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Ontogenetic and spatial variations in brown trout habitat selection

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Abstract – Habitat quality and quantity determine many biological processes and traits that directly affect the population dynamics of stream fishes. Understanding how habitat selection is adjusted to different ecological conditions is essential to improve predictive modelling of population dynamics. We describe brown trout *Salmo trutta* summer habitat selection patterns through univariate and multivariate habitat selection functions across defined river reach typologies. We sampled 44 sites and performed a principal component analysis that defined eight reach types differing in both local site and catchment-scale physical features. We observed ontogenetic changes in habitat selection, as trout preferred deeper and slower flowing water as they increased in size. Likewise, selectivity for different types of structural habitat elements changed through ontogeny. Both patterns were consistent across reach types. Moreover, we detected spatial variations in habitat selection patterns within age-classes among different reach types. Our results indicate that brown trout is a habitat generalist and suggest that spatial variations in habitat selection patterns are driven by physical and environmental factors operating at multiple spatial scales.

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Key words: habitat suitability; resource selection functions; habitat simulation models; PHABSIM; *Salmo trutta*; European Union Water Framework Directive

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Introduction

The River Continuum Concept by Vannote et al. (1980) formalised the hypothesis that systematic habitat changes along a downstream gradient have predictable consequences for biological processes ranging from energy flow to community structure (Rosenfeld et al. 2007). Thereafter, several studies focused on identifying the functional relationships between either fish community or population traits and their habitat (e.g., Blanck et al. 2007). In salmonids, spatio-temporal variations in population abundance and production are closely related to differences and changes in physical habitat conditions (Milner et al. 2003; Lobón-Cerviá & Rincón 2004). Further, together with other essential biotic and abiotic factors, habitat quality and quantity influence many population traits such as survival (Harvey et al. 2005; Lobón-Cerviá 2007), growth (Harvey et al. 2005; Dineen et al. 2007) or migration rates (Belanger & Rodriguez 2002), as well as pervasive biological processes like self-thinning (Lobón-Cerviá 2008), that affect population dynamics. Habitat selection is perceived as an adaptive complex behaviour faced by organisms at the individual level, but shapes many key biological processes whose patterns emerge at higher organisation levels (Grimm & Railsback 2005). It is then essential to understand how individuals adapt to different habitat conditions to predict the effects of habitat changes on stream fish population dynamics.

Habitat selection patterns of brown trout *Salmo trutta* are well established in broad terms (Armstrong et al. 2003), although this species can flexibly modify selection behaviour as a function of habitat features (Klemetsen et al. 2003). It is suggested the species occupy a relatively wide spatial niche with different optima within tolerable limits (Heggenes et al. 1999). Brown trout show a great plasticity in habitat selection, not only on a regional basis (Heggenes 2002) but also at a river reach level (Ayllón et al. 2009). Consequently, the transferability of habitat selection models is generally limited given the complexity to

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separate the effects of local physical conditions from those of factors varying at larger spatial scales (Lamouroux et al. 1999). Mediterranean-type streams are characterised by seasonal events of flooding and drying and strong intra and interannual flow variations (Gasith & Resh 1999). In these systems, aquatic organisms have developed different modes of adaptation (life history, behaviour) in response to the seasonal timing (and its predictability) of flow events (Lytle & Poff 2004). River hydrology may be an important driving force for trout population dynamics in southern Europe (Lobón-Cerviá 2009; Nicola et al. 2009). Given that physical habitat is much determined by the interaction of the structural features of the channel and the hydrological regime (Maddock 1999), brown trout may display a higher plasticity in habitat selection in variable environments than in stable ones. However, this question remains largely unknown despite its implications are essential when defining measures for strategic conservation and management of Mediterranean salmonid populations, which are increasingly threatened by habitat degradation and other anthropogenic impacts (Almodóvar & Nicola 1999, 2004; Almodóvar et al. 2006a,b). Specifically, implementation of the European Water Framework Directive (WFD; 2000/60/EEC) to assess the ecological status of rivers implies a clear knowledge of how species habitat selection patterns adapt to the prevalent habitat conditions at typified river typologies.

The objectives of this study were: (i) to define brown trout habitat selection patterns at river reach types differing in physical and environmental characteristics and (ii) to determine the factors driving selection patterns and the spatial scale over which they operate. For this purpose, habitat selection patterns were expressed as univariate microhabitat preference curves by age-class, so that they could be readily used in physical habitat simulation models. In addition, multivariate resource selection functions (RSF) were developed by age-class and river reach type, as fish typically do not select physical habitat features independently, but profitable combinations of them (e.g., Turgeon & Rodríguez 2005; Ayllón et al. 2009; Dixon & Vokoun 2009).

Study area

Brown trout habitat selection patterns were analysed in 44 study sites located in 20 rivers and streams from the Ebro river basin, a Mediterranean drainage, and 12 rivers and streams from the Bay of Biscay drainage (Fig. 1). The study area was situated between latitudes 42°29′ and 43°21′N and longitudes 0°43′ and 2°20′W. Selected sites cover the existing variability of environmental and geo-morphological conditions within the area. Sampling sites corresponded to first to fourth-order streams and were located at an altitude ranging from 115 to 870 m. Median summer discharge ranged from 0.05 to 1.77 $m^3 \cdot s^{-1}$ and mean daily summer temperature ranged between 11.6 and 16.6 °C. As selected rivers flow in a relatively small area, the differences in water ionic content do not cover a range

