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Pre-reproductive movements of potamodromous cyprinids in the Iberian Peninsula: when environmental variability meets semipermeable barriers

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Abstract

This study aims to describe pre-reproductive movements of *Luciobarbus bocagei* and *Pseudochondrostoma duriense* in a regulated canyon-stretch of the Tormes River (Spain), with high environmental variability, semipermeable barriers, and fishway retrofitting actions. The main objectives were to identify peak migration dates and environmental drivers, test ensemble-learning techniques to model fish migration and propose adaptive management measures. To achieve this, fish movements were 5-year monitored in a stepped fishway and Survival Analysis and Random Forest techniques were used for data analysis and modeling. Results showed that migration occurred in May-July, a wider period than the one previously reported in the literature. Movements were triggered by the increase in water temperature and photoperiod, and were strongly affected by the hydraulic river scenario (water levels and discharge) at the semipermeable barriers. Random Forest was able to include the effect of each barrier and predict accurately timing and number of migrants, classifying and ranking the importance of variables. Moreover, developed models allowed to assess fishway retrofitting actions and to predict positive effects in fish number under new, scheduled and variable environmental flow scenarios. Long-term monitoring together with ensemble-learning methods can allow the definition of cost-effective adaptive management strategies to ensure endemic fish conservation.

Keywords: fish migration, fishway, Iberian barbel, Northern straight-mouth nase, Random Forest

Declarations

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Availability of data and material: All used data as well as annual reports (2012-2015 by University of Valladolid and 2016 by CEIBA Estudios Ambientales S.L.) are publicly available at the Fisheries Service of Junta de Castilla y León (www.jcyl.es) and at the Duero River Basin Water Authority (www.chduero.es).

Code availability: not applicable.

Introduction

Freshwater ecosystems are among the most threatened in the world (Saunders et al., 2002) and the decline of freshwater fish is a generalized global problem (Jenkins, 2003). Freshwater environments are subject to multiple threats and stressors derived from the use that human society makes of rivers (e.g. irrigation, power generation, flood control or industrial and domestic supply). These uses alter the ecological patterns and processes of rivers, including their biodiversity, population dynamics, behavioral responses of organisms, nutrient loading or trophic interactions (Ormerod et al., 2010; Saunders et al., 2015; Branco et al., 2016; Segurado et al., 2016). Dudgeon et al. (2006) identified five major threat categories that affect freshwater biodiversity: overexploitation, water pollution, flow modification, habitat degradation and species invasion. Within these general categories, river fragmentation and alterations on natural river flow and thermal regimes are the most important specific threats affecting freshwater fish (Nilsson et al., 2005; Jones & Petreman, 2015; Feng et al., 2018).

Dams, weirs and other obstacles (e.g. gauging stations, bridge foundations, culverts, etc.) are known to be one of the major sources of river fragmentation and flow alteration (Nilsson et al., 2005), as they directly affect fish by breaking their migration routes to spawning or feeding grounds. These have direct impacts on the natural reproductive behavior of many fish species (spawning delays or spawn in non-adequate locations) (Gosset et al., 2006; Marschall et al., 2011; Van Leeuwen et al., 2016), on their fitness (energy expenditure, injuries, lower access to feeding habitats, alterations in natural diets, etc.) (Baumgartner, 2007; Araújo et al., 2013; Morán-López & Uceda-Tolosa, 2020), their community structure (size population reduction, isolation of populations, diversity reduction and genetic erosion) (Benejam et al., 2014; Branco et al., 2017), and their resistance against diseases and invasive alien species (Marvier et al., 2004), consequently leading to a drastic reduction of fish populations or even disappearance (Elvira, 1996; Dias et al., 2017).

Special attention must be taken to semipermeable barriers (Perkin & Gido, 2012), which are those natural or artificial barriers with conditional permeability according to the hydrological scenario of the river and, therefore, relevant in areas with high hydrological variability such as the Iberian Peninsula. The passability of these structures by fish is usually seasonal, as it depends on the increase in river discharge (i.e. increase in water level) (Norman et al., 2009; Garbin et al., 2019). Hence, river regulation can turn seasonal permeable structures into barriers for fish migration (Alexandre & Almeida, 2010).

Iberian cyprinids have evolved and adapted to survive in the variable environmental conditions of Mediterranean basins (Clavero et al., 2004). The Iberian river's hydrology is featured by seasonality and inter-annual variability. It usually presents floods during autumn, winter and/or spring as well as strong summer droughts (Gasith & Resh, 1999). Therefore, anthropogenic alterations in flow regime may produce the loss of migratory signal, affect the habitat availability and reduce river connectivity (Lucas et al., 2001; Jonsson & Jonsson, 2009). Native Iberian fish fauna present the greatest European percentage of endemism (Clavero et al., 2004) and it is characterized by a low number of families, most belonging to Cyprinidae family (Doadrio, 2002). The most abundant species are barbels (genus *Barbus* and *Luciobarbus*) and nases (genus *Pseudochondrostoma*, and *Parachondrostoma*), which are characteristic and dominate medium-sized rivers in the Iberian Peninsula (Oliveira et al., 2012): Iberian barbel (*Luciobarbus bocagei* Steindachner, 1865*)* and Northern straight-mouth nase (*Pseudochondrostoma duriense* Coelho, 1985) the most representative cyprinids of one of the largest Iberian rivers, the Duero River (Martínez Jiménez, 2006). Both Iberian barbel (hereinafter referred to as barbel) and Northern straight-mouth nase (hereinafter referred to as nase) are endemic potamodromous cyprinids and occupy a wide range of freshwater habitats, from floodplains to headwaters, and play an important role in the trophic interactions within their ecosystems (Collares-Pereira et al., 1996; Kottelat & Freyhof, 2007; Santos et al., 2011). As many other potamodromous species, they need to migrate upstream in order to look for the spawning grounds and reproduce (Lucas et al., 2001). Their reproductive season is usually in spring, between April and June (Lobón-Cerviá & Fernández-Delgado, 1984; Herrera et al., 1988; Rodriguez-Ruiz & Granado-Lorencio, 1992; Herrera & Fernández-Delgado, 1994), and they ascend to headwaters looking for reaches of shallow waters with high oxygen concentration and bottoms of sand and pebbles where they place their eggs (Almaça, 1996; Zbinden & Maier, 1996; Santos et al., 2018). However, there is still scarce information regarding the driving factors and their influence during the upstream migration of these endemic species.

In general, fish use environmental variables such as light (e.g. photoperiod, moon cycle), water temperature, hydrology (e.g. river discharge, water depth), meteorology (e.g. rainfall, barometric pressure, etc.), and other chemical information (e.g. salinity, water quality, etc.) as ecological timers for synchronizing behavioral reactions such migration, feeding and spawning (Smith, 1985; Lucas et al., 2001). Thus, alterations on flow and thermal regimes such as those derived from river regulation, water abstraction or pollution, can lead to a shift on the phenology and a consequent mismatch between available and necessary resources (Otero et al., 2014; García-Vega et al., 2018) endangering the persistence of freshwater fish (Shuter et al., 2012). Future scenarios of climate change show potential alterations, not only in water temperature but also in the magnitude, intensity and frequency of rainfall and consequently in river discharge (Solomon et al., 2007; Van Vliet et al., 2013), which may exacerbate the natural annual variability. This, together with the expected water scarcity as a result of the increasing water demand and pollution for industrial, domestic and agricultural supply and their waste water (Seckler et al., 1999; Pittock & Lankford, 2010), as well as river fragmentation (Nilsson et al., 2005), may negatively affect freshwater populations (Vörösmarty et al., 2000; Almodóvar et al., 2012; Branco et al., 2016; Sánchez-Hernández & Nunn, 2016; Segurado et al., 2016). Therefore, knowledge of migration patterns and environmental cues affecting these movements is vital to identify fish requirements and constraints, as well as for the assessment of anthropogenic impacts and the effectiveness of mitigation measures.

Fishways are the most adopted mitigation measure to solve the impact of river fragmentation when the removal of the obstacle is not feasible (Noonan et al., 2012). Fishways (also known as fish passes) are structures that facilitate or allow the passage of fish from one side to the other in transversal barriers to the river (Clay, 1995; FAO/DVWK, 2002; Larinier, 2002). However, the presence of a fishway does not guarantee the migration (e.g. inadequate design or negligent constructions, lack of maintenance, inadequate operating discharges), being necessary its assessment, monitoring and/or retrofitting (Fuentes-Pérez et al., 2016; Valbuena-Castro et al., 2020). On the other hand, the mitigation measure to regulated flow regimes is the definition of environmental flows. An anvironmental flow is usually defined as the quantity, timing, duration, frequency and quality of water flows required to sustain freshwater, estuarine and near-shore ecosystems and the dependent human livelihoods and well-being (Acreman & Ferguson, 2010). However, the complexities arising from the multidimensional nature of balanced water demands makes difficult its definition (McManamay et al., 2016), and the usual legal path is the implementation of minimum flow regimes in regulated rivers, which may be not enough for species adapted to climatic variability (García de Jalón, 2003).

