RIVER RESEARCH AND APPLICATIONS

River. Res. Applic. **25**: 1051–1065 (2009)

INTERACTIVE EFFECTS OF COVER AND HYDRAULICS ON BROWN TROUT HABITAT SELECTION PATTERNS

D. AYLLÓN,[a] A. ALMODÓVAR,[a]* G. G. NICOLA[b] and B. ELVIRA[a]

[a] *Department of Zoology, Faculty of Biology, Complutense University of Madrid, E-28040 Madrid, Spain*
[b] *Department of Environmental Sciences, University of Castilla-La Mancha, E-45071 Toledo, Spain*

ABSTRACT

Habitat modelling results are extremely sensitive to the habitat suitability criteria (HSC) used in the simulations. HSCs are usually expressed as univariate habitat suitability curves, although such univariate approach has been long questioned, since overlooking interactions between hydraulic variables may misrepresent the complexity of fish behaviour in habitat selection. It could lead to adopt erroneous flow management decisions based on misleading results. Furthermore, the interactive effects of hydraulic variables on habitat selection may be driven by the structural features of the channel, which determine cover availability. Therefore, we compared brown trout habitat selection patterns through multivariate resource selection functions (RSFs) in structurally contrasting rivers to unveil the interactive effects of hydraulics and cover elements and their consequences in univariate HSC results. Microhabitat preferences of young-of-the-year (0+) trout were similar across fast and slow waters, meanwhile juvenile (1+) and adult (>1+) preferences significantly changed. RSFs for young-of-the-year trout were consistent with univariate results and did not differ among water types. However, RSFs for older trout varied among water types and revealed complex interactions among hydraulic variables and between hydraulics and structural elements, which were not described accurately by univariate curves. Therefore, results suggest that interactions between water depth and current velocity have a significant effect on habitat selection patterns in juvenile and adult brown trout, this effect being controlled by cover availability. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: habitat suitability criteria; habitat simulation models; PHABSIM; habitat preference; resource selection functions; *Salmo trutta*; salmonids; Iberian Peninsula

Received 12 June 2008; Revised 15 October 2008; Accepted 16 October 2008

INTRODUCTION

Habitat-induced population limitations are related to the amount and quality of habitat available to fish at critical stages in their life cycle (Bovee *et al*., 1998). Therefore, long-term decreases in habitat availability due to human-induced flow reductions or habitat degradation may cause a decline in population density. Consequently, the knowledge of the habitat requirements of species is essential for assessing different impacts from human activities on fish communities. This is especially relevant in salmonid wild populations of south European countries which are currently threatened by habitat destruction, pollution, introduction of exotic especies, overfishing and introgression of foreign genes as a result of artificial stocking (Almodóvar and Nicola, 1998, 1999, 2004; Almodóvar *et al*., 2001, 2002, 2006a,b; Elvira and Almodóvar, 2001).

Habitat selection in salmonids is based on their competitive abilities and the profitability of territories in terms of both potential net energy intake rate and predation risk (Grand and Dill, 1997; Railsback and Harvey, 2002). The trade-off between energy gain and risk is much determined by the characteristics of the physical habitat, which is, in turn, determined by the interaction of the structural features of the channel and the hydrological regime (Maddock, 1999). Changes in physical habitat quality and quantity related to flow variations or modifications in the channel structure can be assessed with physical habitat simulation models. These models usually couple a hydraulic model with a biological model of habitat selection, the habitat suitability criteria (HSC). The HSC is an analytical tool used to represent preferences of different aquatic species for various instream habitat variables at different life

---

*Correspondence to: A. Almodóvar, Department of Zoology, Faculty of Biology, Complutense University of Madrid, E-28040 Madrid, Spain. E-mail: aalmodovar@bio.ucm.es stages (Bovee *et al*., 1998) and this information is usually expressed as univariate habitat suitability curves. Habitat simulation models can include a wide range of variables, provided that they are related to the hydraulics or the structural characteristics of the stream. However, depth, velocity and substrate size are usually considered the only driving physical attributes (Parasiewicz and Walker, 2007). Quantification of available cover is less widespread regardless of its importance in defining the distribution of individuals in the stream. In many cases, substrate granulometry is not enough to quantify cover, so other elements such as woody debris or overhanging and aquatic vegetation should be considered.

The univariate approach in developing HSCs has been always criticized on the basis that fish do not select physical habitat features independently. This is likely to be true as long as functional habitats have been shown to be associated with distinct combinations of depth and velocity, rather than with depth and velocity separately (Kemp *et al*., 1999). For this reason, several authors (e.g. Orth and Maughan, 1982; Vismara *et al*., 2001) have suggested that ignoring possible interactions between the hydraulic variables could introduce a bias and lead to a misinterpretation of habitat modelling results. Consequently, different multivariate methods have been used in habitat modelling studies to consider the interactions between habitat variables (Ahmadi-Nedushan *et al*., 2006). Within such multivariate approaches, generalized linear models (GLMs) and generalized additive models (GAMs) have been recently employed to model resource selection functions (RSFs) in different fish species (e.g. Labonne *et al*., 2003; Fore *et al*., 2007), including salmonids (e.g. Jones and Tonn, 2004; Jowett and Davey, 2007).

Brown trout *Salmo trutta* physical habitat requirements are in general well established (Armstrong *et al*., 2003 and references therein). However, habitat selection in the wild represents habitat preference under the prevailing biotic and abiotic conditions in any particular stream and may differ greatly among streams (Rosenfeld, 2003), so models developed for one stream type rarely work in other stream types or in other regions (Armstrong *et al*., 2003). As a result, the use of regional or site-specific HSCs in habitat modelling is often more accurate than generic curves (Heggenes and Saltveit, 1990; Greenberg *et al*., 1996). Surprisingly, the number of studies in the literature describing brown trout habitat selection patterns, either HSCs or RSFs, in rivers characterized by a Mediterranean hydrological regime is scarce (e.g. Vismara *et al*., 2001), and inexistent in the Iberian Peninsula (but see Teixeira *et al*., 2006 for Iberian Atlantic rivers).

Habitat modelling results may best be viewed as an indicator of population potential in systems where the analysed physical habitat conditions are known to be major population constraints (Bovee *et al*., 1998). For that reason, habitat simulation models have been increasingly applied in many Iberian salmonid rivers to determine ecological flow regimes in the last decades. However, most of these studies have been based on either suitability curves developed elsewhere or modifications from them, despite the consistency of the results from habitat simulation models relies primarily on the accuracy of the HSC (Heggenes *et al*., 1996). Then, the proliferation of habitat modelling studies in Iberian mountain salmonid rivers presenting a Mediterranean flow regime is not justified according to the existing gap in the knowledge about brown trout habitat selection patterns in such environments.

The objectives of this study were twofold. Firstly, we developed HSC for brown trout to be applied in habitat modelling studies in small and medium sized mountain Mediterranean rivers. Secondly, we examined through a multivariate approach (RSFs) the role of the structural characteristics of the channel and their interaction with hydraulic variables in defining brown trout habitat selection patterns and their consequences in HSC results. For this aim, we compared habitat selection patterns and the corresponding univariate preference curves and multivariate RSFs among four selected study sites in a mountain Mediterranean river, which exhibit contrasting hydraulics (fast vs. slow waters) and structural features. We expected depth and current velocity preferences within age-class to change when the interaction between variables was considered. We also expected habitat selection patterns to change across rivers with varying channel structure.

