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

By J. D. Alcaraz-Hernández[1], R. Muñoz-Mas[1], F. Martínez-Capel[1], V. Garófano-Gómez[1,2,3] and P. Vezza[1,4]

[1]*Institut d'Investigació per a la Gestió Integrada de Zones Costaneres (IGIC), Universitat Politècnica de València, València, Spain;* [2]*Université Clermont Auvergne, Université Blaise Pascal, GEOLAB, Clermont-Ferrand, France;* [3]*Laboratoire de géographie physique et environnementale, CNRS, UMR 6042, GEOLAB, Clermont-Ferrand, France;* [4]*International Centre for Ecohydraulics Research (ICER), University of Southampton, University Rd, Southampton, UK*

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). After 4 years of observations (2003–2006) the data representing trout density 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 a comprehensive trial of all 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 depths, 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 to design effective and science-based restoration measures, and result in a more efficient management of brown trout populations.

Introduction

Over the past decades, ecological models have been applied increasingly 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 on ecological modelling literature in 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 analyse 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 correspond to approximately 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 but also cover (e.g. vegetation, undercut banks or log jams). These particular variables were demonstrated to be relevant for fish habitat selection and 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), Artificial Neural Networks (Brosse and Lek, 2000) and Fuzzy Logic (Muñoz-Mas et al., 2012). 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).

On a larger scale, macro-scale HSM analyse 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, some evidence suggests that the consideration of micro and macro-scale variables in independent studies is not enough to cover all variabilities involving the prediction of fish habitat suitability (Bdour et al., 2004). Additionally, models based on multiple spatial scales usually outperform single-scale analyses (Olden et al., 2006).

A promising approach is therefore the development of cross-scale models including the meso-scale as a relevant component. In modelling 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 shown 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 the distribution of salmonids 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) forecasted distribution shifts of brown trout in Pyrenean rivers based on environmental predictor variables, such as mean annual temperature and precipitation. At a 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, *Salmo trutta*, 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 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 on Mediterranean brown trout demonstrate a lack of information on the regional patterns in the habitat selection as well as the structure, distribution and abundance of their populations (Alcaraz-Hernández et al., 2007), all 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), accessibility and availability of food (Sánchez-Hernández et al., 2011a), global warming (Almodóvar et al., 2012), and intra or inter-specific relationships (Sánchez-Hernández and Cobo, 2012).

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

Materials and methods

Study area

Field surveys were carried out in summer 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 >600 m above sea level) with a Strahler order of 2–3. 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.

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 is in January and March. The average annual rainfall varies slightly between 442 mm and 583 mm. However, 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 14°C in winter, with minimum temperatures usually >5°C, while in summer maximum temperatures usually do not exceed 20°C. The selected reaches are mountainous, with small average width (2.51–5.66 m), average depth (0.26–

Fig. 1. Study area: Ebrón (EB), Vallanca (VA), Palancia (PA) and Villahermosa (VI) rivers, within the Júcar River Basin District (Eastern Spain). Sites were in unregulated sections of the headwaters. Elevations at each site (from 1 to 4): 880, 792, 763 and 743 m.a.s.l. in the EB; 968, 890, 752 and 718 m.a.s.l. in the VA; 769, 688, 655 and 627 m.a.s.l. in the PA, and 728, 647, 621 and 605 m.a.s.l. in the VI. Catchment areas ranged from 123 to 268 km^2
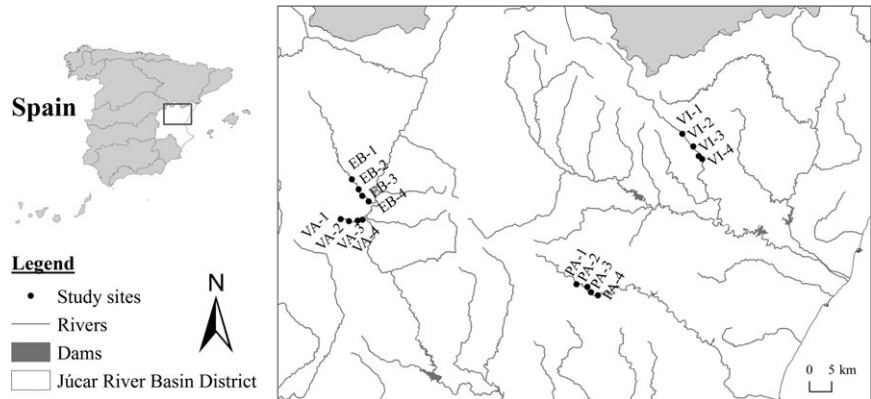
0.49 m) and high average slope (23.0–13.6 m km^{-1}). Detailed environmental descriptions of the reaches are included in Alcaraz-Hernández et al. (2011) and Mouton et al. (2011).

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 years that followed (2004–2006). Years 2005 and 2006 suffered intense drought, where a few of the headwater reaches in the Vallanca and Villahermosa rivers were dry, thus no surveys took place (empty spaces in Table 3 for 2005 and 2006).

