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Spatio-temporal habitat selection shifts in brown trout populations under contrasting natural flow regimes

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ABSTRACT

Understanding the links between instream ecology and hydrology has become a critical task in contemporary river research and management. Habitat selection behaviour is a central dimension in applied ecology because it is a primary way that mobile organisms adapt to changing environmental conditions. Here, we analyzed brown trout habitat selection during two consecutive years in rivers presenting contrasting flow conditions to test the following hypotheses: (1) given that adaptation to flow regimes occurs as a response to the interaction between frequency, magnitude and predictability of mortality-causing events, habitat selection would vary across populations subject to different disturbance regimes; (2) because adaptations are directed towards enduring both intra-annual and interannual variations in flow, habitat selection would shift across years as a response to changing flow conditions and (3) such responses to yearly flow fluctuations would depend on the historical long-term hydrologic regime. We found that trout from rivers with highly variable flow and more frequent, longer and stronger extreme flow events were more willing to occupy positions in high-velocity habitats and showed stronger requirements for velocity refuges, whereas trout inhabiting more stable and benign flow environments selected visually-covered habitats to minimize biotic interactions. Results also revealed that trout shifted habitat selection patterns across years differing in flow conditions irrespective of river typology, but this shift was markedly stronger in rivers with higher flow variability and extremity. Overall, observed ecological patterns have strong implications for predicting the consequences of flow alteration for species adapted to particular flow regimes. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS natural flow regime; disturbance events; ecohydrology; flow alteration; river conservation and management; salmonids; freshwater fish; resource selection functions

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INTRODUCTION

In recent years, understanding the basic processes of ecohydrology has emerged as a critical need for the development of tools for a more sustainable use of water resources and management of natural ecosystems, especially on the light of current and projected climate change (Erol and Randhir, 2012). In this context, the search for links between instream ecology and hydrology has naturally become one of the fundamental issues in contemporary river research and management (Vaughan *et al.*, 2009). Despite other environmental factors (including temperature, water quality, sediment or invasive species) being involved, the hydrologic regime is regarded as the primary driver of riverine ecosystems, because their structure and function, and the adaptations of their constituent freshwater and riparian species are strongly determined by patterns of intra-annual and interannual variation in river flows (Richter *et al.*, 1996; Poff *et al.*, 1997; Lytle and Poff, 2004; Naiman *et al.*, 2008). As a result, it has been hypothesized that rivers with similar hydrological characteristics should share similar community composition, species traits and ecosystem functioning (Poff and Ward, 1989).

The consequences of the hydrologic regime are manifested across both ecological (growth rates, survival and effects of fitness on individuals) and evolutionary time scales. In ecological terms, the primary components of a flow regime are the magnitude, frequency, seasonal timing, predictability, duration and rate of change of flow conditions (Poff *et al.*, 1997). From an evolutionary perspective, extreme events (floods and droughts) exert primary selective pressure for adaptation, because they often represent sources of mortality (Lytle and Poff, 2004). Flow regime adaptations involve life histories, behaviours and morphologies of organisms, with different components of the natural flow regime being relevant for each mode of adaptation (Lytle and Poff, 2004). For example, life history traits of individual aquatic species, and emergent community characteristics, are strongly linked to variability, predictability and seasonality of flow regimes (e.g. Poff and Allan, 1995; Lamouroux *et al.*, 2002; Belmar *et al.*, 2012), so that patterns of life history composition of river basins respond similarly along gradients of hydrologic variability (Olden and Kennard, 2010; Mims and Olden, 2012).

This functional relationship is habitat mediated because, on the one hand, life history strategies summarize how evolution has shaped species to cope with the temporal and

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spatial variability of their present habitat (Southwood, 1977; Poff and Ward, 1989), and on the other hand, the flow regime structures the physical habitat template where biotic interactions take place (Townsend and Hildrew, 1994). Long-term variations in flow magnitude, timing, frequency and duration of flow events, define the physical template over large spatial scales (e.g. basins and subbasins), whereas the short-term history of hydrological events influences habitat availability and connectivity at smaller spatial scales (e.g. within and among river reaches) (Kennard *et al.*, 2007). Habitat use is then necessarily a central aspect in the ecology of a species, because there are close associations between how individuals and populations exploit, compete for and share habitats and food resources in time and space, and their ability to survive and reproduce (Jonsson and Jonsson, 2011; Parra *et al.*, 2011; Ayllón *et al.*, 2012a).

Given that organisms are better adapted to live and reproduce in some places than they are in others, habitat selection represents a stable evolutionary strategy (Morris, 2011). At this respect, salmonids appear to select stream positions that maximize their expectation of reaching reproductive maturity over a time horizon, i.e. habitats that maximize current and future growth potential while minimizing mortality risks (Railsback and Harvey, 2002). Well-fitted to this general fitness-seeking objective, brown trout *Salmo trutta* are highly selective regarding microhabitat position choice (Armstrong *et al.*, 2003; Jonsson and Jonsson, 2011); although it also exhibits a high flexibility in its habitat selection patterns across and within river systems (e.g. Heggenes, 2002). Spatial variations in trout habitat selection patterns are generally driven by physical and environmental factors operating at different spatial scales (Ayllón *et al.*, 2010), factors closely linked to and shaped by hydrologic patterns. In Mediterranean-climate regions, trout have to withstand high intra-annual and interannual hydrological variability, together with frequent natural flow extremes (floods and droughts) (Gasith and Resh, 1999), so it is predictable that the species has developed strong adaptations in various traits, including habitat selection behaviour, to bear such stresses. However, although spatial variations in the primary components of the flow regime are driven by climatic conditions, they are mediated by basin geology, topography and vegetation (Winter, 2001). Therefore, basins sharing a similar climate may have quite different hydrologic regimes when these features differ, exerting in consequence different selective pressures on fish adaptive traits. Consequently, salmonids are expected to modify their habitat selection behaviour as a function of flow regime patterns to cope with the prevalent hydraulic environment and mortality sources (biotic vs abiotic factors). It is clear that such behavioural adaptations are directed towards enduring not only intra-annual but also interannual variations in flow conditions so that fish species would behaviourally react to temporally changing conditions, and importantly, such responses to short-term fluctuations in discharge would depend on the long-term hydrologic regime in which they are nested (Stewart-Koster *et al.*, 2011).