Considering the complexity of interactions presented in some river reaches, modelling techniques based on monitoring time series, that encompass anthropogenic impacts and environmental variables, are essential to define management strategies. Particularly in climate change and flow regulation scenarios, ensemble modelling techniques, such as Random Forest (Breiman, 2001), have the potential to establish and/or asses mitigation measures (e.g. environmental flows, fishways), to set adequate scheduling of river restoration activities or to establish smart management strategies of fisheries stock. These techniques allow to consider the variability of complex scenarios where the fish migration is affected by environmental conditions and anthropogenic impacts (García-Vega et al., 2018, 2020).

This study aims to describe pre-reproductive upstream migration patterns of barbel and nase in a canyon section of the Tormes River (Spain) affected by several semipermeable barriers and the flow regulation induced by a hydropower plant. For this, 5-year monitoring (from 2012 to 2016) of a stepped fishway was carried out. The specific goals were to (1) detect dates with peak migration during their pre-reproductive upstream movements, (2) identify environmental variables affecting these peak movements as well as the influence of semipermeable obstacles along the study reach, (3) model the migration patterns of these potamodromous cyprinids, and (4) evaluate retrofitting actions and propose adaptive management measures to maximize fish migration under semipermeable barriers.

Materials and methods

Study area

The study area was located in the Tormes River, a tributary of the Duero River (Salamanca, Spain). It started (from downstream) at the Cespedosa water supply weir (ETRS89 40º31'00''N, 5º35'10''W), located at the tail of the Santa Teresa Reservoir (496 hm^3), and ended at San Fernando hydropower plant (HPP) dam (ETRS89 40º30'42''N, 5º33'41''W) (**Fig. 1**). This river reach comprises a 1.8 km length river stretch, with an altitude around 900 m a.s.l. and a mean annual discharge of 23.74 m^3/s (under natural conditions, i.e. upstream of the HPP diversion). The reach above Cespedosa weir is mainly a bedrock riffle/cascade dominated canyon with spaced pools where channel material is composed by boulders and cobbles (Rosgen B category (Rosgen & Silvey, 1996)).

The HPP is a run-of-river system, with a dam of 13.4 m height, a rock-cut diversion channel of 525 m (400 m inlet, 125 m outlet, affecting 660 m length of Tormes River mainstem, **Fig. 1**), a reservoir of 1 hm^3 and an operating capacity of 30 m^3/s and 5000 kW. Environmental flows are strictly fulfilled by the HPP, with a minimum of 2.5 m^3/s required in May and June (theoretical spawning season), and 1.05 m^3/s the rest of the year. Fish data were obtained by a trap situated in the stepped fishway associated to this HPP dam (**Fig. 1**). The original fishway consisted of 44 pools (pool length = 1.55 m; pool width = 1.75 m; pool water depth = 0.9-1m) connected each other by a free flow notch (sill height = 0.75 m) and a bottom orifice (0.15 m x 0.2 m), with a water drop between pools of 0.3 m (slope = 17.5%; volumetric dissipated power = 150-175 W/m^3) and a design discharge of 140 L/s. A posterior retrofitting of the fishway was carried out during late summer 2013 (outside of monitoring period). It consisted on the modification of its downstream part (the first upstream 25 pools and cross-walls were preserved as original), to reduce the power dissipation (125 W/m^3) by modifying pool volume (pool length = 1.6 m; pool width = 1.75 m), slope (water drop = 0.25 m; slope = 14.7 %) and connections between pools (submerged notch width = 0.17 m; notch sill = 0.6 m; orifice surface 0.15 m x 0.2 m). In addition, to improve the location of the entrance (located 70 m far from the dam) and guide the fish to it, a weir of 2 m height was built downstream of San Fernando dam and placed next to the fishway entrance (**Fig. 1**). This fish-guiding weir has a lateral notch close to the fishway to concentrate a higher discharge, and to create an attractive velocity and turbulence field in the vicinity of the fishway entrance. However, when moderate-high discharge occurs, the excessive turbulence may hinder the fish entry. Further information about this fishway and river reach assessment can be found in Sanz-Ronda et al. (2015a) and Pedescoll et al. (2019).

Besides barbel and nase, the species composition of the study river reach includes brown trout (*Salmo trutta* Linnaeus, 1758), bermejuela (*Achondrostoma arcasii* Steindachner, 1866), Iberian chub (*Squalius carolitertii* Doadrio, 1987) and calandino (*Squalius alburnoides* Steindachner, 1866). Most part of fish are likely to come from Santa Teresa reservoir, as the canyon section offers reduced feeding and refuge habitats. Before reaching the fishway, fish must overcome three main obstacles from Santa Teresa reservoir (**Fig. 1**):

(1) **Cespedosa water supply weir:** it is a weir of 240 m width and a max height of 2 m. This weir is a semipermeable obstacle, i.e. it is submerged (and passable for fish) when the water level in Santa Teresa reservoir is above 882.6 m a.s.l. (i.e. Cespedosa weir top level). In March 2014 a small nature-like bypass channel (slope 10 % and 3 m width) was built for allowing fish migration in the right bank, but its performance is also conditioned by the reservoir water level and river discharge.

(2) **Gauging structure:** a small permeable weir of environmental discharge control operated by the HPP (1 m height with a central notch of 4 m width and 0.5 m depth).

(3) **Natural waterfalls**: natural barriers with variable water drops (between 1 and 3 m). They are located in the river stretch affected by the discharge diversion of the HPP. Thus, their permeability depends on the discharge through San Fernando dam (i.e. the environmental flow).

Monitoring procedure and environmental variables

Fishway was monitored between mid-April and end-July from 2012 to 2016. Data of fish captures were gathered by HPP staff and authors (see **Availability of data and material** section). During monitoring periods, two sampling methodologies were applied:

(1) **During 2012 and 2013 (original fishway):** a trap in the 5th pool (from upstream, pool size: 3.9 m x 1.7 m) was installed. It consisted in the installation of a mesh in the upper cross-wall for avoiding fish to escape, and a funnel in the downstream notch to allow fish to enter but not to exit (downstream orifice was permanently closed). The trap was checked 2-4 times a week in the morning (9 am; GMT+02:00). During trap checking, fishway gate was closed and thus, the discharge in the whole fishway was interrupted (pools were checked to look for fish before its complete empty). Capturing and handling lasted less than 2 hours. Captured fish were identified, counted and measured (fork length (FL, in cm; ±0.1 cm) and weight (W, in g; ±0.1 g)).

(2) **From 2014 to 2016 (retrofitted fishway):** the trap of the 5th pool was slightly modified with funnels in both downstream notch and orifice. In addition, trap checking periodicity was once a day (9 am) and a discharge bypass was made between 4th and 6th pool, so the fishway discharge was not interrupted during samplings. FL measures (in cm; ±0.1 cm) were only taken in 2014 (in 2015 and 2016 only the species were identified).

In all cases, before measuring, fish were sedated with a solution of 60-100 mg/L MS-222 (tricaine methanesulfonate) as minimum dosage recommended for cyprinids to measure biometric parameters to reduce stress and facilitate handling (Neiffer & Stamper, 2009). As the checking of the trap was made in the first morning hours, captures were assigned to the previous day, as according to the annual monitoring reports, fish likely climbed the fishway during the previous day (median transit time in the fishway < 9 h). Finally, fish were released upstream to continue their migration.

Photoperiod, water temperature, river discharge, and level of Santa Teresa Reservoir were considered as main variables influencing barbel and nase movements. Other variables such as rainfall (highly correlated to river discharge), moon cycle (different correlation in each year; usually more important for diadromous species due to the influence in tide height (Smith, 1985), with low influence reported for potamodromous Iberian cyprinids (Rodriguez-Ruiz & Granado-Lorencio, 1992)) or barometric pressure and chemical (e.g. oxygen, pH, etc.) information (not available data) were discarded for the analysis. Photoperiod (in h) corresponded with the day length (time between sunrise and sunset) and it was calculated with the Brock model (Brock, 1981). Water temperature (in °C) was monitored in the fishway (Orpheus Mini, OTT Hydromet GmbH) during samplings (at 9 am). Missing values were completed with a linear regression ($R^2 = 0.6711$; p-value < 0.0001; $y = 4.5216 + 0.8075 \cdot x$) with previous day air temperature (weather station ref. AV102 Losar del Barco, daily frequency, www.inforiego.org) as response variable (Webb et al., 2003). River discharge data (in m^3/s) were obtained from the gauging station ref. 2081 Puente Congosto (www.miteco.gob.es) located 5 km upstream the study reach before the diversion. Therefore, the environmental discharge, i.e. the discharge through the natural river branch, was estimated by subtracting the discharge diverted towards the HPP from the river discharge gathered in Puente Congosto gauging station, considering the operating range of the HPP (4.5-30 m^3/s) and the minimum environmental discharge required by legal regulations (May and June: 2.5 m^3/s; rest of the year: 1.05 m^3/s). Finally, daily level data of Santa Teresa Reservoir (in m a.s.l.) were obtained from its gauging station, ref. 2038 (www.miteco.gob.es).

Data processing and analysis

All statistical analyses were performed using *R* version 3.5.3 (*R* Core Team, 2019). As the periodicity of the fishway trap checking varied over time, captures were grouped (summed) every three days for all the analyses. In addition, three-day means of environmental variables were calculated.

