Freshwater Biology (2002) **47**, 1353–1365

Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain

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SUMMARY

1. Reproductive traits were studied in seven wild populations of resident brown trout in Spain. We examined whether growth, and certain environmental conditions such as water temperature or food abundance, could explain interpopulation variation in the reproductive characters.
2. The results indicated that nearby populations subjected to a wide variation in environmental conditions exhibited a similar reproductive performance.
3. Age distributions and sex ratios were not significantly different among populations. Age ranged from 0+ to 4+ years but the populations were dominated by the 0+ to 2+ groups. In all rivers females matured at age 2+ as opposed to age 1+ and 2+ for males. Mean length at the end of the growth period differed significantly among populations. However, annual growth rate was similar among rivers and was not significantly correlated with either biomass of the benthos or water temperature during the growth season.
4. Reproductive effort, body condition, fecundity and egg size did not correlate significantly with either the abundance of benthic invertebrates or water temperature. Once the effect of body length on both egg size and number was removed, a significant negative correlation was found between these two traits among populations.

Keywords: growth, life history, reproductive traits, *Salmo trutta*, Spain

Introduction

Life history theory has been used to analyse interpopulation variation in reproductive traits in several fish species (Schaffer & Elson, 1975; Leggett & Carscadden, 1978; Roff, 1992). In particular, a trade-off between reproductive effort and adult growth or survival has been reported in a range of field studies and manipulation experiments (review in Stearns, 1992). Teleost fishes employ multiple life history tactics that maximise the number of reproducing offspring (Wootton, 1998), with fecundity and age and/or size at maturity being the main variables responsible for the observed variability (Winemiller & Rose, 1992). These two traits are extremely plastic and frequently show a huge variation associated with different growth conditions (Jonsson, Hindar & Northcote, 1984; Stearns & Crandall, 1984).

Considerable attention has been focused on predicting the variation in reproductive rate with environmental circumstances if breeding maximises individual fitness (Schaffer & Elson, 1975). Local variation in environmental factors influences growth patterns and therefore reproductive traits such as age and size at maturity (Stearns & Koella, 1986). Furthermore, a negative association between reproductive age and growth rate has been documented in fish, especially in salmonids (e.g. Alm, 1959; Jonsson & Hindar, 1982; Myers, Hutchings & Gibson, 1986;

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Hutchings, 1993), although an increase in asymptotic size may result in higher age at maturity (Jonsson *et al.*, 1984; Jonsson & Jonsson, 1993). Egg production in salmonids varies between populations as a result of environmental factors, such as food supply and temperature (Scott, 1962; McFadden, Cooper & Andersen, 1965; Bagenal, 1969; Fleming & Gross, 1990; Tamate & Maekawa, 2000), as well as to growth rate (Jonsson, Jonsson & Fleming, 1996).

The brown trout (*Salmo trutta* L.) is a geographically widespread species with considerable variation in reproductive traits among populations (Elliott, 1994). The existence of interpopulation differences may indicate local adaptations, either through phenotypic plasticity or genetic variability (Stearns, 1992). Part of this interpopulation variation results from differences in local environmental conditions. Thus, large-scale interpopulation comparisons made by L'Abée-Lund *et al.* (1989), Jonsson *et al.* (1991) and Jonsson & L'Abée-Lund (1993) reported a clinal variation in some reproductive traits of anadromous brown trout in Europe over the latitude range 54–70°N. These authors stated that water temperature was probably the single most important factor responsible for this variation. At a smaller scale, McFadden *et al.* (1965) found a strong influence of ecosystem productivity on maturity and egg production of brown trout. Similarly, Bagenal (1969) showed experimentally that food supply was a major determinant of brown trout maturity and fecundity. Environmental influences on reproductive traits may be particularly marked in stream-dwelling populations of brown trout since, in contrast to anadromous trout, they cannot move to more productive habitats (Jonsson & Jonsson, 1993). In addition, recent studies in brown trout have documented the existence of a trade-off between the number and size of eggs, that is regulated by environmental factors (Lobón-Cerviá *et al.*, 1997; Jonsson & Jonsson, 1999).