In the present study we aimed to test the hypotheses that brown trout habitat selection patterns (1) differ across rivers presenting contrasting flow regimes, (2) change across years showing different flow conditions and (3) these yearly changes vary differentially across rivers with contrasting flow regimes.

METHODS

Study area

This study was carried out in eight localities along five rivers of central Iberian Peninsula; three are tributaries to the River Tajo (Cabrillas, Dulce and Jarama) and two to the River Duero (Cega and Eresma). Specifically, we studied two localities in rivers Cabrillas, Jarama and Eresma and one in rivers Dulce and Cega (Figure 1). The climate is continental Mediterranean, with hot, dry summers and cold, wet winters. Physicochemical characteristics, water temperature and flow regime vary among rivers but may be divided into two groups. The first type (Cega, Eresma and Jarama) have soft, infertile waters running through granite and gneiss catchments, thus being rivers where the greater part of their water comes from surface drainage, becoming torrential at snowmelt in early spring. The rest of the rivers (Cabrillas and Dulce) have hard, fertile waters arising from limestone catchments with an even flow regime throughout the year. Further details of the study area are given in Nicola and Almodóvar (2002), Almodóvar *et al.* (2006) and Nicola *et al.* (2009). Brown trout is the only fish species present throughout the study area, and its populations comprise exclusively resident individuals. The river reaches studied are not currently stocked and are unaffected by land use, pollution or water regulation.

Microhabitat data collection

Habitat surveys were carried out at the end of the spring of years 2010 and 2011, at similar dates both years. We selected these dates as they represent the convergence of the end of a period when extreme flow conditions can cause a high mortality in new recruits (see Nicola *et al.*, 2009), and the onset of the dry season when extreme low flow conditions can exert negative effects on older age classes. Electrofishing using a 2200-watt direct current generator rather than snorkel survey was used to collect habitat use data because some areas within the sampling sites were too shallow to be snorkelled.

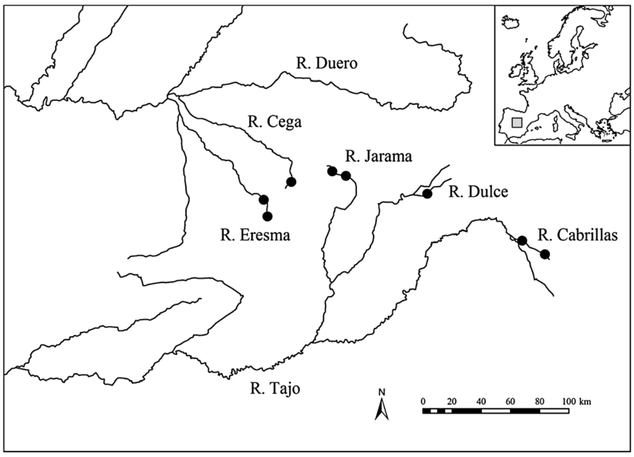

Figure 1. Map of the study area showing the sampling sites.

We preferred to lose accuracy in fish positioning than to introduce a bias through employing different sampling techniques. Turbidity did not affect fish obervations at any site. The same river length was electrofished each year at each sampling site (average length was 73.6 ± 21.1 m). Captured trout were measured (fork length, to the nearest millimetre) and weighed (to the nearest gram), and scales were taken for age determination so that each individual could be assigned to one out of three age classes, i.e. young-of-the-year (YOY; 0+), juvenile (1+) or adult (>1+). The fish were placed into holding boxes to recover and then returned to the stream. Numbered tags were dropped wherever a trout was observed and water depth, current velocity, substrate and cover were measured afterwards in a 1 m^2 quadrat. Depth and mean column velocity were measured once at the exact point where the trout was observed, whereas the proportion of substrate and cover were visually estimated within the surface of the quadrat, with the trout position as the centre of the quadrat. We also calculated the Froude number, a dimensionless ratio of kinetic to potential energy that has been previously proved to be ecologically meaningful regarding the distribution of functional habitats and aquatic organisms (e.g. Kemp *et al.*, 2000; Ayllón *et al.*, 2009, 2010), to characterize the flow's hydraulic properties. 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.

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.*, 2010, 2013). 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 73.6 ± 21.1 m, 5.3 ± 1.9 m and 358.2 ± 127.7 m^2, respectively. Total depth (cm), current velocity ($m\,s^{-1}$), substrate composition and cover were measured. Depth and mean column velocity were measured at the centre of each 1 m^2 quadrat, whereas the proportion (%) of substrate and cover were visually estimated within the surface of the quadrat. The 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.

Characterization of the long-term flow regime

A thorough analysis of historical time series of hydrologic data was performed to classify the studied rivers on the basis of their flow regime (flow types). Flow data were obtained from a database collected by the Hydrological Confederations of River Duero and River Tajo. The selected gauging stations were close to sampling sites, and the analyzed flow records covered 25 years (1985–2009). We calculated a series of hydrologic metrics recommended by Richter *et al.*, 1996 and Olden and Poff (2003) to describe ecologically relevant components of the hydrologic regime in terms of the magnitude, frequency, duration and timing of discharge events, rate of change in discharge events and the temporal variability in these measures. Daily discharge data from each river were processed every year to obtain the hydrologic metrics during two periods: (1) whole hydrologic year (hydrologic year; from 1st October to 30th September) and (2) after recruits emergence and before summer drought (March–June; postemergence). All hydrologic metrics were calculated using the Indicators of Hydrologic Alteration software package (Mathews and Richter, 2007).

