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Original article

Intercohort density dependence drives brown trout habitat selection

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ABSTRACT

Habitat selection can be viewed as an emergent property of the quality and availability of habitat but also of the number of individuals and the way they compete for its use. Consequently, habitat selection can change across years due to fluctuating resources or to changes in population numbers. However, habitat selection predictive models often do not account for ecological dynamics, especially density dependent processes. In stage-structured population, the strength of density dependent interactions between individuals of different age classes can exert a profound influence on population trajectories and evolutionary processes. In this study, we aimed to assess the effects of fluctuating densities of both older and younger competing life stages on the habitat selection patterns (described as univariate and multivariate resource selection functions) of young-of-the-year, juvenile and adult brown trout *Salmo trutta*. We observed all age classes were selective in habitat choice but changed their selection patterns across years consistently with variations in the densities of older but not of younger age classes. Trout of an age increased selectivity for positions highly selected by older individuals when their density decreased, but this pattern did not hold when the density of younger age classes varied. It suggests that younger individuals are dominated by older ones but can expand their range of selected habitats when density of competitors decreases, while older trout do not seem to consider the density of younger individuals when distributing themselves even though they can negatively affect their final performance. Since these results may entail critical implications for conservation and management practices based on habitat selection models, further research should involve a wider range of river typologies and/or longer time frames to fully understand the patterns of and the mechanisms underlying the operation of density dependence on brown trout habitat selection.

1. Introduction

Ecologists have long been interested in the consequences of habitat selection for predicting the distribution and abundance of animals (Morrison et al., 2006). Habitat selection is of great importance in ecological theory because this behaviour is a primary way that mobile organisms adapt to changing conditions (Morris, 2011; Railsback et al., 2003), which is turning an increasingly critical matter in the light of current climate change. Habitat has been in fact the cornerstone for wildlife conservation and management, and so ecologists have developed sophisticated tools to characterize how species use space and resources (McLoughlin et al., 2010). These empirical models are often used to map habitat quality at different spatial scales and to inform managers on the future availability and use of habitats (Morris et al., 2008). At least three fundamental types of predictive models can be used to define habitat selection from correlative data: distributional or macrohabitat models, which predict the presence or absence of species at large spatial scales; capacity models, which predict density or population size when a taxon is present; and microhabitat models, which predict habitat associations at a fine spatial scale (Morrison et al., 2006; Rosenfeld, 2003).

Within the available procedures that quantify relative use of habitat resources, habitat suitability models (HSMs; e.g., Hirzel and Le Lay, 2008), and related resource selection and resource selection probability functions (RSFs; Manly et al., 2002) are probably the most popular. These models are easily linked to geographic information systems (GIS), so the rapid development of this technology and the growing availability of digital landscape data have rendered HSM and RSF models powerful tools for wildlife management and the identification of conservation priority sites (Boyce et al., 2002; Braunisch et al., 2008). Likewise, HSMs or RSFs developed at either the micro or mesohabitat scale have been the biological basis to

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assess instream flow needs and to predict spatio-temporal variations in fish population abundance when linked to hydraulic models within physical habitat simulation systems. Habitat modelling has stood factually in the centre of sustainable river management during the last decades (Ahmadi-Nedushan et al., 2006; Petts, 2009; Tharme, 2003). Yet predicting the proportional probability of use of resources by animals to forecast the future distributions of populations and species without accounting for ecological dynamics may lead to counterproductive conservation and management practices. At this respect, McLoughlin et al. (2010) recently drew attention to the often ignored but critical role of competition on resource use, especially density dependent habitat selection, and its implications for habitat modelling.

Habitat selection represents a stable evolutionary strategy shaped by density dependent selective forces (Morris, 2003). All organisms occupy habitat and most, if not all, are capable of density dependent habitat selection at some life stage and scale (Morris, 2011). Ultimately, habitat selection emerges only because organisms are better adapted to live and reproduce in some places than they are in others (Morris et al., 2008). Individuals choosing among habitats with different fitness functions should occupy those habitats that maximize their expectation of fitness. Yet in a finite world, fitness in a single habitat must, beyond a critical threshold, decline with increasing density (Morris, 2011). Consequently, habitat selection is an emergent property of the habitat quality function (how the fitness potential of an individual animal varies with habitat characteristics) and habitat availability (the characteristics of the available habitat patches) but also of the number of individual animals and the way they compete (Railsback et al., 2003). As a result, habitat selection can change among years, due to fluctuating resources, or to shifts in local distribution that result from changes in the abundance of territorial species (Boyce et al., 2002). In strongly territorial species, such as brown trout *Salmo trutta*, dominant individuals occupying preferred habitat at low densities might force subdominant ones or floaters into low-quality habitat at high densities, so that in years of relatively high abundance, individuals may occupy a wider range of habitats than in years where abundance is lower (Rosenfeld et al., 2005). A failure to take into account such variations can lead to poor model fit or inappropriate inferences of habitat selection patterns (Boyce et al., 2002).