Southern brown trout populations are less studied than temperate conspecifics, despite a large proportion of the evolutionary diversity in this species being found in Mediterranean countries (García-Marín, Utter & Pla, 1999; Machordom *et al.*, 2000). Our purpose was to examine whether the reproductive traits of stream-dwelling brown trout occupying the southern limits (40–41°N) of its native range are influenced by local environmental conditions. Specifically, we hypothesised that the environmental differences among rivers, which may contribute to stream-specific variation in growth, ultimately affect reproductive traits. Thus, the onset of maturity was expected to be delayed where food is scarce and water temperature low. Accordingly, we expected low reproductive effort and fecundity under harsh environmental conditions. To test these predictions, we compared the reproductive traits of seven populations living in neighbouring rivers. These rivers encompassed a wide range of the environmental variables expected to be important for the growth and reproduction of trout.

Methods

Study area

Of the seven study streams, five are tributaries of the River Tagus (Hoz Seca, Cabrillas, Gallo, Dulce and Jarama) and two of the River Douro (Cega and Eresma) (Fig. 1). The Rivers Hoz Seca, Cabrillas, Gallo and Dulce have hard, fertile waters arising from limestone catchments at altitudes from 850 to 1400 m above sea level. The River Hoz Seca is fed by limestone aquifers with stable flow conditions, which maintain water temperature close to 10°C all year-round (Table 1). The Rivers Jarama, Cega and Eresma have soft, infertile waters arising from granite and gneiss catchments at altitudes between 1100 and 1300 m above sea level. Brown trout have established wild populations throughout the study area, which are not artificially stocked in the study streams. The populations, which are exploited by recreational angling, differ significantly in fish density (Table 1). Brown trout is the only or the prevailing fish species present. Bird or mammal predation seems to be scarce.

Physicochemical variables

Physical habitat variables were studied at each site when fish were sampled. A number of transects were spaced 10 m apart and water column depth was measured along the transects at 1 m intervals. Flow data were obtained from a database collected by the Spanish Ministry of Environment. The water temperature was measured by means of data-loggers (Minilog Vemco Ltd) permanently placed in each river during the study period. Mean daily temperature is