For the hydrologic year period, we calculated the coefficient of variation (*CV*) of mean annual daily discharge, the number of zero flow days and the base flow index, along with their *CV*, as well as predictability of daily flow. Predictability is composed of two independent, additive components: constancy, a measure of temporal invariance, and contingency, a measure of periodicity (Colwell, 1974). These two latter measures indicate the degree to which a state stays the same and how closely different states correspond to different time periods, respectively. The index constancy/predictability (C/P) was then used to assess the relative constancy of daily flow, i.e. the proportion of predictability that is explained by constancy, so that larger index values indicate flow stability. In addition, we calculated the magnitude, frequency and rate of change as well as their temporal variability (characterized by the *CV*) of the different types of flow events other than the dominant flow condition (low flows): extreme low flows, high flow pulses, small floods and large floods. Flow values equal or below the 10th percentile of daily low flows were categorized as extreme low flows, whereas all flows over the 75th percentile of daily flows were classified as high flows. All high flow events having a peak flow greater than or equal to the flow value that corresponds to a 2 or 10-year return interval were classified as either small or large floods, respectively. The rate of change in discharge was measured as the mean rate of both positive (rise rate) and negative (fall rate) changes in discharge between consecutive days.

For the postemergence period, we calculated the *CV* of mean annual daily discharge, the predictability of daily flow and the C/P index, as well as the base flow index, the minimum and maximum discharge during 7 and 30 consecutive days, the number and duration of both high and low flow pulses, and the number of reversals (number of times that discharge switches from a rising to a negative, or vice versa, trend in discharge between consecutive days). High and low hydrologic pulses are defined as those periods where the daily discharge rises above the 75th percentile or drops below the 25th percentile of all values for the period. We also computed the *CV* of all these metrics. Irrespective of the time period of the analysis, metrics describing flow magnitude were standardized by dividing by the median daily discharge calculated for the entire record to make them comparable among rivers significantly differing in discharge magnitude.

Multivariate resource selection functions

Brown trout habitat selection patterns were described through multivariate resource selection functions (RSFs). RSFs describe the relationship between habitat availability and the relative probability of habitat use. In consequence, the response variable is the probability that an available habitat position will be used by a trout of a given age class. RSFs were developed by means of mixed-effects logistic regressions. Depth, current velocity and Froude number were used as continuous predictors. Second order terms of continuous variables were included to test for nonlinear effects. Substrate and cover categories were included as independent binary variables. To reduce the number of variables, some of the defined substrate and cover classes were merged into functional groups. Hence, silt and sand were treated as a common category (fines). Cobble and boulder categories were joined and treated as velocity shelters. Substrate shelter was maintained as an independent category, as apart from protecting from high current velocity, it provides a higher degree of visual isolation than cobbles or boulders without interstitial spaces to hide in. We also grouped cover categories that mostly provide visual protection against outstream predators (overhanging vegetation and undercut banks), hereafter referred as visual cover. These elements were differentiated from cover elements that provide simultaneously both refuge against excessively high flow velocities (velocity shelter) and visual isolation from both instream predators and conspecifics (aquatic vegetation, woody debris, combined cover and under cascade), hereafter referred as combined cover.

Two different analyses were performed: (1) within years-across flow types and (2) within flow types-across years. For the first kind of analysis (within years-across flow types), the flow regime type was included as a categorical variable to model changes in habitat selection across sampling sites presenting different flow regimes. For the second kind of analysis (within flow types-across years), the year was included as a categorical variable to model changes in habitat selection across years, and thus to indirectly account for yearly changes in river discharge. The interaction terms between either the flow regime type or the year and each continuous and binary habitat variable were used to assess spatial and temporal, respectively, changes in trout selectivity for the corresponding habitat variable. Because of computation constraints, no interaction terms between habitat variables were considered. Finally, the sampling site was included as a random factor (random intercept) to induce a correlation structure between observations within the same site.

We followed the procedures described by Grueber *et al.* (2011) for the final model selection. All statistical analyses were performed within the R environment (R Development Core Team, 2012). First, the global model with all variables and interaction terms was fitted using the lme4 package (Bates and Maechler, 2009). Once the global model was defined, input continuous variables were standardized and binary variables were centred using the arm package (Gelman *et al.*, 2009). In the next step, all possible submodels from the global model (model set) were generated by means of the MuMIn package (Barton, 2009). Because there is usually no single best model, but there are several models that seem plausible based on information criteria, model averaging was performed. This procedure entails calculating a weighted average of parameter estimates, such that parameter estimates from models that contribute little information about the variance in the response variable are given little weight. We used the Akaike's Information Criterion adjusted for small sample size (AICc) to assess competing models. For model averaging, the top model set, encompassing the model having the lowest AICc value and all models with a $\Delta\mathrm{AICc} < 2$ (Burnham and Anderson, 2002), was obtained from the model set and then averaged using the zero method by means again of the MuMIn package. Finally, the relative importance (defined as the sum of Akaike weights over all models including the explanatory variable) of each variable included in the final averaged model was calculated.

RESULTS

Characterization of the long-term flow regime

The studied rivers exhibited seasonal and among-year variation in water discharge, typical for the Mediterranean climate, but the hydrological pattern differed across rivers during the analyzed time. Two kinds of rivers were accordingly differentiated on the basis of their flow regime type (Table I and Figure 2). Although predictability (P) of daily discharge was very low in general, it was lower in rivers Cega, Eresma and Jarama (ranging between 0.29–0.36) than in rivers Cabrillas and Dulce (0.48–0.54). In addition, in the latter rivers, P was mostly due to constancy (C), whereas in the former it was mostly due to contingency (M). Therefore, the index C/P was much higher (0.81–0.84) in rivers with constant flow (Cabrillas and Dulce; high C/P index group) when compared with rivers with an irregular flow (Cega, Eresma and Jarama; low C/P index group), where the index was between 0.41 and 0.50 (Table I).