Density dependent habitat selection is common in animal populations of many different taxa (e.g., Bartolino et al., 2011; Jensen and Cully, 2005; Manteuffel and Eiblmaier, 2008; Morris and MacEachern, 2010). In salmonids, intracohort density dependent habitat use and selection is well documented too (e.g., Bult et al., 1999; Gibson et al., 2008; Greenberg, 1994; Rosenfeld et al., 2005). However, interactions among competing year classes must be considered as well when developing habitat selection models. The habitat selection patterns of year classes overlap in a greater or lesser degree (e.g., Ayllón et al., 2009, 2010) and therefore there is scope for interactions between them depending on the quantity, quality and spatial arrangement of available habitats (Armstrong et al., 2003). Experimental studies (e.g., Bohlin, 1977; Knight et al., 2008; Vehanen et al., 1999) suggest that intercohort competition is a key mechanism to explain the distribution and abundance of individuals of competing cohorts. There is also increasing evidence that density of not only older but also younger cohorts can affect the numbers and traits of competing cohorts in salmonid wild populations (e.g., Einum et al., 2011; Kvingedal and Einum, 2011; Parra et al., 2012). However, little is known about whether (and if so, how) intercohort density dependence operates on habitat selection in the wild. To solve this question, in the present study we test the hypotheses that habitat selection patterns in the wild of a given brown trout year class would 1) change with density of older year classes, and 2) change with density of younger year classes.

2. Methods

2.1. Study area

Brown trout habitat selection patterns were analysed in three Iberian rivers; two of them (Cega and Eresma) are tributaries of the River Douro and the other one (Cabrillas) is a tributary of the River Tagus. One sampling site was selected in each river. The study area is situated between latitudes 41°45′ and 41°88′N and longitudes 2°07′ and 4°18′E. Physical, environmental and hydrological characteristics of rivers are described elsewhere (e.g., Almodóvar et al., 2006; Nicola and Almodóvar, 2004; Nicola et al., 2009). Brown trout is the prevailing fish species throughout the area, and its populations only comprise freshwater resident individuals.

2.2. Study design

Each sampling site was electrofished at the end of the summer during two consecutive years, 2009 and 2010. Electrofishing within each site took place at similar dates every year (during the last week of September). Prior to sampling, each site was blocked upstream and downstream with nets. The maximum likelihood method (Zippin, 1956) and the corresponding solution proposed by Seber (1982) for three removals assuming constant-capture effort, was applied to estimate fish densities (trout ha^{-1}) with variance for each age class (0+, 1+ and >1+) and sampling site. Significant changes in densities of the different age classes were observed (Table 1). In the River Eresma, 0+ density remained roughly stable across years while the presence of individuals of older age classes was almost inexistent in the year 2009. Hence, potential effects of the densities of older age classes on 0+ habitat selection could be explored. In the River Cega, 1+ density was similar across years while 0+ density was significantly lower in 2009 compared to 2010, whereas it was the opposite for >1+ trout, so it was possible to examine whether 1+ habitat selection was influenced by the densities of older and/or younger age classes. Finally in the River Cabrillas, there were no 0+ individuals any year so there were no 1+ trout in 2010, while >1+ age class was well represented both years. This situation allowed the analysis of potential effects of 1+ density on >1+ habitat selection.

2.3. Habitat data collection

Habitat surveys were carried out at the end of the summer of years 2009 and 2010, at similar dates every year but seven days later in time than quantitative samplings. Electrofishing using a 2200-W DC generator rather than snorkel survey was used to collect habitat use data because some areas within the sampling sites were either too shallow or too turbid to be snorkeled. The same river length was electrofished each year at each sampling site. Captured trout were measured (fork length, to the nearest mm) and weighed (to the nearest g), and scales were taken for age determination so that each individual could be assigned to one of three age classes, i.e. young-of-the-year (YOY; 0+), juvenile (1+) or adult (>1+). The fish were

Table 1
Densities (±standard error of the mean; individuals ha^{-1}) of 0+, 1+ and >1+ brown trout age classes by river and year of sampling.

River	Year	0+	1+	>1+
Eresma	2009	569.1 ± 51.4	28.5 ± 3.2	0.0 ± 0.0
	2010	882.1 ± 69.7	796.7 ± 82.7	1308.9 ± 75.8
Cega	2009	114.0 ± 12.6	615.7 ± 98.2	387.7 ± 24.1
	2010	433.3 ± 45.9	419.3 ± 60.9	114.0 ± 7.1
Cabrillas	2009	0.0 ± 0.0	719.6 ± 77.1	859.7 ± 11.1
	2010	0.0 ± 0.0	0.0 ± 0.0	1229.4 ± 16.9