STUDY AREA

Two selected sites in the river Eska and one site at each of its headwater tributaries, rivers Belagua and Uztarroz, were sampled in summer of 2004. The river Eska is a mountain stream located in the Pyrenees (Northern Spain), and is the main tributary of the river Aragón (Ebro River basin), a Mediterranean drainage (Figure 1). The river

DOI: 10.1002/rra

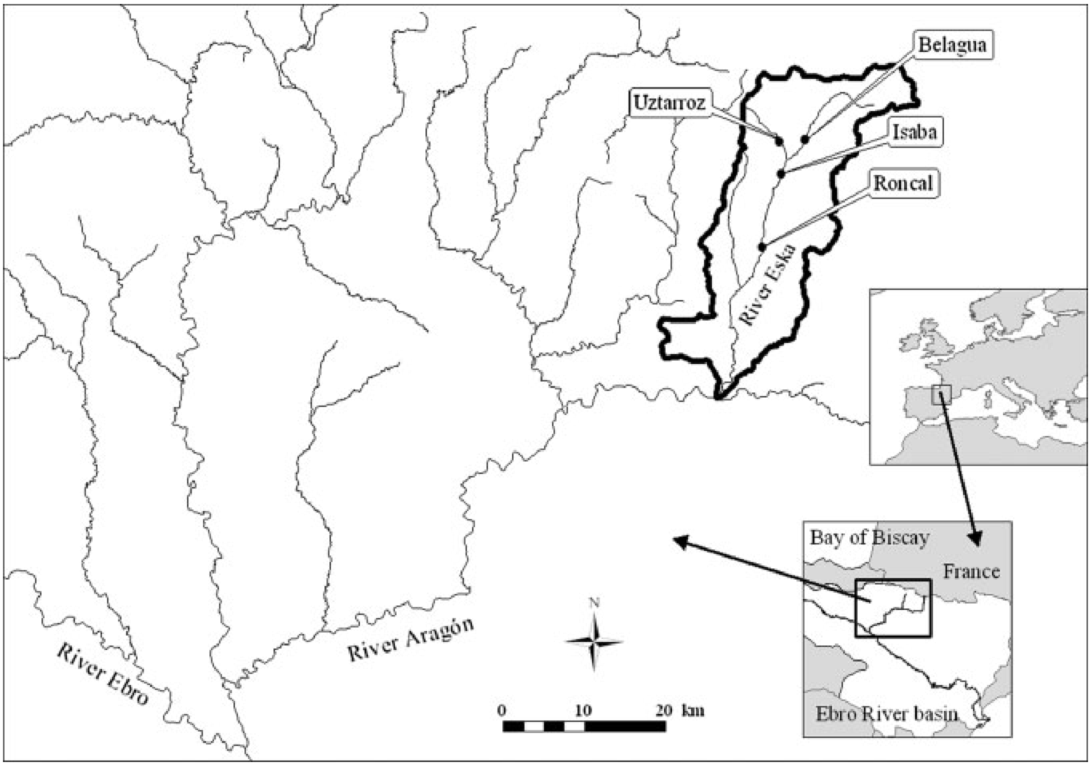

Figure 1. Map of the study area showing the sampling sites at Eska River basin

Eska has hard waters from limestone catchments at elevations ranging between 460 and 2300 m above sea level. The river Eska has a pluvio-nival hydrological regime with maximum mean discharge in winter (11.1 $m^3 s^{-1}$) and a second flow peak in spring (7.6 $m^3 s^{-1}$) after the snowmelt, and minimum flows occurring in summer (0.8 $m^3 s^{-1}$). The daily average water temperature is close to 0–1°C in winter and 16–17°C in summer.

MATERIALS AND METHODS

Data collection

Fish were sampled in each site by electrofishing using a 2200-W DC generator to estimate habitat use. Captured trout were measured (fork length, to the nearest millimetre) and weighed (to the nearest gram). Scales were taken for age determination so that each individual could be assigned to one of three age-classes, young-of-the-year (0+), juvenile (1+) or adult (>1+). The fish were placed in holding boxes to recover and then returned back to the stream. Numbered tags were dropped wherever a trout was captured, and depth, current velocity, substrate and cover were measured afterwards in a 1 m^2 quadrat. The Froude number (FR) of each occupied position was calculated later according to the following equation (Kemp *et al.*, 2000): $FR = V/(gD)^{0.5}$, where V is the mean column velocity, g the acceleration due to gravity and D the water depth.

Physical habitat availability data were collected concurrently with fish sampling at each site. Habitat availability was estimated every 1 m along transects placed perpendicular to the flow. Transects were selected to best describe the longitudinal distribution of all types of mesohabitats present within the site and were weighted by the proportion of site length they represented. For this purpose, at least two transects were located at each mesohabitat type. Sample length at study sites was five to seven times the average channel width, in accordance with the general

DOI: 10.1002/rra

precepts of alluvial river morphology on the spacing of successive riffles (Leopold *et al*., 1964). Average length of study site was 67.8 ± 21.1 m, and average assessed area of study sites was 739.2 ± 404.7 m^2.

Total depth (cm), current velocity ($m\,s^{-1}$), substrate composition and cover were measured. The proportion (%) of substrate and cover were visually estimated in a 1 m^2 quadrat. Substrate was classified according to modified categories from classification by Platts *et al*. (1983) as silt (particle size less than 0.8 mm), sand (0.8–4.7 mm), gravel (4.8–76.0 mm), cobble (76.1–304.0 mm), boulder (more than 304.0 mm) and bedrock. We defined cover as any element other than substrate that can provide protection to fish against predators or adverse environmental conditions. The type of cover was noted as vegetation (aquatic or overhanging), woody debris, undercut bank, combined (combination of vegetation and woody debris) and pools.

Data analyses

The site average Froude number (SFR; ratio sensitive to the proportion of riffles vs. pools in reaches) and Reynolds number (RE; indicator of the level of turbulence), the width to depth ratio (descriptor of channel shape) and the slow (pool) to fast (turbulent and flat) waters (Flosi and Reynolds, 1994) ratio were used to compare the channel morphology and hydraulic geometry among study sites. The site average FR and RE were calculated following Lamouroux and Capra (2002): $\mathrm{SFR} = Q/(g^{0.5}D^{1.5}W)$, where Q is the site discharge, g the acceleration due to gravity, D the site average water depth and W the channel width; $\mathrm{RE} = Q/(\gamma W)$, where γ is the water kinematic viscosity, and Q and W as noted before.

We compared habitat availability between sites, and habitat use between age-classes within a site and between sites by age-classes. We also compared habitat availability and use to test for the existence of habitat selection. Comparisons were made using a Kolmogorov–Smirnov test (KS one- or two-sample test) for continuous frequency distributions and the log-likelihood ratio test (G test) for discrete frequency distributions. We also performed a principal component analysis (PCA) to explore differences in habitat use patterns between age-classes and sites from a multivariate perspective, and to determine the habitat variables driving such variations.

Univariate preference curves for water depth, current velocity and channel index were developed. The channel index is a categorical variable used in habitat simulation models to describe the structural characteristics of the stream channel (see Bovee *et al*., 1998). In the present study, the channel index was established as a combination of substrate and cover features. It was classified in 11 categories according to the substrate and cover classes previously defined. Whenever an element providing cover was present, it was considered the main structural element of the quadrat, whereas dominant substrate represented channel index when no cover elements were available in the quadrat. Preference curves were developed by age-classes according to standard procedures (Bovee, 1986; Mallet *et al*., 2001; Vismara *et al*., 2001). Habitat variables were divided into classes, and histograms of frequencies of use and availability were elaborated. The optimal size interval of depth and velocity frequency distributions was chosen by means of the modified Sturges rule (Cheslak and García, 1988). Preference index was calculated as the ratio between proportional use and availability and then normalized, dividing by the maximum preference value. Polynomial regression functions (from 2nd up to 5th order) were fitted to preference data to derive the suitability curves, so that the best-fit models were selected based on the significance level of the regression coefficients (Student's t-test, $p < 0.05$) and on the coefficient of determination (r^2). Finally, preference curves were normalized so that the minimum value was 0 and the maximum was 1.

A RSF was developed for each age-class to describe the relationship between microhabitat characteristics and the relative probability of habitat use. Functions were developed by means of multiple logistic regressions, following the procedures described by Hosmer and Lemeshow (2000). Depth, current velocity, FR and percentage of each substrate and cover class were used as continuous independent variables, and water type (fast vs. slow waters) was input as a categorical variable. Prior to logistic regression, Pearson correlations among independent variables were examined and highly correlated variables ($r > 0.7$) were excluded. A univariate analysis of each variable was performed afterwards to test for individual significance and to assess nonlinear effects. Meaningful interactions between microhabitat variables were also tested. Finally, competing models were compared by means of the Akaike's information criterion adjusted for small samples for final model selection (Burnham and Anderson, 2002). Area under the receiver operating characteristic (ROC) curve and cross-validated classification accuracy

DOI: 10.1002/rra

were used to evaluate final models, the prediction threshold being chosen as the value where model sensitivity equalled specificity. Significance level was set at $\alpha = 0.1$.

