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Generalized additive models to predict adult and young brown trout (*Salmo trutta* Linnaeus, 1758) densities in Mediterranean rivers

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Summary

Habitat suitability models (HSM) are concerned with the abundance or distribution of species as a consequence of interactions with the physical environment. Generalized Additive Models (GAMs) were used to model brown trout (*Salmo trutta* L.) density as a function of environmental variables at the scale of river reach and hydromorphological units (HMU) in the Júcar River Basin (Eastern Spain). The data representing trout density after 4 years of observation (2003-2006) were split into two categories, young (<2 years) and adult (≥ 2 years), for modelling independently. The environmental descriptors at reach-scale described the geographical position, hydrological conditions, proportions and diversity of habitats. At the scale of HMUs (pool, glide, riffle or rapid), habitat descriptors representing dimensions, substrate, cover and velocity were used. The best and parsimonious GAM for each category was selected after the comprehensive trial of all of the possible combinations of input variables. The models explained 61% (adult) and 75% (young) of the variability of the data (R^2adj). The results demonstrated the relevance of mean width, mean depth, cover index, mean velocity and slope for adult brown trout. Young trout densities were mainly related to maximum depth, cover index, mean velocity, elevation, average distance between rapids and number of slow water HMUs. This article shows the relevance of considering geographical and habitat-related requirements at different scales to describe the patterns of trout density. Furthermore, the importance of considering non-linear relationships with habitat variables was demonstrated. The results are useful for environmental managers designing effective and science-based restoration measures, which may result in a more efficient management of brown trout populations.

Introduction

Over the past decades, ecological models have increasingly been applied to guide conservation and management decisions related to fish species. Models range from individual to population levels and cover diverse aspects such as age structure of the populations, natural and fishing mortality, size of the spawning stock biomass and recruitment patterns as well as growth rate, gene flow, habitat quality and spatial distribution patterns (for a synthesis about ecological modelling literature on stream fish, see Frank et al., 2011). Among the diversity of approaches, habitat suitability models (HSM) are statistical models included within the species distribution models that analyze the relationships between species and their habitats. Studies of fish habitat selection have been extended to the prediction of distribution and abundance (annual summer densities estimated for each age class), in order to understand how they are influenced by the spatiotemporal habitat heterogeneity (Lobón-Cerviá, 2007; Ayllón et al., 2013). HSM have used hydraulic variables (e.g. velocity, depth, substrate) measured at different spatial scales. Commonly used scales include micro, meso and macro-scale which approximately correspond to one or a few squared meters, tens of meters, or an entire catchment area respectively (Bovee et al., 1998).

Initially, HSM for fish were developed at the micro-scale, using an univariate approach based on the relationship between a single variable and its suitability (Bovee, 1982; Bovee et al., 1998). The most common variables were not only hydraulic ones but also cover (e.g. vegetation, undercut banks or log jams). These particular variables were demonstrated to be relevant for fish habitat selection and fish densities (Bovee, 1986; Gibson, 1993), especially for salmonid fish but also for cyprinids (Grossman and De Sostoa, 1994; Martínez-Capel et al., 2009). There are several methods to generate habitat suitability indices for a single variable, but the continuous univariate habitat suitability curves are by far the most common approach in studies involving the physical habitat simulation (Payne and Allen, 2009). However, several authors have suggested that considering each variable independently may be questionable, because it could induce a bias as a result of overlooking possible interactions between variables (Orth and Maughan, 1982; Lambert and Hanson, 1989). To deal with this limitation, the multivariate approach has increased in popularity among researchers (De Pauw et al., 2006). Also, a wide array of techniques have been applied in micro-scale habitat suitability models, such as Logistic Regression (Hayes and Jowett, 1994), Fuzzy Logic (Muñoz-Mas et al., 2012) and Artificial Neural Networks (Brosse and Lek, 2000). In many cases the distribution of the environmental variables violates the assumptions of normality, linearity, independence and homoscedasticity, typical of the popular linear regressions models. Therefore, models that incorporate non-linear behaviours could be more advisable and more realistic for many applications (Venables and Dichmont, 2004). The development of advanced techniques in the machine learning area has allowed the creation of predictive models with the ability to identify non-linear relationships and greater power for explaining and predicting ecological patterns (Olden et al., 2008; Olaya-Marín et al., 2012).

At a larger scale, macro-scale HSM analyze the abiotic factors controlling the spatial patterns of species distributions in river networks, catchments or river basins. This approach has been successfully applied using several techniques, including Generalized Linear Models (Anlauf et al., 2011), Multivariate Adaptive Regression Splines (Leathwick et al., 2005) and Artificial Neural Networks (Olaya-Marín et al., 2012). These studies combined variables derived from several sources and applied different techniques to reveal potentially suitable areas for the target species (Fukuda et al., 2013). However, there is some evidence suggesting that the consideration of micro and macro-scale variables in independent studies is not enough to cover all the variability involving the prediction of fish habitat suitability (Bdour et al., 2004). Additionally, models based on multiple spatial scales usually outperform single-scale analysis (Olden et al., 2006).

Therefore, a promising approach is the development of cross-scale models including the meso-scale as a relevant component. In the modelling of fish species distribution, the meso-scale resolution can be used to capture the confounded effect of biotic and abiotic environmental variables (Vezza et al., 2012) by focusing on the interaction of aquatic species with the spatial arrangement of habitat variables (Addicott et al., 1987). This approach can rely on the concept of Functional Habitat developed by Kemp et al. (1999). The meso-scale was demonstrated to perform well in describing the relationship between fish species distribution or densities and habitat features, such as cover or migration barriers (Fausch et al., 2002; Costa et al., 2012). More recent studies have demonstrated the value of cross-scale investigations in linking fish ecology, flow and physical habitat variability but considering the meso-scale as the central frame (Gosselin et al., 2010; Gosselin et al., 2012).

Some of the aforementioned approaches have been applied to model salmonids distribution, involving several techniques and scales. In the context of Mediterranean rivers at the microhabitat scale, the variables of mean velocity, depth and substrate have been evaluated for the establishment of habitat suitability curves (Ayllón et al., 2009; Muñoz-Mas et al., 2012). At the macrohabitat level, Filipe et al. (2013) have forecasted distribution shifts of brown trout in Pyrenean rivers based on environmental predictor variables, such as mean annual temperature and precipitation. At mesohabitat scale, habitat suitability criteria for mean velocity, depth, substrate and cover have been developed on data collected by HMU (Gortázar et al., 2011; Mouton et al., 2011).