Descriptive statistics

Frequency analysis of the number of captures by species and years were performed. Chi-squared together with post-hoc pairwise chi-square tests were used in order to identify differences in number of captures among years. Kruskall-Wallis (KW) test was performed to find differences in fish size by year. When KW test was significant, post hoc Dunn's multiple comparison test with Bonferroni correction was performed. These non-parametric test were applied as variables were not normally distributed.

To detect whether pattern of movements varied among years, survival analysis techniques were used, by applying the concept of survival time (time (t) until an event occurs) to migration time (time until a fish is captured in the fishway). For this, Kaplan-Meier (KM) survival curves (Kaplan & Meier, 1958) were determined to show possible different patterns and to determine the median migration date (the 3-day period when the 50% of the captures has occurred). Analyses were performed from t = 1 (15th-17th April) to t = 35 (26th-28th July) (each increment corresponds to 3 days, and the analyses covered a total of 3.5 months). Since the fish were not previously tagged, some assumptions were made: (1) Once a fish was captured, it continued its migration, in that, as repeated observations of the same individual could not be distinguished, it was assumed that all fish were only captured once. (2) The captured fish were the only ones that participated in the experiments and the exact survival time (capture date) of all participating individuals (captured fish) was known, i.e. there were not censored data. Log Rank (LR) test was used for KM curve comparison (Mantel, 1966). For survival analysis the *survival R* package (Therneau & Grambsch, 2000) was used.

The environmental variables were compared among years by using KW and Dunn tests.

Random Forest modelling

To determine the influence of the environmental variables on the number of captures, assess the retrofitting actions in the study site, evaluate the effects of semipermeable barriers and propose optimal managing strategies on the site, Random Forest (RF) regression was used. RF is a statistical ensemble method based on the combination of a multitude of decision trees which are used to determine the mean prediction of the individual trees (Breiman, 2001). RF has been widely applied in ecology (Breiman, 2001; Cutler et al., 2007) and more recently in freshwater fish studies showing good performance in fish abundance prediction and response to environmental alterations (Markovic et al., 2012; Ward et al., 2014; Vezza et al., 2015; García-Vega et al., 2018). The *randomForest* (Liaw & Wiener, 2002) *R* package was used, in which the number of trees to grow was set at 500 while the number of variables randomly sampled as candidates at each split was set at the square root of the number of input variables (recommended default settings). In RF, unlike linear regression, interactions between different predictor variables are automatically incorporated into the regression tree model (Smith et al., 2013). In addition, there is no need for a separate test set for cross-validation as it is performed internally during the run (Breiman, 2001), so RF model was built without data splitting to fully extract the ecological information from the observed data.

Due to the possible different requirements of both species (barbel and nase) as well as the methodological variability between the period 2012-2013 (original fishway) and 2014-2016 (retrofitted fishway, attraction weir, bypass in Cespedosa weir and sampling procedure) four RF regression models were developed in order to: (1) reduce possible bias, (2) compare retrofitting effects and (3) compare model results by species. For the regression, the number of captures was considered as the response variable. Three-day mean of photoperiod (P), environmental discharge (Q) (i.e. discharge through the natural river branch), and water temperature (T) (continuous variables) of the moment of the capture (*t*) were selected as predictors. In addition, variation of river discharge (ΔQ) with respect to the previous three-day period (*t*-1) (i.e. $\Delta Q = Q_t - Q_{t-1}$) was also included as a continuous predictor variable. As descriptors of the passability of the semipermeable barriers, two new binary categorical variables (0,1) were created, one related to the passability of Cespedosa weir (Z_{prev}), that depends on the water level of Santa Teresa reservoir, and the other one related to the necessary discharge to overcome the waterfalls (Q_{prev}). For the former, $Z_{prev} = 1$ if the level of the reservoir was greater than a certain limit (Z_{limit}) (a priori unknown but optimized during the run) at least once during the considered period *t-i*, and $Z_{prev} = 0$ if otherwise. For the latter, $Q_{prev} = 1$ if Q was greater than a certain limit (QW_{limit}) at least once during the considered period *t-i*, and $Q_{prev} = 0$ if otherwise. In both conditional variables also water temperature limits (TZ_{limit} and TW_{limit} respectively) were considered due to its influence on swimming and jumping capacity of fish (Larinier et al., 2002; Ruiz-Legazpi et al., 2018). Lastly, to consider the possible effect of an excessive turbulence in the fishway as consequence of the notch at the fish-guiding weir (only for 2014-2016 period), an additional binary predictor was defined ($Q_{entrance}$). For this variable, $Q_{entrance} = 1$ if Q was greater than a certain discharge limit (QE_{limit}) during the moment *t*, and $Q_{entrance} = 0$ if otherwise.

Z_{limit}, TZ_{limit}, QW_{limit}, TW_{limit} and QE_{limit} as well as the considered time period (*t-i*) for the definition of Z_{prev} and Q_{prev} were determined by an automatic optimization search in the four RF models, to maximize the coefficient of determination (R^2) and minimize the mean squared error (MSE).

Additionally, as in RF extreme observations are estimated using averages of response values that are closer to those observations, large values of the regression function may be underestimated and small values of the regression function may be overestimated (Zhang & Lu, 2012). This issue was resolved by applying a linear bias correction.

To get reliable and optimized models, a custom designed backward stepwise procedure was programmed in *R* to discard variables with low or none contribution in the model. Each model started with all *p* predictors. Then, the least important predictor (the one with lower contribution in R^2) was removed and a new RF model was estimated using $p - 1$ predictors, until all selected predictors contributed more than 0.02 units in R^2 respect to the starting full model. The final four models were evaluated by the R^2 for both, the number of captures (migration quantification) and the proportion of captures every 3-day period (migration timing). The importance of the variables was measured using the increase in mean squared error of predictions (%IncMSE), which represents how much the model fit decreases when a variable drops of the model and the increase in node purity (IncNodePurity), that is used to measure the quality of a split for every variable (node) of a tree (it is calculated by the difference between the sum of squared residuals before and after the split on that variable). For both metrics, the higher the number, the more important it is. Partial dependence plots for environmental variables were obtained from RF in order to characterize the marginal effect of a variable in the model (i.e. the impact that a unit change in one of the predictor variables has on the outcome variable while all other variables remain constant).

Lastly, to assess the possible effects of the retrofitting actions during 2014-2016 and to show the potential of RF models as a managing and decision tool, two modelling scenarios were created. On the one hand, the first scenario consisted on the use of 2012-2013 environmental data to predict the potential number of captures if retrofitting actions were previously implemented. For this, the full model of 2014-2016 was applied to the 2012-2013 environmental data, to assess the differences in number of captures and timing with respect to 2012-2013 captures. On the other hand, due to the influence of environmental discharge in the passability of the semipermeable barriers prior to the fishway, a second scenario was proposed. It consisted on a variable managing strategy of the environmental discharge to improve fish migration in the river reach during reproductive season (April-July). For this, data of the period 2014-2016 was used, although with variations in the river discharge of the study section. This variation consisted in the periodical (every *i* three-day) augment of Q (and thus, Q_{prev}) up to QW_{limit} when the temperature was in an adequate range (>TW_{limit}) and such discharge was available in the river. With this modified environmental dataset, 2014-2016 full model was applied and the differences in the number of captures and timing were assessed.

Results

Fish characteristics

In the whole study period, 38908 fish were captured in the fishway during their pre-reproductive upstream migration. Barbel was present in a higher proportion (n = 27890, 72%) than nase (n = 11018, 28%), although inter-annual differences in number were observed (all Chi-squared test p-values < 0.0001) (**Fig. 2**a). According to post-hoc pairwise chi-square tests, barbel only presented no differences in number of migrants in 2013 and 2015 (p-value = 0.18), whereas nase showed non significantly different number of migrants in 2014 and 2016 (p-value = 0.252).

Barbel fork length ranged from 17 to 55 cm (median = 33.5 cm) with significant differences among years (**Fig. 2**b, KW test p-value < 0.0001). Regarding nase, fork length ranged from 7 to 33 cm (median = 15 cm) with also significant differences among years(**Fig. 2**b, KW test p-value < 0.0001) although without differences between 2012 and 2014 according to Dunn pairwise test (2012-2013 p-value = 0.0001; 2012-2014 p-value = 0.0684: 2013-2014 = 0.0001).

Migration patterns and drivers

Most part of total captures in the fishway occurred from mid-May to mid-June (barbel 86.89% and nase 77.89%). However, the percentage of captures during this one-month period varied among years (barbel 2012 = 91.97%, 2013 = 87.22%, 2014 = 81.54%, 2015 = 46.64%, 2016 = 92.97%; nase 2012 = 88.00%, 2013 = 79.25%, 2014 = 60.14%, 2015 = 90.25%, 2016 = 52.25%), with migration extended to mid-July in some years (barbel 2013 and nase 2013, 2014 and 2016) (**Fig. 3** and **Fig. 4**) or low number of captures during May (e.g. nase in 2016). Barbel and nase presented different global migration patterns (**Fig. 4**a; LR test p-value < 0.0001), with median migration dates of t = 18 (5 – 7 June) for barbel and t = 16 (30 May – 1 June) for nase **Fig. 4**a; LR test p-value < 0.0001). In addition, significant differences among years were found (**Table 1**, **Fig. 3** and **Fig. 4**b-f). In 2012, 2014 and 2016, barbel migration occurred earlier than nase, whereas in 2013 and 2015 nase migrated earlier than barbel. In addition, both histograms and KM curves showed that migrations in 2014-2016 occurred in several peaks along the migration period (**Fig. 3** and **Fig. 4**).

