Oecologia (2009) 160:515–524
DOI 10.1007/s00442-009-1317-x

POPULATION ECOLOGY - ORIGINAL PAPER

Influence of hydrologic attributes on brown trout recruitment in low-latitude range margins

Graciela G. Nicola · **Ana Almodóvar** ·
Benigno Elvira

Received: 21 October 2008 / Accepted: 18 February 2009 / Published online: 17 March 2009

Abstract Factors controlling brown trout *Salmo trutta* recruitment in Mediterranean areas are largely unknown, despite the relevance this may have for fisheries management. The effect of hydrological variability on survival of young brown trout was studied during seven consecutive years in five resident populations from the southern range of the species distribution. Recruit density at the end of summer varied markedly among year-classes and rivers during the study period. Previous work showed that egg density the previous fall did not account for more than 50% of the observed variation in recruitment density. Thus, we expected that climatic patterns, as determinants of discharge and water temperature, would play a role in the control of young trout abundance. We tested this by analyzing the effects of flow variation and predictability on young trout survival during the spawning to emergence and the summer drought periods. Both hatching and emergence times and length of hatching and emergence periods were similar between years within each river but varied considerably among populations, due to differences in water temperature. Interannual variation in flow attributes during spawning to emergence and summer drought affected juvenile survival in all populations, once the effect of endogenous factors was removed. Survival rate was significantly related to the timing, magnitude and duration of extreme water conditions, and to the rate of change in discharge during hatching and emergence times in most rivers. The magnitude and duration of low flows during summer drought appeared to be a critical factor for survival of young trout. Our findings suggest that density-independent factors, i.e., hydrological variability, play a central role in the population dynamics of brown trout in populations from low-latitude range margins. Reported effects of hydrologic attributes on trout survival are likely to be increasingly important if, as predicted, climate change leads to greater extremes and variability of flow regimes.

Keywords Hydrological variability · *Salmo trutta* · Marginal populations · Population abundance · Population regulation

Introduction

The persistence of animal populations is due to feedback mechanisms which actually or potentially regulate abundance (Turchin 1999). However, wild populations usually experience high density-independent mortality which severely limits the maximum rate of population growth (Myers et al. 1999). Further, population dynamics vary across a species' range in response to environmental changes (Lawton 1993; Brown et al. 1996; Case and Taper 2000). Population density usually decreases from centre to margin, and the regulation of populations may switch accordingly from density-dependent processes to density-independent ones (Guo et al. 2005; Antonovics et al. 2006). There is evidence that density-independent factors have a greater influence on demographic parameters and produce greater fluctuations in peripheral populations than in central ones (Hoffmann and Blows 1994; Williams et al. 2003; Thingstad et al. 2006).

Communicated by Marc Mangel.

G. G. Nicola (✉)
Department of Environmental Sciences,
University of Castilla-La Mancha, 45071 Toledo, Spain
e-mail: graciela.nicola@uclm.es

A. Almodóvar · B. Elvira
Department of Zoology, Faculty of Biology,
Complutense University of Madrid, 28040 Madrid, Spain

Most information concerning the population dynamics of brown trout *Salmo trutta* comes from central and northern Europe (e.g., Elliott 1994; Milner et al. 2003). However, populations from low-latitude range margins face environmental constraints quite different from those of the main distribution area, e.g., dry and hot summers. It remains little investigated if brown trout populations from peripheral southern areas are primarily limited by abiotic and/or biotic factors. In particular, factors controlling brown trout recruitment in Mediterranean areas are largely unknown, despite the relevance that this may have for fisheries management (Nicola et al. 2008). Mediterranean-type streams are characterized by seasonal events of flooding and drying, and also by a strong interannual flow variation (Gasith and Resh 1999). Thus, hydrology could be an important driving force for trout dynamics in Mediterranean regions. Further, summer drought could be a critical period for populations, since it reduces the volume of water available to the fish, causes adverse water quality, and impedes or prevents migration. The effect of summer drought on brown trout recruitment has not yet been analyzed, except for a study in an English stream, which showed that droughts and high temperatures had marked effects on survival of 0+trout, possibly by reduction of available suitable habitat (Elliott et al. 1997). Modern climate change aggravates environmental constraints for populations of temperate species persisting at low-latitude range margins (Parmesan and Yohe 2003). For instance, the extent and impact of summer drought have been increasing in many Mediterranean regions throughout the last decades, and further increases have been anticipated (IPCC 2007).

In salmonids, population size is frequently determined by the abundance of recruits incorporating into the population (e.g., Knapp et al. 1998; Cattanéo et al. 2002; Lobón-Cerviá 2005). Therefore, a better identification and understanding of the multiple constraints on recruitment of populations is crucial for the design of appropriate conservation strategies. Fry emergence and survival is a critical period in brown trout populations, with survival during this stage having a strong influence on population abundance and cohort strength (Armstrong and Nislow 2006). During the post-emergence phase, populations are regulated by density-dependent processes, mainly competition for territories among fry (Elliott 2001). However, some studies have shown that hydrological variability is also of major importance in determining juvenile density in temperate regions. For instance, functional links between recruitment and hydrological factors have been described for some brown trout populations (e.g., Solomon and Paterson 1980; Jensen and Johnsen 1999; Lobón-Cerviá 2004; Lobón-Cerviá and Rincón 2004). Nowadays, it is widely recognized that the impact of hydrological events does not depend only on their magnitude, but also on their timing and the life stage involved. For example, at the time of incubation, high flow events can produce egg washout and extreme low flows egg desiccation (Spina 2001; Zorn and Nuhfer 2007). During the critical period after emergence, discharge determines the available suitable habitat for young trout, i.e., feeding territories and shelter (Ayllón et al. 2009). The early 0+trout are also particularly sensitive to hydrological variability, owing to their inability to face high current velocities and to find shelter during high flow events (Armstrong et al. 2003).