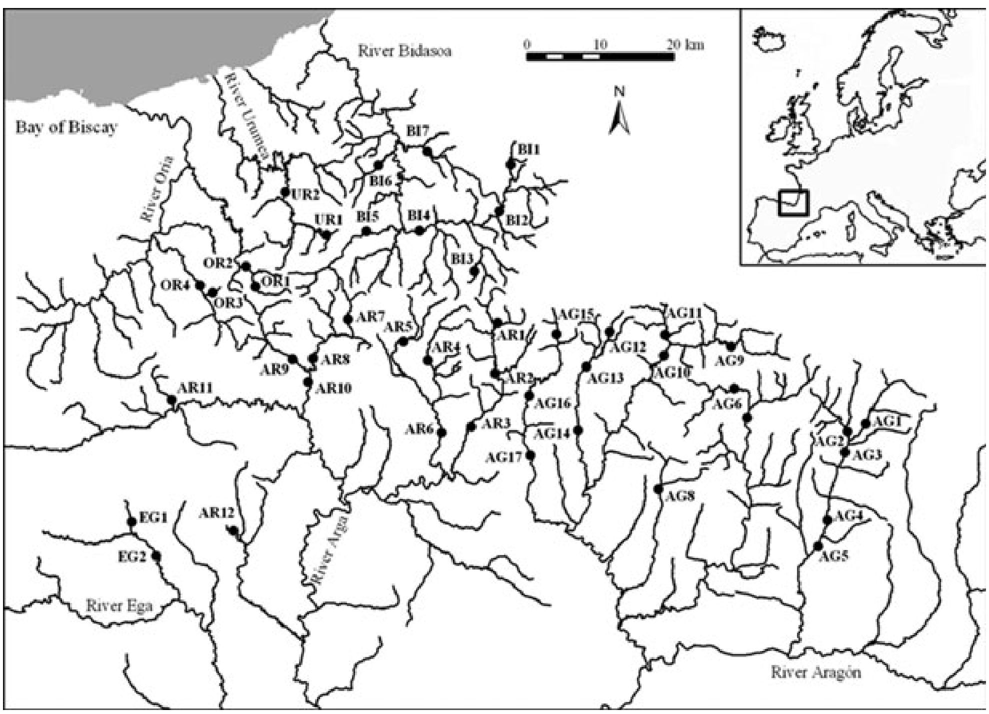

Fig. 1. Map of the study area showing the sampling sites.

wide enough to induce differences in growth and other life-history traits.

Materials and methods

Data collection

The study was carried out during the summer (from 20 July to 11 August) of 2004. Fish were sampled in each site by electrofishing using a 2200-W DC generator. Captured trout were measured (fork length, to the nearest mm) and weighed (to the nearest g). Scales were taken for age determination, so that each individual could be assigned to one of three age-classes, young-of-the-year (YOY, 0+), juvenile (1+) or adult (>1+). The fish were placed into 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 of each occupied position was calculated later according to the following equation (Gordon et al. 2004): $Fr = V/(g \cdot D)^{0.5}$, where V = mean column velocity, g = acceleration due to gravity and D = 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 each site. For this purpose, at least two transects were located at each mesohabitat type. Sample length at study sites was 5–7 times the average channel width, in accordance with the general precepts of alluvial river morphology on the spacing of successive riffles (Leopold et al. 1964). Average length of study sites was 55.2 ± 19.6 m, and average assessed area of study sites was 502.7 ± 285.7 m^2.

Total depth (cm), current velocity ($m \cdot s^{-1}$), substrate composition and cover were measured. The proportion (%) of substrate and cover was 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 <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 classified as vegetation (aquatic or overhanging), woody debris, undercut bank, combined (combination of vegetation and woody debris), pools and under cascade.

River reach classification

To define different river reach types, sites were grouped following a hierarchical, multiple-scale classification approach. For this purpose, 14 climatic, environmental, geological, morphological and hydraulic variables measured at different spatial scales were used (Table 1). Morphological and geological variables were employed to describe physical characteristics at higher spatial scales (watershed and river segment). Variables were calculated by means of ArcGis 9.1 software (ESRI Inc., Redlands, CA, USA). At the reach level, in addition to typical descriptors such as channel wetted width and mean and maximum water depth, the reach Froude number (ratio sensitive to the proportion of riffles vs. pools in reaches) and Reynolds number (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 & Reynolds 1994) ratio were used to compare the channel morphology and hydraulic geometry among study sites. The site average Froude and Reynolds numbers were calculated following

Table 1. Variables used to characterise the study sites and the spatial scale they apply.

Spatial scale	Descriptor	Variable	Description (units)
Watershed	Morphological	Watershed size	Surface drainage area (km^2)
		Distance from the origin	Kilometres from the main water source
		Stream order	Strahler method
	Geological	Basin shape	Drainage area/distance from the origin
Segment	Morphological	Slope	Mean river segment slope (%)
Reach	Morphological	Channel width	Reach-averaged wetted width at median summer discharge (m)
		Width/depth ratio	Width to depth ratio at median summer discharge
	Hydraulic	Mean depth	Reach-averaged water depth at median summer discharge (cm)
		Maximum depth	Maximum water depth at median summer discharge (cm)
		Froude number	Reach average Froude number
		Reynolds number	Reach average Reynolds number
		Slow/fast waters ratio	Relationship between slow and fast-flowing mesohabitat types
	Climatic	Water temperature	Summer average (°C)
	Environmental	Shadow	% of shadowed area in the channel

Lamouroux & Capra (2002). Water temperature and percentage of shadowed wetted channel area were considered as a result of their influence in microhabitat selection as individuals may seek thermal refugia under extreme temperature conditions. A principal component analysis (PCA) was performed then to summarise physical and environmental complexity, to explain spatial variability and to group similar sites. Alternatively, grouping of sites was also explored by means of a cluster analysis using Ward's method and Manhattan distances.

Microhabitat preference curves

First, differences in habitat use among age-classes by reach type and among sites by age-class were evaluated. We also compared habitat availability and use at each reach type to test for the existence of habitat selection. Continuous variables (water depth and velocity) were contrasted using a one-way analysis of variance (ANOVA), with a subsequent Tukey's test for comparison of means. A log-likelihood ratio test (*G*-test) was used for contrasting the categorical variable (channel index). As previous studies (e.g., Parra et al. 2009) have shown spatial variations in brown trout body size within the study area and habitat use is generally not only age but also size-dependent, individual length was included as a covariate in comparisons of habitat use among reach types by age-class. For all analyses, significance level was set at $\alpha = 0.05$.

Univariate preference curves for water depth, current velocity and channel index were developed by age-class. The channel index is a categorical variable used in habitat simulation models to describe the structural characteristics of the stream channel (see Bovee 1986). In this study, the channel index was established as a combination of the substrate and cover features previously defined. Channel index was classified in seven categories as some of the defined substrate and cover classes were merged into functional groups. Hence, cobble and boulder categories were grouped and considered as substrate velocity shelters. Silt and sand were treated as common category (fines). All cover categories were grouped as they refer to elements which mostly provide visual shelter against predators in locations near banks.