Large inter-annual variation in environmental conditions was found (**Fig. 3** and **Table SI.1** in **Supplementary Information**). Most part of fish captures in the fishway occurred between 16 and 21ºC of mean water temperature (73% and 94% of total captures of barbel and nase respectively), although with different thermal ranges varying among years and species (**Fig. 3** and **Fig. SI.1** in **Supplementary Information**). For example, in 2016 there was an important peak of barbel movements (31% of 2016 captures) between 12 and 14ºC (**Fig. 3**), whereas the 58.5% of 2013 nase captures occurred near 15ºC (**Fig. 3**). Regarding river discharge, most of the captures of barbel in the fishway occurred with river discharges from 2.5 to 3 m^3/s in 2012 (89%), 2014 (73%) and 2016 (67%) whereas they were above 4 m^3/s in 2013 (88%) and 2015 (90%). For the nase, most of the captures in 2012 (88%) and 2016 (96%) occurred with discharge from 2.5 to 3 m^3/s. In 2014 the range of peak captures (97%) in the fishway varied between 2.5 and 4 m^3/s, whereas they were between 3.5 and 8 m^3/s in 2013 (100%) and 2015 (91%).

Full RF models showed a good performance in the prediction of both number and timing of captures, with similar or even better results after variable reduction procedure (**Table 2** and **Fig. 5** in **Appendix A**. Auxiliary figures).Variable importance was different for both species as well as different between periods 2012-2013 and 2014-2016 (**Fig. 6** in **Appendix A**. Auxiliary figures). In the case of barbel, backward stepwise procedure showed that model of the period 2012-2013 considered as most explicative predictors those related to the 3-day periods of the capture (entrance in the fishway) (**Fig. 6**a), whereas in the period 2014-2016 the variables associated with previous obstacles were needed to explain its capture patterns (**Fig. 6**b). In the case of the nase, optimized models of the two periods considered only variables related to the capture, with a strong importance of the water temperature and photoperiod in both periods (**Fig. 6**c and d).

According to global partial dependence plots (**Fig. 7** in **Appendix A**. Auxiliary figures), barbel captures are expected with increasing photoperiod as well as increasing water temperature up to reach the maximum expected peak near 15 h, for both 2012-2013 and 2014-2016, and 18.5ºC and 19.5ºC respectively (**Fig. 7**a) (there are secondary peaks with lower values, such as 14.65 h and 13ºC probably associated with 2016 captures, **Fig. 3**). In addition, more barbel captures will occur when increases in discharge also occur. However, the effect of discharge was in a different magnitude for both models, with moderate discharge increases (near 10 m^3/s) for the model 2012-2013 respect to the model 2014-2016 (peak near 20 m^3/s), and more importance of the level of the reservoir for the former. Furthermore, more captures of barbel are expected when high discharges occur during previous days (Q_{prev}), and thus discharge reductions (ΔQ) will occur when approximate to the fishway (although with lower effect in 2012-2013 model). A low discharge related to the entrance had also positive effects in the number of barbel captures.

Nase models showed that more captures are expected with lower values of photoperiod (max in 14.9 h and 14.45 h for 2012-2013 and 2014-2016 models respectively) and water temperature (max in 15ºC and 16.5ºC for 2012-2013 and 2014-2016 models respectively) than barbel (**Fig. 7**b). Water level of the reservoir above Cespedosa weir (Z_{prev}) and moderate increases (Q and ΔQ) in river discharge will be also associated with more captures. However, discharge during previous days had lower effect in the models and no clear relation with the discharge for the entrance were found.

Scenario modelling

Simulated patterns for 2012-2013 scenario showed a potential greater number of captures for both barbel and nase when considering retrofitting actions (2014-2016 model) (**Fig. 8**a). In the case of the second modeling scenario, with a periodical increase in mean environmental river flow of 10 m^3/s in a 3-day period (QW_{limit}) every 15 days (i = 5) (only when river discharge was higher than QW_{limit} and temperature was equal or higher than TW_{limit}, **Table 2**), a greater number of captures was expected with these releases of environmental discharge (**Fig. 8**b).

Discussion

In this paper, pre-reproductive upstream migration patterns of Iberian barbel and Northern straight-mouth nase in a canyon section of the Tormes River (Iberian Peninsula), with semipermeable barriers of human and natural origin, have been described. The strong variability detected in the study reach over the 5-year study period related to the environmental variables, capture methodology, retrofitting actions and number of captures as well as to the presence of semipermeable barriers and the flow abstraction for energy production, made difficult to establish accurate ranges in such complex scenarios. However, the used ensemble modeling techniques have shown their potential to accurately model, assess effects of environmental variables and simulate both observed and hypothetical scenarios, showing the need of providing river connectivity (i.e. functional fishways) as well as to adequate schedule the timing and quantity of environmental discharges.

Migration patterns and drivers

Specialized literature report reproductive migration between April and June for the nase whereas from February to June for the barbel (Lobón-Cerviá & Fernández-Delgado, 1984; Herrera et al., 1988; Rodriguez-Ruiz & Granado-Lorencio, 1992; Herrera & Fernández-Delgado, 1994). In some agreement with this information and based on well-known fish handbooks (e.g. Doadrio, 2002; Kottelat & Freyhof, 2007), annual fishing closure in the study reach was stablished between 15th May to 15th June (regulated by annual rules, www.medioambiente.jcyl.es) and a greater minimum environmental discharge was set up in May-June (2.5 m^3/s) than the rest of the year (1.05 m^3/s) by the River Authority for this HPP. However, this study reports that pre-reproductive migration of these species occurred in pulsed movements with variable peak migration maxima among years, which also extended until July, outside literature limits as well as fishing closures. In addition, despite nase is considered the first cyprinid to perform reproductive migration (Doadrio, 2002), this 5-year study did not allow to establish a clear order of migration between barbel and nase. It seems, that the strong environmental variability as well as the flow depending semipermeable nature of the studied reach may actuate as a break to fish movement, delaying the movement of fish as well as diluting the natural migration order.

Nase migration was strongly affected by photoperiod and water temperature and with expected lower ranges than barbel, which agrees with a possible earlier migration. Other studies have shown that water temperature is the major factor that controls migration of Iberian cyprinids (Rodriguez-Ruiz & Granado-Lorencio, 1992; Santos et al., 2002) with ranges between 17-19ºC in the Guadalete River (SW Spain) (Rodriguez-Ruiz & Granado-Lorencio, 1992) or near 16ºC in the Vilariça River (NE Portugal) (Boavida et al., 2018). Benitez and Ovidio (2018) found that temperature requirements during cyprinid spawning migration may differ between rivers and also depending on the river position. Nevertheless, in absence of an adequate discharge in a semipermeable pathway, where passability is function of water levels and river discharge (Ovidio & Philippart, 2002), its migration can be delayed (Newton et al., 2018; Kelson et al., 2020), showing a strong variability between years in accordance with the timing of environmental variables. The combination of natural variability of the Mediterranean climate together with complex geomorphological and anthropized river systems strongly conditions the movement of fish. Thus, research studies in highly variable scenarios should include multiple-year monitoring in order to get reliable results.

During 2012 (the year with the lowest number of captures), the level of the reservoir did not reach the top of the Cespedosa weir (without bypass channel during this year). Thus, fish had low possibilities to surpass this weir and all captured migrants were likely to correspond to individuals residing between this first weir and the fishway. In 2013 the number of captures increased, in accordance with a higher reservoir level but still conditioned by the inadequate location and attraction of the old fishway entrance. The increase was noticeable for the barbel, but not for the nase, as nase presents stricter thermal requirements than barbel (Souchon & Tissot, 2012) and adequate temperature for the this species occurred when the level of the reservoir had already decreased. In 2014, captures of both species continued increasing, favored by all the retrofitting actions and by high water levels of the reservoir. In 2015, barbel captures went down to a similar number of 2013, which may be explained by the lower discharge (< 8 m^3/s) for this species during the time window with favorable reservoir water level (i.e. > 882.3 m) to pass the weir at the beginning of the season, concentrating most of the captures in mid-July after discharge rates increases (10-15 m^3/s). In contrast, 2015 was the year with most captures of nase. These captures were concentrated during the adequate water level window of the reservoir level and with an adequate temperature range (18-20ºC) for this species. During 2016 the highest number of barbel captures was reported. Despite colder temperatures occurred (near 13ºC) than the range of the RF model within more captures were expected (i.e. above 16ºC with a peak near 19.5ºC), it seems that photoperiod and discharge during previous days could have induced their movements. In contrast, for nase (for which the temperature was the most important trigger according to developed models), movements were observed only when water temperature exceeded 16ºC, obtaining a similar number to those from 2014. A complementary explanation of differences between barbel and nase could arise from the differences in swimming performance and size of these two species. Barbel, that presented larger size than nase, are able to swim greater distances than nases at higher flow velocities (Sanz-Ronda et al., 2015b), what could make them more efficient to surpass velocity barriers created by higher river discharges, as well as to provide greater values of fishway efficiency than nase (for this particular fishway (Sanz-Ronda et al., 2015a; Pedescoll et al., 2019)).