placed into holding boxes to recover and then returned back to the stream. Numbered tags were dropped wherever a trout was captured and water depth, current velocity, substrate and cover were measured afterwards in a 1 m^2 quadrat. Depth and current velocity were measured once at the exact point where the trout was captured, while the proportion of substrate and cover were visually estimated within the surface of the 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, which were selected to best describe the longitudinal distribution of all types of mesohabitats present within each site (for further details on the methodology see Ayllón et al., 2009, 2010). Selected transects were marked in the field so that the same transects were used to collect availability data at both years. Average length, width and assessed area of sampling sites were 85.5 ± 31.3 m, 5.3 ± 2.5 m and 374.5 ± 56.2 m^2, respectively. Total depth (cm), current velocity ($m\ s^{-1}$), substrate composition and cover were measured. Depth and velocity were measured at the centre of each 1 m^2 quadrat, while the proportion (%) of substrate and cover were visually estimated within the surface of the 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 substrate shelter as any interstitial space available as shelter for the fish. 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.

2.4. Microhabitat suitability curves

Univariate suitability 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. In the present study, the channel index was established as a combination of the substrate and cover features previously defined. The channel index was classified in nine categories since some of the defined substrate and cover classes were merged into functional groups. Hence, silt and sand were treated as a common category (fines). We grouped cover categories which mostly provide visual protection against predators (overhanging vegetation and undercut banks), hereafter referred as Visual cover. These elements were differentiated from cover elements which provide both visual protection and refuge against excessively high flow velocities (aquatic vegetation, woody debris, combined cover and under cascade), hereafter referred as Combined cover.

Initially, channel index suitability curves were built through use-to-availability ratios: histograms of frequencies of use and availability were elaborated for each channel index category, and the corresponding suitability index was calculated as the ratio between proportional use and availability and then normalized, dividing by the maximum suitability value. Subsequently, univariate resource selection functions (RSF) were developed to calculate depth and velocity suitability 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 the use-to-availability ratio method since 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 and Lemeshow (2000). Linear and polynomial functions were fitted to data and year was included as a categorical variable to test for significant changes in depth and velocity functions across years. Competing models were compared by means of the Akaike's Information Criterion adjusted for small samples for final model selection (Burnham and Anderson, 2002). Significance level was set at $\alpha = 0.1$. Finally, RSFs were normalized so that the minimum value was 0 and the maximum was 1.

2.5. 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 continuous variable was performed to test for individual significance and to assess non-linear effects. Meaningful interactions between microhabitat variables were also tested. Year was also included as a categorical variable to model changes in habitat selection across years, and thus to indirectly account for yearly changes in the density of accompanying age classes. 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 and Anderson, 2002). The model with the lowest AICc was considered the best fit, as long as all variables included in the model were significant. Following recommendations from Hosmer and Lemeshow (2000), significance level was also set at $\alpha = 0.1$, since 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 was used to evaluate final models, the prediction threshold being chosen as the value where model sensitivity equalled specificity.

2.6. Data analysis

We compared river discharge during habitat survey periods between years at each river by means of one-way analysis of variance (ANOVA). We also tested for changes across years in habitat availability. Continuous variables (water depth and velocity) were contrasted using ANOVA, while log-likelihood ratio test (G test) was used for contrasting the categorical variable (channel index). For all analyses, significance level was set at $\alpha = 0.05$.

3. Results

There were no significant differences (ANOVA, $P > 0.05$) in river discharge between years in rivers Eresma and Cega. Consequently, there were no significant differences (ANOVA, $P > 0.05$) in water depth and current velocity across years in either river. Likewise, the structural characteristics of the channel did not differ significantly between years in either river (G test, $P > 0.05$). By contrast, in the River Cabrillas discharge was significantly higher (ANOVA, $P < 0.01$) in the year 2009, resulting in deeper and faster flow (ANOVA, $P < 0.01$). However, there were no significant differences (G test, $P > 0.05$) in the structural features of the channel between years. Values of habitat variables are shown in Table 2.

3.1. Effects of 1+ and >1+ densities on 0+ habitat selection

Univariate logistic regressions indicated that water depth and current velocity preferences of 0+ age class significantly changed across years in the River Eresma. In the absence of older individuals

Table 2
Characteristics of available habitat during years 2009 and 2010 in the study rivers. Standard deviation values are shown for mean depth and velocity.