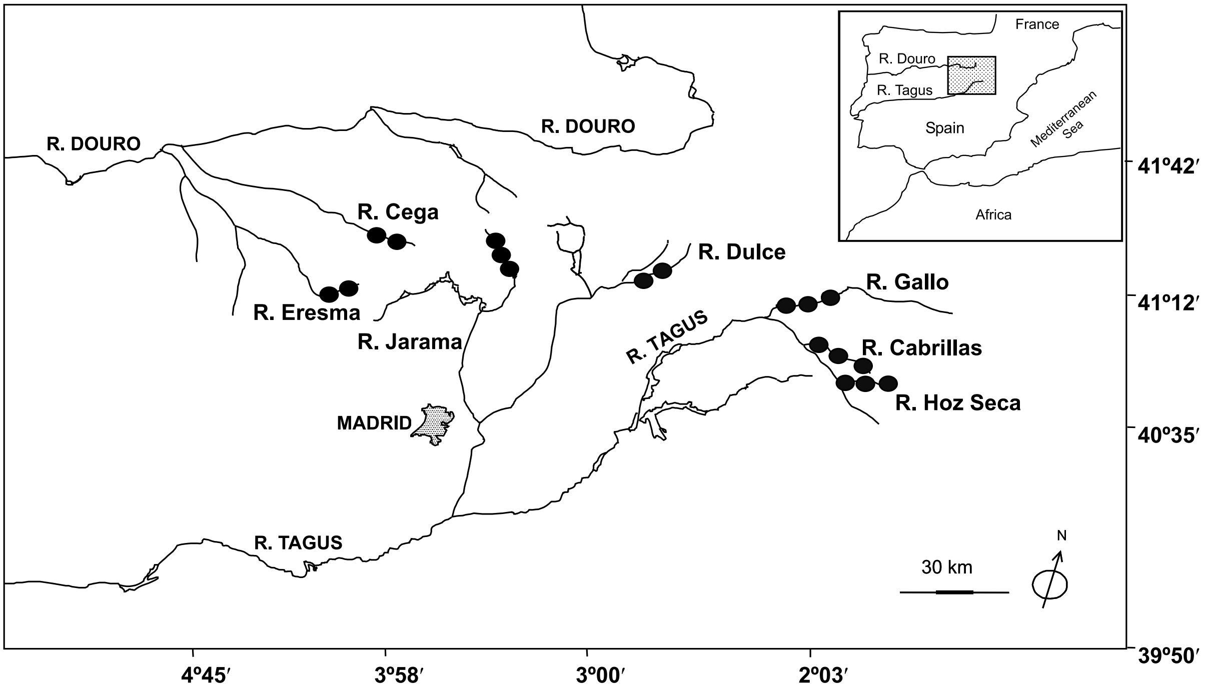

Fig. 1 Map of the study area, showing the location of the sampling sites (closed circles) surveyed during the period from 1996 to 1998.

given as the mean of the maximum and minimum readings in each 24 h period. Samples were taken annually from two sites in each river under wet and dry weather conditions to determine conductivity (μS), pH, alkalinity, sulphate, calcium and magnesium and analysed according to AMERICAN PUBLIC HEALTH ASSOCIATION (APHA) (1985). Conductivity and pH were measured *in situ*.

Macroinvertebrates

Assessment of benthic macroinvertebrates provided an estimate of food availability at each sampling point. At each site, benthic macroinvertebrates were sampled in riffles every third month from January 1996 to December 1998. On each occasion, three sample-units per site were taken with a Neil cylinder sampler with a 250 μm mesh net. Samples were preserved in 10% formalin for later laboratory sorting, identification and counting. Specimens were dried in an oven at 60°C for 24 h and weighed.

Brown trout

Electrofishing took place at each site every third month from January 1996 to December 1998 using a 220 W DC generator. Fish caught were anaesthetised with tricaine methane-sulphonate (MS-222 SANDOZ) and their fork length (FL, 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. Trout density was estimated by applying the three catch removal method (Zippin, 1956) and the numerical age-composition was determined. Annual growth rates in length (G, year^{-1}) were estimated separately for the dominant year-classes (0+ to 2+), as:

$$G = \log_e L_n - \log_e L_{n-1} \qquad (1)$$

where L_{n-1} and L_n (in cm) were the mean fork length of each year-class at the end of the growth season. The annual growth rate was then calculated using eqn 1 for the intervals 0+ to 1+ and 1+ to 2+.

During 1998, reproductive traits were studied from monthly samples. Sampling dates were the same for all rivers. Each fish was packed in plastic bags and frozen immediately after capture on dry ice at –80°C until analysed in the laboratory. A total of 671 individuals were analysed; River Hoz Seca ($n = 101$), River Cabrillas ($n = 97$), River Gallo ($n = 87$), River Dulce ($n = 90$), River Jarama ($n = 96$), River Cega ($n = 93$) and River Eresma ($n = 107$). In the laboratory,

Table 1 Physical, chemical and biological characteristics of the rivers studied. Mean stream values (minimum-maximum in brackets) of physical variables were calculated from measurements in each sampling point during the entire study period 1996–98. Mean water temperature during the growing season (T °C growing season) was estimated for the period between March and September. Chemical determinants were estimated from samples taken annually at high and low flows in two points per river during 1996–98. Abundance of benthic macroinvertebrates and trout was assessed in each sampling point every third month from 1996 to 1998. Differences in river characteristics were tested using a multivariate analysis of variance (MANOVA, $F_{60,15} = 0.13$, $P < 0.001$); the significance level of subsequent univariate ANOVAS (not shown) was established using the Bonferroni correction (Scheiner, 1993)