Habitat data acquisition

Some 23 environmental variables were collected and used in the development of density models for brown trout, *Salmo trutta* (Table 1). The environmental variables corresponded to different spatial scales: the reach-scale and HMU or meso-scale. Reach-scale variables included elevation above sea level (ELE, m) and mean slope of the study reach (SLO, m m^{-1}), measured using a geographic information system (Arc-GIS^{TM} 9.3.1). The spring (FSP, m^3 s^{-1}) and annual (FAN, m^3 s^{-1}) flows were provided by the Júcar River Basin Authority. HMU data were assessed in each reach using an adapted version of the BVET (Hankin and Reeves, 1988; Dolloff et al., 1993). Firstly, each reach was stratified visually 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 their classification 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 variables assessed at reach scale and meso-scale (hydromorphological units, HMU), 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, diameter >256 mm (%)
	Medium substrate	SME	Medium substrate, diameter 2–256 mm (%)
	Fine substrate	SFI	Fine substrate, 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	Amount 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: Mean length of the HMU (LEN, m) with a measuring tape; mean width of water surface (WID, m) 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:

SIN = 0.08 × bedrock + 0.07 × boulder + 0.06 × cobble + 0.05 × gravel + 0.04 × fine gravel + 0.03 × 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 the equation:

$$CIN = \frac{C_b + C_s + C_{sub} + C_{sv} + C_d}{4}$$

where, C_b is the available refuge due to the presence of undercut banks or caves; C_s is the refuge produced by shading; C_{sub} produced by substrate types; C_{sv} produced by submerged vegetation and C_d by the depth of the water column. At five categories of cover, this index assigns scores from zero to five (0 no refuge, and five maximum score) using the recommendations in Table 2. A total of 93 HMU were sampled, with fifty corresponding to slow water HMU (pools and glides) and 43 to fast water HMU (riffles and rapids).

Biological data acquisition

During the summers of 2003–2006, the biological survey took place by electrofishing in each of the selected HMU, one fast and one slow. The electrofishing equipment consisted of a 950 W electric generator connected to an electric rectifier for a continuous current and to 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.

Fork length (mm) and weight (g) of each individual were measured. In addition, scales were extracted from individuals older than 1 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 divided into young (DYO, <2 years) and adult (DAD, ≥2 year) for the data analyses. 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 over-dispersion in the statistical GAMs analyses (Zuur et al., 2009). The values of young and adult brown trout densities by river, reach, HMU and year are shown in Table 3.

Data analysis

Generalized Additive Models (GAMs) were used to model brown trout density, as they are useful in dealing with nonlinear 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 performances in modelling habitat: fish relationships at the meso-scale (Costa et al., 2012). Furthermore, this technique allows the modeller to include normal and non-normal variables in the model. GAMs follow the equation:

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

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

Table 2
Scores of the cover index (CIN) based on availability of different cover types: bank shelter (C_b), shading (C_s), riverbed substrate (C_{sub}), submerged vegetation (C_{sv}), depth (C_d)

Score	C_b	C_s (%)	C_{sub}	C_{sv} (%)	C_d (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

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

River	Reach	HMU	2003		2004		2005		2006	
			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

to each variable involved. 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 (e.d.f.) 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 combinations of variables were generated (of 2, 3, 4 variables, etc.) and the combinations where any relevant Spearman's Rho was observed in 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 possible combinations of datasets including variables in different sets, comprising two to eight variables. Each combination met the aforementioned requirements (non-correlation and non-collinearity of variables).

Among the function families tested, the 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 modelling 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 was 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 then the final selection; 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 <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 square sum 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 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 GAM and GLM functions 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 transfer difficulties, questioning its generalization ability (Fukuda, 2010). Due to the multiple factors affecting fish habitat selection, generally recommended is the generation of site-specific models of habitat suitability, especially for the application of physical habitat modelling and environmental flow assessments (Moyle and Baltz, 1985; Bovee et al., 1998).

Results

The process in combining variables to generate GAMs resulted in a total of 59 009 models for GAM as well as for GLM: 210 composed two variables, 1149 three variables, 4009 four, 9383 five, 15 069 six, 16 667 seven and 12 522 eight variables. All of 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 for 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, a number of slow (NSL) and fast (NFA) habitats, and the Shannon-Weaver diversity habitat index (DIV, 0–1); this 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 *Salmo trutta*. For the adult trout, the 10% of marginal improvement ratio was used for final selection of the best model with five variables. Regarding GLM, the adult
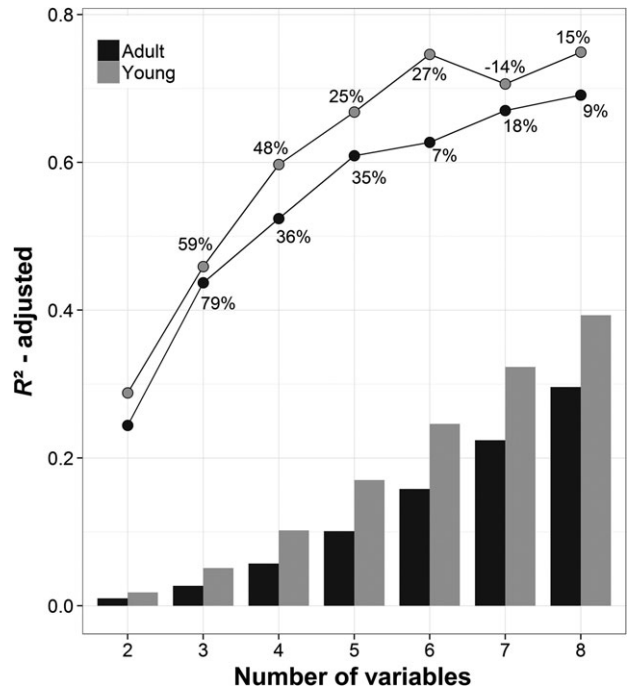