Variable	Eresma		Cega		Cabrillas	
	2009	2010	2009	2010	2009	2010
Mean depth (cm)	15.1 ± 9.6	11.3 ± 3.7	24.0 ± 15.7	23.4 ± 14.6	29.1 ± 11.9	14.9 ± 9.2
Maximum depth (cm)	37	27	63	64	66	47
Mean velocity (m s^{-1})	0.29 ± 0.31	0.24 ± 0.33	0.14 ± 0.24	0.20 ± 0.37	0.70 ± 0.45	0.40 ± 0.26
Fines (%)	0.0	0.0	2.4	7.7	0.0	0.0
Gravel (%)	6.7	16.0	2.4	6.5	3.2	9.1
Cobble (%)	43.3	32.0	9.8	8.9	9.7	4.6
Boulder (%)	0.0	6.0	17.1	23.1	3.2	0.0
Bedrock (%)	0.0	6.0	0.0	0.0	36.1	28.8
Substrate shelter (%)	41.3	36.0	21.9	15.4	2.4	8.0
Visual cover (%)	4.3	2.0	4.9	0.0	22.6	22.7
Combined cover (%)	4.3	2.0	17.1	20.8	22.8	22.3
Pool (%)	0.0	0.0	24.4	17.7	0.0	4.5

(year 2009), 0+ trout selected deeper and slower habitats (Fig. 1). Likewise, structural elements used by 0+ trout changed across years (*G* test, $P < 0.05$) so that selectivity for combined cover and substrate shelters increased while selectivity for boulders decreased when older individuals were absent.

The observed changes in cover and substrate univariate selection patterns were reflected in the multivariate RSF, while changes in the selectivity for hydraulic variables were not significant after controlling for the effects of structural elements (Table 3). In the absence of older individuals, 0+ trout selected positions presenting substrate shelters (included in the RSFs developed for both 1+ and >1+ age classes in the year 2010) and combined cover (included in the RSF developed for 1+ trout in the year 2010) that were not selected when older age classes were present.

3.2. Effects of 0+ and >1+ densities on 1+ habitat selection

Univariate logistic regressions showed that water depth and current velocity preferences of 1+ age class did not differ significantly across years in the River Cega (Fig. 2). By contrast, use of structural elements by 1+ trout significantly varied between years (*G* test, $P < 0.01$). Selectivity for visual and combined cover and pools increased while selectivity for gravels and boulders decreased in the year 2010, when >1+ density decreased.

RSF developed for 1+ age class showed that positions with substrate shelters or combined cover were selected irrespective of densities of accompanying age classes, but selectivity for boulders and visual cover changed with year of sampling (Table 4). Positions offering visual cover, which were highly selected by >1+ trout,

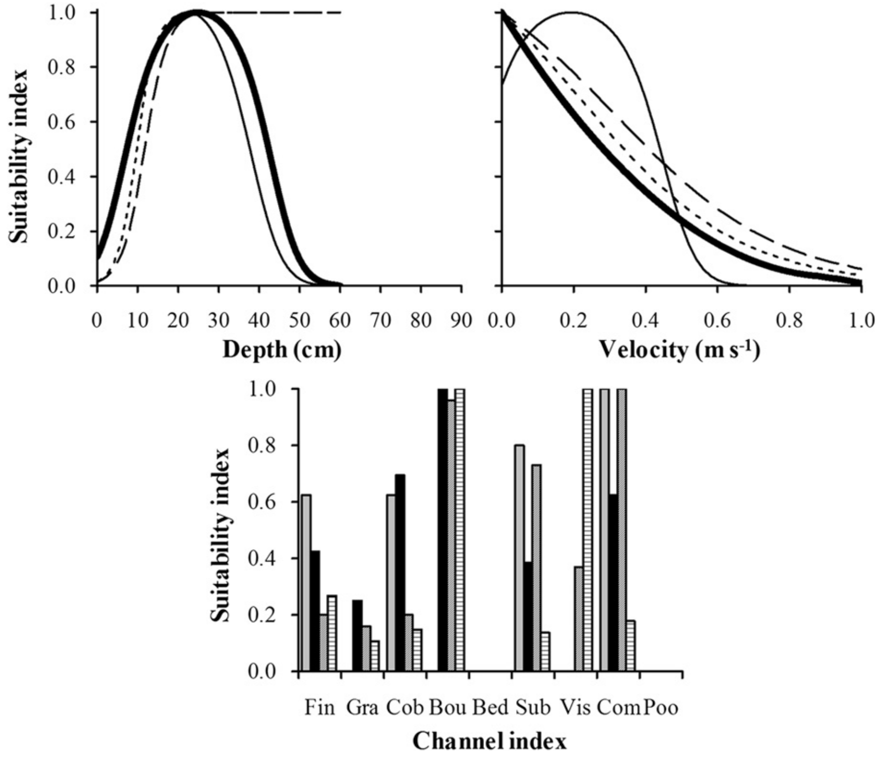

Fig. 1. Univariate preference curves of depth, velocity and channel index for 0+, 1+ and >1+ age classes at River Eresma. Thick and thin lines represent preference curves of 0+ age class at year 2009 and 2010, respectively. Dotted and dashed lines correspond to preference curves of 1+ and >1+ age classes, respectively, at year 2010. Channel index categories refer to fines (Fin), gravel (Gra), cobble (Cob), boulder (Bou), bedrock (Bed), substrate shelters (Sub), visual cover (Vis), combined cover (Com) and pool (Poo). Grey and black bars represent preference of 0+ age class at year 2009 and 2010, respectively. Leaning- and flat-stripped bars correspond to preference curves of 1+ and >1+ age classes, respectively, at year 2010.