Channel index preference curves were built according to standard procedures (Bovee 1986), while univariate RSFs were developed to calculate depth and velocity preference curves. RSFs described the relationship between water depth and current velocity availability and the relative probability of habitat use. A RSF is then a probabilistic form of habitat suitability criteria (Ahmadi-Nedushan et al. 2006). RSFs were preferred over traditional standard methods as they are statistically and quantitatively more rigorous (Boyce et al. 2002). Functions were developed by means of logistic regressions, following the procedures described by Hosmer & Lemeshow (2000). Linear and polynomial functions were fitted to data. Significance level was set at $\alpha = 0.1$. Area under the receiver operating characteristic (ROC) curve was used to evaluate the accuracy of developed models. Finally, RSFs were normalised so that the minimum value was 0 and the maximum was 1.

Finally, we established three descriptors (optimum value, range of suboptimal values and usable range) to characterise the shape and position of calculated preference curves. The optimum value was defined as the value of the microhabitat variable that matches the maximum preference index, the range of suboptimal values as the range of the microhabitat variable having a preference index >0.6 and the usable range as the full range of conditions presenting a preference index over 0. Pair-wise correlation analyses (Pearson *r*) between descriptors of preference curves and hydraulic and physical variables were performed to determine factors driving possible differences in developed habitat suitability criteria among river reach types.

Multivariate resource selection function

Multivariate RSFs were also developed by means of multiple logistic regressions, according to the same procedures described for univariate RSFs. Depth, current velocity and Froude number were used as continuous predictors. The categories of channel index were included as categorical independent variables. A univariate analysis of each variable was performed to test for individual significance and to assess nonlinear effects. Meaningful interactions between microhabitat variables were also tested. For final model selection, the best subsets variable selection method was used, competing models being compared by means of the Akaike's Information Criterion adjusted for small samples (AICc; Burnham & Anderson 2002). The AICc allows objective selection of the model most consistent with the data while balancing the trade-off between precision and bias. The model with the lowest AICc was considered the best fit. Following recommendations from Hosmer & Lemeshow (2000), significance level was also set at $\alpha = 0.1$, as the use of a more traditional level (such as 0.05) may fail to identify variables known to be relevant for brown trout habitat selection. Area under the ROC curve and cross-validated classification accuracy were used to evaluate final models, the prediction threshold being chosen as the value where model sensitivity equalled specificity.

Results

River reach classification

The PCA revealed three main axes accounting for 70.3% of the total variance of physical and environmental characteristics among study sites (Table 2). The first factor was highly correlated to all variables describing geo-morphological features of sites at large spatial scales (watershed and river segment) as well as to variables measured at the reach scale that covariate with those ones, such as channel wetted width or Reynolds number. All variables characterising morphological and hydraulic attributes of river channel at the reach level scored highly in the second factor, except wetted width and Reynolds number. Finally, the third factor loaded heavily on water temperature and shadowed channel area, reflecting environmental characteristics that may affect position choice under extreme weather conditions. Visual inspection of the plots of the first and second components differentiated eight river reach types (RT; Fig. 2), this differentiation being confirmed by the cluster analysis. Scores of PC1 significantly differed between RTs (ANOVA, $F_{7,35} = 49.15$, $P < 0.001$). The Tukey test for unequal sample size showed two contrasting groups formed by RT1 and 2 and RT7 and 8, respectively, while the rest of RTs had scores that varied along the first axis in a gradient. In the same fashion, factor scores of PC2 significantly differed between RTs (ANOVA, $F_{7,35} = 32.12$, $P < 0.001$). The *post hoc* test defined two contrasting groups of reach types encompassing RTs 4 and 7, and RTs 2, 6 and 8, respectively, the rest of reach types following a gradient through the morpho-hydraulic axis. Therefore, sites were firstly clustered by attributes varying at large spatial scales, homogeneous groups being differentiated afterwards by reach-scale conditions. Physical and environmental characteristics of defined river reach types are summarised in Table 3.

Table 2. Factor loadings (unrotated) for the first three principal components (PCs) from principal components analysis of variation in physical and environmental characteristics of sampling sites in the study area.

Variable	PC1	PC2	PC3
Watershed size	**−0.834**	−0.116	−0.116
Distance from the origin	**−0.794**	−0.354	0.170
Stream order	**−0.770**	−0.104	0.129
Basin shape	**−0.736**	−0.015	−0.346
Slope	**0.686**	−0.070	−0.354
Channel width	**−0.835**	−0.255	−0.157
Width/depth ratio	−0.435	**−0.748**	−0.260
Mean depth	−0.484	**0.750**	0.083
Maximum depth	−0.483	**0.707**	0.155
Froude number	−0.232	**−0.568**	−0.208
Reynolds number	**−0.762**	0.239	−0.028
Slow/fast waters ratio	−0.328	**0.627**	−0.353
Water temperature	−0.228	−0.336	**0.792**
Shadow	0.478	−0.034	**0.565**
Variance explained (%)	39.9	21.0	9.4

Loadings in bold were significant ($P < 0.05$).

Microhabitat preference curves

Young-of-the-year trout used significantly shallower habitats than older trout in all RTs (ANOVA, $P < 0.001$), while juveniles and adults selected similar water depths except in pool-dominated reach types, RT4 and 7 (ANOVA, $P < 0.05$). However, 1+ trout never occupied positions at the deepest areas of the stream channel. All age-classes occupied positions with similar water velocities across different river typologies except in reaches presenting deeper pools, RTs 4, 5 and 7 (ANOVA, $P < 0.05$). In these reach types, water velocities used by juveniles were significantly lower than those used by YOY, while were significantly higher than those used by adults. In RT2, adult trout used significantly lower water velocities than younger individuals (ANOVA, $P < 0.001$). Finally, YOY trout used habitats presenting different structural attributes than habitats occupied by older individuals in all RTs (*G*-test, $P < 0.001$). Similarly, the use of structural elements of the channel differed between juveniles and adult trout in all RTs (*G*-test, $P < 0.05$).