The magnitude and frequency of high flow pulses, and small and large floods, as well as the rise rate of discharge during these events, were significantly higher in the rivers conforming the low C/P index group. By contrast, flow peak during extreme flow events was significantly lower in the rivers having a low C/P index, and these extreme flow events were also significantly more frequent in this kind of rivers. As a result, the base flow index was significantly lower, and the number of days with zero flow higher in rivers with a low C/P index. In general, the interannual variability of studied metrics was lower in the rivers characterized by a low C/P index (Table I).

During the postemergence period, daily flow was also more irregular in the rivers Cega, Eresma and Jarama (low C/P index group). These rivers had a significantly lower base flow index, and maximum and minimum flow peaks were

Table I. Hydrologic metrics calculated for hydrologic year and postemergence periods from a 25-year time series (1985–2009) at rivers studied. Rivers having a high constancy to predictability ratio (C/P index) are shown separated from those having a low one. *CV* represents the coefficient of variation.

	High C/P index		Low C/P index		
	Cabrillas	Dulce	Eresma	Cega	Jarama
Hydrologic year metrics					
CV mean annual daily flow	1.09	0.88	1.38	1.52	2.94
Flow predictability	0.54	0.48	0.36	0.35	0.29
Constancy/predictability	0.81	0.84	0.44	0.41	0.50
Number of zero days ***	0.00	0.00	7.87	12.96	6.70
Base flow index ***	0.40	0.39	0.07	0.03	0.11
CV number of zero days	—	—	2.55	2.12	2.98
CV base flow index	0.40	0.58	1.03	1.58	1.41
Extreme low peak ***	0.50	0.24	0.05	0.08	0.14
Extreme low frequency *	1.65	0.74	2.52	2.78	2.44
High flow peak ***	3.63	2.71	5.85	5.81	6.84
High flow frequency **	4.83	3.04	8.48	8.39	7.30
High flow rise rate ***	0.61	0.58	1.01	1.02	2.59
High flow fall rate ^{ns}	−0.38	−0.29	−0.45	−0.42	−0.92
Small flood peak ***	10.24	7.27	13.27	12.79	40.65
Small flood frequency *	0.61	0.70	1.78	1.44	1.65
Small flood rise rate *	2.39	1.81	3.48	3.35	8.67
Small flood fall rate ^{ns}	−1.41	−0.97	−1.29	−1.47	−4.50
Large flood peak ***	18.14	13.91	23.73	25.61	143.30
Large flood frequency *	0.17	0.43	0.74	0.74	0.91
Large flood rise rate ^{ns}	8.41	7.15	6.71	7.29	29.02
Large flood fall rate ^{ns}	−2.57	−1.86	−2.14	−1.93	−15.03
CV extreme low peak	0.19	0.36	0.54	0.66	0.47
CV extreme low frequency	1.66	2.13	1.30	0.91	0.86
CV high flow peak	0.40	0.32	0.34	0.28	0.36
CV high flow frequency	0.53	0.88	0.38	0.30	0.42
CV high flow rise rate	0.68	0.67	0.31	0.34	0.49
CV high flow fall rate	−0.39	−0.64	−0.46	−0.30	−0.44
CV small flood peak	0.20	0.18	0.17	0.12	0.29
CV small flood frequency	1.90	1.66	1.08	1.13	1.23
CV small flood rise rate	0.60	0.57	0.35	0.62	0.61
CV small flood fall rate	−0.29	−0.33	−0.25	−0.23	−0.44
CV large flood peak	0.20	0.21	0.14	0.30	0.28
CV large flood frequency	2.82	2.17	1.24	1.10	1.81
CV large flood rise rate	0.71	0.50	0.85	0.52	0.55
CV large flood fall rate	−0.46	−0.29	−0.35	−0.53	−0.34
Postemergence metrics					
CV mean annual daily flow	0.96	0.72	1.17	1.20	2.71
Flow predictability	0.47	0.51	0.37	0.35	0.28
Constancy/predictability	0.89	0.91	0.73	0.68	0.60
Base flow index ***	0.53	0.54	0.18	0.18	0.23
7-day minimum *	1.06	0.79	0.50	0.65	0.62
30-day minimum ^{ns}	1.25	0.98	0.92	1.04	1.18
7-day maximum *	5.52	3.17	8.58	8.42	24.33
30-day maximum *	3.50	2.19	0.78	0.75	0.82
CV base flow index	0.32	0.38	5.59	5.50	13.38
CV 7-day minimum	0.48	0.56	0.92	1.37	0.95
CV 30-day minimum	0.45	0.49	0.72	1.09	1.46
CV 7-day maximum	0.90	0.65	0.51	0.77	1.70
CV 30-day maximum	0.68	0.55	0.47	0.75	1.76
Low pulse count *	0.00	0.87	1.17	1.65	1.74
Low pulse duration *	—	8.96	26.33	97.32	59.22
High pulse count ^{ns}	1.48	1.13	1.87	1.26	1.83
High pulse duration *	6.58	9.49	12.88	12.74	17.35
CV low pulse count	0.00	2.53	2.82	0.81	1.01
CV low pulse duration	—	0.84	1.67	0.59	1.08
CV high pulse count	0.93	1.08	0.78	1.13	1.74
CV high pulse duration	1.13	0.72	0.79	1.52	1.84
Number of reversals ***	10.61	18.57	32.83	28.48	29.74
CV number of reversals	0.59	0.60	0.20	0.22	0.54

For estimators of the central tendency of hydrologic metrics, *represents significant differences between all rivers conforming the high C/P index group and all rivers conforming the low C/P index group with at least a probability of $p < 0.05$, **with at least a probability of $p < 0.01$, and ***with at least a probability of $p < 0.001$; ^{ns} means that no significant differences were found among all sites of different groups.