The main purpose of this study was to analyze the effects of hydrological variability on recruitment survival of brown trout in five resident populations from the southern limits of its native range. A previous study of the same populations indicated that, although density-dependent mechanisms seemed to regulate the fish abundance in some cases, environmental factors and harvesting appeared generally to preclude populations from reaching densities high enough for negative feedbacks to operate (Nicola et al. 2008). Population density alone did not account for more than 50% of the observed variation in recruitment density, so that the unexplained variability is probably due to local environmental conditions. We hypothesized that juvenile survival may be driven by hydrologic attributes during two critical periods, spawning to emergence and summer drought. We expected that climatic patterns, as determinants of discharge and water temperature, would play a role in determining young trout abundance. We tested this hypothesis by analyzing the relationship between young trout survival and flow variability and predictability over seven consecutive years.

Materials and methods

Study area

This study was carried out in 12 localities along five rivers of central Spain; three are tributaries to the River Tajo (Hoz Seca, Cabrillas and Dulce) and two to the River Duero (Cega and Eresma) (Table 1). The climate is continental Mediterranean, with hot, dry summers and cold winters. Physical characteristics, water temperature, and flow regime vary among rivers, but may be divided into two groups. The first type (Cega and Eresma) are softwater rivers, where the greater part of their water comes from surface drainage, becoming torrential at snowmelt in early spring. The mean water temperature in winter is close to 0°C and in summer to 13°C. The rest of rivers (Hoz Seca, Cabrillas and Dulce) have hard, fertile waters with an even flow regime throughout the year. The Cabrillas and Dulce have average winter temperatures around 7°C and summer means close to 17°C. The Hoz Seca is fed by limestone

Table 1 Physical and chemical characteristics of the rivers studied

	Hoz Seca	Cabrillas	Dulce	Cega	Eresma
River basin	Tajo	Tajo	Tajo	Duero	Duero
Altitude (m)	1,360	1,267	885	1,250	1,290
Width (m)	12.8 (11.7–14.3)	4.3 (2.1–6.5)	4.9 (4.0–6.1)	5.8 (4.9–7.2)	6.3 (5.1–8.0)
Dominant substrate	Gravel	Cobble	Sand	Boulder	Boulder
Conductivity (μS cm^{-1})	598.1 ± 35.8	606.1 ± 22.6	602.4 ± 15.7	17.7 ± 1.2	65.3 ± 4.1
Alkalinity ($CaCO_3$ mg l^{-1})	265.0 ± 12.8	281.7 ± 13.7	303.3 ± 1.8	19.2 ± 2.1	27.0 ± 2.6
pH	8.2 ± 0.2	7.8 ± 0.1	7.7 ± 0.1	7.1 ± 0.1	7.1 ± 0.1
Spawning to emergence period					
Velocity (m s^{-1})	0.70 (0–1.6)	0.67 (0–2.6)	0.85 (0–3.5)	0.50 (0–3.2)	0.72 (0–4.1)
Mean discharge (m^3 s^{-1})	8.5 (1.7–159.9)	1.4 (0.5–16.1)	1.7 (0.5–14.2)	6.5 (1.0–67.6)	4.6 (0.4–35.4)
Mean discharge high flow pulses (m^3 s^{-1})	5.3	0.7	0.9	7.3	6.3
Peak discharge high flow pulses (m^3 s^{-1})	10.2 (8.3–12.1)	1.4 (0.8–2.1)	1.3 (0.9–1.8)	15.4 (6.2–27.6)	17.7 (10.4–28.5)
Mean discharge small floods (m^3 s^{-1})	13.0	2.2	2.1	14.8	11.2
Peak discharge small floods (m^3 s^{-1})	95.3 (13.8–159.9)	10.4 (7.8–16.1)	9.8 (2.6–14.2)	46.8 (28.8–67.6)	33.4 (30.8–35.4)
Temperature (°C)	9.5 (8.1–11.9)	6.4 (5.9–15.2)	9.5 (6.9–14.8)	3.9 (0.3–10.4)	3.5 (0.3–10.3)
Summer drought period					
Velocity (m s^{-1})	0.29 (0–0.5)	0.27 (0–1.1)	0.38 (0–1.5)	0.18 (0–1.5)	0.37 (0–1.4)
Mean discharge (m^3 s^{-1})	1.4 (1.0–2.8)	0.5 (0.2–0.8)	0.5 (0.3–0.9)	2.8 (0.03–1.8)	0.4 (0–1.3)
Mean discharge extreme low floods (m^3 s^{-1})	0.94 (0.78–1.02)	0.30 (0.19–0.31)	-	0.11 (0.03–0.14)	0.13 (0–0.22)
Temperature (°C)	11.3 (10.2–12.0)	14.4 (10.5–16.0)	16.2 (12.1–18.6)	11.3 (7.8–13.4)	11.9 (9.2–13.2)

Stream values of physical variables (mean, min–max) and chemical determinants (mean ± SD) were calculated from seasonal measurements at each sampling point during the entire study period of 1992–1998

aquifers and therefore water temperature remains close to 10°C all year round. Further details of the study area are given in Nicola and Almodóvar (2002) and Almodóvar and Nicola (2004). Brown trout is the only fish species present throughout the study area and its populations comprise exclusively resident individuals. The rivers are not currently stocked and are unaffected by land use, pollution, or water regulation, except for the Hoz Seca, which has been regulated in its lower reaches by a hydropower station since the end of 1993.

Brown trout sampling

Fish were sampled every third month from December 1992 to December 1998 at each locality by electrofishing using a 2,200-W generator. Trout were anaesthetized with tricaine methane-sulphonate (MS-222) and their fork length (to the nearest mm) and weight (to the nearest g) were measured. Scales were taken for age determination. The fish were placed in holding boxes to recover and then returned to the stream.