In general, a positive trend in number of migrants was observed along the years. However, the high environmental variability during the 5-year study period made difficult to see the effect of a certain retrofitting action in such short term monitoring period. For instance, the number of barbel in 2013 (original fishway) and 2015 (retrofitted fishway) were similar, but in 2015 the level of the reservoir was lower. This can be translated in, that with worse environmental conditions in 2015, which could affect the fish passage through the identified semipermeable barriers, the number of barbel was similar to 2013. When comparing years with similar favorable environmental conditions, such as mid-May to mid-June of 2013 (original fishway) and 2014 (retrofitted fishway), it can be seen that the number of captures is significantly greater once retrofitting actions have been carried out, concluding that these improvements were likely to be positive for fish.

The variability related to the capture methodology, retrofitting actions and number of captures in each year made complex to use a single model to characterize fish response to environmental variables. Nonetheless, developed models showed a good performance to predict both number and migration timing. For the period 2012-2013, optimized models explained migration based only in predictors related to the 3-day periods of the capture (P, Q, T and ΔQ). This reinforces the assumption that the collected data during these years likely correspond to some individuals residing between Cespedosa weir and the fishway (2012), or that fish that entered the study area before did not localize the old fishway entrance in the optimized time period ($i = 5$), reducing the effect of Q_{prev} and Z_{prev} (2013). Many studies have shown that inadequate locations and/or poor fishway attraction may suppose a bottleneck in fish movements, resulting in one of the most critical aspects for the efficiency of a fishway (Bunt et al., 2012; Noonan et al., 2012), as if fish do not recognize the entrance, they may remain in the vicinity for a prolonged period, delaying migration or even resulting in the no ascension of the fishway and/or fallbacks (Cooke & Hinch, 2013; McLaughlin et al., 2013).

In the case of the optimized model 2014-2016 for nase, predictors related to obstacles were also discarded during the backward stepwise procedure. However, these variables were indispensable to explain barbel captures, which reinforces the assumption of the probable major efficiency of the barbel when surpassing obstacles during higher river discharges and velocities (Sanz-Ronda et al., 2015b). Models showed that more barbel captures are expected with discharges equal or higher than 10 m^3/s during previous days of the capture to allow the passage through the natural waterfalls.

Scenario modelling

Restoration measures and retrofitting actions can have an important influence on fish population size (Cowx & Gerdeaux, 2004). Simulated scenarios showed a considerable increase of expected captures during 2012-2013 considering the predictive model after the retrofitting actions. However, it is important to note that fish population size is not only dependent on the environmental conditions during migration, but also during recruitment, as non-adequate conditions during early life-stages (e.g. reduction in flow) can condition juvenile survival (Nicola & Almodóvar, 2002; Lobón-Cerviá & Rincón, 2004). This could have introduced a bias in the simulation results. Furthermore, as the number of potential migrants in the large Santa Teresa reservoir was unknown, it was assumed constant along the study period, what may have introduced another source of bias. However, during years with low reservoir levels when migration path is interrupted, such as those in 2012, fish could have spawned in suboptimal conditions in the Santa Teresa reservoir tail, just downstream Cespedosa weir.

Iberian cyprinids have evolved and adapted to survive in the variable environmental conditions of Mediterranean basins (Clavero et al., 2004), thus they require such conditions to complete their life cycle. For these species, anthropogenic alterations in flow regime may produce the loss of migratory signal, affect the habitat availability and reduce river connectivity (Lucas et al., 2001; Jonsson & Jonsson, 2009). In the study site, flow regulation is characterized by an important decrease of river discharge and a removal of variability (i.e. constant discharge), with a minimum environmental discharge near the 10% of the mean annual flow during May-June and 5% the rest of the year. This supposes a strong alteration of the natural flow regime, which may have compromised the natural fragile equilibrium between fish and this river reach. It is clear from our analysis that high flow peaks are essential not only to trigger fish movements but also to make obstacles permeable.

Moreover, connectivity is not only necessary to allow spawning migrations, since different life stages are likely to exhibit different habitat requirements, with these habitat-use patterns being mediated by migratory processes (Northcote, 1978). For example, juveniles of cyprinid species, which primarily respond to instream factors, are also vulnerable to the lack of connectivity in total or semipermeable barriers, as their distribution in upstream river reaches may be restrained (Santos et al., 2011). This enhances the need of functional fishways, as well as, the optimal design of environmental flows, which considers variable flow scenarios along the year instead of setting only a constant discharge. On the other hand, due to the high variability of the Mediterranean climate, a variable migration window is expected, thus appropriate fishing closure season has to be re-defined to guarantee the spawning of these endemic species.

Modelling techniques such as Random Forest (among others) allow to consider the variably of complex scenarios where the passage is a function of environmental conditions (García-Vega et al., 2018, 2020) and have demonstrated here to be useful to establish a regime of variable environmental flows. Results show that establishing periodical (once every 2 weeks) water releases (i.e. reach a 3-day mean discharge of 10 m^3/s), when possible (i.e. river discharge available) and considering water temperature ($\geq$ 13ºC, due to its influence on swimming ability (Ruiz-Legazpi et al., 2018) and effects on internal processes of maturation and migratory motivation (Lucas et al., 2001; Lahnsteiner & Leitner, 2013)), significantly enlarges the migratory window, increasing the total number of captured fish. In addition, and according to the frequency distribution of migrants, it seems important that also discharges < 4 m^3/s are needed in order to optimize fishway attraction and entrance in the current situation (a configuration that distributed the discharge along the whole weir crest could improve the fishway entrance if > 4 m^3/s in this particular case). These flow events have to be designed by considering an adequate duration and intensity to avoid negative effects in fish populations (Alonso-González et al., 2008).

Nevertheless, it is worth mentioning that the cost of such strategies needs to be further analyzed in terms of energy production and fish recruitment increment, making compatible fish conservation and energy production.

Ensemble learning methods, such as RF models, allow to develop “smart management strategies” by adapting the ongoing management, in real time or under the uncertainty of unforeseen climate variations, and to propose new ones. In addition, new observations can be used to feedback the predictive model and continuously propose better strategies, including a cost-benefit analysis of each measure and/or action, to elaborate optimized plans, allowing a comparative analysis of the ecological benefits and the hydropower production.

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Appendix A. Auxiliary figures

Fig. 5 Evaluation of model performance for both number of captures (n) and migration timing (proportion along time): comparison among the observed fish proportion in time t, the predicted with the full model and the predicted with the optimized (after variable reduction) model.

Fig. 6 Variable importance in terms of (1) increase in the mean squared error of predictions (%IncMSE), which represents how much the model fit decreases when a variable drops of the model and (2) increase in node purity (IncNodePurity), which measures the quality of a split (reduction in the sum of squared errors) (for both, the higher number, the more important). (T = water temperature; Q = river discharge; P = photoperiod; Z = reservoir level).

Fig. 7 Partial dependence plots to characterize the marginal effect of a variable in the model (i.e. the impact that a unit change in one of the predictor variables has on the outcome variable while all other variables remain constant).

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Tables

Table 1 Median migration dates (the 3-day period when the 50% of the total number of captures has occurred; captures were grouped every 3 days from t = 1 (15 th-17th April) to t = 35 (26th-28th July)) and Long Rank (LR) tests for curve comparison among years and by species (n = fish number; 0.95LCL = lower 95% confidence limit; 0.95UCL = upper 95% confidence limit; p = p-value).

Species	Year	n	Median	Median (date)	0.95LCL	0.95UCL	Min	Max	LR test
Barbel	2012	384	14	24-26 May	14	14	10	25	All and pairwise: $p < 0.05$
	2013	2191	21	14-16 June	21	21	9	30	
	2014	2827	18	5-7 June	18	18	7	32	
	2015	2037	22	17-19 June	21	22	9	29	
	2016	20451	19	8-10 June	18	18	5	32	
Species	**Year**	**n**	**Median**	**Median (date)**	**0.95LCL**	**0.95UCL**	**Min**	**Max**	**LR test**
Nase	2012	25	17	2-4 June	16	18	14	25	All and pairwise: $p < 0.05$
	2013	53	17	2-4 June	17	18	9	30	
	2014	2027	21	14-16 June	21	21	8	32	
	2015	7026	12	18-20 May	12	12	9	31	
	2016	1887	21	14-16 June	21	23	17	32	

LR test	Global	2012	2013	2014	2015	2016
Barbel vs Nase	< 0.0001	0.0001	0.2	< 0.0001	< 0.0001	< 0.0001

Table 2 RF models will all p predictors (full model) and after back stepwise procedure (optimized model) (i = 5, Z_{limit} = 882.3 m a.s.l. for barbel and Z_{limit} = 882.4 m a.s.l. for nase (no influence of a TZ_{limit} was detected during optimization), QE_{limit} = 4 m^3/s, QW_{limit} = 10 m^3/s and TW_{limit} = 13ºC).