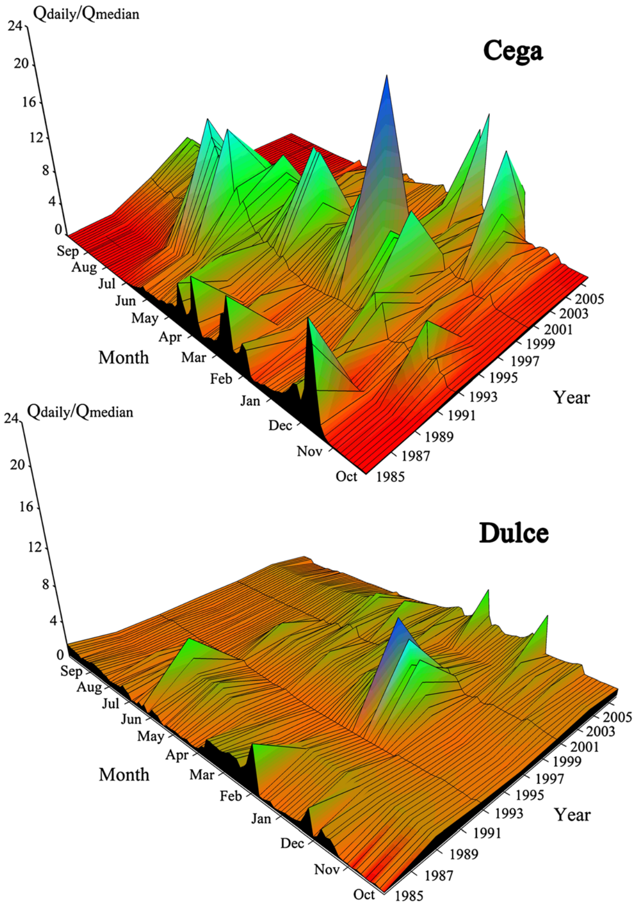

Figure 2. Hydrographs of rivers presenting contrasting flow regimes: river Cega exemplifies study rivers with a low constancy to predictability ratio (low C/P index group), whereas river Dulce illustrates rivers having a high C/P index (high C/P index group). Daily discharge was standardized by dividing by the median daily discharge calculated for the entire record.

significantly higher and lower, respectively, than in rivers with a more constant flow. Consequently, the number and duration of both high and low flow pulses, as well as the number of reversal, were in general significantly higher in the rivers presenting a low C/P index (Table I).

Finally, mean daily discharge during the whole post-emergence period, just during June and the 15 days previous to habitat samplings was significantly higher in year 2010 than in 2011 at all rivers studied (analysis of variance; ANOVA, $p < 0.05$). According to the previous characterization of flow regimes, discharge at year 2010 corresponded to high flow events, whereas discharge at year 2011 were characterized as low flows at all rivers. Interannual changes in discharge resulted in significant variations in channel hydraulics (ANOVA, $p < 0.05$) and structure (G-test, $p < 0.01$) across years at sites conforming both flow-type groups (Table II). Hydraulic conditions (ANOVA, $p < 0.05$) and structural characteristics of the channel (G-test, $p < 0.001$) significantly differed across flow types at high flows (year 2010). By contrast, distribution of structural elements of the channel were homogenized (G-test, $p > 0.2$) at low flows (year 2011) and only significant differences in water depth, and thus in the Froude number (ANOVA, $p < 0.05$) were observed across flow types (Tables II).

Multivariate resource selection functions

RSFs for 0+ trout differed across rivers with contrasting flow types at both years studied (Table III). Likewise, within flow types-across years analyses showed that 0+ trout changed selection patterns across years irrespective of the river typology (Table IV). In 2010, 0+ trout selected positions with very low Froude number though avoiding pool habitats at both kinds of river flow types. In addition, 0+ trout showed a high selectivity for positions linked to velocity and substrate shelters as well as to gravel in rivers having a low C/P index, whereas selected habitats with combined cover in rivers having a high C/P index. Besides, 0+ trout had a higher selectivity for high Froude number in rivers from the low C/P index group (Table III). Trout markedly increased selectivity for visual cover and decreased selectivity for combined cover in year 2011 compared with year 2010 at both kinds of river types. However, 0+ trout inhabiting rivers having a low C/P index also increased selectivity for velocity shelters and decreased their avoidance for pool habitats, whereas trout from rivers with a high C/P index increased their selectivity only for positions with higher Froude number (Table IV). As a result,

Table II. Characteristics of available habitat during years 2010 and 2011 across river flow types. Standard deviation values are shown for mean depth, velocity and Froude number.

	High C/P index		Low C/P index	
Variable	2010	2011	2010	2011
Mean depth (cm)	40.6 ± 20.6	32.5 ± 24.3	31.4 ± 23.5	19.8 ± 15.8
Maximum depth (cm)	120	110	130	92
Mean velocity ($\mathrm{m\,s^{-1}}$)	0.38 ± 0.40	0.28 ± 0.32	0.47 ± 0.39	0.33 ± 0.27
Mean Froude number	0.10 ± 0.22	0.13 ± 0.27	0.17 ± 0.40	0.27 ± 0.52
Bedrock (%)	9.1	1.6	2.0	1.0
Velocity shelter (%)	15.5	18.8	28.3	24.5
Gravel (%)	2.7	9.5	2.0	10.5
Fines (%)	2.1	2.9	1.6	6.5
Pool (%)	6.1	12.9	16.4	9.5
Substrate shelter (%)	12.0	17.7	24.6	22.8
Visual cover (%)	16.7	10.6	10.9	6.0
Combined cover (%)	35.8	26.1	14.2	19.3

Table III. Summary of multivariate resource selection functions (RSFs) of different brown trout age classes after model averaging: effects of each parameter on probability of habitat use within each year studied (2010 vs 2011) across river flow types. Parameter estimates and relative importance (values greater than 0.5 marked in bold) are shown. Depth, velocity (Vel) and Froude number (Frou) are continuous variables, whereas substrate categories (bedrock, Bed; cobble + boulders, VelShel; gravel, Gra; fines, Fin) as well as cover categories (Pool; substrate shelter, Subst; visual cover; and combined cover, Comb) are binary variables.