After controlling for the effects of trout length, YOY fish used significantly different water depths (ANCOVA, $F_{7,427} = 5.06$, $P < 0.001$), velocities (ANCOVA, $F_{7,427} = 8.45$, $P < 0.001$) and structural elements (*G*-test, $G_{42} = 148.76$, $P < 0.001$) among the diverse RTs. Water depths (ANCOVA, $F_{7,368} = 8.32$, $P < 0.001$) and velocities (ANCOVA, $F_{7,368} = 7.29$, $P < 0.001$) as well as substrate and cover features (*G*-test, $G_{42} = 152.04$, $P < 0.001$) used by juvenile trout differed among RTs too. Finally, adults occupied habitats differing in depth (ANCOVA, $F_{7,474} = 9.05$, $P < 0.01$), velocity (ANCOVA, $F_{7,474} = 10.81$, $P < 0.001$) and structural (*G*-test, $G_{42} = 241.85$, $P < 0.001$) conditions across different RTs.

All age-classes were selective with regard to water depth at all reach types (ANOVA, $P < 0.05$), except 1+ age-class at RT7 where no selection occurred. Water velocities used by YOY trout differed from its availability in all reach types (ANOVA, $P < 0.05$) except in RT3 and 7. Juvenile trout showed a differential use of water velocity (ANOVA, $P < 0.05$) at RTs 2, 3 and 6, while adult individuals used a narrower range of water velocities than what was available (ANOVA, $P < 0.05$) at all reach types except at RTs 5, 7 and 8. All age-classes highly selected specific substrate and cover features at all RTs (*G*-test, $P < 0.001$).

Spatial (among RTs) and ontogenetic variations in microhabitat use resulted in differences in the shape

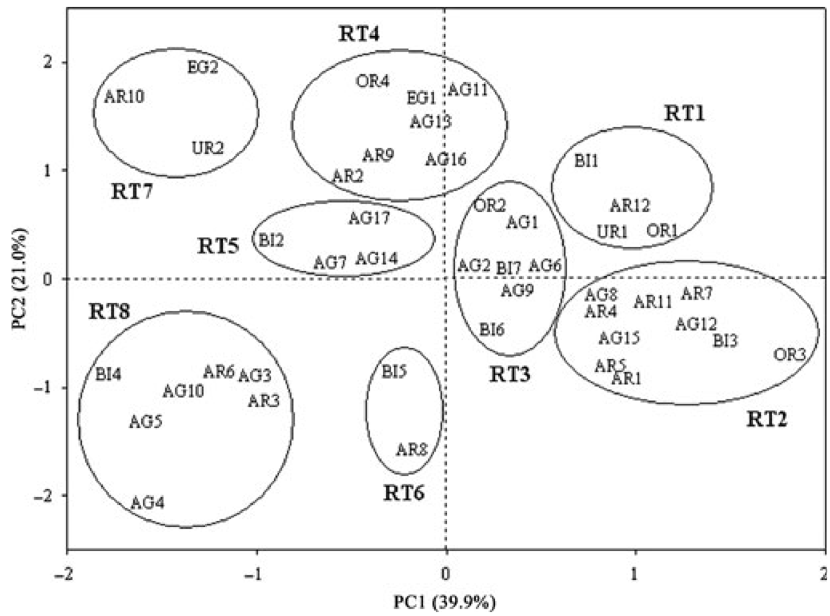

Fig. 2. Plot of the factor scores for physical and environmental characteristics of study sites on the first two principal components. Drawn ellipses encompass study sites with similar morphological, geological and hydraulic characteristics, thus defining eight river reach types (RT1-8).

Table 3. Physical and environmental characteristics of defined river reach types. Mean ± SD values of variables are shown, except in stream order where mode (range) is specified.

Variable	RT1	RT2	RT3	RT4	RT5	RT6	RT7	RT8
Watershed size (km^2)	12.5 ± 2.3	18.0 ± 11.6	51.6 ± 21.5	52.9 ± 25.9	108.4 ± 28.1	69.5 ± 11.0	129.3 ± 47.1	229.9 ± 72.8
Distance from the origin (km)	3.7 ± 2.7	6.6 ± 2.8	10.9 ± 2.0	11.3 ± 4.7	20.7 ± 6.1	15.3 ± 0.6	14.3 ± 2.6	26.8 ± 4.9
Stream order	2 (1–3)	2 (1–2)	2 (2–3)	3 (1–3)	3 (2–3)	3 (3)	4 (3–4)	4 (3–4)
Basin shape	4.7 ± 2.9	2.6 ± 1.3	4.7 ± 1.7	4.8 ± 2.6	5.5 ± 1.8	4.5 ± 0.5	9.2 ± 4.8	8.6 ± 2.1
Slope (%)	5.1 ± 1.2	4.7 ± 2.8	1.8 ± 1.5	1.2 ± 0.6	0.8 ± 0.1	1.0 ± 0.2	0.7 ± 0.1	0.6 ± 0.3
Channel width (m)	5.9 ± 0.8	4.7 ± 1.2	6.8 ± 1.1	10.0 ± 2.1	9.6 ± 2.1	11.6 ± 0.9	10.4 ± 0.2	16.0 ± 4.3
Width/depth ratio	30.2 ± 9.1	37.0 ± 10.3	34.1 ± 7.5	29.8 ± 3.6	34.4 ± 3.8	73.6 ± 11.9	26.1 ± 3.5	75.9 ± 24.6
Mean depth (cm)	20.6 ± 6.6	12.9 ± 2.3	20.3 ± 3.4	33.5 ± 5.1	27.9 ± 4.4	16.1 ± 3.9	39.2 ± 7.0	21.6 ± 3.9
Maximum depth (cm)	69.5 ± 11.0	37.1 ± 7.3	64.9 ± 12.2	93.3 ± 23.4	89.5 ± 21.8	51.5 ± 12.0	118.7 ± 32.0	59.4 ± 16.9
Froude number	0.09 ± 0.04	0.12 ± 0.05	0.14 ± 0.04	0.06 ± 0.02	0.11 ± 0.03	0.18 ± 0.02	0.14 ± 0.04	0.16 ± 0.06
Reynolds number	0.003 ± 0.001	0.001 ± 0.0005	0.004 ± 0.001	0.004 ± 0.001	0.005 ± 0.003	0.004 ± 0.001	0.010 ± 0.001	0.006 ± 0.003
Slow/fast waters ratio	0.6 ± 0.2	0.05 ± 0.1	0.5 ± 0.2	1.3 ± 0.6	0.4 ± 0.3	0.2 ± 0.3	1.1 ± 1.1	0.3 ± 0.3
Mean summer water temperature (°C)	12.7 ± 1.8	13.1 ± 1.5	13.5 ± 1.6	13.2 ± 1.1	15.3 ± 1.0	15.0 ± 0.9	13.2 ± 0.7	14.4 ± 1.1
Shadow (%)	47.0 ± 36.6	69.0 ± 27.7	34.2 ± 38.0	52.1 ± 37.1	21.4 ± 17.5	64.2 ± 36.2	31.1 ± 21.0	25.7 ± 17.7