Table 3
Multivariate resource selection functions of different brown trout age classes at River Eresma. Sample size (N), area under the ROC curve and correct classification rate (CCR) at optimum threshold (OT) values are shown.

Age class (year)	Variables	Estimate	P	N	Area ROC	OT	CCR
0+ (2009–2010)	Intercept	−3.11	0.023	76	0.76	0.67	71.1
	Depth	0.42	0.009				
	Depth^2	−0.009	0.024				
	Boulder*Year (2010)	0.84	0.059				
	Substrate shelter*Year (2009)	0.53	0.026				
	Combined cover*Year (2009)	0.98	0.070				
1+ (2010)	Intercept	2.28	0.003	74	0.70	0.75	69.2
	Froude number	−4.73	0.049				
	Boulder	0.90	0.090				
	Substrate shelter	0.94	0.089				
	Combined cover	1.37	0.071				
>1+ (2010)	Intercept	3.55	0.014	71	0.87	0.80	73.7
	Froude number	−9.61	0.018				
	Froude number*Substrate shelter	8.09	0.047				
	Substrate shelter	−1.39	0.015				
	Visual cover	1.90	0.090				

were only selected by 1+ trout when density of older trout was low. However, pool habitats were not included in the model best explaining 1+ habitat selection.

3.3. *Effects of 1+ density on >1+ habitat selection*

In the River Cabrillas, univariate analyses indicated that >1+ trout selected shallower habitats in the year 2010, when the 1+ age class was absent (Fig. 3). No changes in velocity preferences were found. Structural elements used by >1+ trout changed across years (G test, $P < 0.01$) resulting in a higher selectivity for bedrock, substrate shelters and combined cover when 1+ trout were absent.

Developed RSF mirrored univariate selection patterns of hydraulics and combined cover, but did not include any other structural variable that were a main determinant of 1+ position choice (Table 5).

Based on the area under the ROC curve values of regression models, discrimination accuracy between habitat use and availability ranged from acceptable ($c = 0.70$) to excellent ($c = 0.90$). Likewise, correct classification rates at optimum threshold (between 70 and 84%) indicated a good performance for all fitted models (see Tables 3–5).

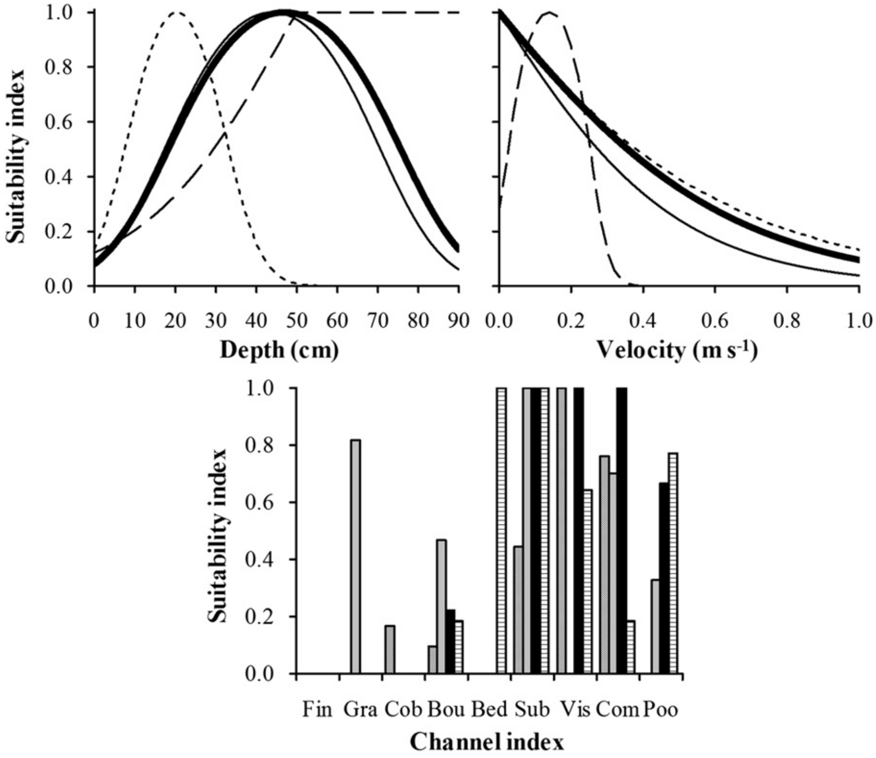

Fig. 2. Univariate preference curves of depth, velocity and channel index for 0+, 1+ and >1+ age classes at River Cega. Thick and thin lines represent preference curves of 1+ age class at year 2009 and 2010, respectively. Dotted lines correspond to preference curves of 0+ age class at year 2010. Dashed lines correspond to preference curves of >1+ age class at year 2009. Channel index categories refer to fines (Fin), gravel (Gra), cobble (Cob), boulder (Bou), bedrock (Bed), substrate shelters (Sub), visual cover (Vis), combined cover (Com) and pool (Poo). Grey and black bars represent preference of 1+ age class at year 2009 and 2010, respectively. Leaning-stripped bars correspond to preference curves of 0+ age class at year 2010. Flat-stripped bars correspond to preference curves of >1+ age classes at year 2009.