	0+				1+				>1+			
	2010		2011		2010		2011		2010		2011	
	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.
(Random intercept)	−20.60	**1.00**	−2.04	**1.00**	−2.02	**1.00**	−2.39	**1.00**	−4.10	**1.00**	−1.63	**1.00**
Depth					0.17	**0.55**	2.82	**1.00**				
Depth^2					−0.23	**0.55**	−0.82	**1.00**				
Vel					−4.62	**1.00**	−3.81	**1.00**				
Vel^2												
Frou	−7.78	**1.00**	−1.90	**1.00**					−23.14	**1.00**	−4.86	**1.00**
Frou^2												
Bed												
VelShel	0.12	**1.00**	0.09	**1.00**	−0.14	0.33	0.28	0.38	−0.64	**0.54**	0.25	**1.00**
Gra	0.05	**0.52**	0.55	**1.00**								
Fin												
Pool	−16.83	**1.00**	−0.17	0.27	2.57	**1.00**	0.06	0.08	1.02	**0.64**	1.33	**1.00**
Subst	0.49	**1.00**	0.29	**1.00**	0.09	**1.00**	0.40	**1.00**	0.08	**1.00**	0.95	**1.00**
Visual			2.29	**1.00**	3.32	**1.00**	2.60	**1.00**	1.36	**1.00**	1.96	**1.00**
Comb	18.56	**1.00**	1.40	**1.00**	0.26	**1.00**	0.24	**0.78**	0.11	**0.92**	1.10	**1.00**
Low C/P*	18.69	**1.00**	0.10	**1.00**	0.79	**1.00**	2.18	**1.00**	3.14	**1.00**	−0.37	**1.00**
Low C/P : Depth							−0.85	0.33				
Low C/P : Depth ^{2}							−3.85	**0.95**				
Low C/P : Vel							1.77	0.43				
Low C/P : Vel^2												
Low C/P : Frou	4.86	**0.54**	0.13	0.09					19.06	**1.00**	−0.07	0.07
Low C/P : Frou^2												
Low C/P : Bed												
Low C/P : VelShel	1.23	**1.00**	1.80	**1.00**					1.02	0.07	2.04	**0.53**
Low C/P : Gra	0.63	**0.52**	2.00	**1.00**								
Low C/P : Fin												
Low C/P : Pool					−1.29	**0.56**			−0.42	**0.64**	−0.74	**0.73**
Low C/P : Subst	1.72	**1.00**	1.68	**1.00**	1.29	**1.00**	1.01	**0.75**	1.35	**1.00**	0.44	**0.57**
Low C/P: Visual			−0.05	0.08	−3.04	**1.00**	−0.65	0.33	0.04	0.08	0.81	0.33
Low C/P : Comb	−17.51	**1.00**	−0.11	0.17	1.37	**1.00**	0.52	**0.77**	0.70	**0.62**	0.78	**0.60**

Coef., coefficient; Imp., relative importance.
*High C/P index group was the reference category

observed variations in 0+ trout habitat selection patterns across river types in year 2011 were basically due to a differential selectivity for substrate features (Table III).

Regarding 1+ trout, differences in habitat selection patterns across river types were found at both years. In 2010, 1+ trout selected positions with low current velocity linked to pool habitats or elements providing visual cover in rivers with high C/P index but linked to substrate shelters or combined cover in rivers with low C/P index (Table III). Although 1+ trout occurring at rivers with low C/P index markedly changed their habitat selection patterns across years, increasing their selectivity for deeper and slower habitats along with positions providing visual cover in year 2011, trout from the other type of rivers did not appreciably modified their selection behaviour (Table IV). Consequently, depth, substrate shelters and elements providing combined cover were central habitat features for 1+ trout in rivers having low C/P index but not in rivers with high C/P index (Table III).

Habitat selection patterns of >1+ trout also differed markedly across rivers characterized by different flow patterns at either year studied. In general, in year 2010 >1+ trout selected positions with a low Froude number linked to pool habitats or visual cover. Apart from this general pattern, trout from rivers having low C/P index selected substrate shelters and combined cover and showed lower selectivity for positions in pools (Table III). Trout from rivers having low C/P index strongly increased their selectivity for visual and combined cover and velocity shelters, whereas it decreased their selectivity for pools in year 2011. On the contrary, trout from rivers having high C/P index just moderately increased selectivity for substrate shelters (Table IV). In consequence, in year 2011, trout significantly differed their selectivity for velocity shelters as well as visual and combined cover across river types (Table III).

DISCUSSION

Results from within years-across flow types analyses showed that RSFs for Mediterranean brown trout differed

Table IV. Summary of multivariate resource selection functions (RSFs) of different brown trout age classes after model averaging: effects of each parameter on probability of habitat use within each river flow type (high vs low C/P index group) across years. Parameter estimates and relative importance (values greater than 0.5 marked in bold) are shown. Depth, velocity (Vel) and Froude number (Frou) are continuous variables, while substrate categories (bedrock, Bed; cobble + boulders, VelShel; gravel, Gra; fines, Fin) as well as cover categories (Pool; substrate shelter, Subst; visual cover; and combined cover, Comb) are binary variables.