and position of preference curves (Fig. 3). In juveniles and adults, the optimum and range of suboptimal and usable water depths increased when increasing the proportion of pools in the reach, and hence mean depth, and with the maximum depth of pools (Table 4). In YOY trout, the range of suboptimal and usable water depths also increased with increasing proportion of pools in the reach. Optimum depth was not related to the slow to fast waters ratio, but increased when increasing the maximum reach depth, although this trend was only marginally significant (Pearson's correlation analysis, $0.05 < P < 0.1$). The area under the ROC curve of the estimated models for YOY trout ranged from 0.67 to 0.77, while ranging between 0.68 and 0.94 for juveniles' models and between 0.70 and 0.96 for adults' functions. These values indicated from exceptional ($c > 0.90$) to low ($c < 0.70$) discrimination accuracies.

The spatial variations observed in the water velocity preference curves were also related to variations in reach-specific morphological and hydraulic conditions (Table 4). Optimum water velocity for YOY trout was higher and the range of suboptimal and useable velocities shrank in reaches presenting higher mean and maximum water depth, and hence lower width to depth ratio. Juvenile trout showed constant velocity optima, but range of suboptimal velocities increased when decreasing the Froude number. In contrast, adults showed a growing preference for slower water velocities as the proportion of pools in the reach increased and thus the Froude number decreased, but the range of suboptimal and usable water velocities

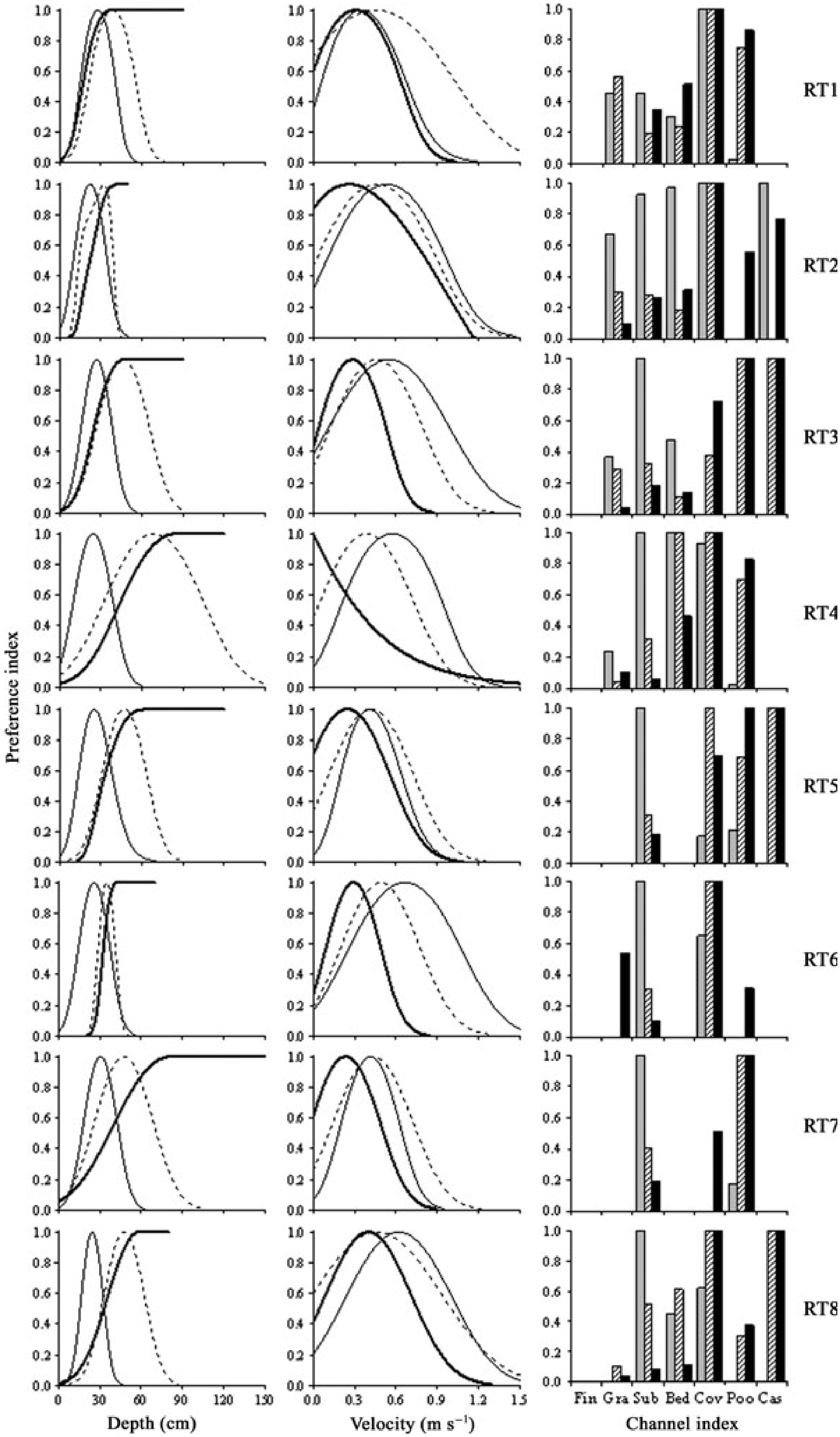

Fig. 3. Preference curves of depth, velocity and channel index for 0+ (thin line; grey bar), 1+ (dashed line; stripped bar) and >1+ (thick line; black bar) age-classes at eight river reach types (RT1 to RT8). Channel index categories refer to fines (Fin), gravel (Gra), cobble and boulder (Sub), bedrock (Bed), bank cover (Cov), pool, (Poo) and under cascade (Cas).