Fish density (trout ha^{-1}) and its variance were estimated separately for each sampling point by applying the maximum likelihood method (Zippin 1956) and the corresponding solution proposed by Seber (1982) for 3-removals assuming constant-capture effort.

Recruitment was measured as the density of 0+trout (trout ha^{-1}) in early September and the parental stock was expressed as the egg density (eggs ha^{-1}) of the parental fish of the cohort (year-class). To evaluate the strength of density-dependence, we employed Ricker's stock-recruitment models (Nicola et al. 2008). The models showed a significant fit to the data in all populations and the proportion of variance explained by the population curves varied between 32 and 51% (Table 2). Recruitment variability unrelated to factors endogenous to the population was then estimated by the differences between observed and expected values (residuals) from the Ricker's stock-recruitment models obtained by Nicola et al. (2008) in the

Table 2 Stock–recruitment relationships ($R = aS \exp^{-bS}$) in the five populations of brown trout *Salmo trutta* studied from 1992 to 1998

River	a	b	F	P	R^2
Hoz Seca	0.005130	0.000005	31.3	<0.01	0.38
Cabrillas	0.009878	0.000003	51.4	<0.01	0.38
Dulce	0.014958	0.000007	38.2	<0.01	0.51
Cega	0.016598	0.000002	17.8	<0.01	0.46
Eresma	0.014244	0.000002	12.5	<0.01	0.32

The estimates of the parameters a and b, the coefficients of determination (R^2) and significance levels for F values are indicated. Data are from Nicola et al. (2008)

study populations. Residuals were then used as indices of survival rates of recruits in subsequent analyses with hydrological variables.

Hydrologic attributes

To evaluate the effect of flow variation and predictability on survival of young trout we estimated several biologically relevant hydrologic parameters, according to Richter et al. (1996) and following the recommendations of Olden and Poff (2003). Flow data were obtained from a database collected by the Spanish Ministry of Environment. The selected gauging stations were close to sampling sites. Daily discharge data from each river were processed every year to obtain twelve variables during two periods: (1) spawning to emergence (Spw-Eme) and (2) summer drought (Dry). Although the concept of drought is well recognized, there is no general agreement on a clear definition (Wilhite and Glantz 1985). Here, the summer drought was defined as a prolonged (over 2 or 3 months sequence) period of dry weather, i.e., extremely low precipitation and very high temperatures. The duration of the drought period was determined by comparing the current situation to the historical average. The average conditions were characterised by the mean daily flow during each period (Mean). The magnitude and duration of extreme water conditions was measured as the minimum and maximum discharge during 7 (7Dmin and 7Dmax) and 30 days (30Dmin and 30Dmax). The frequency and duration of high (HpF and HpD) and low (LpF and LpD) pulses provided a combined extreme event timing measure. 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 time period. The rate of change in discharge was measured as the mean rate of both positive (rise rate, Rr) and negative (falling rate, Fr) changes in discharge between consecutive days. Then, the number of reversals (Rev) was calculated as the number of times that discharge switches from one type of period to another.

Finally, the predictability of daily flow (P) was determined for the study rivers from a 25-year dataset following the method proposed by Colwell (1974) and applied to stream systems by Resh et al. (1988). Predictability is a measure of the relative certainty of knowing a state at a given time and ranges from 0 to 1, with a value of 1 indicating complete predictability. Predictability is composed of two independent, additive components: constancy (C), a measure of temporal invariance, and contingency (M), a measure of periodicity. 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 predictability of a stream with very constant flow will be mostly due to C, while the predictability of a stream with highly variable flow with a fixed periodicity will be mostly due to M. Flow data of each river were cast into a frequency matrix (contingency table) where rows represented flow classes and columns were time categories (see Resh et al. 1988 for specific methods). The frequency of occurrence at each matrix intersection was obtained, from which the indices were computed by mathematical formulae as detailed in Colwell (1974) and Gan et al. (1991). The index C/(C + M) 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.

The annual timing of hatching and emergence was estimated according to Elliott and Hurley (1998) field and laboratory individual-based model on the basis of spawning time and water temperature. The water temperature was measured every 30 min by means of data-loggers (Minilog Vemco) permanently placed in each river during the study period. Mean daily temperature is given as the mean of all readings in each 24-h period. The model describes the relationship between embryonic development and temperature, considering naturally fluctuating temperatures. It accelerates and decelerates development at high and low temperatures, respectively. Egg fertilization dates were fixed as the mid-points for the spawning periods of early, middle, and late spawners. The following equation is the function of temperature that affects the development time to hatching:

$$f_{\mathrm{H}}(T) = C_{\mathrm{H50}}(T_1 - T)(T - T_0)^{-1} \qquad (1)$$

where T is the mean daily water temperature in each locality, T_0 is the lower temperature at which no eggs hatch, T_1 is the theoretical temperature at which eggs hatch instantaneously, and C_{H50} is the degree of curvature of the time response for 50% of the eggs to hatch and is also the number of days taken for eggs to hatch at a constant temperature of $(T_1 + T_0)/2$. For each egg i, a random number generator was used to simulate the relative coefficient of development ε_i from a normal distribution with mean of 1 and standard deviation $\sigma = 0.04833$ (Elliott and Hurley 1998). Daily values of $1/[\varepsilon_i f_{\mathrm{H}}(T)]$ were accumulated until the first day when the value of 1.0 was exceeded, this providing the egg hatching date.

The following equation is the function of temperature that reduces the yolk resource during the alevin stage:

$$f_{\mathrm{A}}(T) = C_{\mathrm{A50}}(T_1 - T)(T - T_0)^{-1} \qquad (2)$$

where C_{A50} is the number of days taken after hatching for 50% of the alevins to become emerging fry. The same values of T_1 and T_0 were used for (1) and (2) functions. Estimates of parameters T_0, T_1, C_{H50} and C_{A50} are given in Elliott and Hurley (1998: Table 3).