RESULTS

Physical characteristics of study sites

Average hydraulic and morphological values showed clear differences of sites at river Eska in comparison to those at rivers Belagua and Uztarroz (Table I). Selected sites at river Eska (fast water-dominated sites, hereafter fast waters) were dominated by fast-flowing habitats (rapids and riffles), so they present shallower and faster conditions than rivers Belagua and Uztarroz (slow water-dominated sites, hereafter slow waters), mainly characterized by the presence of pools. Such variations in reach-scale hydraulic and morphology features would predict differences in fish habitat quality and hence changes in fish habitat selection patterns. Therefore, data were pooled by water type.

Habitat availability and use

No significant differences were detected in univariate water depth and velocity availability between fast and slow waters (KS one-sample test, $p > 0.05$). However, depth–velocity bivariate distributions varied significantly between water types (G test, $p < 0.001$), and maximum depth and proportion of deep-slow habitats were higher in the slow waters. Likewise, the structural characteristics of the channel differed significantly between water types (G test, $p < 0.001$). Despite boulders predominated in both fast and slow waters, the percentage of medium-sized substrate, primarily cobble, was much higher in the fast waters. In the slow waters, cover protection was provided by pool habitats and undercut banks, meanwhile overhanging vegetation, woody debris and a combination of both predominated in the fast waters, elements that were almost inexistent in the slow ones.

The PCA revealed three main axes accounting for 59.5% of the total variance of habitat use between age-classes and streams (Table II). The first factor was highly correlated with cover variables (visual vs. velocity shelters). The second factor encompassed the hydraulic variables and a related one, pool microhabitat. Finally, the third factor reflected substrate use, loading heavily on percentage of boulders, bedrock and gravels. Therefore, hydraulic variables as well as cover and substrate features were determinants of brown trout habitat use patterns. Visual inspection of the plots of the first and second components differentiated four groups of used microhabitats (Figure 2). The first factor defined a first group (1) of visually protected positions used by juvenile and especially adult trout in the fast waters. The second factor clearly separated a second group (2) comprising microhabitats characterized by shallow depths and intermediate-fast current velocities, and hence high FRs (in riffle habitats), from a third set (3) of positions showing a low FR, placed at pool habitats in the slow waters. Finally, a fourth group (4) presenting intermediate depths, moderate velocities and presence of undercut banks could be distinguished.

Table I. Physical (mean ± SD) characteristics of study sites in the Eska River basin

Study site	Belagua	Uztarroz	Isaba	Roncal
Altitude (m)	870	775	760	655
Width (m)	6.5	8.9	20	18.5
Depth (cm)	33.05 ± 17.75	31.01 ± 13.80	25.98 ± 10.30	24.17 ± 9.11
Max depth (cm)	77	58	48	45
Velocity ($\mathrm{m\,s^{-1}}$)	0.36 ± 0.39	0.44 ± 0.42	0.56 ± 0.44	0.72 ± 0.58
Dominant substrate element (%)	Boulder (46)	Boulder (57)	Boulder (40)	Boulder (37)
Dominant cover element (%)	Pool (19)	Undercut bank (13)	Vegetation (5)	Woody debris (8)
Froude number	0.09	0.17	0.27	0.39
Reynolds number	$0.5\ 10^{-5}$	$0.9\ 10^{-5}$	$1.1\ 10^{-5}$	$1.4\ 10^{-5}$
Width/depth ratio	19.7	28.7	75.0	77.1
Slow/fast waters ratio	0.8	0.5	0.1	0.0

Belagua and Uztarroz were classified as slow waters, while Isaba and Roncal were as fast waters.

Table II. Factor loadings (unrotated) for the first three principal components (PCs) from principal components analysis of variation in microhabitat use of brown trout in the study sites

Variable	PC1	PC2	PC3
Depth	0.228	**−0.779**	−0.101
Velocity	−0.466	**0.707**	−0.130
Froude number	−0.404	**0.775**	−0.070
Silt	−0.429	−0.338	−0.203
Sand	−0.053	−0.079	0.298
Gravel	0.175	0.084	**0.586**
Cobble	0.057	0.505	0.282
Boulder	**0.522**	0.235	**−0.763**
Bedrock	−0.469	−0.463	**0.580**
Vegetation	**−0.874**	−0.177	−0.258
Woody debris	**−0.898**	−0.259	−0.146
Undercut bank	0.298	−0.408	−0.251
Combined	**−0.826**	−0.251	−0.193
Pool	0.322	**−0.645**	0.002
Variance explained (%)	26.05	22.15	11.32

Loadings in bold italics were significant ($p < 0.05$).

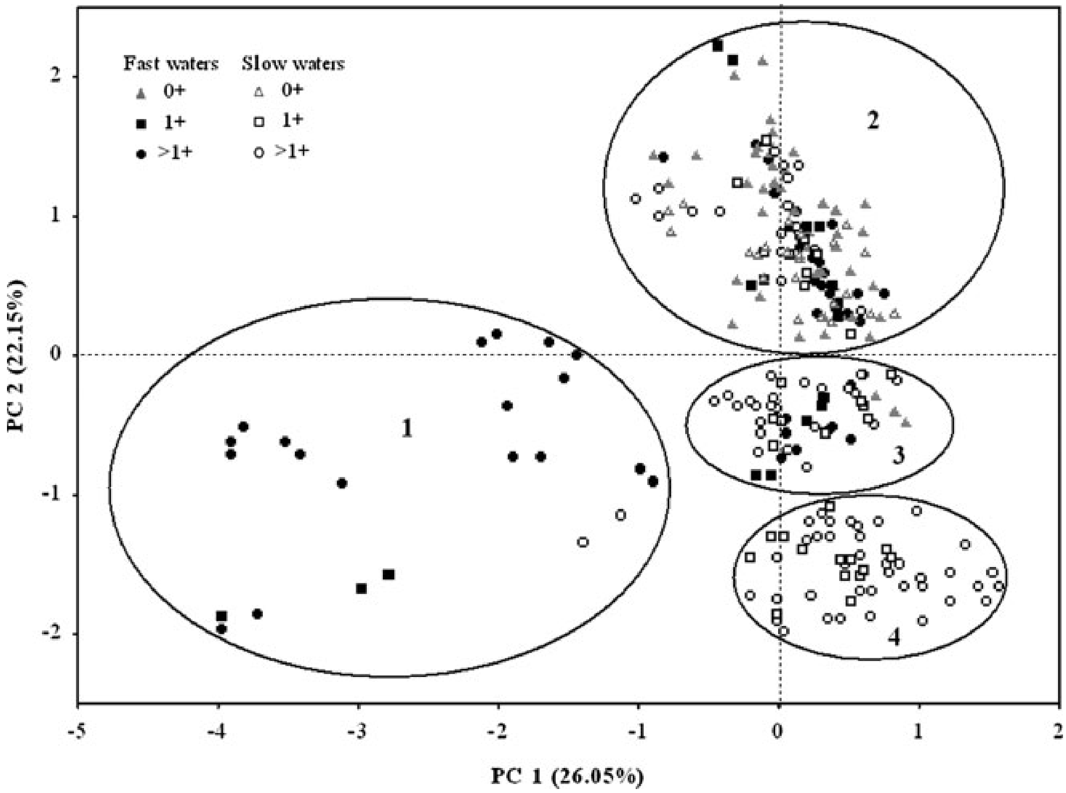

Figure 2. Plot of the factor scores for microhabitat use observations of brown trout individuals on the first two principal components for study sites. Drawn ellipses encompass individuals with similar microhabitat use

DOI: 10.1002/rra

PCA results were consistent with statistical comparisons. Almost all observations of 0+ trout were included in the second PCA group and, therefore, analyses did not reveal differences between water types in the use of water depth and velocity (KS two-sample test, $p > 0.05$) or structural elements (G test, $p > 0.05$). As observed in the PCA, juveniles and adult trout used deeper and slower habitats in the slow waters (KS two-sample test, $p < 0.05$), and the use of substrate and cover elements also changed significantly between water types (G test, $p < 0.05$). When comparisons were made between age-classes, young-of-the-year and adult trout displayed quite different habitat use patterns in both fast and slow waters, while juveniles presented a more plastic behaviour (Figure 2). In the slow waters, 1+ and >1+ trout used similar structural elements (G test, $p > 0.05$), water depths and velocities (KS two-sample test, $p > 0.05$), although only adults occurred at depths over 40 cm (Figure 3). These observations differed significantly from 0+ habitat use (KS two-sample test, G test, $p < 0.05$). In contrast, juveniles and younger individuals used similar structural features (G test, $p > 0.05$) and current velocities (KS two-sample test, $p > 0.05$) in the fast waters.