River	Hoz Seca	Cabrillas	Gallo	Dulce	Jarama	Cega	Eresma
Physical characteristics							
Mean width (min–max, m)	8.6 (3.6–14.3)	4.3 (2.0–6.5)	9.0 (6.6–11.5)	4.9 (4.0–6.0)	5.9 (2.9–9.3)	5.8 (4.9–7.2)	6.3 (5.1–8.0)
Mean depth (min–max, cm)	38.4 (21.4–60.7)	31.9 (9.0–72.5)	50.1 (35.6–78.1)	46.1 (31.1–61.7)	28.6 (12.1–43.7)	29.0 (14.3–38.2)	21.8 (15.2–29.8)
Mean annual discharge (min–max, $m^3 s^{-1}$)	4.9 (0.9–19.7)	1.3 (0.4–4.1)	1.4 (1.0–4.0)	1.2 (0.5–3.5)	7.2 (0.5–27.2)	7.0 (0.4–14.9)	4.0 (0.4–11.2)
Mean annual temperature (min–max, °C)	10.2 (8.4–12.0)	10.2 (4.7–16.0)	12.0 (4.9–17.8)	13.1 (7.6–18.6)	8.6 (0.4–19.9)	6.8 (0.3–15.4)	6.5 (0.3–13.3)
Mean T °C growing season (min–max)	10.8 (8.8–12.0)	12.1 (6.6–16.0)	14.1 (7.9–17.8)	15.0 (10.0–18.6)	9.3 (0.9–15.4)	8.1 (1.3–13.4)	8.1 (2.2–13.3)
Chemical characteristics							
Mean ± SD conductivity ($\mu S\ cm^{-1}$)	611.2 ± 82.8	606.1 ± 135.4	967.0 ± 97.0	602.0 ± 76.7	25.9 ± 5.8	17.7 ± 5.4	65.3 ± 18.0
Mean ± SD alkalinity ($CaCO_3$ mgL^{-1})	366.7 ± 78.9	412.5 ± 15.1	388.4 ± 3.7	309.7 ± 5.0	18.1 ± 11.7	20.7 ± 3.8	29.6 ± 1.1
Mean ± SD pH	8.4 ± 0.1	8.2 ± 0.1	8.2 ± 0.3	7.9 ± 0.2	7.4 ± 0.1	7.2 ± 0.1	7.8 ± 0.3
Mean ± SD sulphate (SO_4^{2-} mgL^{-1})	333.3 ± 28.9	224.2 ± 55.9	141.9 ± 55.6	40.5 ± 8.0	1.7 ± 0.5	1.3 ± 0.5	2.0 ± 0.1
Mean ± SD calcium (Ca^{2+} mgL^{-1})	84.4 ± 4.6	101.3 ± 6.3	85.0 ± 22.3	56.6 ± 17.7	1.2 ± 0.3	2.8 ± 1.0	3.1 ± 0.3
Mean ± SD magnesium (Mg^{2+} mgL^{-1})	25.7 ± 4.1	33.4 ± 4.9	26.4 ± 2.8	22.0 ± 2.9	1.3 ± 1.1	0.9 ± 0.5	0.9 ± 0.1
Biological characteristics							
Mean ± SD benthic density m^{-2}	1355.9 ± 180.8	1702.2 ± 383.8	5946.3 ± 298.2	2045.0 ± 334.3	446.2 ± 24.5	841.1 ± 154.8	677.5 ± 100.1
Mean ± SD dry benthic biomass m^{-2} (g)	1.76 ± 0.65	1.72 ± 0.42	6.15 ± 1.31	2.75 ± 1.16	0.49 ± 0.03	0.56 ± 0.05	0.47 ± 0.13
Mean ± SE trout density ha^{-1}	565.9 ± 57.8	1709.0 ± 379.8	851.5 ± 234.8	1365.3 ± 291.9	1530.0 ± 263.9	2486.7 ± 293.3	4894.5 ± 441.8

fish were measured (fork length, to the nearest mm) and weighed (to the nearest 0.1 g) and a sample of scales were taken to determine their age. While still partly frozen trout were dissected and sex and maturity stage determined. The trout were reweighed completely eviscerated. Gonads were weighed (to the nearest mg) and ovaries were preserved in Gilson's fluid (Bagenal & Braum, 1971) to separate the eggs from the connective tissue.