Fig. 2. Variation of performance criterion (R^2-adjusted; dots) of best model at each iteration (bars) with increasing number of variables in the training dataset of the Generalized Additive Model (GAM) based on 4 years of sampling (2003–2006). Marginal improvement ratio = marginal percentage of improvement in relation to best previous model (dots). The R^2-adjusted of the best two-variable model was used as a base value. 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)

trout models 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 performance reductions are possible with more variables.

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 (e.d.f. > 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 for 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

Table 4
Summary of best Generalized Additive Models (GAMs) for adult and young *Salmo trutta* densities. Final predictive variables: 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	e.d.f.	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

variability, respectfully. The adult model comprised the variables: mean length (LEN), WID, DME, VEL and DBR, whereas the young model comprised WID, DME, coarse substrate (SCO), density of woody debris (WOD), VEL and NFA.

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 an approx. 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 decreased 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 approx. linearly, and remained almost invariable for WID > 5 m.

In Fig. 4 the partial effects of young trout density (DYO) are illustrated, where 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.
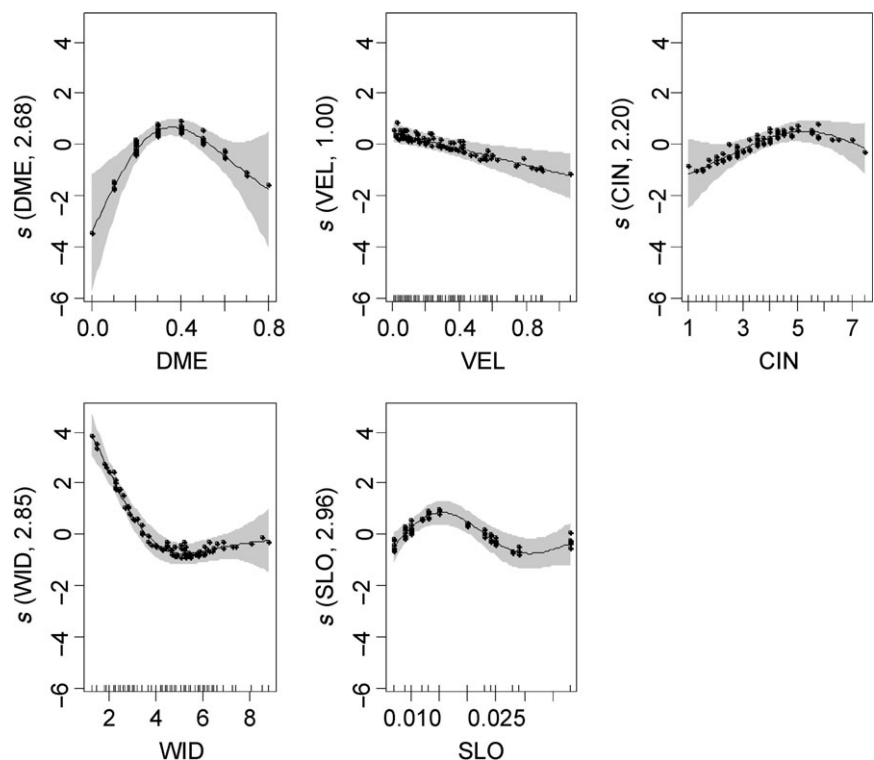