Table 4. Correlation coefficients (Pearson *r*) and their probabilities (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) for comparisons of descriptors of developed water depth and velocity preference curves (optimum value and range of suboptimal and usable values) with descriptors of the physical and hydraulic features of reach types.

Variable	Age-class	HSC descriptor	Channel width	Width/depth ratio	Mean depth	Maximum depth	Froude number	Reynolds number	Slow/fast waters ratio	PC1
Depth	0+	Optimum	0.10	−0.27	0.56	0.67	0.09	0.66	0.52	−0.33
		Suboptimal range	−0.38	−0.62	0.47	0.48	−0.66	−0.01	0.70*	0.27
		Usable range	−0.15	−0.58	0.62	0.71*	−0.35	0.40	0.70*	−0.13
	1+	Optimum	0.34	−0.27	0.73*	0.63	−0.51	0.33	0.76*	−0.41
		Suboptimal range	−0.01	−0.58	0.65	0.73*	−0.74*	0.22	0.87**	−0.12
		Usable range	0.14	−0.53	0.81*	0.78*	−0.61	0.42	0.75*	−0.35
	>1+	Optimum	0.38	−0.34	0.90**	0.83*	−0.32	0.67	0.75*	−0.61
		Suboptimal range	0.16	−0.57	0.95***	0.97***	−0.37	0.66	0.82*	−0.48
		Usable range	0.12	−0.53	0.91***	0.93***	−0.35	0.61	0.77*	−0.44
Velocity	0+	Optimum	0.52	0.75*	−0.35	−0.48	0.49	−0.19	−0.33	−0.26
		Suboptimal range	−0.04	0.48	−0.71*	−0.79*	0.25	−0.66	−0.50	0.34
		Usable range	0.08	0.59	−0.73*	−0.82*	0.26	−0.67	−0.56	0.26
	1+	Optimum	−0.22	−0.21	0.17	0.26	0.38	0.46	−0.21	−0.03
		Suboptimal range	−0.68	−0.67	−0.08	−0.02	−0.70*	−0.39	0.18	0.63
		Usable range	−0.63	−0.30	−0.36	−0.29	−0.19	−0.35	−0.15	0.64
	>1+	Optimum	0.22	0.56	−0.52	−0.46	0.74*	0.04	−0.73*	−0.15
		Suboptimal range	−0.33	0.01	−0.50	−0.47	0.13	−0.26	−0.59	0.34
		Usable range	0.21	−0.02	0.16	0.01	−0.57	−0.22	0.28	−0.05

were not related to any studied variable. The area under the ROC curve of the estimated models ranged from 0.66 to 0.84 in YOY trout, from 0.60 to 0.76 in juveniles and from 0.58 to 0.75 in adults. These values suggested that in some cases the discrimination between water velocity use and availability of developed models was very low, indicating no selection but a higher use of most available water velocities by trout.

Young-of-the-year trout showed the greatest preference for positions dominated by substrate velocity shelters in all RTs, while selectivity for gravels and cover elements increased with PC1 scores (Table 5). Preference for pool habitats increased with maximum reach depth. Juvenile trout mainly selected habitats characterised by presence of cover elements in all RTs (Table 5). Preference for pool habitats increased with their increasing proportion in the reach, as well as with mean and maximum reach depth. Selectivity for gravel and substrate velocity shelters varied with attributes operating at large spatial scales (summarised by PC1), though in opposite directions. Adult trout showed maximum preference for either pool habitats or positions dominated by cover elements depending on reach-specific conditions (Table 5). Contrarily to selectivity for bank cover, preference for pool habitats increased with increasing width to depth ratio and maximum reach depth. Adult selectivity for substrate

Table 5. Correlation coefficients (Pearson *r*) and their probabilities (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) for comparisons of calculated preference indexes of channel index categories with descriptors of the physical and hydraulic features of reach types.

Age-class	Category	Channel width	Width/depth ratio	Mean depth	Maximum depth	Froude number	Reynolds number	Slow/fast waters ratio	PC1
0+	Gravel	−0.84**	−0.44	−0.49	−0.47	−0.51	−0.74*	−0.15	0.92***
	Substrate velocity shelter	0.47	0.27	0.23	0.13	0.40	0.36	0.01	−0.55
	Bedrock	−0.31	−0.19	0.23	−0.34	−0.54	−0.59	0.09	0.46
	Bank cover	−0.39	0.04	−0.53	−0.57	−0.43	−0.81*	−0.18	0.70*
	Pool	0.06	−0.43	0.66	0.75*	−0.08	0.69	0.36	−0.41
1+	Gravel	−0.66	−0.29	−0.48	−0.42	−0.35	−0.59	−0.22	0.75*
	Substrate velocity shelter	0.83*	0.50	0.30	0.18	0.53	0.61	0.03	−0.86**
	Bedrock	0.48	0.25	0.14	−0.02	−0.29	−0.09	0.25	−0.27
	Bank cover	0.05	0.39	−0.53	−0.57	−0.20	−0.68	−0.44	0.30
	Pool	−0.12	−0.66	0.70*	0.76*	−0.38	0.51	0.70*	−0.19
>1+	Gravel	0.22	0.62	−0.41	−0.41	0.49	−0.24	−0.34	0.01
	Substrate velocity shelter	−0.75*	−0.50	−0.25	−0.12	−0.24	−0.24	−0.15	0.63
	Bedrock	−0.48	−0.38	−0.12	−0.16	−0.79*	−0.60	0.27	0.63
	Bank cover	0.03	0.47	−0.63	−0.71*	−0.13	−0.76*	−0.38	0.39
	Pool	−0.44	−0.89**	0.61	0.70*	−0.55	0.32	0.59	0.09

velocity shelters decreased with increasing channel width.

Multivariate resource selection functions

In general, area under the ROC curve and correct classification rate values indicated a good discrimination between habitat use and availability for all obtained multivariate models, although in a few cases the discriminatory power of developed functions was low ($c < 0.70$). Multivariate RSFs were consistent with the spatio-temporal patterns of habitat selection described by univariate preference curves, accurately detecting the most determinant microhabitat variables and their relative influence on habitat selection (Table 6). Interestingly, the Froude number was the best predictor to describe the interactive nature of hydraulic variables in almost all RTs for all age-classes. At channel positions where the Froude number was low, the categorical variable Pool (Po) allowed us to discriminate between pool habitats and areas of low water velocity located at shallow river margins.