Age at maturity was defined as the age at which 50% of a cohort were mature. Individual fecundity (*sensu* Nikolsky, 1969) was recorded by counting the total number of ripe eggs in the ovaries in maturity stage IV to V, that is, when they have achieved their maximum weight and it is assumed that the individual will spawn in the next season. The mean egg diameter for each female was determined from a random sample of 20 ripe eggs in maturity stage IV to V measured with an ocular micrometer (to the nearest 0.1 mm). There were no significant (ANOVA, $P > 0.05$) differences in egg diameter between maturity stages IV and V within populations. Body condition of ripe trout was estimated by means of the residual index (Jakob, Marshall & Uetz, 1996), that is, as the residuals drawn from linear regression between gutted body weight and body length ($\log_{10}$ transformed data). Fish used for estimating fecundity, egg diameter and body condition were caught on spawning grounds from November to December, when trout in the study area spawn. There was no evidence of differences in the mean spawning date among streams or years of the study (1992–98).

Protein and lipid content of somatic (muscle) and gonadal tissue from four ripe females from each river were analysed. Carbohydrates usually constitute a negligible proportion of the tissues of teleost fishes (Elliott, 1976; Craig, 1977) and their content was not determined. The tissues were ground in a mincer and homogenised in a microcutter. Between each sample, the mincer and the microcutter were carefully cleaned, washed and dried. Protein content was determined directly using the Folin reagent, following the method of Lowry *et al.* (1951), from a sample of approximately 10 mg. Lipid content was determined by the chloroform–methanol wet extraction technique (Folch, Lees & Sloane-Stanley, 1957) from a tissue sample of approximately 20 mg. Duplicate determinations were conducted on each subsample. If replicates differed by more than 2%, the analysis was repeated. Protein and lipid composition usually change with fish size (Jonsson & Jonsson, 1997), so that females with similar sizes were selected in order to remove any size effect. Total energy content (kJ per 100 g wet weight) was estimated as the sum of the caloric values of the different tissues, where lipid was assigned a value of 39.5 kJ g^{-1} and protein 23.6 kJ g^{-1} (Craig, Kenley & Talling, 1978). The energy of soma and gonads of the fish were calculated as mean energy content of the tissue (kJ g^{-1}) times their weights (g).

Statistical analysis

Data were analysed using standard parametric techniques and χ^2 tests when assessing sex distributions. To examine age structure, growth and biochemical composition, multifactor analyses of variance (ANOVA) were used, with subsequent Scheffé tests for comparison of means. Interpopulation comparison of body condition, reproductive effort and egg size and number was performed by means of regression analysis with trout length followed by a comparison of residual values through ANOVA tests. All data were $\log_{10}$ transformed before the regressions were performed and subsequent comparisons of any significant effect were done by means of Scheffé tests. As no significant among-rivers difference was found in the slopes of these regressions all data were pooled. Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro–Wilk and Levene's tests, respectively. The significance level for all statistical tests was set at $\alpha = 0.05$.

Results

Environmental conditions

The abiotic and biotic characteristics were significantly different among the studied streams (Table 1). The rivers exhibited seasonal variation in water discharge and temperature, typical for the Mediterranean-climate (Gasith & Resh, 1999). However, the Rivers Jarama, Cega and Eresma were significantly colder and more variable in flow regime than other rivers (Table 1). There were also some differences among streams in concentrations of common ions (Table 1), and the streams can be separated into two different groups as to water productivity. The first group (Rivers Jarama, Cega and Eresma) has soft waters with low conductivity, alkalinity and specific ions, whereas the other rivers (Rivers Hoz Seca, Cabrillas, Gallo and Dulce) have hard water with higher means of these chemical variables. The bottom fauna was significantly more abundant in streams draining limestone areas with a higher mineral content compared with those draining rocks of granite with low ionic and carbonate content (Table 1). This was specially evident in Rivers Gallo and Dulce, which also had a comparatively more stable discharge and were warmer, allowing macrophytes to occur which provide cover for many groups of macroinvertebrates.