Fig. 3. Partial effects of mean depth (DME), velocity (VEL), cover index (CIN), mean width (WID) and slope (SLO) in adult brown trout densities modelled using Generalized Additive Models (GAMs) based on 4 years of sampling (2003–2006). Solid black line = general trend of the considered variable effect on mean adult trout density; shaded areas = 95% confidential intervals. Numbers in *y*-axis = effective degrees of freedom. Black points = training data
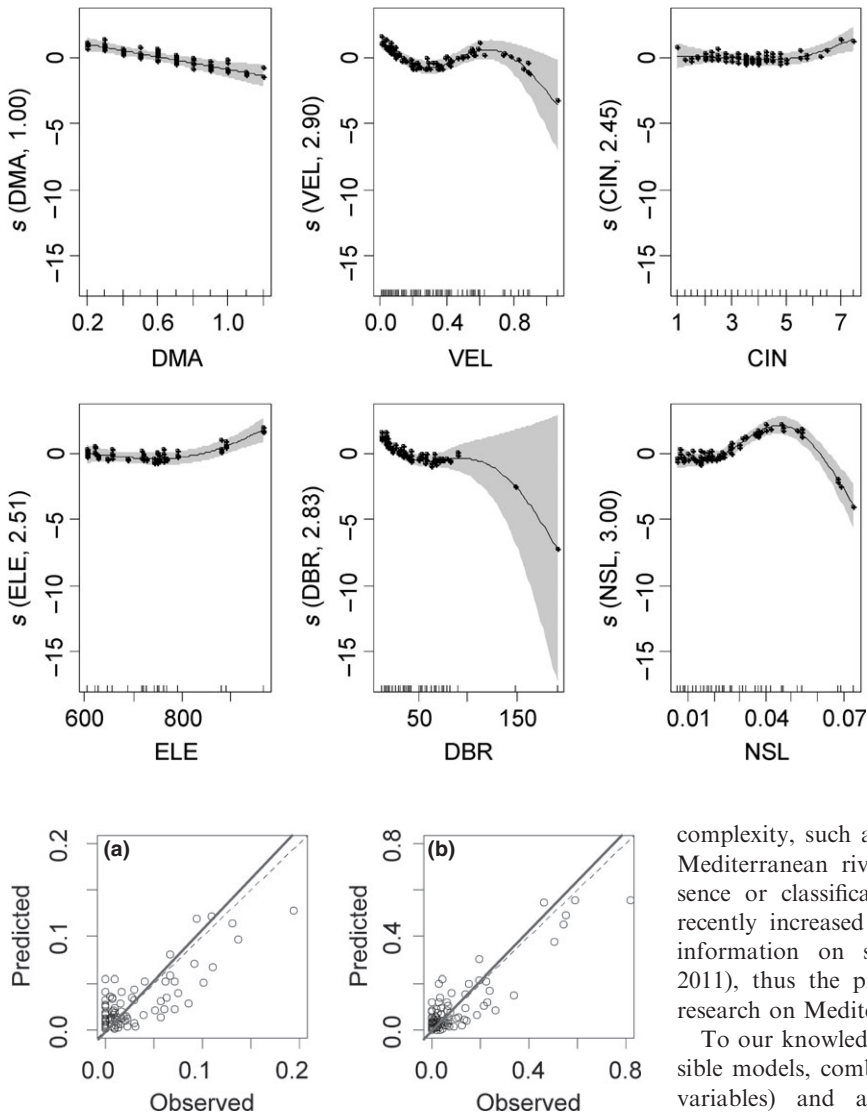
Fig. 4. Partial effects of maximum depth (DMA), velocity (VEL), cover index (CIN), elevation (ELE), distance between rapids (DBR) and number of slow habitats (NSL) in young brown trout densities modelled using Generalized Additive Models (GAMs) based on 4 years of sampling (2003–2006). Solid black line = general trend of the considered variable effect on mean young trout density; shaded areas = 95% confidential intervals. Numbers in y-axis = effective degrees of freedom. Black points = training data

Fig. 5. Observed (x-axis) vs predicted (y-axis) values of adult (a) and young (b) brown trout density by the Generalized Additive Models (GAMs). Thick grey lines = regression line between observed and predicted. Dotted black lines = in 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 brown trout, respectively. These values can be considered similar to those obtained in previous studies based on multivariate approaches (Ayllón et al., 2010, 2013; Vezza et al., 2012), 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, whereas 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 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 selection variables. The comprehensive trial of all possible combinations of input variables and selection of the best parsimonious model after predefined criteria is the only method 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 made 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 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 marked 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 a low to moderate gradient. In accordance with these results Ayllón et al. (2010) and Filipe et al. (2013) found that the slope affects the distribution of trout on a 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 of Hauer et al. (2011) where young trout occupied shallow pool waters and 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, 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, 2014b). Regarding water depth, Baran et al. (1997) found a clear segregation by habitat units between fry and adult stages of brown trout: fry were more frequently detected in riffles and glides, and adults were concentrated in deep-water 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); the possible reduction in expended energy (low energy swimming costs) has also been suggested (Bridcut and Giller, 1995; Railsback and Harvey, 2002).

In Northern Europe, Heggenes et al. (1999) demonstrated that water 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 relationship between large salmonid fish and deep habitats, although there are movements of fish towards shallow microhabitats in summer or winter, depending on habitat availability. Regarding the observed decrease in density at large depths (Fig. 3), this could be produced by the expected reduction in the drift provision; upholding this premise, microhabitat suitability modelling has 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 on 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, 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 are 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 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 provides 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.

Acknowledgements

References

Addicott, J. F.; Aho, J. M.; Antolin, M. F.; Padilla, D. K.; Richardson, J. S.; Soluk, D. A., 1987: Ecological neighborhoods: scaling environmental patterns. Oikos 49, 340–346.

Aertsen, W.; Kint, V.; van Orshoven, J.; Özkan, K.; Muys, B., 2010: Comparison and ranking of different modelling techniques for prediction of site index in Mediterranean mountain forests. Ecol. Model. 221, 1119–1130.

Ahmadi-Nedushan, B.; St-Hilaire, A.; Bérubé, M.; Robichaud, É.; Thiémonge, N.; Bobée, B., 2006: A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Res. Appl. 22, 503–523.