		Barbel		Nase	
		Full model	**Optimized model**	**Full model**	**Optimized model**
2012-2013	**Predictors**	$Z_{prev} + Q_{prev} + \Delta Q + Q + T + P$	$Q + T$	$Z_{prev} + Q_{prev} + \Delta Q + Q + T + P$	$\Delta Q + T + P$
	Global R^2	0.8164	0.8926	0.9714	0.9653
	MSE	3288.16	1923.86	0.57	0.69
	R^2 2012	0.3847	0.3473	0.8655	0.8449
	R^2 2013	0.7654	0.8436	0.9682	0.9847
2014-2016	**Predictors**	$Z_{prev} + Q_{prev} + \Delta Q + Q_{entrance} + Q + T + P$	$Z_{prev} + Q_{prev} + \Delta Q + Q + T + P$	$Z_{prev} + Q_{prev} + \Delta Q + Q_{entrance} + Q + T + P$	$\Delta Q + Q + T + P$
	Global R^2	0.9228	0.928	0.9195	0.9203
	MSE	56125.72	52350.1	11598.6	11483.67
	R^2 2014	0.5331	0.5153	0.5267	0.5806
	R^2 2015	0.4634	0.2658	0.9515	0.9498
	R^2 2016	0.9241	0.9382	0.8795	0.8568

Figures

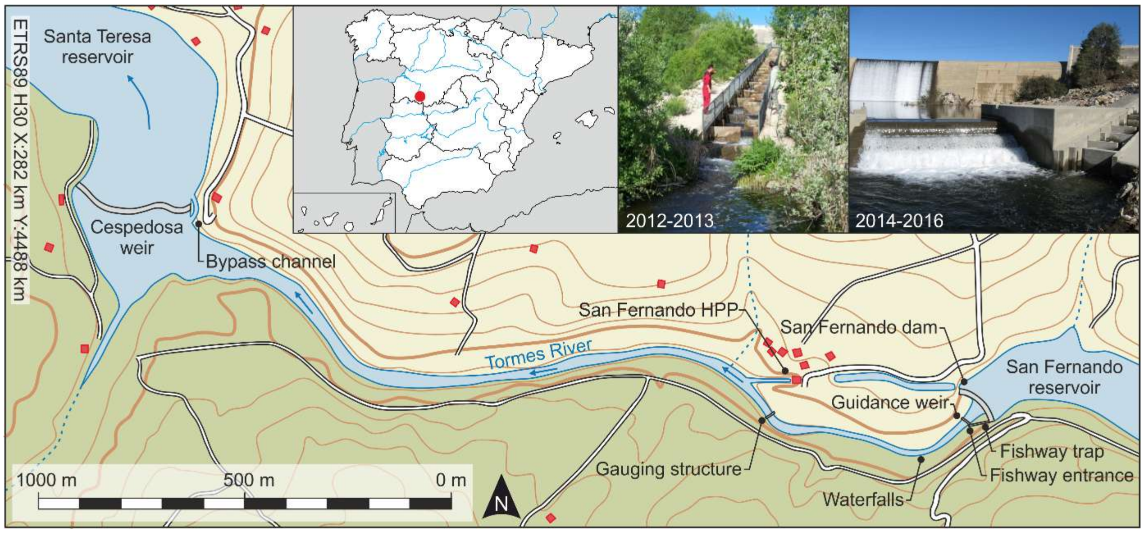

Fig. 1 Location of the study area: from Cespedosa weir to San Fernando dam (arrows indicate the flow direction) and main obstacles for fish migration in the river reach. Pictures of original (2012-2013) and retrofitted fishway with a fish-guiding weir (2014-2016).

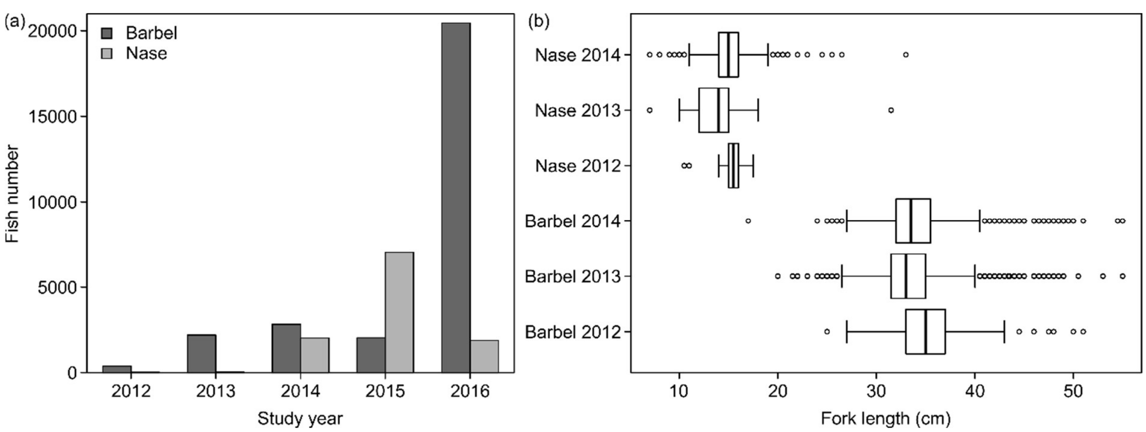

Fig. 2 (a) Number of captures by year and species. (b) Fork length boxplot by species and year (FL data available only in 2012-2014).

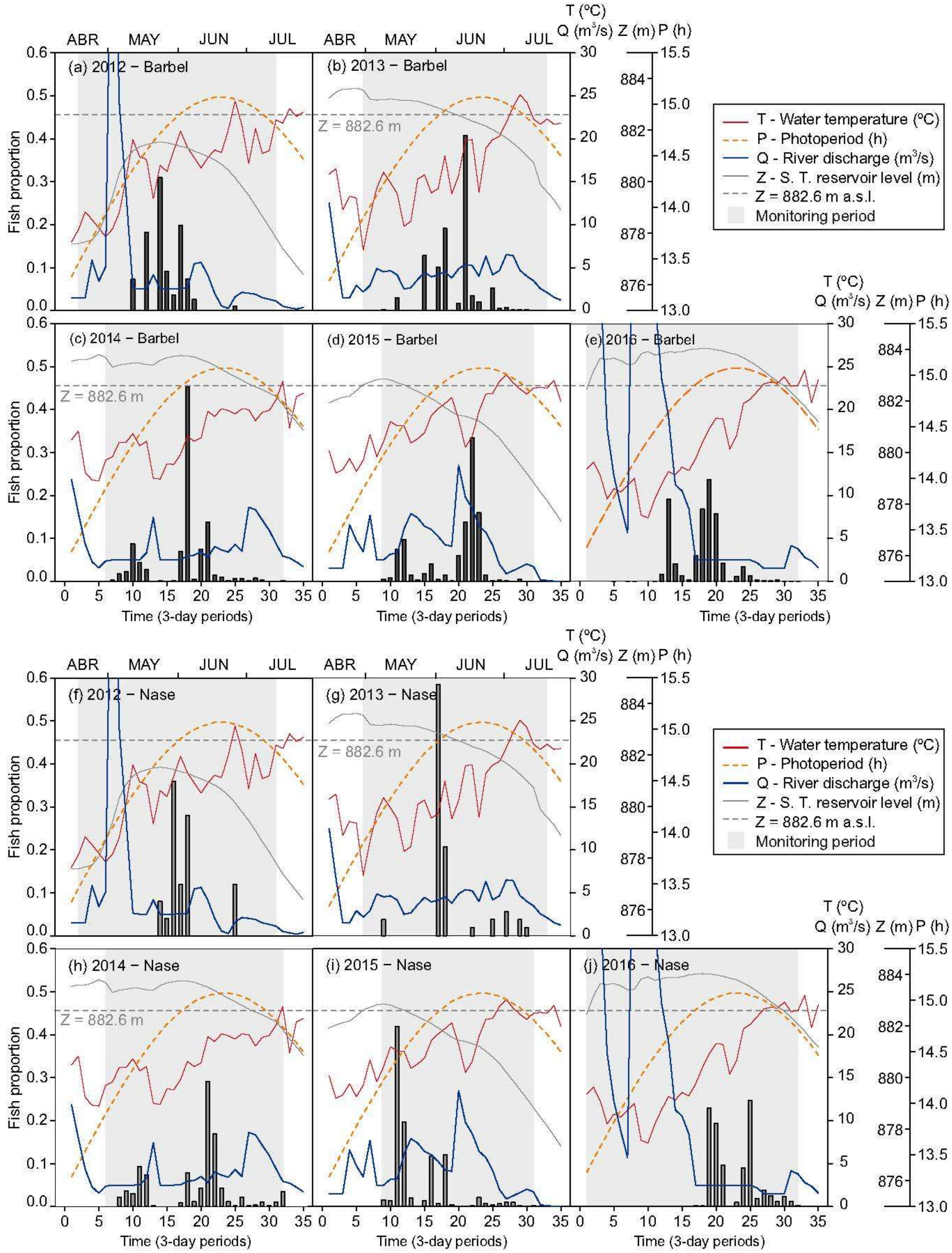

Fig. 3 Proportion of upstream migrants of barbel and nase. Mean (3-day period) of water temperature (T), photoperiod (P), river discharge in the study section (Q) and Santa Teresa reservoir level (Z) (horizontal dashed line = Cespedosa weir level = 882.6 m a.s.l.). Shadow area represents the monitoring period for each year.