Age structure and growth

The age distribution of trout did not differ significantly among rivers (ANOVA, $F_{24,70} = 0.87$, $P > 0.05$). Populations showed a clear dominance of age groups 0+ to 2+ and a maximum longevity between 4 and 5 years. The male to female ratio was not significantly different from 1.0 in any of the populations ($n = 7$, $\chi^2_1 = 0.00$–1.96, $P > 0.05$). There was no significant difference among years in the mean length of trout of ages 0+ to 2+ at each of the sampling points. Therefore, for each site the data on growth for the years 1996–98 were combined. Mean length at the end of the growth period varied significantly among populations (Table 2). Trout from the Rivers Cega and Eresma were significantly smaller in each respective age class (Scheffé test, $P < 0.001$) than in other populations. Mean length for similar aged fish did not vary between the Rivers Hoz Seca and Cabrillas (Scheffé test, $P > 0.05$). There was no significant difference in the annual growth rate within the period from age 0+ to age 1+ among populations (Table 2), with a mean value of 0.57 ± 0.08 year^{-1}. The annual length increment declined with the age of the trout. The reduction in growth from first to second year was about 44%. During the second period of growth (1+ to 2+), significant differences were observed among populations (Table 2), but subsequent comparisons of means only revealed significant differences between the River Hoz Seca, the highest mean value, and Rivers Gallo and Dulce (Scheffé test, $P < 0.05$). These latter populations exhibited the lowest values of all populations. The annual length increment was not significantly correlated with either benthic biomass ($G_{0+\text{-}1+}$, Pearson's $r = -0.53$, $P > 0.05$; $G_{1+\text{-}2+}$, $r = -0.59$, $P > 0.05$) or mean water temperature during the growth season ($G_{0+\text{-}1+}$, $r = -0.12$, $P > 0.05$; $G_{1+\text{-}2+}$, $r = -0.74$, $P > 0.05$). As growth rate was not significantly different among populations, the interpopulation variation in mean trout length for similar aged fish was attributable to the mean length attained by 0+ trout at the end of the first growth season. There is a negative relationship between the date of fry emergence from the stream bed and water temperature, so that the lower the winter temperature, the later the fish emerged. The date of emergence finally determines the length of the first growth season and therefore the size attained by 0+ trout (G.G. Nicola & A. Almodóvar, unpublished).

Table 2 Mean length (cm) ± SD and mean annual growth rates in year^{-1} ± SD of brown trout at the end of each growth season in the seven populations studied 1996–98. The results of the analysis of variance (ANOVA) are given (see Results for multiple comparison Scheffé tests). In the two-way ANOVA, with age and river as classification factors, only the interaction between age and river is shown

	Length			Annual growth	
River	0+	1+	2+	0+ to 1+	1+ to 2+
Hoz Seca	7.7 ± 1.0 (90)	13.5 ± 1.4 (59)	18.8 ± 2.0 (68)	0.60 ± 0.07	0.38 ± 0.04
Cabrillas	8.1 ± 1.1 (246)	14.3 ± 1.4 (79)	19.4 ± 1.3 (97)	0.57 ± 0.03	0.28 ± 0.05
Gallo	9.6 ± 1.4 (57)	15.5 ± 1.5 (78)	19.9 ± 1.5 (131)	0.47 ± 0.11	0.26 ± 0.02
Dulce	9.4 ± 1.2 (73)	17.5 ± 2.0 (73)	22.7 ± 1.9 (68)	0.61 ± 0.02	0.26 ± 0.05
Jarama	7.3 ± 1.6 (191)	12.9 ± 2.0 (202)	16.9 ± 2.3 (129)	0.56 ± 0.07	0.32 ± 0.05
Cega	6.6 ± 0.9 (179)	11.5 ± 1.6 (181)	15.7 ± 1.5 (105)	0.62 ± 0.10	0.33 ± 0.02
Eresma	6.4 ± 0.9 (197)	10.8 ± 1.2 (344)	14.9 ± 1.2 (248)	0.50 ± 0.08	0.31 ± 0.05
	ANOVA (age × river),	$F_{12,2874} = 5.77$***		$F_{6,22} = 2.00$ ns	$F_{6,24} = 4.56$**