Table 4
Multivariate resource selection functions of different brown trout age classes at River Cega. Sample size (*N*), area under the ROC curve and correct classification rate (CCR) at optimum threshold (OT) values are shown.

Age class (year)	Variables	Estimate	*P*	*N*	Area ROC	OT	CCR
0+ (2010)	Intercept	1.57	0.018	91	0.85	0.48	80.0
	Velocity	−6.01	0.024				
	Substrate shelter	1.78	0.004				
	Visual cover	1.45	0.003				
	Combined cover	1.37	0.003				
1+ (2009–2010)	Intercept	−2.99	0.002	108	0.77	0.60	70.4
	Depth	0.17	0.005				
	Depth^2	−0.002	0.053				
	Substrate shelter	0.98	0.004				
	Combined cover	0.84	0.011				
	Boulder*Year (2009)	0.89	0.021				
	Visual cover*Year (2010)	0.95	0.018				
>1+ (2009)	Intercept	0.15	0.806	89	0.82	0.68	74.7
	Froude number	32.49	0.020				
	Froude number^2	−165.37	0.027				
	Substrate shelter	1.10	0.018				
	Visual cover	0.70	0.090				
	Pool	0.93	0.038				

4. Discussion

We observed that all the three brown trout age classes studied were selective in their choice of stream position but changed their selection patterns across years. These changes were consistent with variations in the densities of older age classes but seemed not to be influenced by the density of younger age classes. That is, trout of a given age increased selectivity for positions highly selected by older individuals when they were absent or present at lower densities, but this pattern did not hold when the density of younger age classes varied.

Position choice in salmonids is often traded-off between energy gain and predation risk (Railsback and Harvey, 2002). Yet Ayllón et al. (2009, 2010) showed that, within the limits of this trade-off, YOY brown trout tend to select in summer the most energetically profitable positions in order to maximize growth, probably because of the necessity of reaching a size large enough to survive the first winter. Meanwhile, older trout tend to select increasingly deeper and covered habitats to reduce size-dependent predation risk. That is, the direction of the maximizing growth-minimizing predation risk trade-off would shift along ontogeny. This was evidenced in the River Eresma, where adults highly selected elements providing

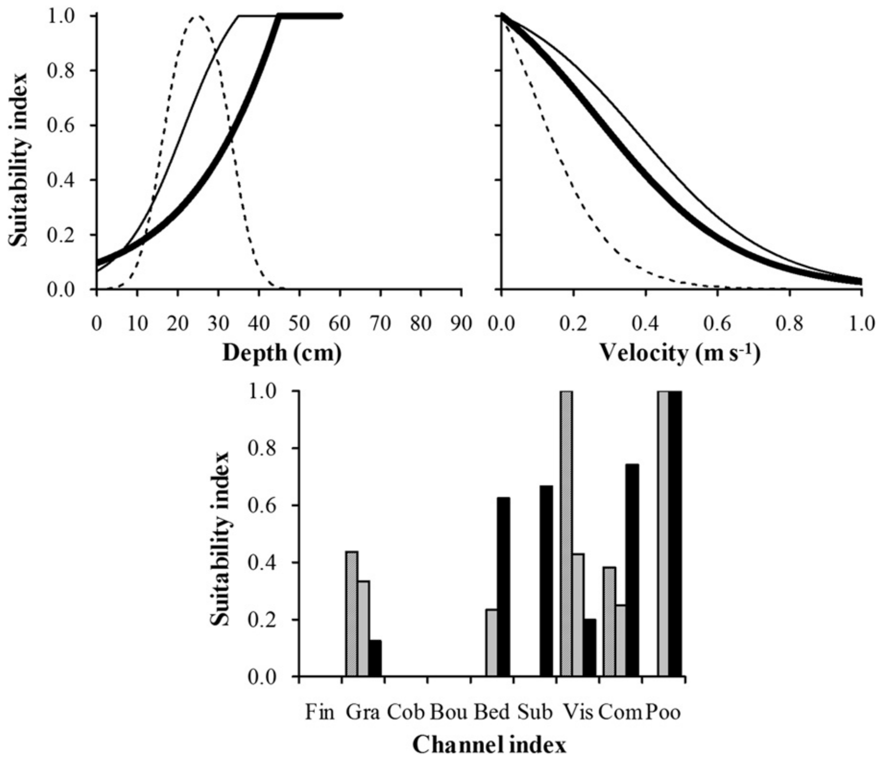

Fig. 3. Univariate preference curves of depth, velocity and channel index for 1+ and >1+ age classes at River Cabrillas. Thick and thin lines represent preference curves of >1+ age class at year 2009 and 2010, respectively. Dotted lines correspond to preference curves of 1+ age class at year 2009. Channel index categories refer to fines (Fin), gravel (Gra), cobble (Cob), boulder (Bou), bedrock (Bed), substrate shelters (Sub), visual cover (Vis), combined cover (Com) and pool (Poo). Grey and black bars represent preference of >1+ age class at year 2009 and 2010, respectively. Stripped bars correspond to preference curves of 1+ age class at year 2009.

