), to maintain essential habitat characteristics and consequently, native populations depending on them (Belmar et al., 2013). To ensure the success of the mitigation measures, it is necessary to deepen the knowledge on the relationship between hydrologic changes, habitat alterations and the ecological response of aquatic biota (Belmar et al., 2013). Restoration measures should focus on maintaining habitat diversity (Almeida, Boavida, & Pinheiro, 2014; Ribbi, Boillat, Peter, & Schleiss, 2014), since well-maintained riparian corridors increase the presence of wooden debris, branches and roots in marginal areas, creating low flow areas. In severely altered rivers with regulated margins, it may be necessary to favour the rehabilitation of riparian galleries by creating new refuge conditions for local fauna (Kauffman, Beschta, Otting, & Lytjen, 1997). According to the results obtained in this study, tagged fish were able to maintain a low level of activity and maintain their position in the river during hydropeaking periods due to their ability to choose suitable habitats with higher refuge value. Thus, it is very important that rivers affected by these types of regulated discharges have a heterogeneous habitat, considering not only all life cycles stages but also the species occurring (Hayes et al., 2019), since preserving the physical habitat of a stream should be considered a major step towards conserving its biota (Ligon, Dietrich, & Trush, 1995).

Operational measures are often applied to hydropower plants production schemes and should include: (a) attenuation of the magnitude of discharge; (b) slowing down the ramping rate and reduce the magnitude of flow variations; and/or (c) limiting and increasing the minimum discharge during critical periods (Charmasson & Zinke, 2011). According to the results obtained by the present study, the magnitude of flow discharge is the most determinant factor on the activity of studied fish. To mitigate this factor, one can propose the reduction of the magnitude of peak flows by reducing the ratio of the flow discharge between ecological and hydropeaking flows (Charmasson & Zinke, 2011). With this proposal, it is assumed that fish will be able to maintain their regular activities without the need to seek refuge and/or interrupt foraging behaviour due to high magnitude discharges. An increase of the transition time between the two types of flow released by hydropower facilities to diminish such impacts can also be proposed. This can be translated into a gradual flow transition between the ecological flow and hydropeaking flow, instead of a sudden and abrupt one like what is often observed in other regulations scenarios, allowing fish to have a better response to the changing current velocity and depth associated with this flow increase.

After the application of mitigation measures, it is important to develop long-term monitoring programs that accompany the development of the applied measures. In case the mitigation goals are not met, it is necessary to identify the causes and correct them, to ensure the success of the applied measures (Bruder et al., 2016). Construction of hydropower production facilities and other hydraulic infrastructures that promote abrupt changes in the natural flow regime of riverine ecosystems continues to be on many countries' agendas, so there is a growing need to understand the consequences of these changes on freshwater habitat and fish populations, to ensure the success of the maintenance and restoration of riverine ecosystems.

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DATA AVAILABILITY STATEMENT

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

ORCID

Ana Sofia Rato https://orcid.org/0000-0002-2311-5594
Carlos Manuel Alexandre https://orcid.org/0000-0003-2567-4434
Pedro Raposo de Almeida https://orcid.org/0000-0002-2776-5420
José Lino Costa https://orcid.org/0000-0002-3843-4635
Bernardo Ruivo Quintella https://orcid.org/0000-0002-0509-4515

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