Herein, we present HSM for brown trout in four rivers of Eastern Spain. The ecological importance of these native trout populations lies in their adaptation to Mediterranean conditions. These conditions are characterized by the marked seasonality in climate events, intermittent periods of torrential rains and droughts, and high inter and intra-annual flow variation (Gasith and Resh, 1999; Baeza et al., 2005). In the long term these populations are declining because of the habitat degradation, flow regulation, river pollution, overfishing, inter-specific competition with exotic species and introduction of foreign trout genes as a result of stocking (Almodóvar et al., 2006; Sánchez-Montoya et al., 2009; Maceda-Veiga, 2013). Furthermore, studies about Mediterranean brown trout demonstrate a lack of information about the regional patterns in the habitat selection as well as the structure, distribution and abundance of their populations (Alcaraz-Hernández et al., 2007) which are influenced by a large number of environmental factors. Some of those factors are the geological history of the area (Machordom et al., 2000), habitat availability (Rincón and Lobón-Cerviá, 1993; Ayllón et al., 2009), hydrological variability (Lobón-Cerviá, 2009; Nicola et al., 2009), global warming (Almodóvar et al., 2012), accessibility and availability of food (Sánchez-Hernández et al., 2011a), and intra or inter-specific relationships (Sánchez-Hernández and Cobo, 2012).

In four Mediterranean rivers, diverse variables of the physical habitat at different scales were considered to predict the abundance of native brown trout. The objectives of this research were: i. to generate predictive Generalized Additive Models for brown trout density in two age groups, independently; ii. to investigate the main factors of the physical habitat which control trout density at the reach scale and meso-scale in Mediterranean rivers; and iii. to compare the performance of Generalized Linear Models and Generalized Additive Models in the modelling of trout density.

Materials and methods

Study area

The field surveys were carried out in summer seasons from 2003 to 2006 in four Mediterranean rivers (Ebrón, Vallanca, Villahermosa and Palancia) of the Júcar River Basin District. All four are within the Valencian Region (Eastern Spain), where brown trout populations are resident and dominant in the fish community (Fig. 1). The study sites were located in unregulated sections of the headwaters (elevations greater than 600 m above sea level) with a Strahler order from 2 to 3. The catchment areas ranged from 123 to 268 km^2 and were dominated by carbonated rocks (pH of 7.9 ± 0.2), favouring the aggregation of the substrate particles and producing an appreciable carbonate layer in some reaches.

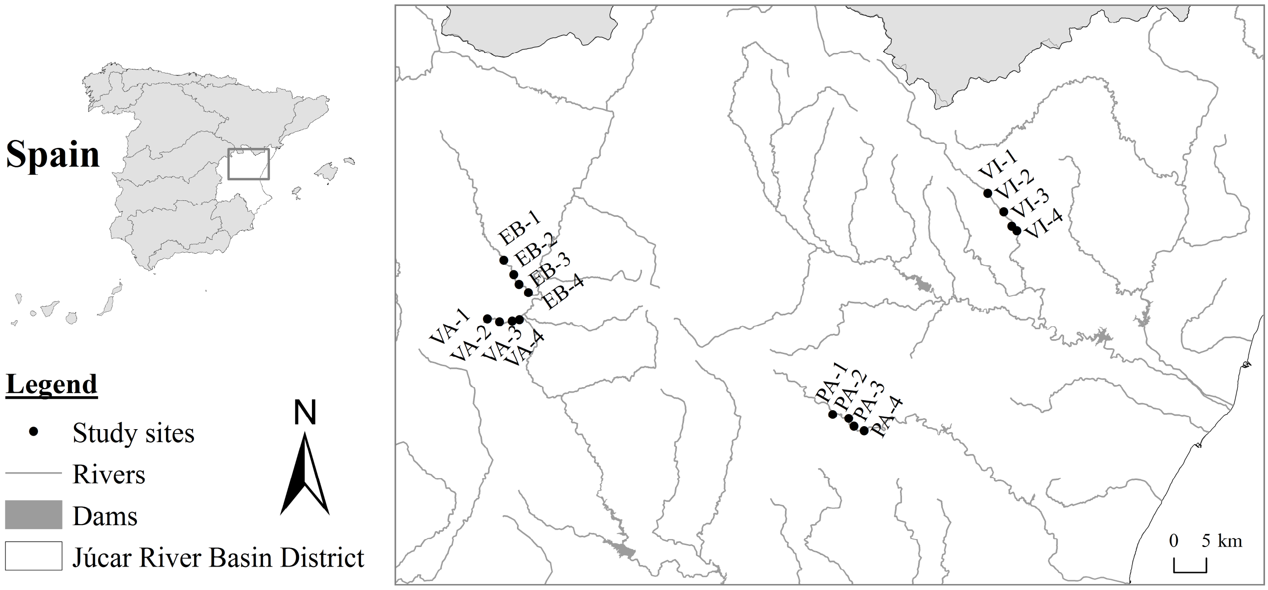

Fig. 1. Location of the study areas in the Ebrón (EB), Vallanca (VA), Palancia (PA) and Villahermosa (VI) Rivers, within the Júcar River Basin District (Eastern Spain). The study sites were located in unregulated sections of the headwaters. The elevations at each of the sites (from 1 to 4) are: 880, 792, 763 and 743 m asl. in the EB; 968, 890, 752 and 718 m asl. in the VA; 769, 688, 655 and 627 m asl. in the PA, and 728, 647, 621 and 605 m asl. in the VI. The catchment areas ranged from 123 to 268 km^2.

The climate is typically Mediterranean, with rainfall concentrated at the end of winter and the beginning of spring resulting in low flows during the summer. The largest inter-annual variation occurs in January and March. The average annual rainfall slightly varies between 442 mm and 583 mm. However, the mean annual flows vary from 0.26 to 1.13 m^3 s^{-1}. The mean annual water temperature is very homogeneous in the four rivers. Water temperature oscillates between 12 and 14ºC in winter, with minimum temperatures usually greater than 5ºC, while in summer maximum temperatures do not usually exceed 20ºC. The selected reaches are mountainous, with small average width (2.51-5.66 m), average depth (0.26-0.49 m) and high average slope (23.0-13.6 m km^{-1}). A detailed environmental description of the reaches was included in Alcaraz-Hernández et al. (2011) and Mouton et al. (2011).

Study design

Four reaches were selected in each river where brown trout are usually present. Data from two reaches were collected in each of the Ebrón, Vallanca and Villahermosa Rivers during the first year (2003), whereas four reaches were surveyed in each of the four rivers during the following years (2004-2006). Years 2005 and

2006 suffered intense drought; then a few of the headwater reaches in the Vallanca and Villahermosa Rivers were dried, thus the survey did not take place (empty cells under 2005 and 2006 in Table 3).