Discussion

In this study, we observed broad spatial differences in brown trout habitat selection. Our results defined brown trout as a habitat generalist species and suggested that spatial variations in habitat selection patterns are driven by physical and environmental factors operating at multiple spatial scales. We also observed variations in habitat selection through ontogeny that were consistent across reach types, although the overlap levels in habitat preferences between life stages varied with reach type. Ontogenetic changes in habitat selection have been widely described in brown trout (see reviews by Armstrong et al. 2003 and Klemetsen et al. 2003; and references therein) and other species of freshwater fishes (e.g., Schlosser 1985; Sempeski & Gaudin 1995; Mann 1996; Hedger et al. 2005). Further, variations in habitat selection patterns have been observed in brown trout populations at shorter temporal scales, from seasonal (Rincón & Lobón-Cerviá 1993; Mäki-Petäys et al. 1997; Bremset 2000; Riley et al. 2006) to diel (Harris et al. 1992; Shuler et al. 1994; Bremset 2000; Bardonnet et al. 2006) time periods.

The larger fish-deeper habitat pattern held true across river reach typologies, as did the selection of slower water habitats as trout increased in size. These patterns are consistent with the ontogeny of habitat selection previously observed in the species, i.e. YOY trout inhabit fast-flowing riffles while older trout occupy deeper and slower water habitats (e.g., Heggenes 1996; Armstrong et al. 2003). The results of multivariate RSFs corroborated univariate patterns observed as YOY trout maximised habitat selectivity

Table 6. Multivariate resource selection functions of different brown trout age-classes by reach type.

Age-class	Reach type	Function	Area ROC	OT	CCR
0+	RT-1	$y = 5.93\ \mathrm{FR} - 6.86\ \mathrm{FR}^2 + 0.47\ \mathrm{COV} - 0.63\ \mathrm{PO} - 1.12$	0.735	0.37	70.5
	RT-2	$y = 7.47\ \mathrm{FR} - 7.79\ \mathrm{FR}^2 + 0.33\ \mathrm{SUB} + 0.52\ \mathrm{COV} + 0.52\ \mathrm{BE} - 0.76$	0.708	0.32	66.7
	RT-3	$y = 6.53\ \mathrm{FR} - 8.56\ \mathrm{FR}^2 + 1.20\ \mathrm{SUB} + 0.79\ \mathrm{BE} - 1.77$	0.775	0.21	72.7
	RT-4	$y = 15.56\ \mathrm{FR} - 18.16\ \mathrm{FR}^2 + 0.73\ \mathrm{SUB} + 1.40\ \mathrm{COV} - 0.76$	0.854	0.27	75.5
	RT-5	$y = 18.27\ \mathrm{FR} - 26.83\ \mathrm{FR}^2 + 0.57\ \mathrm{SUB} - 3.57$	0.851	0.23	79.9
	RT-6	$y = 6.77\ \mathrm{FR} - 7.16\ \mathrm{FR}^2 + 0.44\ \mathrm{SUB} - 2.40$	0.844	0.31	74.8
	RT-7	$y = 23.28\ \mathrm{FR} - 43.38\ \mathrm{FR}^2 + 1.39\ \mathrm{SUB} - 4.36$	0.882	0.14	84.3
	RT-8	$y = 2.32\ \mathrm{FR} - 10.95\ \mathrm{FR}^2 + 1.31\ \mathrm{SUB} + 1.25\ \mathrm{COV} - 2.32$	0.780	0.24	73.0
1+	RT-1	$y = 2.84\ \mathrm{FR} - 3.21\ \mathrm{FR}^2 + 0.49\ \mathrm{COV} + 0.34\ \mathrm{PO} - 0.26$	0.656	0.37	58.5
	RT-2	$y = 9.37\ \mathrm{FR} - 16.57\ \mathrm{FR}^2 + 0.82\ \mathrm{COV} - 0.68$	0.758	0.34	67.3
	RT-3	$y = 10.01\ \mathrm{FR} - 14.61\ \mathrm{FR}^2 + 0.56\ \mathrm{PO} - 0.66\ \mathrm{BE} - 2.22$	0.781	0.25	70.1
	RT-4	$y = 16.41\ \mathrm{FR} - 22.15\ \mathrm{FR}^2 + 1.64\ \mathrm{FR}\bullet\mathrm{SUB} + 1.54\ \mathrm{COV} + 1.0\ \mathrm{PO} - 0.83$	0.815	0.20	75.7
	RT-5	$y = 12.18\ \mathrm{FR} - 20.54\ \mathrm{FR}^2 + 1.23\ \mathrm{COV} + 0.76\ \mathrm{PO} - 1.28$	0.815	0.17	74.3
	RT-6	$y = 20.63\ \mathrm{FR} - 42.89\ \mathrm{FR}^2 + 0.98\ \mathrm{COV} - 3.05$	0.852	0.10	72.5
	RT-7	$y = 12.48\ \mathrm{FR} - 13.17\ \mathrm{FR}^2 + 0.75\ \mathrm{PO} - 4.07$	0.769	0.13	74.1
	RT-8	$y = 4.48\ \mathrm{FR} - 8.51\ \mathrm{FR}^2 + 0.40\ \mathrm{COV} - 2.12$	0.653	0.10	64.9
>1+	RT-1	$y = 5.74\ \mathrm{FR} - 12.89\ \mathrm{FR}^2 + 0.49\ \mathrm{COV} + 0.26\ \mathrm{PO} + 0.17$	0.686	0.48	61.5
	RT-2	$y = 0.14\ D + 1.40\ \mathrm{COV} + 0.93\ \mathrm{SUB} + 1.11\ \mathrm{BE} - 3.26$	0.851	0.26	74.8
	RT-3	$y = 20.72\ \mathrm{FR} - 61.85\ \mathrm{FR}^2 + 0.82\ \mathrm{COV} + 0.87\ \mathrm{PO} - 0.26$	0.757	0.34	67.0
	RT-4	$y = 7.73\ \mathrm{FR} - 17.34\ \mathrm{FR}^2 + 1.54\ \mathrm{COV} + 1.41\ \mathrm{PO} - 0.30$	0.797	0.38	79.9
	RT-5	$y = 7.01\ \mathrm{FR} - 18.77\ \mathrm{FR}^2 + 1.16\ \mathrm{COV} + 1.37\ \mathrm{PO} - 0.32$	0.852	0.37	76.5
	RT-6	$y = 26.07\ \mathrm{FR} - 76.94\ \mathrm{FR}^2 + 0.76\ \mathrm{COV} - 1.93$	0.818	0.16	75.3
	RT-7	$y = 3.87\ \mathrm{FR} - 6.27\ \mathrm{FR}^2 + 0.93\ \mathrm{COV} + 0.47\ \mathrm{PO} - 0.81$	0.696	0.18	64.4
	RT-8	$y = 9.37\ \mathrm{FR} - 19.56\ \mathrm{FR}^2 + 0.88\ \mathrm{COV} + 0.63\ \mathrm{PO} - 0.81$	0.785	0.09	67.7