Each egg i has a yolk resource r_i to be utilized during the alevin stage and emergence occurs when the resource is exhausted. The parameter r_i also has a normal distribution with a mean of 1 and a standard deviation of $\delta = 0.01192$ (Elliott and Hurley 1998). The value of the yolk resource, r_i, for each egg i was computed from $r_i = 1-\delta\ (\varepsilon_i-1)\sigma^{-1}$ and then reduced on each subsequent day by $1/f_A(T)$ until the yolk was exhausted, this providing the fry emergence date. The entire procedure was repeated five times each year to provide a more precise estimate of dates.

Data analyses

Multivariate analyses were performed in SIMCA-P + 12.0. Partial least squares regression (PLS) was used to analyze the relationships between hydrological variables and survival of recruits (Geladi and Kowalski 1986; Abdi 2003). Separate PLS models were developed for each river. All variables were verified for normal distribution through Shapiro–Wilk test and log $(x + 1)$ transformed to receive normal distribution. The data were divided into X and Y blocks. The Y block (response variable) consisted of survival rates and hydrological variables constituted the X block. All models were constructed with the autofit function in order to obtain the highest predictive (Q^2) value. A Q^2 value above 0.4 was considered good (Eriksson et al. 2006). To determine the importance of X variables in predicting Y variable the variable influence on projection (VIP) statistic was used. A VIP value greater than 1.0 was considered to be highly influential, whereas a lower value was considered to be of less influence (Eriksson et al. 2006). The significance level for all statistical tests was set at $\alpha = 0.05$.

Results

Hydrological variability

The studied rivers exhibited seasonal and among-year variation in water discharge, typical for the Mediterranean climate, but the hydrological pattern was different among sites during the study period. The hydrologic conditions showed marked differences between years 1992–1995 and 1996–1998 in Hoz Seca, Cabrillas, and Dulce (Fig. 1), where dry and wet periods were respectively detected. However, hydrologic attributes were similar in Eresma and Cega among study years. Frequent high flow pulses and occasional small floods typically occur in Eresma and Cega during winter and spring. In contrast, during summer, extreme low flow episodes are very frequent (Table 1). The rest are groundwater rivers little affected by surface run-off at times of heavy rainfall or snowmelt. High flow pulses occur during autumn and spring, but their magnitude and frequency was much lower than in Eresma and Cega (Fig. 1). Small floods were very scarce and only occurred during winter and spring of years 1996–1998. Extreme low flows during summer were only detected in Hoz Seca and Cabrillas.

The summer drought which characterizes Mediterranean climate lasted for 3 months, from mid-July to mid-October, in all rivers. Low discharge during the dry season is

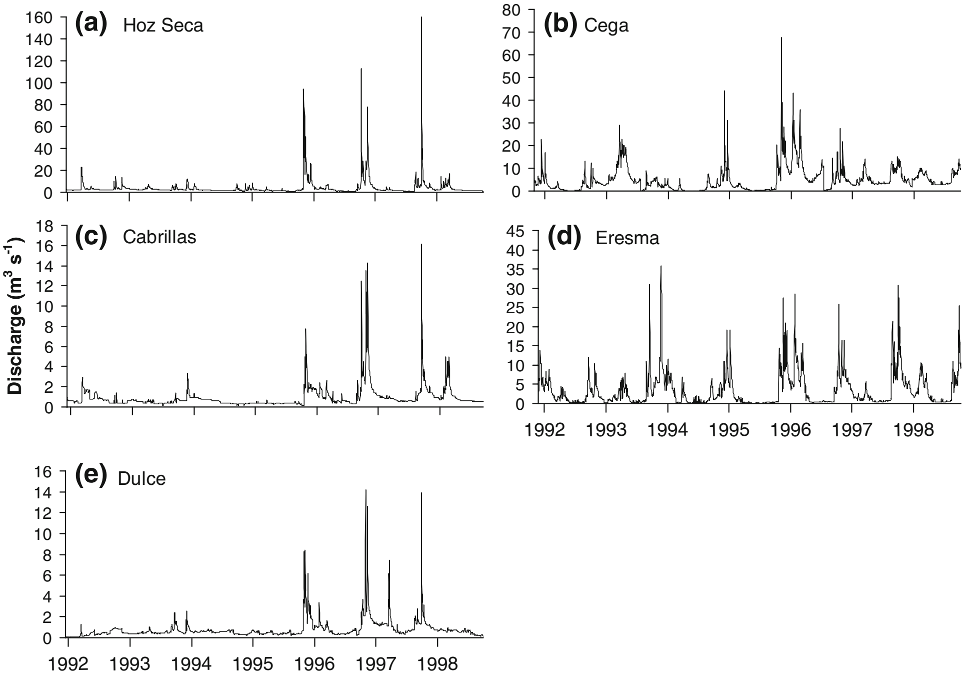

Fig. 1 Daily discharge ($m^3\ s^{-1}$) in the five study rivers (Hoz Seca, Cabrillas, Dulce, Cega, and Eresma) during 1992–1998

Table 3 Mean dates for hatching and emergence of brown trout and mean water temperature (°C) during incubation (T_{incub}) and emergence (T_{emerg}) periods during 1992–98 in the five rivers studied

River	Hatching	T_{incub}	Emergence	T_{emerg}
Hoz Seca	7–22 Jan	9.0 (8.1–10.0)	21–28 Feb	9.9 (8.2–11.9)
Cabrillas	17 Jan–5 Feb	7.5 (5.9–9.5)	11–21 Mar	9.5 (6.2–15.2)
Dulce	6–20 Jan	9.3 (6.9–11.2)	15–24 Feb	11.9 (7.7–14.8)
Cega	26 Apr–19 May	2.6 (0.0–8.4)	15–25 Jun	6.3 (0.4–10.4)
Eresma	4 Apr–11 May	2.8 (0.3–5.3)	20–30 Jun	5.9 (2.3–10.3)

Data ranges are indicated in parentheses

coupled with higher temperatures, especially in Cabrillas and Dulce (Table 1). Predictability (P) of daily discharge was similar among streams and ranged from 0.50 to 0.60. However, in Hoz Seca, Cabrillas, and Dulce, P was mostly due to C, whereas in Cega and Eresma it was mostly due to M. Therefore, the index C/P was much higher (0.71–0.78) in rivers with constant flow (Hoz Seca, Cabrillas, and Dulce) when compared to rivers with an irregular flow (Cega and Eresma), where the index was between 0.35 and 0.41.