***$P < 0.001$, **$P < 0.01$ and ns = not significant. The sample sizes are shown in brackets.

Age and size at maturity

Females matured at 2+ years in all rivers, except in the River Dulce, where females matured at age 1+ (Table 3). Males were more heterogeneous than females and matured at 1 and 2 years old. The youngest mature trout were 1 year old in all rivers, excluding males from Rivers Dulce and Gallo which began to mature as 0+. The mean length of the smallest mature trout was not significantly different among males from different populations (Table 3). The mean length of the smallest mature female showed significant differences among populations (ANOVA, $F_{6,19} = 7.54$, $P < 0.001$), and a posteriori comparison of means indicated that differences occurred (Scheffé test, $P < 0.01$) between the Rivers Cega and Eresma, with an average around 13–14 cm, and the remaining populations, with an average around 16–17 cm except for River Hoz Seca, which had an average of 14.5 ± 1.3 cm. This latter was significantly different from the Rivers Cabrillas, Gallo and Jarama (Scheffé test, $P < 0.05$), but did not differ significantly from the Rivers Cega and Eresma.

Reproductive effort and physiological costs of reproduction

Gonad weight (GW) was positively related to fork length in both sexes

$$\text{Females: } \log_{10}\text{GW} = -4.16 + 4.03\log_{10}\text{FL}(r^2 = 0.90, \text{d.f.} = 46, P < 0.001) \quad (2)$$

$$\text{Males: } \log_{10}\text{GW} = -3.18 + 2.65\log_{10}\text{FL}(r^2 = 0.63, \text{d.f.} = 86, P < 0.001) \quad (3)$$

The adjusted means of female GW obtained from eqn 2 were significantly different among rivers (Table 4). Subsequent comparisons of means revealed significant differences only between the low values of the River Hoz Seca and the highest means of the Rivers Gallo and Dulce (Table 4). With respect to males, there were also significant differences among populations (Table 4), mainly because of the minimum value showed by the River Jarama and the highest means showed by the Rivers Dulce and Eresma (Table 4). The energy content of female gonads (ECG, kJ) was also significantly related to female length:

$$\log_{10}\text{ECG} = -3.11 + 4.05\log_{10}\text{FL}(r^2 = 0.88, \text{d.f.} = 46, P < 0.001) \quad (4)$$

The relationship was very similar to that obtained with gonad weight. The adjusted means of ECG obtained from eqn 4 differed significantly among populations (Table 4), but comparisons *a posteriori* showed that the only significant difference was between River Dulce and River Hoz Seca (Table 4). River Dulce showed the highest mean of ECG. Both GW and ECG were not significantly correlated with either benthos biomass (GW, $r = 0.44$, $P > 0.05$; ECG, $r = 0.22$, $P > 0.05$) or mean water temperature during growth season (GW, $r = 0.19$, $P > 0.05$; ECG, $r = 0.36$, $P > 0.05$).

Linear regression models of body mass on fork length were fitted for adults

$$\text{Females: } \log_{10} W = -1.80 + 2.88\log_{10}\text{FL}(r^2 = 0.97, \text{d.f.} = 46, P < 0.001)$$

$$\text{Males: } \log_{10} W = -1.84 + 2.94\log_{10}\text{FL}(r^2 = 0.98, \text{d.f.} = 86, P < 0.001)$$

The comparison of the residuals from eqns 5 and 6 revealed significant differences between sexes (ANOVA, $F_{1,109} = 4.08$, $P < 0.05$), with the highest body condition in males. However, female body condition varied significantly among rivers (Table 4), and the slimmest fish were not found in the least productive rivers, but in the Rivers Cabrillas and