Habitat data acquisition

Twenty three environmental variables were collected and used in the development of density models for brown trout (Table 1). The environmental variables corresponded to different spatial scales, reach scale and HMU or meso-scale. The reach-scale variables included, elevation above sea level (ELE, m) and mean slope of the study reach (SLO, m m^{-1}); these were measured using a geographic information system (ArcGIS™ 9.3.1). Additionally, spring flow (FSP, m^3 s^{-1}) and annual flow (FAN, m^3 s^{-1}) were provided by the Júcar River Basin Authority. The HMU data were assessed in every reach using an adapted version of the BVET (Hankin and Reeves, 1988; Dolloff et al., 1993). Firstly, each reach was visually stratified according to its different biotopes, mesohabitats or HMUs using the BVET protocol. Measurement of their main physical characteristics such as length, width, depth and substrate (instead of a visual estimation) allowed them to be classified into four types: pool, glide, riffle and rapid (Alcaraz-Hernández et al., 2011). These characteristics were quantified in reaches 300 m long. In this sense, several authors have recommended a similar sampling site length for habitat characterization (Leopold et al., 1964; Meador et al., 1993). These data were used to obtain other variables such as the number of slow (NSL, slow habitats m^{-1}; i.e. pool and glide) and fast HMU (NFA, fast habitats m^{-1}; i.e. riffle and rapid). The diversity of habitat types was calculated using the Shannon-Weaver index (DIV, 0-1) and the average distance between rapids (DBR, m) or average length between pairs of consecutive fast HMU were also considered.

Table 1. Description of the variables assessed at reach scale and meso-scale (hydromorphological units; HMU) at the Ebrón, Vallanca, Palancia and Villahermosa Rivers (Júcar River Basin District, Eastern Spain).

Spatial scale	Variable	Code	Description (units)
Reach	Altitude	ELE	Elevation above sea level (m)
	Slope	SLO	Mean slope of the study reach (m m^{-1})
	Spring flow	FSP	Mean spring flow rate (m^3 s^{-1})
	Annual flow	FAN	Mean annual flow rate (m^3 s^{-1})
	Number of slow habitats	NSL	Number of slow habitats in the reach (slow habitats m^{-1})
	Number of fast habitats	NFA	Number of fast habitats in the reach (fast habitats m^{-1})
	Diversity habitat index	DIV	Shannon-Weaver diversity index of habitat types (0-1)
	Distance between rapids	DBR	Average distance between rapids (m)
HMU	Mean length	LEN	Mean length of surface water of the HMU (m)
	Mean width	WID	Mean width of surface water of the HMU (m)
	Mean depth	DME	Mean depth of the HMU (m)
	Maximum depth	DMA	Maximum depth of the HMU (m)
	Area	ARE	Area of each HMU (m^2)
	Volume	VOL	Volume of the HMU (m^3)
	Shading	SHA	Shading over the HMU (%)
	Embeddedness	FCO	Riverbed covered by fine materials (%)
	Coarse substrate	SCO	Coarse substrate with diameter > 256 mm (%)
	Medium substrate	SME	Medium substrate with diameter 2-256 mm (%)
	Fine substrate	SFI	Fine substrate with diameter < 2 mm (%)
	Substrate index	SIN	Substrate index (3, sand; 8, bed rock)
	Velocity	VEL	Velocity of the HMU (m s^{-1})
	Woody debris	WOD	Number of woody debris on the reach (woody m^{-1})
	Cover index	CIN	Refuge index (0, no refuge; 10, excellent)

The main physical characteristics of each HMU were measured each year at each site as follows. Mean length of the HMU (LEN, m) with measuring tape. Mean width of water surface (WID, m) was obtained from three cross-sections corresponding to ¼, ½, and ¾ of the total length of the HMU. Mean depth (DME, m) was calculated from nine points corresponding to measurements taken at each cross-section where width was estimated, and maximum depth (DMA, m) was measured in the corresponding point. These measurements were used to calculate the area of HMU (ARE, m^2) by simplifying its calculation as the product of length and width. Volume of HMU (VOL, m^3) was calculated as the product of length, width and mean depth. Other variables were visually estimated. Shading, was determined as the percentage cover of shade over the channel (SHA, %). The percentage of embeddedness (FCO, %) and substrate (%) were divided into three categories: coarse (SCO, ø > 256 mm), medium (SME, ø 2-256 mm) and fine (SFI, ø < 2 mm). Substrate composition was converted into a single substrate index (SIN) by summing weighted percentages of each substrate type (Jowett et al., 1991). The weights were slightly modified from the original substrate codes of the Instream Flow Incremental Methodology (Bovee, 1982; Mouton et al., 2011) as follows:

SIN = 0.08 x bedrock + 0.07 x boulder + 0.06 x cobble + 0.05 x gravel + 0.04 x fine gravel + 0.03 x sand. In addition, mean velocity in the HMU (VEL, m s^{-1}) was calculated by dividing the gauged flow and the mean cross section area. Density of woody debris (WOD, pieces of wood per m^2) and cover index (CIN, from 0 – no refuge to 10 –excellent) by García de Jalón and Schmidt (1995) were determined. Cover index followed this equation:

$$CIN = Cb + \frac{Cs + Csub + Csv + Cd}{4}$$

where, Cb is the available refuge due to the presence of undercut banks or caves; Cs is the refuge produced by shading; Csub produced by substrate types; Csv produced by submerged vegetation and Cd by the depth of the water column. At five categories of cover, this index assigns scores from zero to five (being 0 no refuge and 5 maximum score) using the recommendations in Table 2. A total of ninety three HMU were sampled, with fifty corresponding to slow water HMU (pools and glides) and forty three to fast water HMU (riffles and rapids).

Table 2. Scores of the cover index (CIN) based on the availability of different cover types: bank shelter (Cb), shading (Cs), river bed substrate (Csub), submerged vegetation (Csv) and depth (Cd).

Score	Cb	Cs (%)	Csub	Csv (%)	Cd (cm)
0	None	0	Rock surface	None	< 15
1	Aerial undercut bank	< 10	Sand	< 1	15-50
2	Submerged undercut	10-25	Fine gravel	1-5	50-80
3	Deep submerged undercut	25-50	Gravel	5-15	80-100
4	Riparian roots	50-75	Cobbles	15-30	100-150
5	Deep undercut and roots	> 75	Boulder	> 30	> 150

Biological data acquisition

During summers of the years 2003-2006, the biological survey took place by electrofishing in each one of the selected HMU, one fast and one slow. The electrofishing equipment consisted of a 950 W electric generator connected to an electric rectifier to get continuous current and select the appropriate voltage. Each HMU was surveyed at least three times without replacement, after placing nets at both extremes of the HMU. The number of captures, in each of the independent size classes (see below) was divided by the sampling area, which ranged from 11 to 399 m^2.