Recruitment variability

There was a good agreement between the hatching and emergence model predictions and the annual observations of alevins and fry during winter and spring samplings in each river. Both the hatching and emergence times and the length of hatching and emergence periods were very similar between years within each river, but varied considerably among populations (Table 3). The Cega and Eresma were significantly colder than the rest of rivers during the period from spawning to emergence. Therefore, eggs hatched between April and May and emergence took place in June. In the rest of the rivers, eggs usually hatch in January and early February, and the alevin stage ends from mid-February to mid-March, when the fry disperse from the redd.

Recruit density at the end of summer varied markedly among year-classes and rivers during the study period (Fig. 2), showing statistically significant differences among years within each river and among populations (Nicola et al. 2008). Mean estimates of young trout density during the period 1992–1998 ranged from 649.8 trout ha^{-1} in Dulce to 1,242.8 trout ha^{-1} in Eresma (Fig. 3). Recruitment was most variable in Cega and Eresma, with coefficients of variation around 50%.

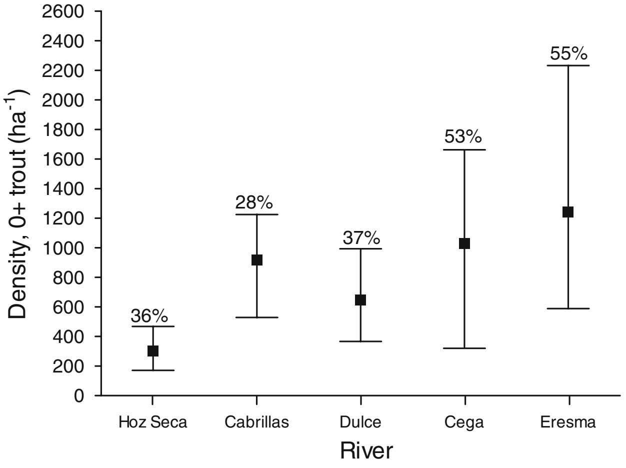

Fig. 2 Density (mean, minimum, maximum, and coefficient of variation CV%) of young brown trout *Salmo trutta* of age 0+in early September in the study rivers during 1992–1998

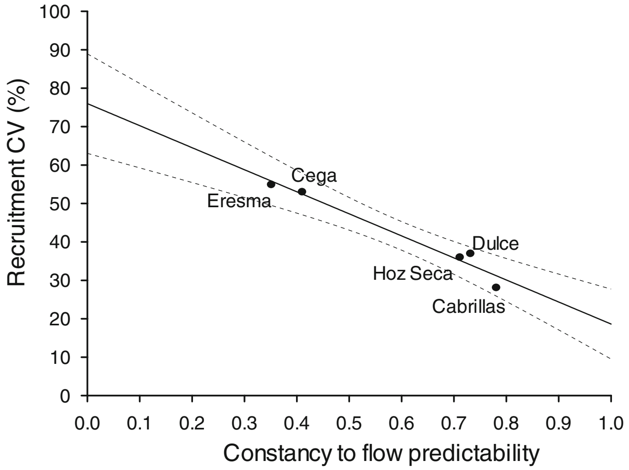

Fig. 3 Relationship (with 95% confidence intervals) between predictability of daily flow, expressed as the index between constancy and predictability (see "Materials and methods" for more details), and the coefficient of variation for recruitment (0+trout density) during 1992–1998 in five streams from central Spain

Effects of hydrologic conditions on recruitment

Interannual variation in flow conditions during spawning to emergence and summer drought affected juvenile survival of brown trout in all populations, once the effect of endogenous factors, i.e., egg density the previous fall, was removed. The obtained PLS models showed that the first two latent factors explained more than 90% of the total variance of survival rate (Hoz Seca, $R^2 = 0.97$, $P < 0.001$; Cabrillas, $R^2 = 0.96$, $P < 0.001$; Dulce, $R^2 = 0.91$, $P < 0.01$; Eresma, $R^2 = 0.94$, $P < 0.01$; Cega, $R^2 = 0.98$, $P < 0.001$) and had relatively good predictive power (Hoz Seca, $Q^2 = 0.78$; Cabrillas, $Q^2 = 0.67$; Dulce, $Q^2 = 0.38$; Eresma, $Q^2 = 0.38$; Cega, $Q^2 = 0.74$).