Habitat preference

Comparisons of used and available habitat (Figures 3 and 4) showed that all age-classes were selective with regard to velocity and water depth (KS one-sample test, $p < 0.05$) and channel index (G test, $p < 0.05$). However, no differences (i.e. no preference) were found between water depths used by 0+ trout and its availability in the fast waters.

Water depth preference curves differed between age-classes (Table III, Figure 3) with optimum depth increasing with age. Young-of-the-year trout showed a strong preference for shallow areas (optimum depth was 25 cm in both rivers) while older trout preferred deeper habitats (maximum preference between 35 and 50 cm for 1+ and 40 and 60 cm for >1+). Nevertheless, the shape of the curves varied between 1+ and >1+ age-classes, since the corresponding preference curves for 1+ displayed a bell shape. Preference curves for 0+ age-class were similar between water types, but somewhat different for 1+ and >1+, as most preferred depth increased with maximum available depth. However, the larger-trout/deeper-water pattern was maintained across water types.

Older trout selected slower habitats than younger ones in both fast and slow waters, although some differences between water types were observed (Table III, Figure 3). The most preferred current velocities of all age-classes in the fast waters (ranging from 0.8 $\mathrm{m\,s^{-1}}$ for 0+ to 0.5 $\mathrm{m\,s^{-1}}$ for >1+) were higher than in the slow waters (ranging from 0.4 $\mathrm{m\,s^{-1}}$ for 0+ to 0.2 $\mathrm{m\,s^{-1}}$ for >1+), even though 0+ trout also showed a high preference for fast current velocities in the slow waters.

Young-of-the-year were highly selective for boulders, used as velocity shelters, in both water types (Figure 4), thus explaining their greater preference for high to moderate current velocities. Juvenile and adult preferences were similar, although they changed between water types due to habitat availability. Therefore, 1+ individuals showed a moderate preference for boulders in spite of they exhibited a greater preference for the combination of vegetation and woody debris at the fast waters, and pools and undercut banks at the slow waters (Figure 4). A similar pattern was observed in adults, although they showed a lower selectivity for boulders. Larger trout mainly selected pool habitats in the slow waters, where the availability of pools was much higher, and this fact was reflected in the velocity preference curves, which presented the optimum value at low current velocities. In contrast, the presence of deep pools was almost negligible in the fast waters, wherein the deepest zones were located at the channel banks where the overhanging vegetation and tree roots provided velocity and visual protection (Figure 4).

Resource selection models revealed that all age-classes selected specific microhabitats when compared to availability. Habitat selection patterns of juveniles and adults differed between fast and slow waters ($p < 0.01$), as expected from univariate results. Consequently, separate RSFs were developed for each water type. According to the Hosmer–Lemeshow test, all regression models presented a high goodness-of-fit ($p > 0.76$). In the same fashion, the area under the ROC curve suggested a very good discrimination between habitat use and availability for all obtained models ($c > 0.841$).

The regression model for 0+ trout indicated that water depth and current velocity had significant nonlinear effects ($p < 0.005$, Table IV). Young-of-the-year trout also positively selected positions dominated by boulders ($p < 0.001$), meanwhile avoided undercut banks ($p < 0.1$). Sensitivity equalled specificity at approximately 0.21, where the correct classification rate (CCR) of the model was 79%.

DOI: 10.1002/rra

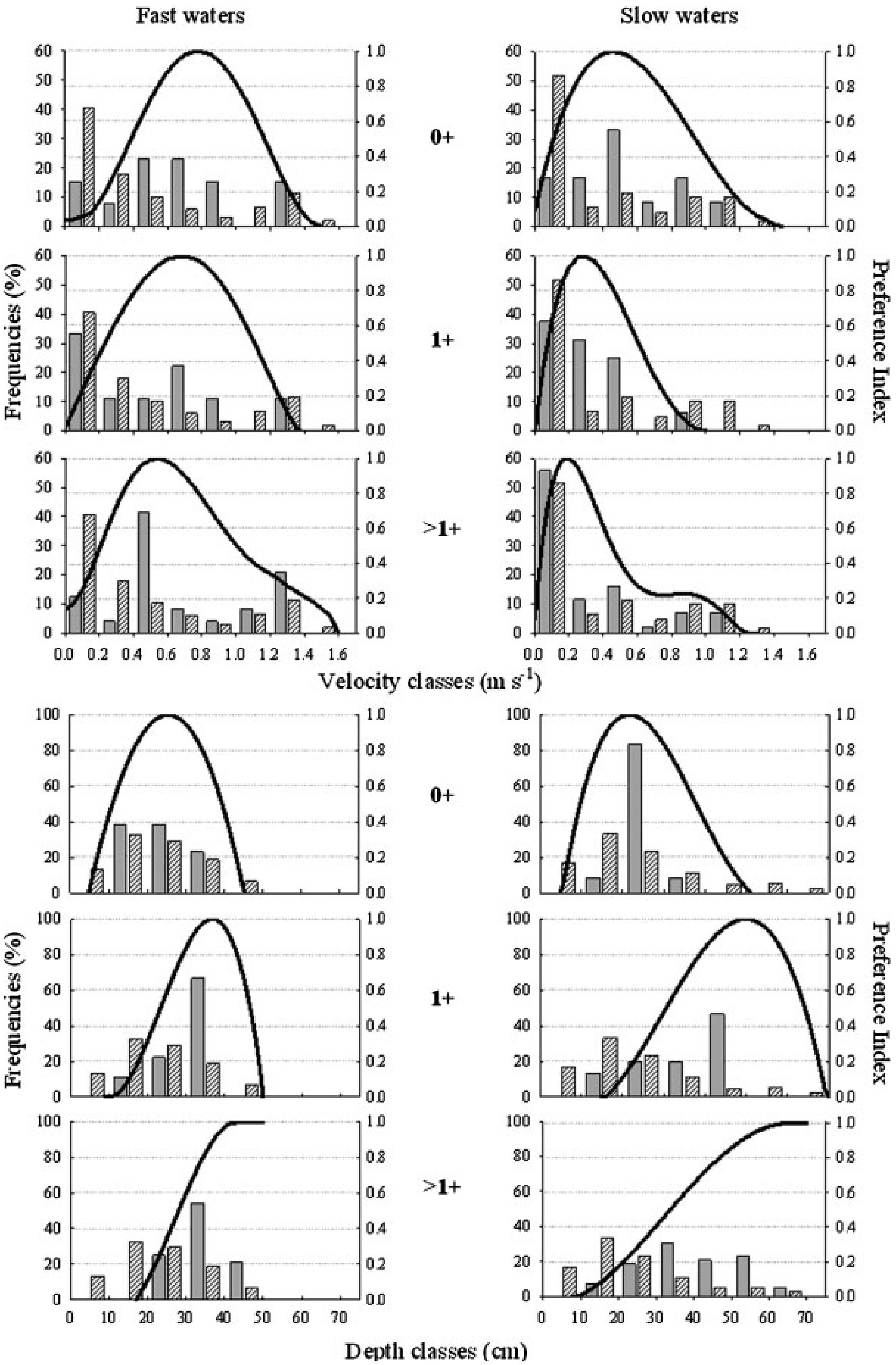

Figure 3. Frequency distributions of used (grey bars) and available (stripped bars) water depths and velocities at fast and slow waters for 0+, 1+ and >1+ age-classes. The black lines are the normalized preference curves