The fork length (mm) and weight (g) of each individual were measured. In addition, scales were extracted from the individuals older than one year to verify the longitudinal-age classification and the length frequency analysis of the captured fish. Two independent scale readers analysed the age and in case of unclear scales the fish was discarded. Trout densities (trout m^{-2}) were calculated using the weighted maximum likelihood of Carle and Strub (1978) and were divided into young (DYO, < 2 years) and adult (DAD, ≥ 2 year) for the data analysis. The age classes 0+ and 1+ were classified into the same category (DYO, < 2 years) because they had disappeared from some reaches as a consequence of extreme events (floods and droughts) that occurred during the years of the study. Therefore, the data corresponding to fry and juvenile brown trout included more zeros than expected. Zero inflated databases can lead to some problems. Firstly, the estimated parameters and standard errors may be biased. Secondly, the excessive number of zeros can cause overdispersion in the statistical analysis with GAMs (Zuur et al., 2009). The values of young and adult brown trout densities by river, reach, HMU and year are shown in Table 3.

Table 3. Young (DYO) and adult (DAD) brown trout densities (trout m^{-2}) recorded by river, reach, hydromorphological unit (HMU) simplified as fast or slow, and year of sampling.

			2003		2004		2005		2006	
River	Reach	HMU	DYO	DAD	DYO	DAD	DYO	DAD	DYO	DAD
Ebrón	1	Fast	0.000	0.010	0.000	0.000	0.000	0.007	0.022	0.000
	1	Slow	0.035	0.013	0.006	0.000	0.019	0.010	0.010	0.010
	2	Fast	-	-	0.031	0.000	0.055	0.000	0.046	0.009
	2	Slow	-	-	0.011	0.000	0.045	0.006	0.028	0.022
	3	Fast	-	-	0.018	0.023	0.226	0.016	0.080	0.101
	3	Slow	-	-	0.017	0.063	0.122	0.041	0.036	0.051
	4	Fast	0.016	0.000	0.000	0.000	0.043	0.000	0.032	0.000
	4	Slow	0.014	0.057	0.014	0.000	0.060	0.000	0.000	0.000
Vallanca	1	Fast	-	-	0.541	0.000	0.000	0.000	0.000	0.000
	1	Slow	-	-	0.237	0.086	0.000	0.000	0.000	0.000
	2	Fast	-	-	0.196	0.071	0.549	0.000	0.068	0.000
	2	Slow	-	-	0.133	0.111	0.461	0.194	0.153	0.017
	3	Fast	0.060	0.012	0.068	0.011	0.505	0.031	0.195	0.020
	3	Slow	0.030	0.005	0.028	0.057	0.335	0.010	0.213	0.015
	4	Fast	0.092	0.092	0.075	0.030	-	-	-	-
	4	Slow	0.063	0.094	0.065	0.131	0.589	0.109	0.817	0.136
Palancia	1	Slow	-	-	0.000	0.000	0.000	0.000	0.000	0.000
	2	Fast	-	-	0.000	0.006	0.013	0.000	0.007	0.000
	2	Slow	-	-	0.000	0.010	0.021	0.017	0.022	0.004
	3	Fast	-	-	0.014	0.000	0.185	0.007	0.014	0.007
	3	Slow	-	-	0.007	0.013	0.066	0.019	0.000	0.030
	4	Fast	-	-	0.021	0.000	0.000	0.017	0.034	0.000
	4	Slow	-	-	0.000	0.000	0.008	0.008	0.000	0.000
Villahermosa	1	Fast	-	-	0.005	0.005	-	-	-	-

1	Slow	0.024	0.000	0.000	0.007	-	-	-	-
2	Fast	-	-	0.018	0.012	-	-	-	-
2	Slow	-	-	0.000	0.062	-	-	-	-
3	Fast	-	-	0.260	0.023	0.223	0.039	0.138	0.000
3	Slow	-	-	0.052	0.071	0.143	0.075	0.101	0.060
4	Fast	-	-	0.037	0.008	0.136	0.010	0.108	0.000
4	Slow	0.073	0.030	0.022	0.067	0.029	0.066	0.036	0.027

Data analysis

Generalized Additive Models (GAMs) were used to model brown trout density, as they are useful to deal with non-linear relationships between species abundance and environmental variables. Additionally, the models are additive, hence they can examine the effect of several independent variables on the dependent variable (James et al., 2013). GAMs have shown an acceptable or good performance in modelling habitat-fish relations at the meso-scale in previous studies (Costa et al., 2012). Furthermore, this technique allows the modeller to include normal and non-normal variables in the model. GAMs follow the next equation:

$$E(y) = \beta_0 + s_1(x_1) + s_2(x_2) + s_3(x_3) + \ldots$$

where y represents the response variable, β_0 the constant parameter of the model, s_1, s_2 and s_3 the smoothing functions and x_1, x_2 and x_3 the predictive variables (Wood, 2001). This model adjusts a response to the aggregation of each variable modelled through the application of multiple constrained splines, providing a smooth response according to each of the involved variables. Therefore, the non-parametric transformation of the predictive variables was implemented using a smoothing function. The choice of the degrees of freedom of the smoothing function (*edf*) was carried out by applying a penalized spline regression (Wood, 2006).

A pre-processing procedure of the entire database was executed in order to discard correlations and collinearity among variables in the models, according to Zuur et al. (2009). Firstly, all the combinations of variables were generated (of 2, 3, 4 variables, etc.) and the combinations where any relevant Spearman's Rho was observed by pairs (Rho > 0.5) were discarded for the modelling. In addition, the Variance Inflation Factor (VIF) was used to check collinearities among the predictive variables, and variables with VIF > 5 were discarded (Zuur et al., 2009). Finally, to select the variables involved in the generation of the GAM, young and adult brown trout regression models were iteratively calculated by trying all of the possible combinations of datasets including variables in different sets, comprising of two to eight variables. Each combination met the aforementioned requirements (non-correlation and non-collinearity of variables).