Alcaraz-Hernández, J. D.; Martínez-Capel, F.; Peredo-Parada, M.; Hernández-Mascarell, A. B., 2007: Relaciones entre densidades y biomasas de Salmo trutta fario y mediciones del mesohábitats en tramos trucheros de la Comunidad Valenciana. Limnetica 26, 159–167.

Alcaraz-Hernández, J. D.; Martínez-Capel, F.; Peredo-Parada, M.; Hernández-Mascarell, A. B., 2011: Physical heterogeneity of hydromorphological units in Mediterranean streams (East Spain). Limnetica 30, 363–378.

Almodóvar, A.; Nicola, G. G.; Elvira, B.; García-Marín, J. L., 2006: Introgression variability among Iberian brown trout Evolutionary Significant Units: the influence of local management and environmental features. Freshw. Biol. 51, 1175–1187.

Almodóvar, A.; Nicola, G. G.; Ayllón, D.; Elvira, B., 2012: Global warming threatens the persistence of Mediterranean brown trout. Glob. Change Biol. 18, 1549–1560.

Anlauf, K. J.; Jensen, D. W.; Burnett, K. M.; Steel, E. A.; Christiansen, K.; Firman, J. C.; Feist, B. E.; Larsen, D. P., 2011: Explaining spatial variability in stream habitats using both natural and management-influenced landscape predictors. Aquat. Conserv. Mar. Freshw. Ecosyst. 21, 704–714.

Armitage, D. W.; Ober, H. K., 2010: A comparison of supervised learning techniques in the classification of bat echolocation calls. Ecol. Info. 5, 465–473.

Armstrong, J. D.; Kemp, P. S.; Kennedy, G. J. A.; Ladle, M.; Milner, N. J., 2003: Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. 62, 143–170.

Ayllón, D.; Almodóvar, A.; Nicola, G. G.; Elvira, B., 2009: Interactive effects of cover and hydraulics on brown trout habitat selection patterns. River Res. Appl. 25, 1051–1065.

Ayllón, D.; Almodóvar, A.; Nicola, G. G.; Elvira, B., 2010: Ontogenetic and spatial variations in brown trout habitat selection. at. Ecol. Freshw. Fish 19, 420–432.

Ayllón, D.; Nicola, G. G.; Parra, I.; Elvira, B.; Almodóvar, A., 2013: Intercohort density dependence drives brown trout habitat selection. Acta Oecol. 46, 1–9.

Baeza, D.; García de Jalón, D.; Gutiérrez, B.; Vizcaíno, P., 2005: Basin influence on natural variability of rivers in semi-arid environments. Int. J. River Basin Manag. 3, 247–259.

Baran, P.; Delacoste, M.; Lascaux, J. M., 1997: Variability of meso-habitat used by brown trout populations in the French Central Pyrenees. Trans. Am. Fish. Soc. 126, 747–757.

Bdour, A.; Papanicolaou, A. N.; Talebbeydokhti, N., 2004: Comparison of watershed macroscale approaches against microscale for the South Fork Clearwater River, Idaho. In World Water and Environmental Resources Congress 2001. Orlando, FL.

Bisson, P. A.; Montgomery, D. R.; Buffington, J. M., 2006: Valley segment, stream reaches, and channel units. In: Methods in stream ecology. F. R. Hauer and G. A. Lamberti (Eds). Academic Press, San Diego, pp. 23–49.

Bonnlander, B. V.; Weigend, A. S., 1996: Selecting input variables using mutual information and nonparametric density estimation. In: International Symposium on Artificial Neural Networks. Taiwan, pp. 42–50.

Bovee, K. D., 1982: Guide to stream habitat analysis using the instream flow incremental methodology. Report PB 83-131052. National Technical Information Service. Springfield, VA.

Bovee, K. D., 1986: Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Paper #21 FWS/OBS-86/7. Fish and Wildlife Service, U.S. Department of the Interior, Washington, p. 235.

Bovee, K. D.; Lamb, B. L.; Bartholow, J. M.; Stalnaker, C. B.; Taylor, J.; Henriksen, J., 1998: Stream habitat analysis using the

instream flow incremental methodology. Report USGS/BRD-1998–0004. U. S. Geological Survey, Biological Resources Division, Fort Collins, 131 pp.

Bridcut, E. E.; Giller, P. S., 1995: Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. Can. J. Fish Aquat. Sci. **52**, 2543–2552.

Brosse, S.; Lek, S., 2000: Modelling roach (*Rutilus rutilus*) microhabitat using linear and nonlinear techniques. Freshw. Biol. **44**, 441–452.

Carle, F. L.; Strub, M. R., 1978: A new method for estimating population size from removal data. Biometrics **34**, 621–630.

Costa, R. M. S.; Martínez-Capel, F.; Muñoz-Mas, R.; Alcaraz-Hernández, J. D.; Garófano-Gómez, V., 2012: Habitat suitability modelling at mesohabitat scale and effects of dam operation on the endangered Júcar nase, *Parachondrostoma arrigonis* (river Cabriel, Spain). River Res. Appl. **28**, 740–752.

De Pauw, N.; Gabriels, W.; Goethals, P. L. M., 2006: River monitoring and assessment methods based on macroinvertebrates. In: Biological monitoring of rivers: applications and perspectives. G. Ziglio, M. Siligardi and G. Flaim (Eds). John Wiley & Sons, Ltd, Chichester, England, pp. 111–134.