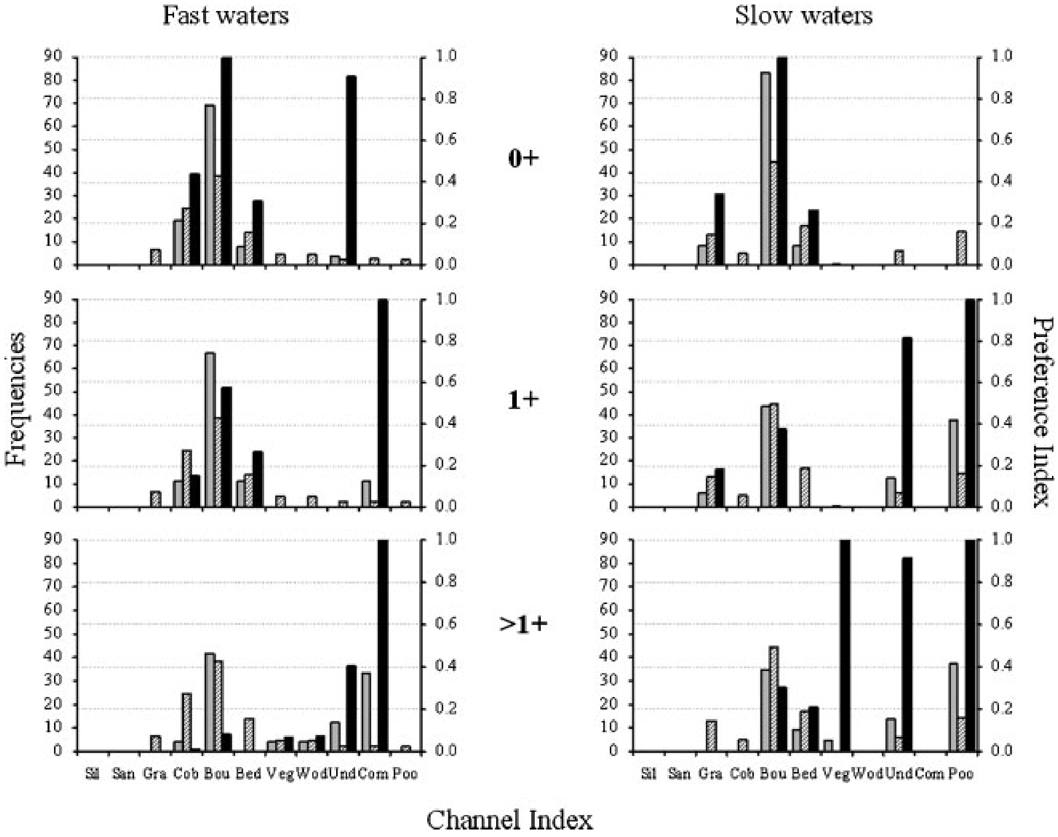

Figure 4. Frequency distributions of use (grey bars), availability (stripped bars) and preference index (black bars) of channel index categories: silt (Sil), sand (San), gravel (Gra), cobble (Cob), boulder (Bou), bedrock (Bed), vegetation (Veg), woody debris (Wod), undecut bank (Und), combined (Com) and pool (Poo), at fast and slow waters for 0+, 1+ and >1+ age-classes

Table III. Normalized water depth and current velocity preference functions for brown trout at different water types for 0+, 1+ and >1+ age-classes

Water type	Variable	Age-class	Function	r^2	p
Slow waters					
	Depth (d)				
		0+	$\mathrm{PI}=6\text{E-}5d^3+0.0065d^2+0.2005d--0.88782$	0.97	<0.05
		1+	$\mathrm{PI}=-3\text{E}-5d^3+0.0029d^2-0.0448d+0.1247$	0.97	<0.05
		>1+	$\mathrm{PI}=-8\text{E}-6d^3+0.0008d^2-0.0013d-0.0535$	0.98	<0.01
	Velocity (v)				
		0+	$\mathrm{PI}=2.2421v^3-6.3454v^2+4.4194v+0.0913$	0.96	<0.05
		1+	$\mathrm{PI}=8.1888v^3-15.115v^2+6.9236v+0.0547$	0.89	<0.05
		>1+	$\mathrm{PI}=15.679v^5-60.236v^4+84.78v^3-52.223v^2+12.116v+0.0789$	0.99	<0.05
Fast waters					
	Depth (d)				
		0+	$\mathrm{PI}=-8\text{E}-6d^3-0.0018d^2+0.1086d-0.4585$	0.88	<0.05
		1+	$\mathrm{PI}=-0.0001d^3+0.0074d^2-0.1164d+0.5354$	0.98	<0.01
		>1+	$\mathrm{PI}=-7\text{E}-5d^3+0.0054d^2-0.0951d+0.3997$	0.98	<0.01
	Velocity (v)				
		0+	$\mathrm{PI}=-1.1297v^2+1.763721v-0.04535$	0.68	<0.05
		1+	$\mathrm{PI}=0.275v^3-2.7074v^2+3.2053v+0.0557$	0.91	<0.05
		>1+	$\mathrm{PI}=-1.8814v^3-5.7687v^2+4.3859v+0.014$	0.83	<0.05

PI represents the normalized preference index. Coefficient of determination (r^2) and p-values (p) are also shown.

DOI: 10.1002/rra

Table IV. Coefficients of logistic regression models for resource selection functions of different brown trout age-classes by water type

Water type	Fast and slow waters		Fast waters				Slow waters			
Age-class	0+		1+		>1+		1+		>1+	
	b_i (SE)	*p*	b_i (SE)	*p*	b_i (SE)	*p*	b_i (SE)	*p*	b_i (SE)	*p*
Intercept	−10.832 (2.399)	<0.001	−107.108 (53.783)	0.046	−8.320 (1.905)	<0.001	−6.412 (2.762)	0.020	−3.529 (1.024)	0.001
Depth (cm)	0.593 (0.193)	0.002	6.503 (3.340)	0.052	0.109 (0.045)	0.016	0.234 (0.129)	0.069	0.088 (0.024)	<0.001
Depth^2	−0.120 (0.004)	0.003	−0.100 (0.052)	0.053			−0.002 (0.001)	0.092		
Velocity (m s^{-1})	5.267 (1.811)	0.004								
Velocity^2	−3.452 (1.207)	0.004								
Froude number					10.298 (4.927)	0.037	35.698 (13.010)	0.006	9.091 (4.544)	0.050
Froude number^2					−12.638 (5.937)	0.033	−70.126 (29.526)	0.018	−14.907 (6.468)	0.021
Boulder (%)	0.025 (0.006)	<0.001	0.021 (0.012)	0.092	0.032 (0.012)	0.010	−0.035 (0.017)	0.035	−0.023 (0.012)	0.068
Vegetation (%)										
Woody debris (%)										
Undercut bank (%)	−0.610 (0.034)	0.075			0.088 (0.048)	0.070				
Combined (%)			0.030 (0.019)	0.092						
Froude number × boulder									0.061 (0.036)	0.089
Froude number × vegetation					0.062 (0.031)	0.047				
Froude number × woody debris					0.223 (0.093)	0.017				

DOI: 10.1002/rra

Similarly, linear and quadratic terms of water depth ($p < 0.05$), and percentage of boulders ($p < 0.05$) were included in the model developed for 1+ trout in the slow waters (Table IV). The interaction between depth and velocity described by the FR was also included in the model ($p < 0.05$). In contrast, RSF for juvenile trout in the fast waters depended on water depth in a nonlinear way ($p < 0.05$), percentage of boulders and combined cover ($p < 0.1$), but not on water velocity. Sensitivity and specificity were equal at approximately 0.26 and 0.13, respectively. Cross-validated CCRs were 81.7 and 88.6%.