Between the function families tested, quasipoisson distribution function was selected for modelling trout density and an offset was introduced (offset = Log ARE) in accordance with other studies with a similar modeling procedure (Nislow et al., 2011). The number of knots in the splines was limited to four. The signification of the *F* test was used to discard any combination where any of the variables did not have a signification smaller than 0.1. None of the variables were transformed for the modelling process.

The R^2*-adjusted* (hereafter R^2adj) was the performance criterion selected to choose the best model with the least number of variables (Aertsen et al., 2010). The model with the best performance from each iteration was the one finally selected; in this case the model with the largest R^2adj for each number of variables was retained. The selection of the final model was based on the marginal improvement ratio of the R^2adj. No more variables were added when the marginal improvement ratio of R^2adj was less than 10 %. There are other statistics to select the subsets of predictors in order to improve prediction accuracy and model interpretability, such as Cp, AIC or BIC. These three and R^2adj are based on penalizing the residual sum of square by the number of observations and predictor variables. The statistics R^2adj, Cp, AIC and BIC are reliable in scenarios where the sample size is very large and their results are asymptotic (James et al., 2013). In this study the sample size was relatively small but as the asymptote of R^2adj is always 1, it was decided to use R^2adj. In addition, Generalized Cross Validation score (GCV), visual inspection of the response of each variable and its error distribution were considered in the selection of the best GAMs (Wood, 2006; Pierce et al., 2007). The residuals were plotted against the predictive variables to investigate the violation of the assumption of independence.

Finally, generalized linear models (GLMs) were calculated, with the same procedure used to generate the GAMs. Specifically, the models were generated with each of all the possible combinations of variables, with similar requirements (non-correlation and non-collinearity), using the same function family and the same performance criterion R^2adj. The entire process was carried out with the functions gam and glm of the packages *mgcv* (Wood, 2006) and *stats* developed in R 2.15 for Windows (R Development Core Team, 2010).

The models were generated for the entire data set including all four rivers, as the data collection covered a relatively small area in the headwaters of the Júcar River Basin District, and multi-site models are very interesting for supporting habitat management and river restoration (Lamouroux et al., 1999). Previous studies have demonstrated that multi-site or regional models do not necessarily reflect broad ranges of suitable conditions (Lamouroux et al., 1999). Several studies have succeeded in developing regional models (Hayes and Jowett, 1994; Lamouroux et al., 1999; Nykänen and Huusko, 2004). However, several models at catchment scale showed difficulties to be transferred, questioning its generalization ability (Fukuda, 2010). Due to the multiple factors affecting fish habitat selection, it is generally recommended the generation of site-specific models of habitat suitability, especially for the application of physical habitat modelling and environmental flows assessments (Moyle and Baltz, 1985; Bovee et al., 1998).

Results

The process to combine variables and generate GAMs resulted in a total of 59009 models for GAM as well as for GLM. A total of 210 composed of two variables, 1149 of three variables, 4009 of four, 9383 of five, 15069 of six, 16667 of seven and 12522 of eight variables. All these models met the selection criteria (non-correlation and non-collinearity among variables).

Figure 2 illustrates the R^2adj of the best model at each iteration, given the number of variables in the training dataset for the GAM as well as the marginal improvement ratio. Adult density presented a monotonic increment of the performance criteria as the number of variables included increased. However, the young trout presented a maximum with a decrease from the six-variable model to the seven-variable model. This decrease was due to the presence of an undesired combination of variables, as explained herein. The seven-variable model included among others, the number of slow (NSL) and fast (NFA) habitats, and the Shannon-Weaver diversity habitat index (DIV, 0-1). That model was rejected because the former (six-variable model) indirectly included the concept of diversity, as it included NSL and NFA. Therefore, the model with six variables was selected for young brown trout. For the adult trout, the 10% of marginal improvement ratio was used to finally select the best model with five variables. Regarding GLM, the models for adult trout showed an R^2adj equal to 18% with five variables and 15% with six, whereas the models for young trout showed an R^2adj of 23% with six variables and 19% with seven. The R^2adj penalizes the number of variables, thus the reductions of performance are possible with more variables.

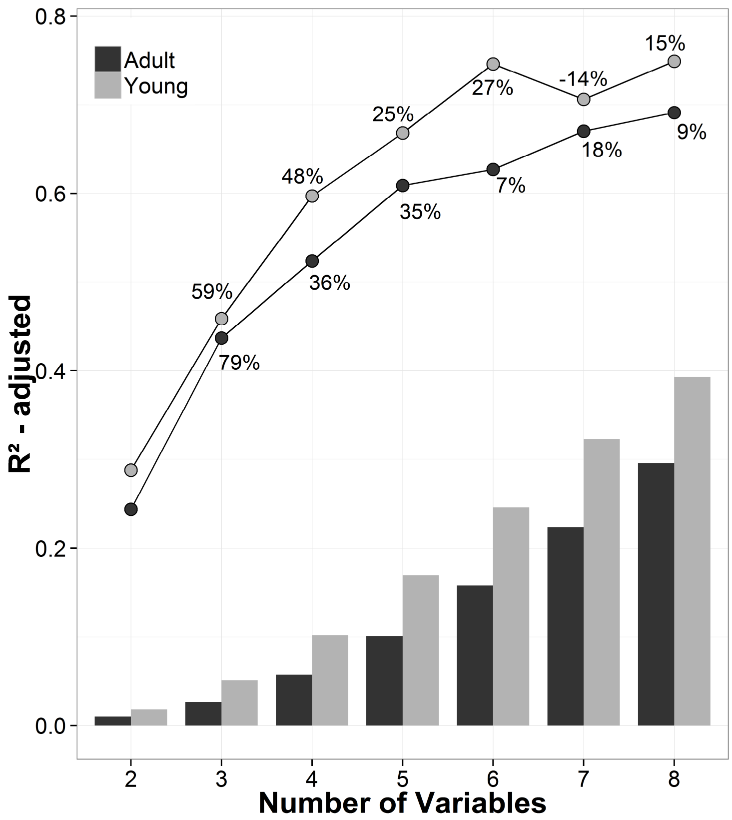

Fig. 2. Variation of the performance criterion (*R^2-adjusted; dots*) of the best model at each iteration (bars) with increasing number of variables in the training dataset of the Generalized Additive Model (GAM) based on 4 years of sampling (2003-2006). The marginal improvement ratio corresponds to the marginal percentage of improvement in relation to the best previous model (dots). The *R^2-adjusted* of the best two-variable model was used as a base value. The best model for adult trout included five variables (mean depth, velocity, cover index, mean width and slope), and six variables for young trout (maximum depth, velocity, cover index, elevation, distance between rapids and number of slow habitats).