For brevity in Table 4, only the PLS regresion coefficients and VIP scores which measure the relative contributions of the hydrological variables in explaining the variance of juvenile survival, are shown. According to

Table 4 Regression vector standardized PLS partial coefficients (coeff) and VIP scores (scores) of the hydrologic attributes for the regression models obtained for the survival rates of brown trout in the five rivers studied

	Hoz Seca		Cabrillas		Dulce		Eresma		Cega	
	Coeff	Scores	Coeff	Scores	Coeff	Scores	Coeff	Scores	Coeff	Scores
$7Dmin_{Spw\text{-}Eme}$			0.17	1.37						
$7Dmax_{Spw\text{-}Eme}$									−0.14	1.53
$30Dmax_{Spw\text{-}Eme}$					−0.09	1.22			−0.15	1.67
$HpF_{Spw\text{-}Eme}$	−0.11	1.37			−0.09	1.22			−0.13	1.65
$HpD_{Spw\text{-}Eme}$					−0.08	1.20			−0.09	1.08
$LpF_{Spw\text{-}Eme}$							−0.24	1.62		
$Rr_{Spw\text{-}Eme}$	−0.12	1.41							−0.14	1.68
$Fr_{Spw\text{-}Eme}$									0.15	1.78
$Rev_{Spw\text{-}Eme}$			−0.25	1.82			−0.06	1.26	−0.13	1.50
$7Dmax_{Dry}$			0.11	1.12	0.24	1.82	0.21	1.76	0.08	1.05
$30Dmax_{Dry}$			0.20	1.47	0.18	1.31				
HpF_{Dry}	0.12	1.42								
Rr_{Dry}							0.20	1.78		
Rev_{Dry}	−0.14	1.23								

Only the coefficients having a VIP score greater than 1 are shown (see “Materials and methods” for details)

Table 4, the relative influence of flow regime variables during the two critical periods varied among rivers. However, a more close inspection of data showed some patterns in Spw-Eme and Dry periods.

During the Spw-Eme period, in Hoz Seca, Dulce, and Cega, the frequency and duration of high flow events during both hatching and emergence times were major attributes driving juvenile survival. In Cabrillas, the survival of 0+trout increased when the magnitude and stability of discharge augmented during spawning. In Eresma, low pulse episodes during emergence time negatively influenced survival, probably decreasing the availability of suitable habitat for fry. Finally, recruitment in Hoz Seca, Eresma, and Cega was also negatively influenced by daily flow fluctuations during emergence.

During the Dry period, both the magnitude and duration of maximum discharge episodes and flow stability were highly important for predicting 0+trout survival in all rivers. In Hoz Seca, the negative influence of daily flow fluctuations (reversals) on recruitment during summer may be attributed to the frequent changes in water level generated by flow regulation, which substantially alter the availability of suitable microhabitat for 0+trout.

Finally, the coefficient of variation for 0+trout density during the period 1992–1998 was found to be negatively correlated ($r = -0.96$, $P < 0.01$) to the index C/P within the study area, which is indicative of the relative constancy of daily flow. Thus, interannual variation of recruitment tends to be higher in populations under irregular hydrologic conditions (Fig. 3).

Discussion

Interannual variation in flow conditions during both spawning to emergence and summer drought periods affected juvenile survival of brown trout in all the study populations. However, the relative importance of hydrologic features on recruitment varied among rivers. First, flow characteristics during the incubation period seemed to be of minor importance in all populations. On the contrary, survival rate was negatively correlated with the frequency and duration of high flow events during both hatching and emergence times in three rivers (Hoz Seca, Dulce, and Cega). High discharge could result in loss rates by displacing alevins and fry downstream or to nonoptimal habitats with higher energy costs or lower food availability. Higher flows and colder temperatures probably interact to increase the chances of displacement of fry and to decrease the availability of favourable foraging locations (Nislow et al. 2000). Displacement of brown trout fry during high stream flows has been reported previously (e.g., Ottaway and Forrest 1983; Heggenes and Traaen 1988; Daufresne et al. 2005). First-feeding juveniles tend to occupy relatively low-velocity, shallow locations near water-body margins or shelters, where some of them defend small territories (Grant et al. 1998; Ayllón et al. 2009). Heggenes and Traaen (1988) experimentally confirmed that brown trout at the swim-up stage were washed out by water velocities from 0.10 to 0.25 m s^{-1}, as a consequence of their inability to maintain their stream position or to find shelter. These velocities are common in the study rivers during the emergence periods of some years (Table 1). In addition, high flow pulses in the study area are typically associated with sediment transport increases followed by further accumulation in the stream bed, which can physically trap alevins, preventing their emergence (Acornley and Sear 1999; Hartman and Hakala 2006).

In Hoz Seca, Eresma, and Cega, survival rate was also negatively influenced by the rate of change in discharge (reversals and rise rate) during the emergence period, which can quickly influence habitat availability and suitability for young trout (Olden and Poff 2003; Ayllón et al. 2009), and therefore limit recruit abundance within the sites. In Hoz Seca, Almodóvar and Nicola (1999) observed a loss in recruitment due to the violent fluctuations in the water level generated by flow regulation, which causes a loss of suitable habitat for young trout.

In Cabrillas, there was a significant positive correlation between minimum discharge during the spawning period and survival of young trout. Low discharges are believed to adversely affect spawning success and limit salmonid abundance (Frenette et al. 1984; Gibson and Myers 1988). A lower discharge during the spawning period may diminish fry production by decreasing the amount of suitable habitat for gravel nests (Elliott and Hurley 1998; Fukushima et al. 1998; Einum et al. 2003) or may impede the intragravel flow of water, thereby deteriorating conditions for incubating brown trout embryos.

Hydrologic influences on brown trout year-class strength have been previously observed mostly in high-gradient, mountainous streams in Europe (e.g., Jensen and Johnsen 1999; Cattanéo et al. 2002; Lobón-Cerviá 2004; Lobón-Cerviá and Rincón 2004) and in introduced populations from the USA and New Zealand (e.g., Strange et al. 1992; Hayes 1995), as well as in low-gradient streams in the USA (Zorn and Nuhfer 2007). All these works pointed out that 0+trout density was negatively influenced by high stream discharge during or shortly after emergence, resulting in weak year-classes. Most of these studies were based on general estimates of emergence times and scarce flow features (mainly average conditions). Our findings for Mediterranean-type streams support the observed pattern in temperate streams in a broad sense. However, average conditions were not significantly related to survival rates, whereas the timing, magnitude, and duration of extreme water conditions and the rate of change in discharge were of major importance. Further, the use of more precise calculations of hydrologic attributes and hatching/emergence times showed a variable influence of flow features on young trout survival, which basically depended on the physical habitat of study rivers, i.e., the availability of microhabitat and cover for young trout and the suitable habitat for gravel nests.