Since adult trout selected depth and velocity in opposite direction, the FR was an excellent predictor of their microhabitat selection patterns (Table IV). In both models, selectivity increased linearly with depth ($p < 0.05$) and nonlinearly with the FR ($p < 0.05$). The value at which the FR optimized selectivity was lower in the slow waters, where adults highly inhabited pool habitats. Adult trout selected boulders in the fast waters, while avoided them in the slow ones ($p < 0.05$). However, the model developed in the slow waters showed that adults selected substrate of boulders when occupying positions of higher FR (i.e. in riffles; $p < 0.1$). Finally, >1+ fish in the fast waters selected microhabitats connected to undercut banks ($p < 0.05$), as well as vegetation and woody debris but only when the FR increased ($p < 0.1$). Sensitivity and specificity curves crossed at 0.51 (slow waters) and 0.15 (fast waters). CCRs at optimum thresholds were 78.1 and 87.7%, respectively.

DISCUSSION

We observed a spatial segregation of age-classes in the depth gradient, a behaviour previously described in brown trout populations (e.g. Greenberg *et al*., 1996; Mäki-Petäys *et al*., 1997; Roussel and Bardonnet, 1997; Teixeira *et al*., 2006). Despite physical habitat is the major determinant of spatial variations in the abundance and distribution of most salmonid populations (Milner *et al*., 2003), the distribution of younger individuals at a reach scale is affected by older fish through intercohort competition or predation (Bult *et al*., 1999; Vehanen *et al*., 1999; Nordwall *et al*., 2001; Vik *et al*., 2001). This results in deeper areas being occupied by larger trout and younger individuals living in shallow habitats. In fact, in our studied rivers the use of pool habitats by juvenile and especially adult brown trout grew disproportionately when the availability of these habitats increased. We could also observe that juveniles were excluded from the deepest areas probably as a result of habitat competition with older individuals.

Most preferred territories for young-of-the-year trout were those with water depths between 20 and 35 cm, current velocities between 0.5 and 0.8 m s^{-1} and dominance of boulders. It contrasts with the majority of previous studies, which described the highest velocity preferences at low velocity values. However, it has been shown that for 0+ trout feeding on drift, habitats with fast currents close to velocity shelters where fish can rest after feeding are the most suitable, since they are the most profitable in terms of energy gain (Fausch and White, 1981; Fausch, 1984; Hughes and Dill, 1990). Further, Greenberg *et al*. (1996) also reported a preferred velocity for stone sheltered 0+ trout of 0.5–0.8 m s^{-1}, much higher values than those selected by similar sized trout in the open water. Young-of-the-year trout have a high motivation for foraging in summer (Vehanen *et al*., 2000) as a result of the necessity of reaching a size large enough to survive the first winter. In consequence, they would select the most energetically profitable positions in order to maximize growth. Therefore, according to our findings, current velocity would be the driving hydraulic variable provided that velocity shelters were abundant. Nevertheless, since most of used physical habitat models are still not capable of simulating such interaction, simulations based on curves presenting optimum preferences values at low current velocity are prone to predict biased maximum WUA values at very low flows (Railsback, 1999). This bias could be roughly overcome by using velocity curves as presented here conditioned by velocity shelter criteria.

Multivariate criteria can be used to deal with the fact that fish select suitable combinations of the hydraulic variables rather than in an independent way. Yet HSC bivariate models have not proved to be more realistic than univariate models in some cases (e.g. Lambert and Hanson, 1989), as it happened in our study for 0+ age-class. On the other hand, microhabitat selection patterns of juvenile and adult trout were best described by depth–velocity interactions, measured through the FR. Bivariate models suggest that depth could be the controlling factor between the hydraulic variables (Vismara *et al*., 2001) and our multivariate results confirmed that point. Contrarily to young-of-the-year trout, which would prefer to maximize energy intake, juvenile and adult trout would tend to diminish

DOI: 10.1002/rra

size-dependent predation risk and minimize energy expenditure by selecting deep slow-flowing habitats. Swimming performance increases with body size so larger trout can forage at larger distances to offset the possible reduction in food availability in these habitats. Consequently, the relative influence of current velocity in habitat selection may decrease as trout grow and depth may become the main limiting factor.

RSFs suggested that the interaction between depth and velocity was, however, somewhat driven by the structural features of the stream channel. Whenever present, adult trout mainly selected deep pools, partly as a form of overhead cover. In the slow waters, the largest proportion of adults was found in pool habitats with water depths over 45 cm and low FRs (<0.2). In contrast, when this habitat is absent, adult trout may use shallower water areas provided that overhead cover is present. This was illustrated in the fast waters, wherein the largest proportion of $>1+$ individuals occupied positions with water depths ranging 30–40 cm associated with undercut banks or a combination of overhanging vegetation and tree roots, avoiding the more exposed shallow pools. In water depths below 30 cm, adult trout were observed in fast-flowing riffles, selecting positions connected to velocity shelters such as large boulders and woody debris, which also act as visual shelters by creating surface turbulence (Smith and Brannon, 2007) and increasing habitat complexity and thus visual isolation (Dolinsek *et al*., 2007). These complex patterns were well described by the resource selection models developed in the present study through interaction terms between the FR and cover and substrate variables. It revealed a plastic behaviour where adults would use shallower and faster conditions than expected as long as cover elements are provided. In addition, we observed a visible shift in the habitat selection pattern of juveniles among water types, which was evidenced by the multivariate analyses (both PCA and RSFs), as a consequence of differences in cover availability and typology. In the fast waters, juvenile trout displayed a similar behaviour to young-of-the year trout while they behaved more alike to adult trout in the slow waters. This context-dependent pattern suggests that 1+ trout would select deep, slow-flowing habitats providing visual protection against predators whenever either its availability is high or adult density is low. In contrast, juveniles would use shallower and less covered positions whenever they are scarce or competition with adults is high. Thus the influence of cover on habitat selection remains along the whole life cycle of brown trout, being probably the most important single site attribute determining salmonid abundance (Armstrong *et al*., 2003).

Salmonids are quite plastic in their habitat use so that generalizations of HSC can be spread at most at a regional spatial scale (Mäki-Petäys *et al*., 1997). This has resulted in quite different HSC developed for brown trout in diverse locations (see Vismara *et al*., 2001, and HSC reviewed therein). While the larger fish-deeper habitat pattern is widely recognized, defined patterns for the rest of microhabitat variables remains elusive, especially for current velocity. This may be the consequence of the interactive nature of hydraulics and channel structure in creating suitable microhabitats. Our results suggest that in mountain Mediterranean streams structural features are at least as determinant in habitat selection as hydraulic conditions, since the presence or absence of visual and velocity shelters modified the preference of brown trout for depth and velocity conditions. Mediterranean hydrological regime is characterized by a winter and spring wet seasons followed by a marked dry season in summer, concurrently with the highest air temperatures. These adverse environmental conditions make pools and visually isolated areas increasingly preferred as trout age, the selection of protected areas at river margins increasing with growing river width, and younger individuals selecting boulder sheltered positions. This pattern matches with observations from other southern brown trout populations (Vismara *et al*., 2001; Teixeira *et al*., 2006), although not with northern populations where adult trout select pool habitats but avoid river margins, and younger individuals prefer instream vegetation at river margins over boulder sheltered positions (e.g. Greenberg *et al*., 1996; Mäki-Petäys *et al*., 1997; Heggenes, 2002).