The results of the best GAM (Table 4) indicated that adult trout density was successfully explained by mean width (WID), mean depth (DME), cover index (CIN), velocity (VEL) and slope (SLO). The model for young trout included maximum depth (DMA), CIN, VEL, elevation (ELE), distance between rapids (DBR) and NSL. The models for adult and young trout density explained 61% and 75% of the variability of the data (R^2adj), respectively. Both models showed non-linear relationships with some of the explanatory variables, with effective degrees of freedom larger than 1 (*edf* > 1). There was a linear relationship between adult trout density and one predictor variable (VEL) as well as between young trout and DMA. In addition, most of the variables were highly significant ($p < 0.001$), except CIN and VEL in the adult model and CIN in the young trout model (Table 4). Relevant statistical differences between GAMs and GLMs were noted. GLM models for adult and young trout density with the same number of variables as the GAM models, explained 18% and 23% of the data variability, correspondingly. The adult model comprised the following variables: mean length (LEN), WID, DME, VEL and DBR. While the young model was comprised of: WID, DME, coarse substrate (SCO), density of woody debris (WOD), VEL and NFA.

Table 4. Summary of the best Generalized Additive Models (GAMs) for adult and young brown trout density. The predictive variables finally selected by the models were mean width (WID), mean depth (DME), cover index (CIN), mean velocity (VEL) and slope (SLO) for adult brown trout; and maximum depth (DMA), cover index (CIN), mean velocity (VEL), elevation (ELE), distance between rapids (DBR) and number of slow habitats (NSL) for young brown trout.

Age group	Predictive variable	GAM			
		R^2-adjusted	*edf*	*P-value*	*F*
Adult	WID	0.61	2.85	< 0.001	42.102
	DME		2.67	< 0.001	7.244
	CIN		2.20	0.035	3.180
	VEL		1.00	0.002	9.917
	SLO		2.96	< 0.001	5.822
Young	DMA	0.75	1.00	< 0.001	17.452
	CIN		2.45	0.052	4.259
	VEL		2.90	< 0.001	10.289
	ELE		2.51	< 0.001	7.506
	DBR		2.83	< 0.001	11.197
	NSL		3.00	< 0.001	21.807

The partial effects of each individual predictor variable on adult trout density (DAD) at the meso-scale (leaving other parameters fixed) are shown in Fig. 3. DAD increased with DME in an approximately linear fashion from 0 to 0.4 m and decreased slowly with increasing DME, thus showing approximately a bell-shaped effect. A less marked bell-shaped effect was shown by CIN and SLO. DAD increased slightly with CIN when CIN < 5 and decreased when CIN > 5. Slope influenced DAD positively, with an optimum at 0.015 m m^{-1} and decreasing thereafter. DAD slightly increased with SLO when slopes were over 0.04 m m^{-1}, presenting another peak. However, VEL and WID demonstrated an opposite trend. Adult density slowly decreased with VEL, decreased with WID from 0 to 5 m in approximately linearly, and remained almost invariable for WID > 5 m.

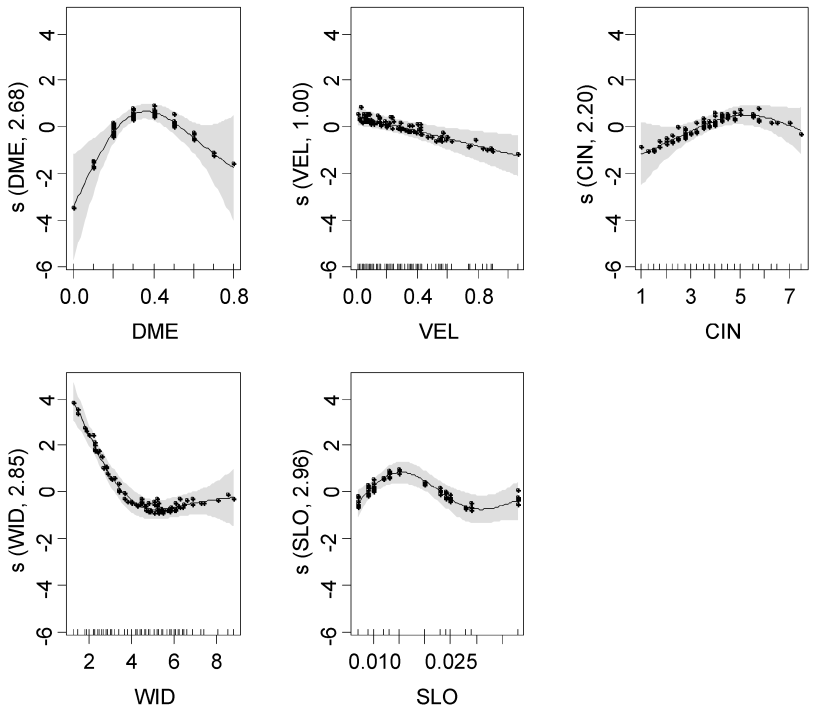

Fig 3. Partial effects of mean depth (DME), velocity (VEL), cover index (CIN), mean width (WID) and slope (SLO) in adult brown trout densities modelled using Generalized Additive Models (GAMs) based on 4 years of sampling (2003-2006). The solid black line is the general trend of the effect of the considered variable on the mean adult trout density, while the shaded areas represent 95% confidential intervals. The numbers in the labels of y-axis denote the effective degrees of freedom. Training data are shown as black points.

In Fig. 4 the partial effects of young trout density (DYO) are illustrated, DYO decreased linearly as DMA increased. The response demonstrated inverted s-shaped curves for VEL and DBR with a positive effect at low values, and a central range with an invariable effect and a negative effect at higher values (over 0.8 m s^{-1} for VEL and 125 m for DBR). DYO was invariable with CIN from 0 to 4 points and increased slightly thereafter. A similar partial effect was shown by ELE. Specifically, DYO exhibited similar values from 600 to 750, increasing slightly thereafter. Alternatively, a normal distribution was observed when DYO was plotted against NSL. With DYO increasing slowly with low NSL values, being optimum at 0.05 and tailing off linearly with larger NSL values. Finally, Fig. 5 depicts the comparison between observed and predicted values of DYO and DAD as assessed by the GAMs (using five variables for adult trout and six variables for young trout). As depicted, differences between observed and predicted values were small with Rho values of 0.89 and 0.81 for DYO and DAD, respectively.