Dolloff, C. A.; Hankin, D. G.; Reeves, G. H., 1993: Basinwide estimation of habitat and fish populations in streams. USDA Forest Service General Technical Report SE-GTR-83. 25 pp.

Elliott, J. M., 1990: Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. III. The role of territorial behaviour. J. Anim. Ecol. **59**, 803–818.

Elso, J. I.; Giller, P. S., 2001: Physical characteristics influencing the utilization of pools by brown trout in an afforested catchment in Southern Ireland. J. Fish Biol. **58**, 201–221.

Fausch, K. D.; Torgersen, C. E.; Baxter, C. V.; Li, H. W., 2002: Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience **52**, 483–498.

Ferreira, T.; Oliveira, J.; Caiola, N.; De Sostoa, A.; Casals, F.; Cortes, R.; Economou, A.; Zogaris, S.; Garcia-Jalon, D.; Ilh, É. U. M.; Martinez-Capel, F.; Pont, D.; Rogers, C.; Prenda, J., 2007: Ecological traits of fish assemblages from Mediterranean Europe and their responses to human disturbance. Fish. Manage. Ecol. **14**, 473–481.

Filipe, A. F.; Markovic, D.; Pletterbauer, F.; Tisseuil, C.; De Wever, A.; Schmutz, S.; Bonada, N.; Freyhof, J., 2013: Forecasting fish distribution along stream networks: brown trout (*Salmo trutta*) in Europe. Divers. Distrib. **19**, 1059–1071.

Frank, B. M.; Piccolo, J. J.; Baret, P. V., 2011: A review of ecological models for brown trout: towards a new demogenetic model. Ecol. Freshw. Fish **20**, 167–198.

Fukuda, S., 2010: Assessing transferability of genetic algorithm-optimized fuzzy habitat preference models for Japanese Medaka (*Oryzias latipes*). In: 4th International Workshop on Genetic and Evolutionary Fuzzy Systems, GEFS 2010, Mieres, pp. 57–62.

Fukuda, S.; Mouton, A. M.; De Baets, B., 2011: Abundance versus presence/absence data for modelling fish habitat preference with a genetic Takagi-Sugeno fuzzy system. Environ. Monit. Assess. **184**, 6159–6171.

Fukuda, S.; De Baets, B.; Waegeman, W.; Verwaeren, J.; Mouton, A. M., 2013: Habitat prediction and knowledge extraction for spawning European grayling (*Thymallus thymallus* L.) using a broad range of species distribution models. Environ. Model. Software **47**, 1–6.

García de Jalón, D.; Schmidt, G., 1995: Manual práctico para la gestión sostenible de la pesca fluvial. Asociación para el Estudio y Mejora de los Salmónidos (AEMS), Madrid, 169 pp.

Gasith, A.; Resh, V. H., 1999: Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annu. Rev. Ecol. Syst. **30**, 51–81.

Gibson, R. J., 1993: The Atlantic salmon in fresh water: spawning, rearing and production. Rev. Fish Biol. Fish **3**, 39–73.

Gortázar, J.; Parasiewicz, P.; Alonso-González, C.; García de Jalón, D., 2011: Physical habitat assessment in the Tajuña River (Spain) by means of the MesoHABSIM approach. Limnetica **30**, 379–392.

Gosselin, M. P.; Petts, G. E.; Maddock, I. P., 2010: Mesohabitat use by bullhead (*Cottus gobio*). Hydrobiologia **652**, 299–310.

Gosselin, M. P.; Maddock, I.; Petts, G., 2012: Mesohabitat use by brown trout (*Salmo trutta*) in a small groundwater-dominated stream. River Res. Appl. **28**, 390–401.

Grossman, G. D.; De Sostoa, A., 1994: Microhabitat use by fish in the lower Rio Matarraña, Spain, 1984–1987. Ecol. Freshw. Fish **3**, 123–136.

Guisan, A.; Edwards, T. C. Jr; Hastie, T., 2002: Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. **157**, 89–100.

Hankin, D. G.; Reeves, G. H., 1988: Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Can. J. Fish Aquat. Sci. **45**, 834–844.

Hauer, C.; Unfer, G.; Tritthart, M.; Formann, E.; Habersack, H., 2011: Variability of mesohabitat characteristics in riffle-pool reaches: testing an integrative evaluation concept (FGC) for MEM-application. River Res. Appl. **27**, 403–430.

Hauer, C.; Unfer, G.; Graf, W.; Leitner, P.; Zeiringer, B.; Habersack, H., 2012: Hydro-morphologically related variance in benthic drift and its importance for numerical habitat modelling. Hydrobiologia **683**, 83–108.

Hayes, J. W.; Jowett, I. G., 1994: Microhabitat models of large drift-feeding brown trout in three New Zealand rivers. N. Am. J. Fish. Manage. **14**, 710–725.

Heggenes, J.; Baglinière, J. L.; Cunjak, R. A., 1999: Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. Ecol. Freshw. Fish **8**, 1–21.