The RSFs presented in this study are the first developed for brown trout in Mediterranean rivers, so comparisons with previous models were not possible. In addition, they are hardly comparable to the GAMs (including only hydraulic variables) developed by Jowett and Davey (2007) from one of New Zealand's largest rivers, where brown trout is besides an exotic species. However, our findings are consistent with previous studies describing abundance and distribution of brown trout in mountain streams. Our results suggest a high preference of young-of-the-year trout for positions in riffles, and despite juveniles and adults displayed a high plasticity in habitat selection, both age-classes selected deep slow-flowing habitats over fast-flowing habitats when the possibility of choice did exist. These models are in accordance to abundance patterns in mesohabitat types described by Baran *et al*. (1997) in Pyrenean Atlantic streams, which showed a high variability in juveniles, probably resulting from their high adaptability in habitat selection. Moreover, trout abundance in Pyrenean mountain streams is enhanced by water depth and habitat diversity, density in deep habitats being increased with the proportion of rapids and riffles in the reach as a consequence of habitat partitioning between 0+ and older trout (Baran *et al*., 1997). Our results for 1+ and >1+ trout are also consistent with Lamouroux and Capra's (2002) regional models, which predict increasing reach habitat quality and quantity for juveniles and adults at decreasing average reach SFR. Though, their results for 0+ trout contrast with ours, since we observed this age-class as a riffle-dweller (i.e. high SFR) and not a pool-dweller.

The use of joint frequency distributions of depth and velocity leads to a more realistic description of hydraulic conditions in stream reaches (Schweizer *et al*., 2007). It renders possible to best describe habitat preferences and to understand how fish change habitat selection patterns consistently to spatial variations in bivariate depth and velocity distributions, as we observed in juvenile and adult brown trout. However, our multivariate RSFs highlight that distribution of fish cannot be only defined by hydraulic patterns, depicting a scenario where position choice is driven by biologically important interactions among microhabitat variables. Consequently, as Smith and Brannon (2007) pointed out, models that simulate complex flow patterns in streams resulting from the interaction of cover and flow (Leclerc *et al*., 1995; Ghanem *et al*., 1996; Crowder and Diplas, 2000, 2002) may improve our ability to predict distribution and abundance of fish. Moreover, other important components of cover such as surface turbulence (Smith *et al*., 2005) should be also included in habitat models by using the FR (Bovee *et al*., 1998) which has been proved to be ecologically meaningful (Kemp *et al*., 2000; present study). Overlooking the interactive effects of the hydraulic variables and structural elements, which may play a key role on habitat selection in salmonids, could derive in unreliable habitat simulation results in relation to the shape, position and amount of habitat predicted by the WUA-discharge curves. It could lead to adopt erroneous management decisions concerning instream flows, since recommended flow regimes may influence habitat or aquatic populations in a negative way. Therefore, the application of RSF models coupled with GIS and complex two-dimensional flow models would be an effective tool for fish habitat assessment and management.

ACKNOWLEDGEMENTS

This study was funded by the Government of Navarre by means of an agreement with the Complutense University of Madrid. We thank two anonymous referees and the editor for their helpful comments on an earlier draft of the paper.

REFERENCES

Ahmadi-Nedushan B, St-Hilaire A, Berube M, Robichaud E, Thiemonge N, Bobee B. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. *River Research and Applications* **22**: 503–523. DOI: 10.1002/rra.918

Almodóvar A, Nicola GG. 1998. Assessment of a brown trout *Salmo trutta* population in the river Gallo (central Spain): angling effects and management implications. *Italian Journal of Zoology* **65**: 539–543.

Almodóvar A, Nicola GG. 1999. Effects of a small hydropower station upon brown trout *Salmo trutta* L. basin in the Hoz Seca River (Tagus, Spain) one year after regulation. *Regulated Rivers: Research and Management* **15**: 477–484. DOI: 10.1002/(SICI)1099-1646(199909/10)15:5<477::AID-RRR560>3.0.CO;2-B

Almodóvar A, Nicola GG. 2004. Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta* L. *Fisheries Management and Ecology* **11**: 173–182. DOI: 10.1111/j 1365-2400. 2004.00402.x

Almodóvar A, Nicola GG, Elvira B. 2006a. Spatial variation of brown trout production: the role of environmental factors. *Transactions of the American Fisheries Society* **135**: 1348–1360. DOI: 10.1577/T05-189.1

Almodóvar A, Nicola GG, Elvira B, García-Marín JL. 2006b. Introgression variability among Iberian brown trout Evolutionary Significant Units: the influence of local management and environmental features. *Freshwater Biology* **51**: 1175–1187. DOI: 10.1111/j. 1365-2427. 2006.01556.x

Almodóvar A, Nicola GG, Suárez J. 2002. Effects of fishery management on populations of brown trout *Salmo trutta* in central Spain. In *Conservation of Freshwater Fishes: Options for the Future*, Collares-Pereira MJ, Cowx I, Coelho MM (eds). Fishing News Books, Blackwell Science: Oxford; 337–345.

Almodóvar A, Suárez J, Nicola GG, Nuevo M. 2001. Genetic introgression between wild and stocked brown trout *Salmo trutta* in the Douro River Basin (Spain). *Journal of Fish Biology* **59**: 68–74. DOI: 10.1111/j. 1095-8649. 2001.tb01379.x

Armstrong JD, Kemp PS, Kennedy GJA, Ladle M, Milner NJ. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**: 143–170. DOI: 10.1016/ S0165-7836(02) 00160-1

Baran P, Delacoste M, Lascaux JM. 1997. Variability of mesohabitat used by brown trout populations in the French central Pyrenees. *Transactions of the American Fisheries Society* **126**: 747–757. DOI: 10.1577/1548-8659 (1997)26<0747:VOMUBB>2.3.CO;2

Bovee KD. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Washington, DC: USDI Fish and Wildlife Service. *Instream Flow Information Paper #21 FWS/OBS-86/7*. 235. http://www.fort.usgs.gov/Products/Publications/pub_abstract.asp?PubID=1183

Bovee KD, Lamb BL, Bartholow JM, Stalnaker CB, Taylor J, Henriksen J. 1998. Stream habitat analysis using the instream flow incremental methodology. *U.S. Geological Survey, Biological Resources Division Information and Technology Report USGS/BRD-98/04*. 131. http://www.mesc.usgs.gov/products/publications/3910/3910.pdf

Bult TP, Riley SC, Haedrich RL, Gibson RJ, Heggenes J. 1999. Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 1298–1306. DOI: 10.1139/cjfas-56-7-1298

Burnham KP, Anderson DR. 2002. *Model Selection and Multimodel Inference*: a Practical Information—Theoretic Approach (2nd edn). Springer-Verlag: New York.

Cheslak EF, García JC. 1988. An evaluation of the effects of various smoothing and curve-fitting techniques on the accuracy of suitability functions. *U.S. Fish and Wildlife Service Biological Report* **88**(11): 259–286.

Crowder DW, Diplas P. 2000. Evaluating spatially explicit metrics of stream energy gradients using hydrodynamic model simulations. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 1497–1507. DOI: 10.1139/cjfas-57-7-1497

Crowder DW, Diplas P. 2002. Vorticity and circulation: spatial metrics for evaluating flow complexity in stream habitats. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 633–645. DOI: 10.1139/f 02-037

Dolinsek IJ, Biron PM, Grant JWA. 2007. Assessing the effect of visual isolation on the population density of Atlantic salmon (*Salmo salar*) using GIS. *River Research and Applications* **23**: 763–774. DOI: 10.1002/rra.1024

Elvira B, Almodóvar A. 2001. Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. *Journal of Fish Biology* **59**: 323–331. DOI: 10.1111/j. 1095-8649. 2001.tb01393.x

Fausch KD. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* **62**: 441–451. DOI: 10.1139/z 84-067

Fausch KD, White RJ. 1981. Competition between brook trout (*S. fontinalis*) and brown trout (*S. trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1220–1227. DOI: 10.1139/f 81-164

Flosi G, Reynolds FL. 1994. California salmonid stream habitat restoration manual. California Department of Fish and Game, *Technical Report*, Sacramento.

Fore JD, Dauwalter DC, Fisher WL. 2007. Microhabitat use by smallmouth bass in an Ozark stream. *Journal of Freshwater Ecology* **22**: 189–199.