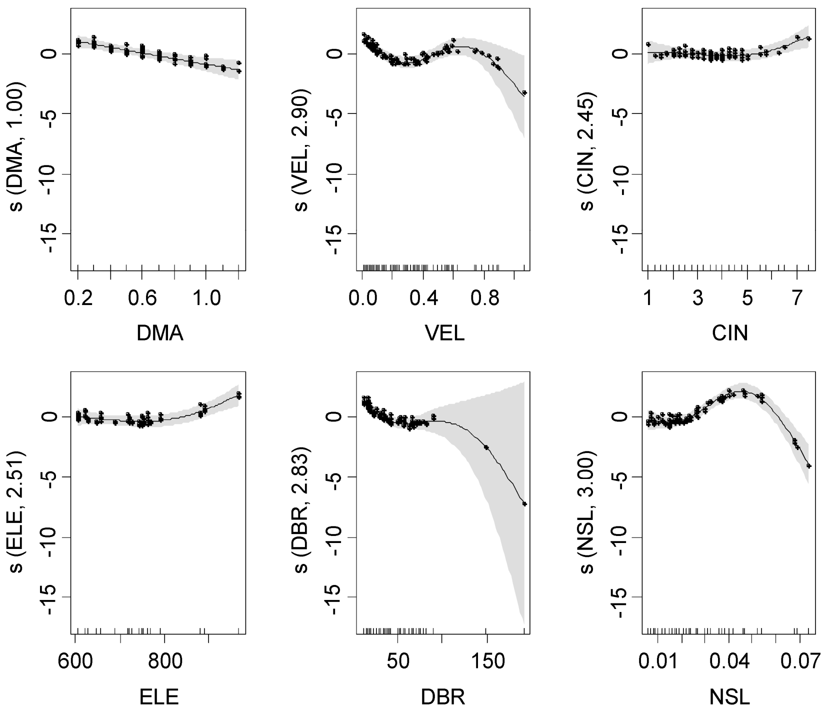

Fig 4. Partial effects of maximum depth (DMA), velocity (VEL), cover index (CIN), elevation (ELE), distance between rapids (DBR) and number of slow habitats (NSL) in young brown trout densities modelled using Generalized Additive Models (GAMs) based on 4 years of sampling (2003-2006). The solid black line is the general trend of the effect of the considered variable on the mean young trout density, while the shaded areas represent 95% confidential intervals. The numbers in the labels of y-axis denote the effective degrees of freedom. Training data are shown as black points.

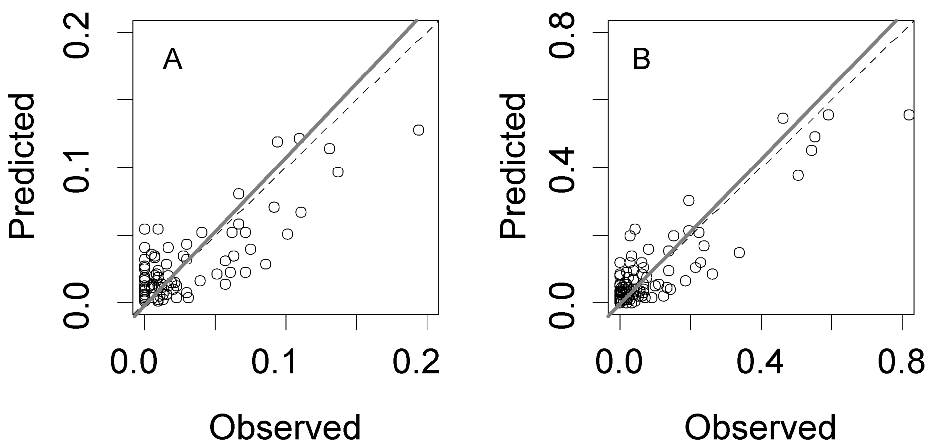

Fig. 5. Observed (x-axis) *versus* predicted (y-axis) values of adult (A) and young (B) brown trout density by the Generalized Additive Models (GAMs). The thick grey lines represent the regression line between observed and predicted, whereas the dotted black lines represent the perfect agreement.

Discussion

The present study provides an appropriate methodology to generate predictive fish density models with GAMs, focusing on the best subset selection. The exhaustive selection of variables led to the production of optimal models, with performance (R^2adj) of 0.61 and 0.75 for adult and young, respectively. These values can be considered similar to those obtained in previous studies based on multivariate approaches (Ayllón et al., 2010; Vezza et al., 2012; Ayllón et al., 2013), and equivalent or superior (specifically for young trout) to the study performed with random forests and fuzzy logic upon the same Valencian rivers (Mouton et al., 2011). Although the present study selected more predictive variables than the aforementioned studies, it is remarkable that we dealt with a problem that is considered as a further degree in complexity, such as fish density. While previous studies in Mediterranean rivers afforded the problem of presence/absence or classification. Interest in fish density models has recently increased because they may provide more gradual information on species habitat selection (Fukuda et al., 2011), thus the present approach is a step forward in the research on Mediterranean brown trout.

To our knowledge, this is the first study generating all the possible models combining the predictor variables (from 2 to 8 variables) and analysing the best parsimonious GAM, instead of using step-forward or step-backward algorithms of variables selection. The comprehensive trial of all of the possible combinations of input variables and selection of the best parsimonious model after predefined criteria is the only method that is guaranteed to determine the optimal set of input variables (Bonnlander and Weigend, 1996).

The presented methodology was considered computationally affordable and more systematic than previous approaches (Tutz and Binder, 2006), because no preliminary assumptions must be done and the systematic search provides us with the best combination of predictors for the optimal model. In the future, a new sample design will be necessary to acquire enough data to develop density models by age classes. Another potential limitation in this study was the over-fitting, which was limited by setting a maximum of four knots in the models due to the limited number of observations.

Moreover, the data-driven procedure to generate GLM resulted in models with a limited predictive power, thus other techniques of higher complexity are recommended (e.g. GAM). This result has been confirmed in other studies on fish habitat requirements (Olden and Jackson, 2002; Ahmadi-Nedushan et al., 2006; Armitage and Ober, 2010; Vezza et al., 2014a). Indeed, GAMs are considered an important methodological step forward in regression analyses because they are a semi-parametric extension of GLM with the only underlying assumption that the functions are additives and the components are smooth (Guisan et al., 2002).

Regarding our second objective, the models for adult and young Mediterranean trout remarked the importance of considering a hierarchical approach for modelling fish-habitat relationships (Armstrong et al., 2003; Olden et al., 2006; Ferreira et al., 2007). A great proportion of the selected variables operate at the reach-scale (slope, elevation, distance between rapids and number of slow habitats), especially for young trout, but there is a considerable improvement in performance with HMU variables (depth, mean velocity, cover).