The magnitude and duration of low flow during summer was a critical factor for 0+trout survival in the study streams. Recruitment was better when discharge was higher, probably by increasing the amount of available juvenile habitat in all rivers and also by reducing the thermal and oxygen stress in the warmest rivers. High stream flow during summer likely increases the number of territories, particularly along the streambank, where 0+trout usually occur. Also, an increase of stream flow in summer enhances the production of invertebrates (Boulton 2003), which serve as food for young brown trout.

The effects of drought on brown trout were only noted by Elliott et al. (1997) in England, who found that severe summer droughts greatly reduced the density of 0+trout, whereas milder droughts had a less severe effect. However, in Elliott et al.'s (1997) study, summer droughts were occasional (7 in 30 years), whereas in our study rivers summer droughts cause prolonged periods of low flow and high water temperature each year. It is the relative severity of drought which affects young trout survival in Mediterranean-type streams. There is some evidence that droughts may result in significant population fluctuations in other native fish species from Mediterranean-type streams (e.g., Bernardo et al. 2003; Magalhaes et al. 2007). Reported effects are likely to be increasingly important if, as predicted, climate change leads to an increased frequency and severity of droughts in the Mediterranean region (IPCC 2007; Giorgi and Lionello 2008).

Our findings support the hypothesis that the survival of 0+trout in streams under a Mediterranean climate is influenced by the local discharge regime. Density-dependence explained between 32 and 51% of recruitment variability in the study populations (Nicola et al. 2008), whereas hydraulic features explained from 91 to 97% of the survival variability, once the effect of endogenous factors was removed. Our analyses support the pattern observed in other taxa where populations are more variable towards the periphery of species' ranges, mainly as a result of a higher variability in abiotic factors, such as climatic conditions (e.g., Mehlman 1997; García and Arroyo 2001; Williams et al. 2003; Thingstad et al. 2006). Density-independent factors, i.e., hydrological variability, could play a central role in the population dynamics of brown trout in populations from low-latitude range margins. Our results point out the importance of extreme flow events and daily flow changes during winter–spring to brown trout recruitment, and highlight the influence of summer drought on population dynamics. In these populations where numbers of swim-up fry in most years are not high enough to bring density-dependent mortality into play, hydrologic variability during critical periods is a major determinant of year-to-year variation of recruitment. Furthermore, the constancy of flow regime was related to the temporal variability of abundance within the study area. Contrary to the situation in central Europe, brown trout in low-latitude range margins may have population dynamics which are driven more by external factors.

Acknowledgments This study was supported by the Spanish National Institute of Agricultural Research (INIA) through research projects SC-9645 and SC-95/005. All field procedures complied with the current laws of Spain. We also acknowledge the very constructive criticism of three anonymous referees and the editor, Marc Mangel.

References

Abdi H (2003) Partial least squares (PLS) regression. In: Lewis-Black M, Bryman A, Liao TF (eds) The SAGE encyclopedia of social sciences research methods. Sage Press, Thousand Oaks, pp 792–795

Acornley RM, Sear DA (1999) Sediment transport and siltation of brown trout (*Salmo trutta* L.) spawning gravels in chalk streams. Hydrol Process 13:447–458

Almodóvar A, Nicola GG (1999) Effects of a small hydropower station upon brown trout *Salmo trutta* L. in the River Hoz Seca (Tagus basin, Spain) 1 year after regulation. Regul Rivers Res Mgmt 15:477–484

Almodóvar A, Nicola GG (2004) The effects of fishery management on conservation of Spanish stream-dwelling brown trout *Salmo trutta* L. Fisheries Manag Ecol 11:173–182

Antonovics J, McKane AJ, Newman TJ (2006) Spatiotemporal dynamics in marginal populations. Am Nat 167:16–27

Armstrong JD, Nislow KH (2006) Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). J Zool 269:403–413

Armstrong JD, Kemp PS, Kennedy GJA, Ladle M, Milner NJ (2003) Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish Res 62:143–170

Ayllón D, Almodóvar A, Nicola GG, Elvira B (2009) Interactive effects of cover and hydraulics on brown trout habitat selection patterns. River Res Appl. doi:10.1002/rra.1215

Bernardo JM, Ilhéu I, Matono P, Costa AM (2003) Interannual variation of fish assemblage structure in a Mediterranean river: implications of streamflow on the dominance of native or exotic species. River Res Appl 19:521–532

Boulton AJ (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrates assemblages. Freshw Biol 48:1173–1185

Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. Annu Rev Ecol Syst 27:597–623

Case TJ, Taper ML (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. Am Nat 155:583–605

Cattanéo F, Lamouroux N, Breil P, Capra H (2002) The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. Can J Fish Aquat Sci 59:12–22

Colwell RK (1974) Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148–1153

Daufresne M, Capra H, Gaudin P (2005) Downstream displacement of post-emergent brown trout: efects of development stage and water velocity. J Fish Biol 67:599–614

Einum S, Fleming IA, Côté IM, Reynolds JD (2003) Population stability in salmon species: effects of population size and female reproductive allocation. J Anim Ecol 72:811–821

Elliott JM (1994) Quantitative ecology and the brown trout. Oxford University Press, New York

Elliott JM (2001) The relative role of density in the stock-recruitment relationship of salmonids. In: Prévost E, Chaput C (eds) Stock, recruitment and reference points: assessment and management of Atlantic salmon. INRA, Paris, pp 25–66

Elliott JM, Hurley MA (1998) An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. J Fish Biol 53:414–433