James, G.; Witten, D.; Hastie, T.; Tibshirani, R., 2013: An introduction to statistical learning with applications R. Springer, New York, 441 pp.

Jowett, I. G.; Davey, A. J. H., 2007: A comparison of composite habitat suitability indices and generalized additive models of invertebrate abundance and fish presence-habitat availability. Trans. Am. Fish. Soc. **136**, 428–444.

Jowett, I. G.; Richardson, J.; Biggs, B. J. F.; Hickey, C. W.; Quinn, J. M., 1991: Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. N. Z. J. Mar. Freshw. Res. **25**, 187–199.

Kemp, J. L.; Harper, D. M.; Crosa, G. A., 1999: Use of 'functional habitats' to link ecology with morphology and hydrology in river rehabilitation. Aquat. Conserv. Mar. Freshw. Ecosyst. **9**, 159–178.

Lambert, T. R.; Hanson, D. F., 1989: Development of habitat suitability criteria for trout in small streams. Regulated Rivers – Res. Manage. **3**, 291–303.

Lamouroux, N.; Capra, H.; Pouilly, M.; Souchon, Y., 1999: Fish habitat preferences in large streams of southern France. Freshw. Biol. **42**, 673–687.

Leathwick, J. R.; Rowe, D.; Richardson, J.; Elith, J.; Hastie, T., 2005: Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshw. Biol. **50**, 2034–2052.

Leopold, L. B.; Wolman, M. G.; Miller, J. P., 1964: Fluvial processes in geomorphology. WH Freeman, San Francisco.

Lobón-Cerviá, J., 2007: Numerical changes in stream-resident brown trout (*Salmo trutta*): uncovering the roles of density-dependent and density-independent factors across space and time. Can. J. Fish Aquat. Sci. **64**, 1429–1447.

Lobón-Cerviá, J., 2009: Why, when and how do fish populations decline, collapse and recover? The example of brown trout (*Salmo trutta*) in Rio Chaballos (northwestern Spain). Freshw. Biol. **54**, 1149–1162.

Maceda-Veiga, A., 2013: Towards the conservation of freshwater fish: Iberian Rivers as an example of threats and management practices. Rev. Fish Biol. Fish **23**, 1–22.

Machordom, A.; Suárez, J.; Almodóvar, A.; Bautista, J. M., 2000: Mitochondrial haplotype variation and phylogeography of Iberian brown trout populations. Mol. Ecol. **9**, 1324–1338.

Maki-Petäys, A.; Muotka, T.; Huusko, A.; Tikkanen, P.; Kreivi, P., 1997: Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. Can. J. Fish Aquat. Sci. **54**, 520–530.

Martínez-Capel, F.; Bargay-Juan, M.; Hernández-Mascarell, A. B.; Alcaraz-Hernández, J. D.; Garófano-Gómez, V. 2007: Estimación de las curvas de preferencia de microhábitat para determinadas especies piscícolas representativas como paso intermedio en el establecimiento del régimen de caudales medioambientales en los ríos de la Demarcación Hidrográfica del Júcar. Informe técnico de la Universidad politécnica de Valencia para la Confederación Hidrográfica del Júcar. Valencia, Spain.

Martínez-Capel, F.; García De Jalón, D.; Werenitzky, D.; Baeza, D.; Rodilla-Alamá, M., 2009: Microhabitat use by three endemic Iberian cyprinids in Mediterranean rivers (Tagus River Basin, Spain). Fish. Manage. Ecol. **16**, 52–60.

Meador, M. R.; Cuffney, T. F.; Gurtz, M. E., 1993: Methods for sampling fish communities as part of the National Water-Quality Assessment Program. Open-File Report 93-104. USGS: 40 pp.

Mouton, A. M.; Alcaraz-Hernández, J. D.; De Baets, B.; Goethals, P. L. M.; Martínez-Capel, F., 2011: Data-driven fuzzy habitat suitability models for brown trout in Spanish Mediterranean rivers. Environ. Model. Software **26**, 615–622.

Moyle, P. B.; Baltz, D. M., 1985: Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Trans. Am. Fish. Soc. **114**, 695–704.

Muñoz-Mas, R.; Martínez-Capel, F.; Schneider, M.; Mouton, A. M., 2012: Assessment of brown trout habitat suitability in the Jucar River Basin (Spain): comparison of data-driven approaches with fuzzy-logic models and univariate suitability curves. Sci. Total Environ. **440**, 123–131.

Nicola, G.; Almodóvar, A.; Elvira, B., 2009: Influence of hydrologic attributes on brown trout recruitment in low-latitude range margins. Oecologia **160**, 515–524.

Nislow, K. H.; Hudy, M.; Letcher, B. H.; Smith, E. P., 2011: Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. Freshw. Biol. **56**, 2135–2144.

Nykänen, M.; Huusko, A., 2004: Transferability of habitat preference criteria for larval European grayling (*Thymallus thymallus*). Can. J. Fish Aquat. Sci. **61**, 185–192.

Olaya-Marín, E. J., 2013: Ecological models at fish community and species level to support effective river restoration. PhD Dissertation. Universitat Politècnica de València.