Four reach-scale predictor variables were selected. Slope was selected for the adult trout density model, whereas elevation, distance between rapids and number of slow habitats were selected for young trout. After examining the results, the optimal slope value for adult trout was around 0.015 m m^{-1}, i.e. reaches characterized by low to moderate gradient. In accordance with these results Filipe et al. (2013) and Ayllón et al. (2010) found that the slope affects the distribution of trout at large scale. Macro-scale topographic variables were important to determine the micro-climate variability present within the study area, thus improving the model predictions.

Elevation can be seen as a surrogate of water temperature, which has been revealed as a key driver of young brown trout distribution. It is expected that higher temperatures predicted for the future would limit the fry growth (Parra et al., 2012) and would lead headwaters to become refuge areas for brown trout (Almodóvar et al., 2012). Young trout responded to the sequence of habitat units, especially with adequate proportion of pools along the reach and short distances between rapids. The resulting partial plots indicated an optimum degree of habitat diversity (Fig. 4). This result supports the studies by Hauer et al. (2011) where young trout occupied shallow waters in pool and run habitat types close to rapids, finding lower velocities, higher water temperatures and appropriate concentrations of dissolved oxygen. As trout density depends on the HMU configuration in the river segment (i.e. proportions and sequence), density models could improve if they were estimated upon combinations of HMU, specifically on density data at the scale of morphologically representative reaches. For example, as the summed abundance at different HMU weighted by habitat-specific densities (Hankin and Reeves, 1988; Rosenfeld, 2003; Hauer et al., 2011).

Three predictor variables were selected at meso-scale, i.e. depth, mean velocity and cover, in accordance with previous studies in Mediterranean rivers (Mouton et al., 2011; Vezza et al., 2012; Vezza et al., 2014b). Regarding water depth, Baran et al. (1997) found a clear segregation by habitat units between fry and adult stages of brown trout, because fry were more frequently detected in riffles and glides, and adults were concentrated in deep habitats. Elso and Giller (2001) found that trout fry utilize faster flowing habitats rather than slower habitats until they reach a certain size, after which they move into pools. This behaviour can been explained by intra-specific competition or territoriality (Elliott, 1990; Elso and Giller, 2001) and the reduction of energy expenses (low energy swimming costs) has been also suggested (Bridcut and Giller, 1995; Railsback and Harvey, 2002).

In Northern Europe, Heggenes et al. (1999) demonstrated that depth is the most important habitat variable for brown trout in small rivers, especially during low flow. Maki-Petäys et al. (1997) observed that in general there is a relation between large salmonid fish and deep habitats, although there are movements of fish towards shallow microhabitats in summer or winter, depending on the habitat availability. Regarding the observed decrease of density in large depths (Fig. 3), it could be produced by the expected reduction in the drift provision; upholding that premise, microhabitat suitability modelling has been recently improved with the consideration of macroinvertebrate drift as an input variable (Hauer et al., 2012).

On the contrary, mean velocity for adult trout showed a negative linear trend (Fig. 3). For young trout there was a negative effect at high velocity, in agreement with a previous microhabitat study in Spain (Ayllón et al., 2013). In comparison with the adult data, the partial plot for young trout demonstrated certain dispersion at higher velocities. The results of the two size classes mostly concur with studies in Mediterranean rivers where velocity curves showed an optimum at low velocity and a decreasing trend (Martínez-Capel et al., 2007; Ayllón et al., 2010; Muñoz-Mas et al., 2012; Ayllón et al., 2013) but a similar discrepancy about the suitability of the null velocity being present. This result it not surprising, because trout fry consume a relevant percentage of invertebrates living on erodible substrate (i.e. faster flowing habitat) whereas adult trout tend to feed on prey available in the water column (Sánchez-Hernández and Cobo, 2012). The differences between age groups could mean an interaction of velocity with other variables, e.g. substrate, because coarse substrate may produce velocity shelters at higher velocities and suitable niches for feeding, which can be more relevant for fry in smaller rivers with a medium-high gradient.

The adult trout density presented a maximum positive effect at intermediate values of cover index, decreasing where cover is scarce or extremely abundant. However, the effect of cover on young trout seems to be of very little importance. Some studies at the micro-scale indicated that older trout tend to select increasingly deeper and covered habitats to reduce size-dependent predation risk (Ayllón et al., 2009, 2010; Ayllón et al., 2013). However, such studies used cover as a categorical variable, thus the cover index provides us with a more gradual perspective and an integrative combination of cover types. Our results could be the product of excessive cover, which could make access to the best bio-energetic positions difficult for the adult trout (Sánchez-Hernández et al., 2011b).

The presented results were mostly in agreement with Mouton et al. (2011) who trained two models based on fuzzy logic and Random Forests, and selected width, cover index and mean velocity as the most relevant variables for trout (all ages combined). As width was here inversely correlated with elevation, it could be considered that in general, elevation was positively related with density. We hypothesize that the influence of human activities is partly explanatory, because flow regulation and river pollution increase in the downstream direction. Another reason can be that the limitations in river connectivity (especially for weirs in the Vallanca River) do not allow a good dispersion of the fish as they grow. Therefore, the high densities in the headwaters of the Vallanca (including very narrow reaches) may produce this trend which is not transferable to the majority of other trout rivers.

This article demonstrates that modelling habitat suitability at different scales can provide interesting insights on fish density patterns, in agreement with other authors (Bisson et al., 2006; Mouton et al., 2011), especially when non-linear techniques are applied. The modelling procedures demonstrated that young and adult brown trout density depend on meso-scale variables and reach-scale variables. Therefore, river restoration actions in Mediterranean rivers should include the assessment of river connectivity and habitat diversity to quantify the ratio and distribution of slow and fast habitats. In the Júcar river Basin, the positive effect of small weir removal has already been demonstrated (Olaya-Marín et al., 2012), as has the accessibility to lateral tributaries (and the corresponding catchment area) in highly fragmented river systems (Olaya-Marín, 2013).

Our models provide useful information for the design of effective restoration measures by environmental and water managers. Models at the meso-scale allow the assessment of habitat suitability for fish in response to flow management or other river restoration actions. Accordingly, meso-scale multivariate models with GAM have been used in studies of eco-hydraulics to assess environmental flows with excellent results (Jowett and Davey, 2007; Costa et al., 2012). The exhaustive search for the best subset of environmental predictors was a relevant aspect of the model selection, in contrast with previous studies.

Thus, this study has provided valuable guidelines in modelling habitat requirements for freshwater fish species as well as a better insight on habitat suitability for brown trout in the Mediterranean context.

Acknowledgments

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