Elliott JM, Hurley MA, Elliott JA (1997) Variable effects of droughts on the density of a sea-trout *Salmo trutta* population over 30 years. J Appl Ecol 34:1229–1238

Eriksson L, Johansson E, Kettaneh-Wold N, Trygg J, Wilkström C, Wold S (2006) Multi- and megavariate data analysis basic principles and applications. Umetrics, Umea

Frenette M, Caron M, Julie P, Gibson RJ (1984) Interaction entre le débit et les populations de tacons (*Salmo salar*) de la riviere Matamec, Québec. Can J Fish Aquat Sci 41:954–963

Fukushima M, Quinn TJ, Smoker WW (1998) Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. Can J Fish Aquat Sci 55:618–625

Gan KC, McMahon TA, Finlayson BL (1991) Analysis of periodicity in streamflow and rainfall data by Colwell's indices. J Hydrol 123:105–118

García JT, Arroyo BE (2001) Effects of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. Ecography 24:393–402

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

Geladi P, Kowalski BR (1986) Partial least-square regressions: a tutorial. Anal Chim Acta 185:1–17

Gibson RJ, Myers RA (1988) Influence of seasonal river discharge on survival of juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 45:344–348

Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Global Planet Change 63:90–104

Grant JWA, Steingrimsson SO, Keeley ER, Cunjak RA (1998) Implications of territory size for the measurement and prediction of salmonid abundance in streams. Can J Fish Aquat Sci 55:181–190

Guo Q, Taper M, Schoenberger M, Brandle J (2005) Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108:47–57

Hartman KJ, Hakala JF (2006) Relationships between fine sediment and brook trout recruitment in forested headwater streams. J Freshw Ecol 21:215–230

Hayes JW (1995) Spatial and temporal variation in the relative density and size of juvenile brown trout in the Kakanui River, North Otago, New Zealand. N Z J Mar Freshw Res 29:393–408

Heggenes J, Traaen T (1988) Downstream migration and critical water velocities in stream channels for fry of four salmonid species. J Fish Biol 32:717–727

Hoffmann AA, Blows MW (1994) Species borders: ecological and evolutionary perspectives. Trends Ecol Evol 9:223–227

IPCC (2007) Climate Change 2007 The physical science basis. Cambridge University Press, New York

Jensen AJ, Johnsen BO (1999) The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Funct Ecol 13:778–785

Knapp RA, Vredenburg VT, Matthews KR (1998) Effects of stream channel morphology on golden trout spawning habitats and recruitment. Ecol Appl 8:1104–1117

Lawton JH (1993) Range, population abundance and conservation. Trends Ecol Evol 8:409–413

Lobón-Cerviá J (2004) Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. Can J Fish Aquat Sci 61:1929–1939

Lobón-Cerviá J (2005) The importance of recruitment for the production dynamics of stream-dwelling brown trout (*Salmo trutta*). Can J Fish Aquat Sci 62:2484–2493

Lobón-Cerviá J, Rincón PA (2004) Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. Oikos 105:641–646

Magalhaes MF, Beja P, Schlosser IJ, Collares-Pereira MJ (2007) Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams. Freshw Biol 52:1494–1510

Mehlman DW (1997) Change in avian abundance across the geographic range in response to environmental change. Ecol Appl 7:614–624

Milner NJ, Elliott JM, Armstrong JD, Gardiner R, Welton JS, Ladle M (2003) The natural control of salmon and trout populations in streams. Fish Res 62:111–125

Myers RA, Bowen KG, Barrowman NJ (1999) Maximum reproductive rate of fish at low densities. Can J Fish Aquat Sci 56:2404–2419

Nicola GG, Almodóvar A (2002) Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. Freshw Biol 47:1353–1365

Nicola GG, Almodóvar A, Jonsson B, Elvira B (2008) Recruitment variability of resident brown trout in peripheral populations from southern Europe. Freshw Biol 53:2364–2374

Nislow KH, Folt CL, Parrish DL (2000) Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. Trans Am Fish Soc 129:1067–1081

Olden JD, Poff NL (2003) Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. River Res Appl 19:101–121

Ottaway EM, Forrest DR (1983) The influence of water velocity on the downstream movement of alevins and fry of brown trout, *Salmo trutta* L. J Fish Biol 23:221–227

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. J N Am Benthol Soc 7:433–455

Richter BD, Baumgartner JV, Powell J, Braun DP (1996) A method for assessing hydrologic alteration within ecosystems. Conserv Biol 10:1163–1174

Seber GAF (1982) The estimation of animal abundance and related parameters. Griffin, London

Solomon DJ, Paterson D (1980) Influence of natural and regulated streamflow on survival of brown trout (*Salmo trutta* L.) in a chalk stream. Environ Biol Fish 5:379–382

Spina AP (2001) Incubation discharge and aspects of brown trout population dynamics. Trans Am Fish Soc 130:322–327

Strange EM, Moyle PB, Foin TC (1992) Interactions between stochastic and deterministic processes in stream fish community assembly. Environ Biol Fish 36:1–15

Thingstad PG, Nyholm NEI, Fjeldheim B (2006) Pied flycatcher Ficedula hypoleuca population dynamics in peripheral habitats in Scandinavia. Ardea 94:211–223

Turchin P (1999) Population regulation: a synthetic view. Oikos 84:153–159

Wilhite DA, Glantz MH (1985) Understanding the drought phenomenon: the role of definitions. Water Int 10:111–120

Williams CK, Ives AR, Applegate RD (2003) Population dynamics across geographical ranges: time-series analyses of three small game species. Ecology 84:2654–2667

Zippin C (1956) An evaluation of the removal method of estimating animal population. Biometrics 12:163–189

Zorn TG, Nuhfer AJ (2007) Influences on brown trout and brook trout population dynamics in a Michigan river. Trans Am Fish Soc 136:691–705