Area under the ROC curve and correct classification rate (CCR) at optimum threshold (OT) values are shown.
FR, Froude number; *D*, water depth; SUB, substrate shelters; BE, bedrock; COV, cover; PO, pool.

at higher Froude values (>0.35) than juveniles (0.30–0.45) and adults (<0.25). According to Jowett (1993), these values categorise YOY stage as riffle-dwellers and adults as pool dwellers, whereas juvenile trout show a context-dependent behaviour. The observed spatial segregation between age-classes may be explained by the trade-off between energy gain and predation risk which tends to drive position choice in salmonids (Railsback & Harvey 2002). Thus, growing trout would select increasingly deeper habitats to obtain higher territory volumes to fulfil increasing metabolic demands (Ayllón et al. 2010) and reduce predation risk (Harvey & Stewart 1991). Furthermore, the Froude value of positions selected by different age-classes was highly correlated with the selection of substrate and cover elements. Kemp et al. (2000) showed that the occurrence of different structural elements in a river could be described by the Froude number. The range of Froude values that maximised habitat selectivity of brown trout in this study matches with that of the range of optimum values reported by Kemp et al. for substrate and cover conditions most frequently selected by different age-classes.

In homogeneous fast-flowing reach types, intercohort niche overlap was high, competition being relaxed with increasing stream size, as adult trout occupied covered positions at deep banks while younger individuals selected substrate sheltered microhabitats. Irrespective of stream size, intercohort segregation along the depth and velocity gradients increased with increasing proportion of pools relative to fast-flowing habitats and maximum depth. However, selectivity of pool habitats by adult trout was largely related to maximum depth of pools and interaction with stream size. That is, adults tend to select shallow pools in small streams, but not so in more exposed wide rivers in which only deep pools were selected. Besides, preference for pools by adults increased with the proportion of pools available in a given reach in a nonlinear fashion. This is consistent with the notion that fish density in deep habitats increases with the proportion of riffles available in a reach due to habitat partitioning between YOY and older trout (Baran et al. 1997), probably as a result of pool isolation (Lonzarich et al. 2000).

Multivariate RSFs identified substrate shelters as the most determinant structural feature of YOY trout habitat, whereas cover elements were highly selected only in headwater streams and homogeneous reach types. The analyses also showed that cover elements and pool habitat, when present, were the preferred structural features of juvenile and adult brown trout. The lack of pool habitat has been considered the main limiting factor for large trout, especially in small streams (Heggenes 1996). However, our results suggest that cover structures may play a similar role. Recent studies have also highlighted the pervasive function of cover elements in structuring the spatial distribution of brown trout individuals within streams (e.g., O′Connor & Rahel 2009). Considering the evolution of habitat selection through ontogeny observed in our study, cover availability may be regarded as the single most important attribute determining salmonid abundance, as suggested by Armstrong et al. (2003). The observed positive effects of restoration projects performing instream cover enhancement on fish populations support that point (Smokorowski & Pratt 2007).

Previously reported hydraulic and structural features selected by brown trout (e.g., Greenberg et al. 1996; Mäki-Petäys et al. 1997; Vismara et al. 2001; Heggenes 2002; Strakosh et al. 2003) differed between streams, but are within the ranges described in our study. These differences are not surprising, as habitat selection may change with variation of physical and environmental factors across geographic regions. In addition, many biotic factors that influence habitat selection may vary over space as well. In salmonid populations, different forms of competition and predation drastically alter habitat selection patterns (Grand 2002). On one hand, the type, number and size of predators affect prey size distribution (Byström et al. 2003), promoting differential behavioural responses of life stages concerning habitat selection. On the other hand, habitat selection varies for salmonids in sympatry as opposed to salmonids in allopatry (Näslund et al. 1998; Blanchet et al. 2007) and differs between populations closed to anadromy and populations where resident and anadromous forms coexist (Morinville & Rasmussen 2006).

The observed broad differences in habitat selection across reach types suggest a flexible habitat generalist strategy. Heggenes (2002) previously described such plastic behaviour in brown trout Atlantic populations and our study extends it to Mediterranean streams. The hierarchical ‘landscape filters’ concept by Poff (1997) predicts that distribution and abundance of species reflect their specific traits that allow them to pass through multiple habitat filters. At very large spatial scales, a wide variation in habitat selection patterns is expected for habitat generalist species when biotic and abiotic constraints differ between regions. In this study, we observed differences in selection patterns in streams within a relatively small study area and even within the same river basin, or stream. Optimal and suboptimal habitat preferences widely varied within usable limits among reach types, this variability being explained by changes in both local site features and catchment-scale variables. Variations in selection patterns observed along the morpho-geological watershed-scale gradient may represent the adaptation of individuals to downstream patterns of physical and biological factors along the river continuum. Site-specific hydraulic and morphological features finally shape general selection trends into reach type-specific patterns. This study represents a step forward from previous works (e.g., Heggenes 2002) in that it provides the general functional links between main physical attributes defining reach types and related habitat selection patterns. However, special emphasis should be placed in defining those links in a wider range of river typologies to improve results from physical habitat simulations or predictive population models.

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