	0+				1+				>1+			
	High C/P		Low C/P		High C/P		Low C/P		High C/P		Low C/P	
	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.	Coef.	Imp.
(Random intercept)	−16.40	**1.00**	−2.48	**1.00**	−2.19	**1.00**	−0.82	**1.00**	−3.36	**1.00**	−1.58	**1.00**
Depth					0.04	0.11	0.33	**0.87**				
Depth^2					−0.11	0.11	−2.75	**1.00**				
Vel					−5.14	**1.00**	−3.64	**1.00**				
Vel^2												
Frou	−3.61	**1.00**	−2.39	**1.00**					−17.32	**1.00**	−5.28	**1.00**
Frou^2												
Bed												
VelShel			0.57	**1.00**	−1.48	0.11	−0.07	0.26	0.17	0.24	0.05	**0.57**
Gra			1.98	**1.00**								
Fin												
Pool	−7.36	**0.77**	−3.56	**1.00**	2.85	**1.00**	0.19	**0.61**	1.33	**0.64**	0.75	**1.00**
Subst			1.49	**1.00**			1.27	**1.00**	0.05	**1.00**	1.65	**1.00**
Visual	0.33	**1.00**	−0.23	**1.00**	3.74	**1.00**	0.33	**0.91**	1.13	**1.00**	1.86	**1.00**
Comb	15.98	**1.00**	1.39	**1.00**	1.45	**0.89**	1.27	**1.00**	0.21	**1.00**	0.71	**1.00**
Year 2011*	14.78	**1.00**	0.84	**1.00**	−1.81	**1.00**	0.09	**0.83**	2.94	**1.00**	−0.62	**1.00**
Year 2011 : Depth							0.95	**0.65**				
Year 2011 : Depth ^{2}							−0.10	0.09				
Year 2011 : Vel					−3.53	0.36	−0.11	0.08				
Year 2011 : Vel^2												
Year 2011 : Frou	3.20	**0.67**							14.66	**1.00**	−1.29	0.20
Year 2011 : Frou^2												
Year 2011 : Bed												
Year 2011 : VelShel			0.88	**0.77**			0.25	0.22			0.75	**0.53**
Year 2011 : Gra			0.05	0.09								
Year 2011 : Fin												
Year 2011 : Pool			2.02	0.15			0.80	**0.61**			−0.14	0.28
Year 2011 : Subst			0.04	0.10					0.65	**0.55**		
Year 2011 : Visual	2.67	**0.87**	2.03	**1.00**	0.06	0.14	1.09	**0.65**	−0.03	0.13	1.12	**0.82**
Year 2011 : Comb	−13.97	**0.83**	−0.58	**0.54**					0.22	0.44	1.35	**0.71**

Coef., coefficient; Imp., relative importance.
*Year 2010 was the reference category

across rivers with contrasting flow types at both years studied. Likewise, within flow types-across years analyses revealed that trout changed their habitat selection patterns across years irrespective of the river typology, but observed changes were significantly more marked in rivers having a more irregular flow regime (low C/P index). Results from both kinds of analyses were consistent between each other, and altogether they confirmed the three hypotheses being tested.

Previous studies have described ontogenetic variations in brown trout habitat selection, YOY individuals aiming at maximizing potential growth by selecting shallow, slow flowing and protected (by substrate features) positions close to fast currents, whereas adult trout tend to minimize size-dependent predation risk by selecting pools or visually covered habitats (Ayllón *et al.*, 2009, 2010). Habitat selection patterns observed in the present study conform to this general species' context; although patent variations in habitat selection occurred across rivers having contrasting flow conditions. These variations, which occurred at both high and low flow conditions irrespective of whether available habitat conditions differed across rivers with different flow types or not, can be only understood under the light of this age-dependent niche separation pattern though. Trout showed a significantly higher selectivity for positions linked to elements providing protection against fast currents such as substrate features (especially in the case of YOY trout) and combined cover (in juveniles and adults) in the rivers from the low C/P index group. These rivers have very low flow predictability with highly variable flow with a fixed periodicity and more frequent, longer and stronger in magnitude extreme flow events than rivers from the high C/P index group, which showed more constant flow and more benign flow events. In addition, daily changes in flow conditions are stronger and more variable in their direction (rising vs falling flow trends) in the rivers from the first typology. It is well-known that not only floods but also more modest high-flow peaks during the postemergence period can exert a great mortality in new recruits (e.g. Cattanéo *et al.*, 2002; Nicola *et al.*, 2009; Ayllón *et al.*, 2012b) and depress individual growth of older cohorts (e.g. Jensen and Johnsen, 1999) in salmonid populations. Therefore, it is coherent that trout living in rivers with high variability and extremity in flow conditions are better adapted to exploit positions in high-velocity habitat patches and had developed strong requirements for habitat features providing refuge against such fast currents. By contrast, trout inhabiting rivers with more even flow should focus on avoiding predation or competition, selecting positions connected to visual and/or combined cover. This pattern is supported by the general notion that highly variable and/or unpredictable flow regimes provide a physical habitat template in which abiotic factors are of predominant importance in controlling lotic processes and contributing to observed ecological patterns, whereas more benign or predictable flow environments are conducive to the development of stronger biotic interactions such as competition or predation, which can directly influence observed patterns (Poff and Ward, 1989).