Olaya-Marín, E. J.; Martínez-Capel, F.; Soares Costa, R. M.; Alcaraz-Hernández, J. D., 2012: Modelling native fish richness to evaluate the effects of hydromorphological changes and river restoration (Júcar River Basin, Spain). Sci. Total Environ. **440**, 95–105.

Olden, J. D.; Jackson, D. A., 2002: A comparison of statistical approaches for modelling fish species distributions. Freshw. Biol. **47**, 1976–1995.

Olden, J. D.; Poff, N. L.; Bledsoe, B. P., 2006: Incorporating ecological knowledge into ecoinformatics: an example of modeling hierarchically structured aquatic communities with neural networks. Ecol. Inform. **1**, 33–42.

Olden, J. D.; Lawler, J. J.; Poff, N. L., 2008: Machine learning methods without tears for ecologists. Q. Rev. Biol. **83**, 171–193.

Orth, D. J.; Maughan, O. E., 1982: Evaluation of the incremental methodology for recommending instream flows for fishes. Trans. Am. Fish. Soc. **111**, 413–445.

Parra, I.; Almodóvar, A.; Ayllón, D.; Nicola, G. G.; Elvira, B., 2012: Unravelling the effects of water temperature and density dependence on the spatial variation of brown trout (*Salmo trutta*) body size. Can. J. Fish Aquat. Sci. **69**, 821–832.

Payne, T. R.; Allen, M. A., 2009: Application of the use-to-availability electivity ratio for developing habitat suitability criteria in PHABSIM instream flow studies. In: Proceedings of the 7th International Symposium on Ecohydraulics, Concepción, Chile, January 12–16, 2009.

Pierce, G. J.; Santos, M. B.; Smeenk, C.; Saveliev, A.; Zuur, A. F., 2007: Historical trends in the incidence of strandings of sperm whales (*Physeter macrocephalus*) on North Sea coasts: an association with positive temperature anomalies. Fish. Res. **87**, 219–228.

R Development Core Team, 2010: R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Railsback, S. F.; Harvey, B. C., 2002: Analysis of habitat-selection rules using an individual-based model. Ecology **83**, 1817–1830.

Rincón, P. A.; Lobón-Cerviá, J., 1993: Microhabitat use by stream-resident brown trout: bioenergetic consequences. Trans. Am. Fish. Soc. **122**, 575–587.

Rosenfeld, J., 2003: Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Trans. Am. Fish. Soc. **132**, 953–968.

Sánchez-Hernández, J.; Cobo, F., 2012: Summer differences in behavioural feeding habits and use of feeding habitat among brown trout (Pisces) age classes in a temperate area. Ital. J. Zool. **79**, 468–478.

Sánchez-Hernández, J.; Vieira-Lanero, R.; Servia, M.; Cobo, F., 2011a: Feeding habits of four sympatric fish species in the Iberian Peninsula: keys to understanding coexistence using prey traits. Hydrobiologia **667**, 119–132.

Sánchez-Hernández, J.; Vieira-Lanero, R.; Servia, M.; Cobo, F., 2011b: First feeding diet of young brown trout fry in a temperate area: disentangling constraints and food selection. Hydrobiologia **663**, 109–119.

Sánchez-Montoya, M. M.; Vidal-Abarca, M. R.; Puntí, T.; Poquet, J. M.; Prat, N.; Rieradevall, M.; Alba-Tercedor, J.; Zamora-Muñoz, C.; Toro, M.; Robles, S.; Álvarez, M.; Suárez, M. L., 2009: Defining criteria to select reference sites in Mediterranean streams. Hydrobiologia **619**, 39–54.

Tutz, G.; Binder, H., 2006: Generalized additive modeling with implicit variable selection by likelihood-based boosting. Biometrics **62**, 961–971.

Venables, W. N.; Dichmont, C. M., 2004: GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fish. Res. **70**, 319–337.

Vezza, P.; Parasiewicz, P.; Rosso, M.; Comoglio, C., 2012: Defining minimum environmental flows at regional scale: application of mesoscale habitat models and catchments classification. River Res. Appl. **28**, 717–730.

Vezza, P.; Parasiewicz, P.; Calles, O.; Spairani, M.; Comoglio, C., 2014a: Modelling habitat requirements of bullhead (*Cottus gobio*) in Alpine streams. Aquat. Sci. **76**, 1–15.

Vezza, P.; Parasiewicz, P.; Spairani, M.; Comoglio, C., 2014b: Habitat modeling in high-gradient streams: the mesoscale approach and application. Ecol. Appl. **24**, 844–861.

Wood, S. N., 2001: Mgcv: GAMs and generalized ridge regression for R. R. News **1–2**, 20–25.

Wood, S. N., 2006: Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton, 392 pp.

Zuur, A. F.; Ieno, E. N.; Walker, N.; Saveliev, A. A.; Smith, G. M., 2009: Mixed effects models and extensions in ecology with R. Springer, New York, 574 pp.

Author's address: Juan Diego Alcaraz-Hernández, Institut d'Investigació per a la Gestió Integrada de Zones Costaneres (IGIC), Universitat Politècnica de València. C/ Paranimf 1, 46730 Grau de Gandia, València, Spain.
E-mail: jdalcaraz@gmail.com