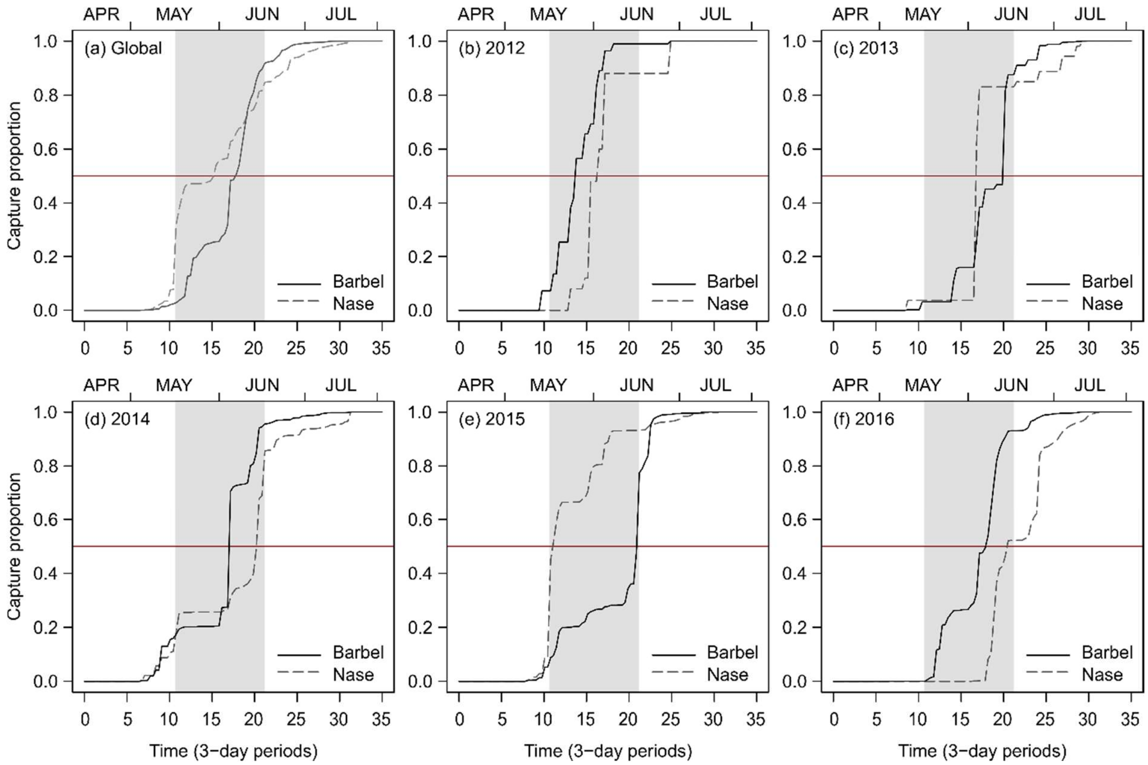

Fig. 4 Migration patterns (KM survival curves) by year and species (horizontal line = 50% of captures; shadow area: fishing closure period, from 15th May to 15th June).

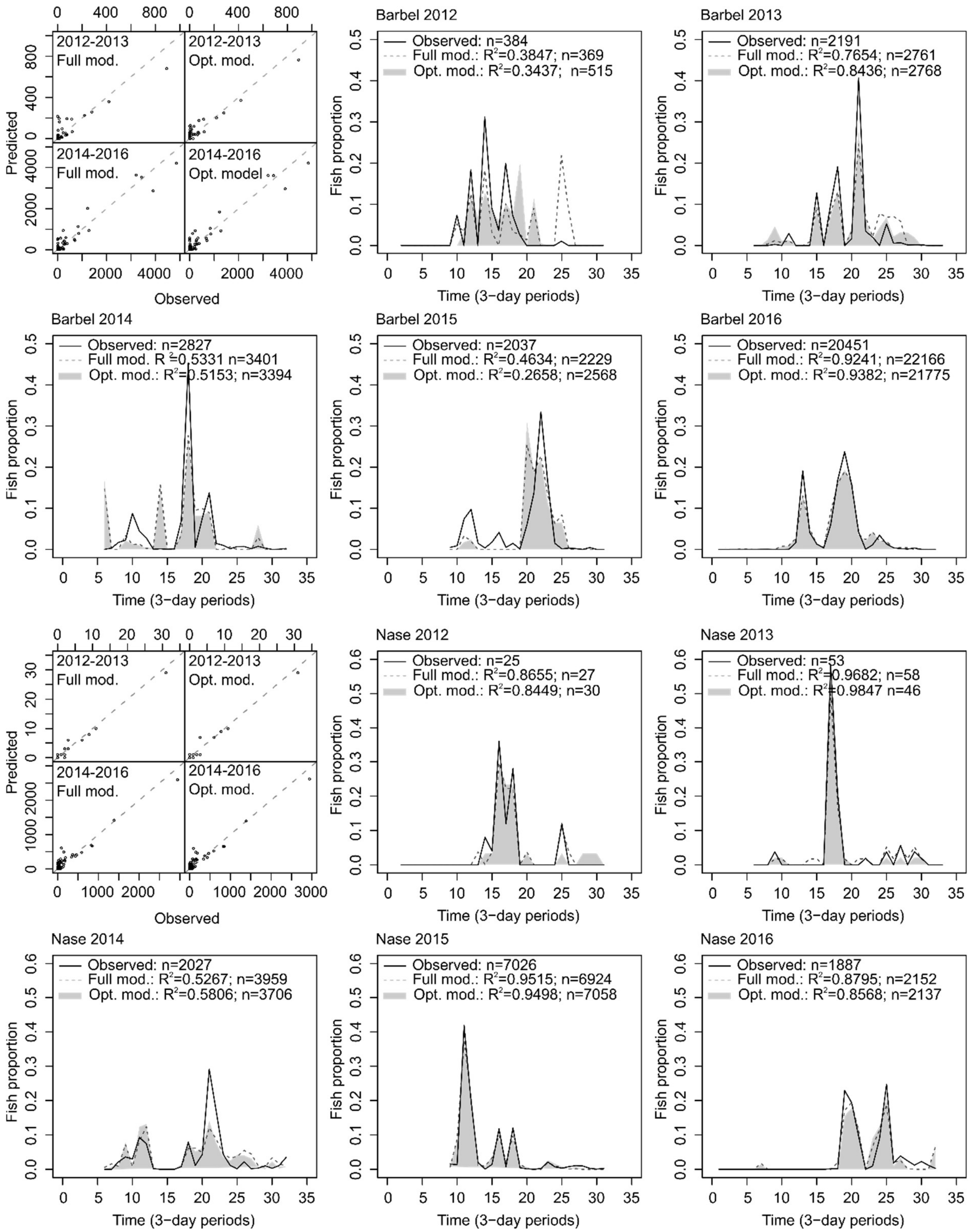

Fig. 5 Evaluation of model performance for both number of captures (n) and migration timing (proportion along time): comparison among the observed fish proportion in time t, the predicted with the full model and the predicted with the optimized (after variable reduction) model.

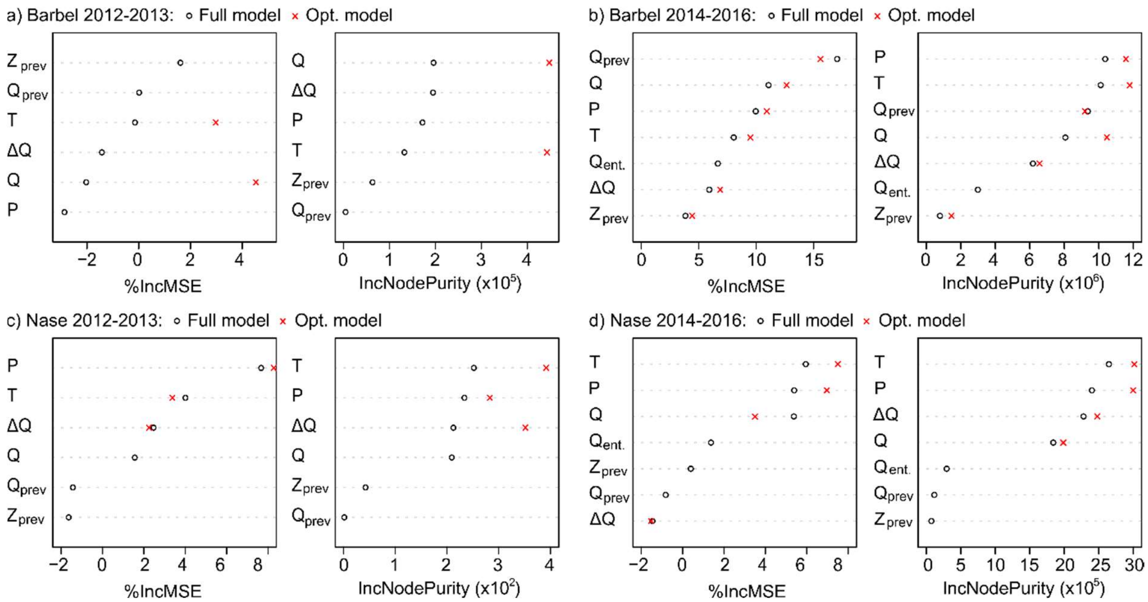

Fig. 6 Variable importance in terms of (1) increase in the mean squared error of predictions (%IncMSE), which represents how much the model fit decreases when a variable drops of the model and (2) increase in node purity (IncNodePurity), which measures the quality of a split (reduction in the sum of squared errors) (for both, the higher number, the more important) (T = water temperature; Q = river discharge; P = photoperiod; Z = reservoir level).