Table 5
Multivariate resource selection functions of different brown trout age classes at River Cabrillas. Sample size (*N*), area under the ROC curve and correct classification rate (CCR) at optimum threshold (OT) values are shown.

Age class (year)	Variables	Estimate	*P*	*N*	Area ROC	OT	CCR
1+ (2009)	Intercept	1.45	0.009	77	0.90	0.68	83.6
	Velocity	−8.84	0.003				
	Visual cover	−1.32	0.005				
>1+ (2009–2010)	Intercept	0.75	0.290	120	0.89	0.60	80.0
	Depth	0.05	0.072				
	Velocity	−5.55	<0.001				
	Depth*Year (2010)	0.03	0.005				
	Pool*Year (2009)	0.88	0.072				
	Combined cover*Year (2010)	0.55	0.052				

visual cover while only selected substrate sheltered positions when connected to fast currents (high Froude number). In this river, juvenile and YOY trout were excluded by adults from the visually covered habitats, but while juveniles selectively occupied shallower positions presenting substrate shelters or elements providing combined cover, YOY individuals were left to use more exposed positions behind boulders. Nevertheless, when older trout were absent, YOY trout expanded their range of habitats, selecting deeper and slower positions linked to substrate shelters or elements providing combined cover but not to elements providing only visual cover. This suggests that juvenile trout dominate over YOY trout when competing for positions they both find suitable, as observed by Bohlin (1977) and Vehanen et al. (1999) in experimental conditions.

We observed a similar pattern in the River Cega since adult trout highly selected the habitats with the lowest predation risk (pools and habitats connected to elements providing visual cover). When coexisting with older trout, juveniles avoided these habitats, but when density of adults decreased, juveniles selectively occupied those covered positions and avoided positions dominated by gravels or boulders. However, although selectivity for pools increased, pool habitats were not actively selected by juveniles. This suggests that at low densities, adult trout were concentrated on pool habitats and even a low number of individuals could preclude juveniles from using pools. In general, the occupation of pool habitats by juveniles is highly context-dependent (Ayllón et al., 2009, 2010), so that under certain circumstances juvenile salmonids prefer runs and riffles over pools even in the absence of older individuals, pools being selected then only at high juvenile densities (Bult et al., 1999; Greenberg, 1994), while in other conditions pool habitats are preferred since they are energetically more profitable than riffles (Jenkins and Keeley, 2010).

Juveniles did not change however their distribution patterns across the depth and velocity gradients when YOY density was lower. We toy with two possible explanations for this fact. First, YOY most preferred positions could be not sub-optimal but rather marginal habitats for juveniles so that even a low YOY density may render these positions unsuitable in terms of energy gain through both exploitative and interference competition. Alternatively, juveniles could be below carrying capacity the sampled year because of a previous bottleneck so that intracohort competition levels were not high enough to induce subordinate individuals to use marginal habitats. In the case of adult trout, it was more difficult to disentangle the intercohort density effects from the environmental ones since depth and current velocity availability changed across years in the River Cabrillas. The changes in selection patterns of adult trout were partly explained by the changes in their hydraulic environment. Adults showed a higher preference for pool habitats when mean and maximum depth, and thus the range of available depths, was higher (at increased river discharge). As observed in previous studies (e.g. Ayllón et al., 2010), adult brown trout's preference for pools decreases as does pool depth since predation risk increases. Consequently at lower river discharge, adult trout increased their selectivity for shallower positions offering combined cover. Nevertheless, adults did not select habitats highly selected by juveniles when they were absent despite the fact that those habitats were unoccupied. Hence, adult trout seemed to select stream positions independently of juvenile densities.