Ghanem AH, Steffler PM, Hicks FE, Katopodis C. 1996. Two-dimensional hydraulic simulation of physical habitat conditions in flowing streams. *Regulated Rivers: Research and Management* **12**: 185–200. DOI: 10.1002/(SICI)1099-1646(199603)12:2/3<185::AID-RRR389>3.0.CO;2-4

Grand TC, Dill LM. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behavioral Ecology* **8**: 437–447. DOI: 10.1093/beheco/8.4.437

Greenberg L, Svendsen P, Harby A. 1996. Availability of microhabitats and their use by brown trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in the river Vojman, Sweden. *Regulated Rivers: Research and Management* **12**: 287–303. DOI: 10.1002/(SICI)1099-1646(199603)12:2/3<287::AID-RRR396>3.0.CO; 2-3

Heggenes J. 2002. Flexible summer habitat selection by wild allopatric brown trout in lotic environments. *Transactions of the American Fisheries Society* **131**: 287–298. DOI: 10.1577/1548-8659 (2002) 131<0287:FSHSBW>2.0.CO;2

Heggenes J, Saltveit SJ. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L. *Journal of Fish Biology* **36**: 707–720. DOI: 10.1111/j. 1095-8649. 1990. tb04325.x

Heggenes J, Saltveit SJ, Lingaas O. 1996. Predicting fish habitat use responses to changes in water flow: Modelling critical minimum flows for Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*. *Regulated Rivers: Research and Management* **12**: 331–344. DOI: 10.1002/(SICI)1099-1646(199603)12:2/3<331::AID-RRR399>3.0.CO;2-E

Hosmer DW, Lemeshow S. 2000. *Applied Logistic Regression* (2nd edn). John Wiley and Sons, Inc, New York.

Hughes NF, Dill LM. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 2039–2048. DOI: 10.1139/f90-228

Jones NE, Tonn WM. 2004. Resource selection functions for age-0 Arctic grayling (*Thymallus arcticus*) and their application to stream habitat compensation. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1736–1746. DOI: 10.1139/F04-116

Jowett IG, Davey AJH. 2007. A comparison of composite habitat suitability indices and generalized additive models of invertebrate abundance and fish presence-habitat availability. *Transactions of the American Fisheries Society* **136**: 428–444. DOI: 10.1577/T06-104.1

Kemp JL, Harper DM, Crosa GA. 1999. Use of functional habitats to link ecology with morphology and hydrology in river rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**: 159–178. DOI: 10.1002/(SICI)1099-0755(199901/02)9:1<159::AID-AQC3 19>3.0.CO;2- M

Kemp JL, Harper DM, Crosa GA. 2000. The habitat-scale ecohydraulics of rivers. *Ecological Engineering* **16**: 17–29. DOI:10.1016/S0925-8574(00) 00073-2

Labonne J, Allouche S, Gaudin P. 2003. Use of a generalised linear model to test habitat preferences: the example of *Zingel asper*, an endemic endangered percid of the river Rhone. *Freshwater Biology* **48**: 687–697. DOI: 10.1046/j. 1365-2427. 2003.01040.x

Lambert TR, Hanson DF. 1989. Development of habitat suitability criteria for trout in small streams. *Regulated Rivers: Research and Management* **3**: 291–303. DOI: 10.1002/rrr.3450030128

Lamouroux N, Capra H. 2002. Simple predictions of instream habitat model outputs for target fish populations. *Freshwater Biology* **47**: 1543–1556. DOI: 10.1046/j. 1365-2427. 2002.00879.x

Leclerc M, Boudreault A, Bechara JA, Corfa G. 1995. Two-dimensional hydrodynamic modeling: a neglected tool in the instream flow incremental methodology. *Transactions of the American Fisheries Society* **124**: 645–662. DOI: 10.1577/1548-8659 (1995)24<0645:TDHMAN>2.3.CO;2

Leopold LB, Wolman MG, Miller JP. 1964. *Fluvial Process in Geomorphology*. W.H. Freeman and Co.: San Francisco, CA.

Maddock I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* **41**: 373–391. DOI: 10.1046/j.1365-2427. 1999.00437.x

Mäki-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. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 520–530. DOI: 10.1139/cjfas-54-3-520

Mallet JP, Lamouroux N, Sagnes P, Persat H. 2000. Habitat preferences of European grayling in a mediun size stream, the Ain River, France. *Journal of Fish Biology* **56**: 1312–1326. DOI: 10.1006/jfbi.2000.1252

Milner NJ, Elliott JM, Armstrong JD, Gardiner R, Welton JS, Ladle M. 2003. The natural control of salmon and trout populations in streams. *Fisheries Research* **62**: 111–125. DOI: 10.1016/S0165-7836(02) 00157-1

Nordwall F, Naslund I, Degerman E. 2001. Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 2298–2308. DOI: 10.1139/cjfas-58-11-2298

Orth DJ, Maughan OE. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. *Transactions of the American Fisheries Society* **111**: 413–445. DOI: 10.1577/1548-8659 (1982) 11<413:EOTIMF>2.0.CO;2

Parasiewicz P, Walker JD. 2007. Comparison of MesoHABSIM with two microhabitat models (PHABSIM and HARPHA). *River Research and Applications* **23**: 904–923. DOI: 10.1002/rra.1043

Platts WS, Megahan WF, Minshall GW. 1983. Methods for evaluating stream, riparian and biotic conditions. General Technical Report 138, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 76. http://www.treesearch.fs.fed.us/pubs/29138

Railsback S. 1999. Reducing uncertainties in instream flow studies. *Fisheries* **24**: 24–26.

Railsback SF, Harvey BC. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* **83**: 1817–1830. DOI: 10.1890/0012-9658 (2002)083[1817:AOHSRU]2.0.CO;2

Rosenfeld J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. *Transactions of the American Fisheries Society* **132**: 953–968. DOI: 10.1577/T01-126

Roussel JM, Bardonnet A. 1997. Diel and seasonal patterns of habitat use by fish in a natural salmonid brook: an approach to the functional role of the riffle-pool sequence. *Bulletin Français de la Pêche et de la Pisciculture* **346**: 573–588.

Schweizer S, Borsuk ME, Jowett I, Reichert P. 2007. Predicting joint frequency distributions of depth and velocity for instream habitat assessment. *River Research and Applications* **23**: 287–302. DOI: 10.1002/rra.980

Smith DL, Brannon EL. 2007. Influence of cover on mean column hydraulic characteristics in small pool riffle morphology streams. *River Research and Applications* **23**: 125–139. DOI: 10.1002/rra.969

Smith DL, Brannon EL, Odeh M. 2005. Response of juvenile rainbow trout to turbulence produced by prismatoidal shapes. *Transactions of the American Fisheries Society* **134**: 741–753. DOI: 10.1577/T04-069.1

Teixeira A, Cortes RMV, Oliveira D. 2006. Habitat use by native and stocked trout (*Salmo trutta* L.) in two Northeast streams, Portugal. *Bulletin Français de la Pêche et de la Pisciculture* **382**: 1–18.

Vehanen T, Bjerke PL, Heggenes J, Huusko A, Mäki-Petäys A. 2000. Effect of fluctuating flow and temperature on cover type selection and behaviour by juvenile brown trout in artificial flumes. *Journal of Fish Biology* **56**: 923–937. DOI: 10.1006/jfbi.1999. 1215

Vehanen T, Mäki-Petäys A, Aspi J, Muotka T. 1999. Intercohort competition causes spatial segregation in brown trout in artificial streams. *Journal of Fish Biology* **55**: 35–46. DOI: 10.1006/jfbi.1999. 0971

Vik JO, Borgstrom R, Skaala O. 2001. Cannibalism governing mortality of juvenile brown trout, *Salmo trutta*, in a regulated stream. *Regulated Rivers: Research and Management* **17**: 583–594. DOI: 10.1002/rrr.647

Vismara R, Azzellino A, Bosi R, Crosa G, Gentili G. 2001. Habitat suitability curves for brown trout (*Salmo trutta fario* L.) in the river Adda, Northern Italy: comparing univariate and multivariate approaches. *Regulated Rivers: Research and Management* **17**: 37–50. DOI: 10.1002/1099-1646(200101/02)17:1<37::AID-RRR606>3.0.CO;2-Q