Results also supported the hypothesis that trout would shift habitat selection patterns across years varying in discharge conditions. Physical disturbances, like high flows in rivers, are typically regarded as a major source of habitat shift, presumably affecting cover use (Winterbottom *et al.*, 1997). It is also widely accepted that natural changes in water flow is one of the main drivers of seasonal changes in salmonid habitat use and selection (e.g. Rincón and Lobón-Cerviá, 1993; Heggenes *et al.*, 1996; Vehanen *et al.*, 2000). Further, it has been shown that salmonids change their microhabitat choice in response to fluctuating flows under daily or longer periodic flow changes (e.g. Shirvell, 1994), but not under short-term (minutes to hours) fluctuations (e.g. Heggenes, 1988; Vehanen *et al.*, 2000; Kemp *et al.*, 2003). However, little heed have been paid to determine whether yearly variations in discharge may alter fish habitat selection behaviour. In our study, trout shifted habitat selection patterns across years differing in flow conditions, but this shift was significantly stronger in rivers with higher flow variability and extremity. In this kind of rivers, YOY and juvenile trout increased selectivity for pools and visual cover under low flow conditions despite that their availability in the streams decreased, whereas adults selected even in higher proportion habitats with visual and combined cover. That is to say, a fraction of individuals of any age class was willing to assume the costs in the form of reduced availability of food associated to visually-isolated positions to diminish predation risk. In that sense, decreased selectivity of YOY trout for combined cover was likely more related to exclusion through intercohort competition than to real avoidance. On the other side of the track, although predation risk increases under low flow conditions compared with high flow events, the amount of optimal habitat for foraging increases too. As a result, we observed an increased selectivity for velocity shelters under low flows even though its availability was fairly constant across years. The use of cover may reflect a trade-off between demands for growth and sheltering, so individuals with stronger motivation for foraging and growth are expected to hold positions close to velocity shelters because it may be considered more efficient shelter from a foraging point of view than the rest of cover types, as it does not prevent visual contact with the environment (Vehanen *et al.*, 2000).

By contrast, trout from rivers exhibiting a more benign and constant flow environment hardly shifted their habitat selection patterns in spite of the observed changes in habitat conditions, and only YOY individuals appreciably modified their position choice. This result validated our last hypothesis: trout from rivers with highly irregular flow, and recurrent and strong flow events were more willing to shift selected habitats than trout living in more stable environments. In general, population resilience after disturbance events results from individual traits that confer rapid population growth, or that favour the use of spatially more or less distinct refugia, or both; thus a high mobility (promoting refuge use and recolonization) is a resilience feature highly favoured in fluctuating habitats (Townsend and Hildrew, 1994). In addition, environmental perception differs among organisms, which is partly captured by scaling temporal environmental heterogeneity to length of life (Townsend and Hildrew, 1994). That is, an individuals' perception of mortality risks associated to flow events should partly depend on the frequency and predictability of such events. Local adaptations cannot occur when disturbance events are highly unpredictable (Lytle and Poff, 2004; Lytle *et al.*, 2008). In our study, trout from highly variable rivers with recurrent extreme events showed a higher selectivity for velocity refuges under high flows, perhaps anticipating potential flood events; meanwhile they significantly increased selectivity for combined and visual cover under low flows, perhaps preparing for facing a potential summer drought (extreme low flow event) that would increase the intensity of biotic interactions such as predation and competition (Magoulick and Kobza, 2003; Naiman *et al.*, 2008). This suggests that populations occurring at highly variable rivers would have a higher potential for adaptation to cope with the projected changes in climatic conditions in the Mediterranean region (increased water temperature and flow variability, and higher frequency in extreme events), an area where brown trout is expected to face the greatest risks from climate change within its distribution range (Almodóvar *et al.*, 2012). It is worth noting that not only mechanisms aimed at enhancing survival would be involved in observed patterns, because habitat shifts could be also directed towards streamlining the use of food resources considering that patterns of invertebrate drift change with flow hydraulics and channel flow resistance (e.g. Wilcox *et al.*, 2008). At any rate, our findings would suggest that stronger tendency to shift habitat selection behaviour may be not only genetic based but could also emerge from adaptive ontogenetic learning, as YOY trout from rivers having more stable flow were more willing to change microhabitat selection than older individuals. Testing this hypothesis through field experiments involving the transference of individuals inhabiting rivers with variable flow conditions to more stable ones and vice versa remains an interesting open line of research.

Understanding natural patterns of hydrology in time and space and the associated ecological consequences of altering these patterns of flow variability has become fundamental to the assessment and management of environmental water allocations for river systems and environmentally sustainable water management planning (Kennard *et al.*, 2010; Olden *et al.*, 2012). This is robustly founded on the notion that ecological responses to a given anthropogenic change in flow regime should be similar in rivers of a similar initial natural flow regime (Poff *et al.*, 2010). Our study indicates that the way salmonids use and exploit habitats through their spatial (across rivers) and temporal (across short-time frames) dimensions is dependent on the long-term flow regime. Therefore, the consequences of anthropogenic changes to flow timing, magnitude and frequency would differ among populations inhabiting rivers with contrasting hydrologic patterns. This fact has strong implications for predicting the consequences of flow alteration for species adapted to particular flow regimes and for informing flow management recommendations. For example, flow changes resulting in altered disturbance regimes that are less predictable than before (e.g. irregular drought occurrence due to water diversion or unnatural flow peaks due to hydropeaking operations) are more prone to cause greater mortality events in populations occurring in stable flow environments. Further, given that population habitat selection patterns vary across river typologies, restoration projects aiming at enhancing instream habitat that do not take into account the habitat-mediated functional links between population traits and hydrologic regime may turn out a complete failure. Finally, environmental flow standards for regulated rivers or other management practices designed on the basis of habitat suitability models or resource selection probability functions of target species without accounting for ecological dynamics, such as density dynamics (e.g. Boyce *et al.*, 2002; Ayllón *et al.*, 2013) or fluctuating resources (see for e.g. McLoughlin *et al.*, 2010; or this study), may lead to counter-expected ecological responses. Since our results may entail therefore critical implications for conservation and management practices based on habitat selection models, further research should involve a wider range of flow typologies and/or longer time frames to fully understand the ecological and evolutionary effects of hydrological patterns on brown trout habitat selection.

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