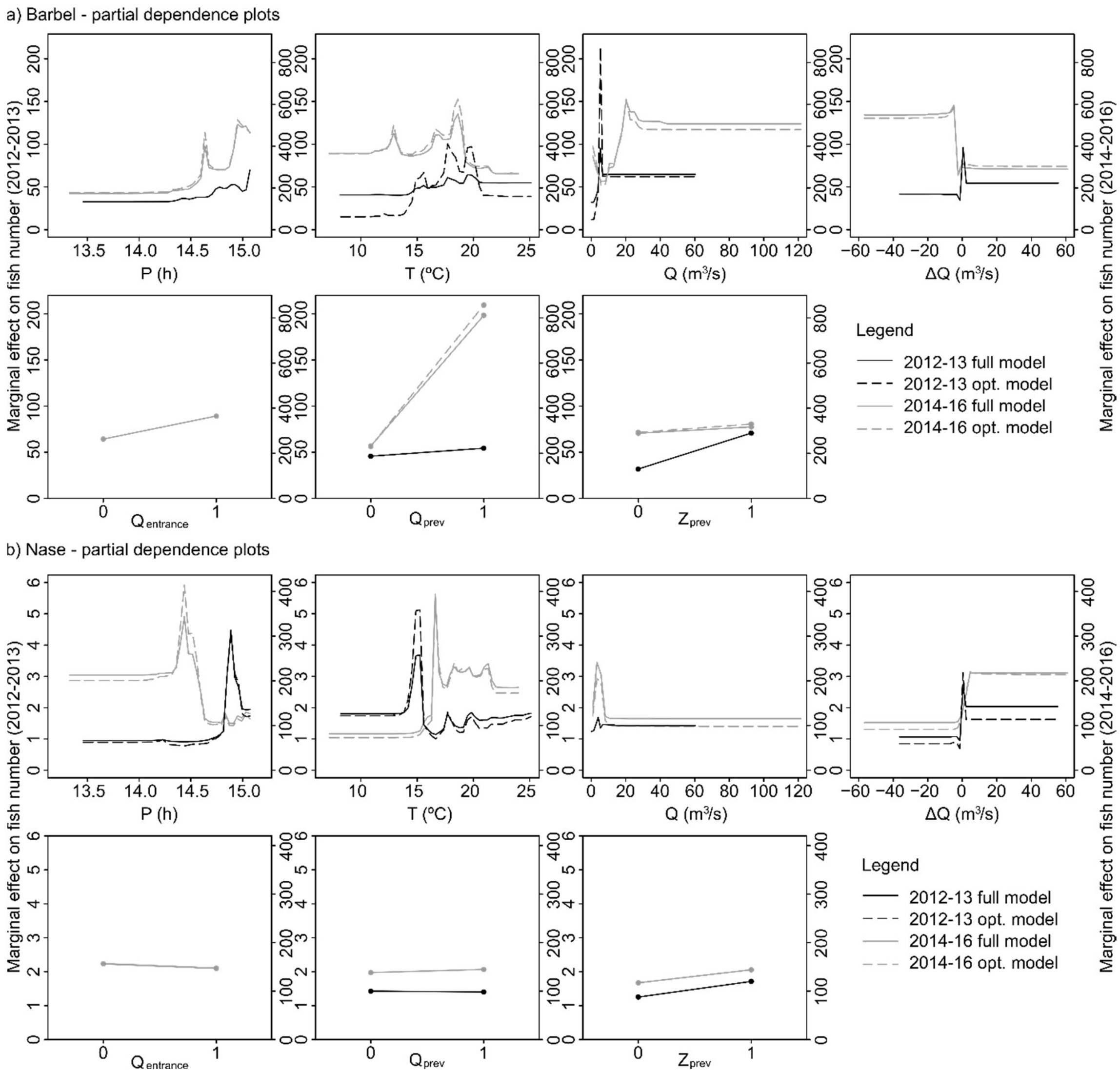

Fig. 7 Partial dependence plots to characterize the marginal effect of a variable in the model (i.e. the impact that a unit change in one of the predictor variables has on the outcome variable while all other variables remain constant).

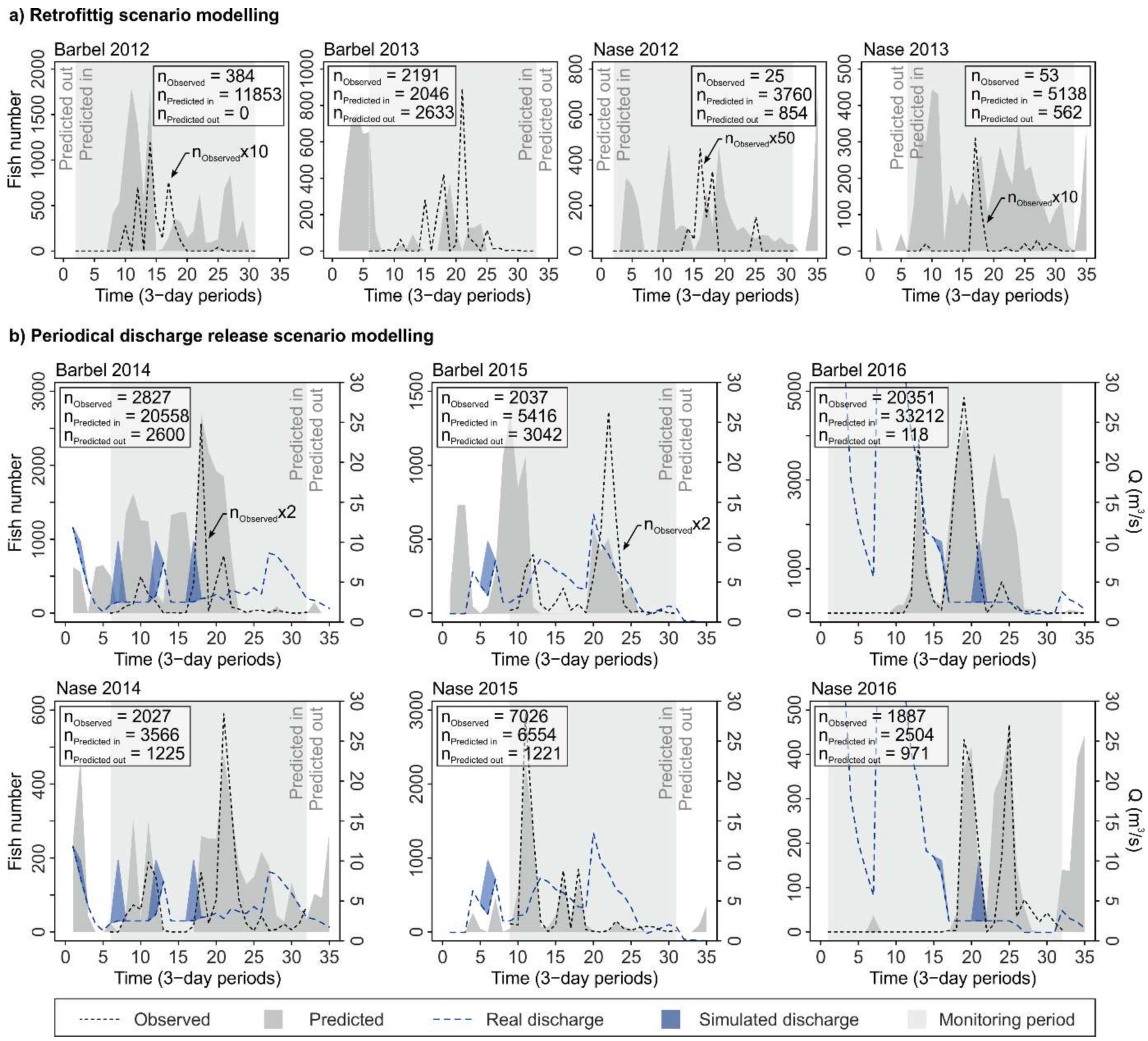

Fig. 8 Simulated scenarios with full models. (a) 2012-2013 environmental data but considering the fishway improvements, attraction weir and bypass in Cespedosa weir. (b) 2014-2016 release of 10 m^3/s of environmental flow every 15 days (arrows indicate the simulated discharge releases). Number (n) of predicted inside (in) and outside (out) of the monitoring period (shadow area). It must be noted that to improve the illustration, different y-axis ranges have been used between graphs, and number of observed fish has been scaled in some of the graphs (i.e. $n_{observed}$ x factor).