Habitat quantity and quality is a resource that, by limiting carrying capacity, typically creates a bottleneck that increases both intra and intercohort competition, thus stimulating the operation of density dependence (Milner et al., 2003). In stage-structured populations, the transition between life stages and between habitats can act as a significant demographic and selective bottleneck, and in particular, competition with older and larger conspecifics may influence the number and traits of individuals successfully making the transition (Samhouri et al., 2009). In salmonid populations, survival and movement (Nordwall et al., 2001), individual growth rate (Kaspersson and Höjesjö, 2009), body size and energetics (Einum and Kvingedal, 2011; Nordwall et al., 2001) of a cohort are significantly affected by the density of older cohorts. Reciprocally, Einum et al. (2011) and Kvingedal and Einum (2011) showed that individual growth rate and energetics of yearling Atlantic salmon are influenced by the density of younger individuals, while Parra et al. (2012) observed that mean body size of juvenile and adult brown trout decreased with increasing density in suitable habitat of younger life stages likewise. In this study, we have shown that elevated density of older cohorts restricts the range of habitats used by younger individuals, which would ultimately lead to decreased carrying capacity and hence increased intracohort competition. By contrast, fluctuations in the density of younger cohorts did not result in substantial changes in the habitat selection patterns of older ones. Kvingedal and Einum (2011) observed that salmon yearlings do not appear to consider the density of younger individuals when distributing themselves, even if they appear to have a negative effect on their growth performance, which suggests that older fish distribute themselves according to other factors than growth potential per se. So the overall net effect of increasing density of younger cohorts would be a decrease in habitat quality for older ones through increased energetic costs derived from increased competition but not a change in their habitat selection patterns.

These mechanisms are of critical importance for the dynamics of peripheral populations facing severe environmental constraints. In the rivers studied, recruitment varies markedly across years, this variability being significantly related to the timing, magnitude and duration of extreme flow events during hatching, emergence and summer drought (Nicola et al., 2009). The fact that younger cohorts are more capable of homogenizing densities across unoccupied habitats than older ones favours the temporal succession of weak and strong cohorts, since new recruits are able of expanding into free habitats when the numbers of weakened cohorts are insufficient to saturate their available habitat along ontogeny. This density dependent dynamic habitat selection also implies that management actions after a drastic reduction in population numbers resulting from catastrophic events should focus on increasing the density of the youngest age classes as they are more capable of using unoccupied habitats than older ones. By extension, management practises leading to an oversaturation of the habitat for a certain cohort may result in strong intracohort density dependent mortality or growth if the individuals of the cohort are not capable of occupying available habitats or competing year classes are at carrying capacity.

The size and shape of the realized niche, and thus patterns of resource selection, depend on several factors other than resource availability, including critical processes, such as competition and predation (Hirzel and Le Lay, 2008). Most animals must acquire resources while avoiding predators (Stearns, 1992), so any model developed to accurately predict the distribution of individuals and the emerging population properties must account for the habitat selection trade-off between maximizing foraging success and minimizing predation risk. Although HSMs and RSFs incorporate foraging competition and predation risk only as qualities of the fixed landscape or riverscape, ignoring possible intraspecific and predator–prey interactions, they explicitly address spatial resource and risk distributions (Biesinger et al., 2011). This partly explains why these models have been so widely used as a tool in species management, ecological impact assessment, ecological restoration studies and conservation planning.

Our findings may entail however critical consequences for ecological management practices based on HSMs or RSFs outputs. We observed that RSFs changed across years as a result of the fluctuations in the densities of competing cohorts. It is clear that HSMs and RSFs for a life stage based on habitat selection by dominant fish alone (or all fish at low densities) would more accurately represent the best quality habitats but would also underestimate the quality of unoccupied habitat that might still be suitable for growth (Rosenfeld et al., 2005). In the same way, modelling habitat selection patterns of one life stage when competing life stages are absent or significantly well below their habitat capacity would overestimate its range of selected habitats. It would predict consequently an overestimated potential available habitat, and thus carrying capacity, for the life stage under normal conditions. The implications for fish population management are harsh given that carrying capacity is a central parameter to determining the conservation status of populations (Almodóvar et al., 2012; Ayllón et al., 2012) or the probability of population persistence (Hilderbrand, 2003), as well as to calibrating population dynamics models (Dumas and Prouzet, 2003). Likewise, management actions aimed at improving the quantity and/or quality of the habitat of a life stage that represents a limiting bottleneck for the adult population based on biased HSMs or RSFs would yield counterintuitive population responses. For example, manipulations of the habitat of a limiting life stage based on an overestimated RSF may indeed increase the numbers of competing life stages which would actually decrease the habitat capacity for the limiting life stage. Therefore, studies at fine scales that fail to incorporate density are bound to yield biased estimates of resource selection whenever density alters the proportional use of resources, which could have profound effects on the success of management actions. This work represents a step forward in that sense, although studies involving a wider range of river typologies or longer time periods are still needed to fully understand the patterns of and the mechanisms underlying the operation of density dependence on brown trout habitat selection. Further research should focus on elucidating whether observed patterns are stable along time and whether they change across rivers with contrasting habitat characteristics or hydrological regime. However, the feasibility of conducting that sort of studies in the wild is often limited compared to controlled studies in artificial streams, as densities or discharge conditions cannot be manipulated. In this context, field manipulation studies (e.g., Einum et al., 2011; Kaspersson and Höjesjö, 2009) provide a useful alternative as in such experimental settings it is possible to control cohort densities while working in natural streams.

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