Table 3 Age at maturity and mean length (cm) ± SD of the smallest mature trout caught in males and females in each of the populations studied. The results of the analysis of variance (ANOVA) are also given (see Results for multiple comparison Scheffé tests)

	Males		Females	
River	Age at maturity	Length	Age at maturity	Length
Hoz Seca	1+ (18)	13.88 ± 2.17	2+ (29)	14.47 ± 1.27
Cabrillas	2+ (23)	13.43 ± 1.08	2+ (21)	16.18 ± 0.84
Gallo	2+ (21)	13.20 ± 2.40	2+ (27)	16.45 ± 1.77
Dulce	1+ (23)	14.14 ± 1.58	1+ (23)	15.60 ± 0.57
Jarama	1+ (30)	13.86 ± 1.16	2+ (17)	16.73 ± 0.21
Cega	2+ (26)	12.32 ± 1.61	2+ (25)	14.13 ± 0.70
Eresma	2+ (22)	12.46 ± 1.04	2+ (26)	13.30 ± 0.97
		$F_{6,24}$ = 0.93 ns		$F_{6,19}$ = 7.54***

***$P < 0.001$ and ns = not significant. The sample sizes are shown in brackets.

Table 4 Summary of comparison of some adjusted life-history variables among rivers using analysis of variance (ANOVA) and results of Scheffé multiple comparison tests (only significant comparisons are given)

	d.f.	F	*P*	Scheffé test
Males				
GW	6,81	3.98	< 0.001	Jarama < Dulce, Eresma; *P* < 0.05
Body condition	6,81	6.69	< 0.001	Eresma, Jarama < Hoz Seca, Gallo; *P* < 0.05
Females				
GW	5,42	5.73	< 0.001	Hoz Seca < Gallo, Dulce; *P* < 0.001
ECG	5,42	3.64	< 0.01	Hoz Seca < Dulce; *P* < 0.05
Body condition	5,42	4.77	< 0.001	Cabrillas, Dulce < Gallo, Hoz Seca; *P* < 0.05
Fecundity	6,82	3.78	< 0.01	Eresma, Cega < Hoz Seca; *P* < 0.01
Egg size	6,46	8.71	< 0.001	Hoz Seca < rest of rivers; *P* < 0.001

GW = gonad weight (g), ECG = energy content of gonads (kJ).

Dulce (Table 4). The body condition of males also varied significantly among rivers with minimum values in the Rivers Eresma and Jarama (Table 4). Protein and lipid content of somatic tissue were not significantly different among populations (Table 5), attaining average values of 31.4 ± 4.7% g^{-1} wet weight and 0.07 ± 0.04% g^{-1} wet weight, respectively. Energetic content did not exhibit significant differences among populations (Table 5), with an overall average value of 7.6 ± 1.11 kJ g^{-1} wet weight. The body condition of females was not significantly correlated with either benthic biomass ($r = 0.52$, $P > 0.05$) or mean water temperature during the growth season ($r = -0.01$, $P > 0.05$).

Fecundity and egg quality

Egg number (*F*) increased significantly with female length

$$\log_{10} \mathrm{F} = -0.93 + 2.66 \log_{10} \mathrm{FL}(r^2 = 0.84, \mathrm{d.f.} = 87, P < 0.001) \qquad (7)$$

The populations did differ significantly in adjusted mean fecundity (Table 4). Thus, the populations of Rivers Eresma and Cega had a significantly lower adjusted mean fecundity than that of the River Hoz Seca (Table 4), but the other populations did not show significant differences in their adjusted mean fecundity. The mean absolute fecundity ranged from 228.9 ± 47.0 eggs in the River Jarama to 710.1 ± 224.1 eggs in the River Dulce (Fig. 2). Egg size was homogeneous within each female, with coefficients of variation around 2%. Moreover, there were no significant differences in the coefficient of variation within samples from different rivers (average 9.4%, ANOVA, $F_{6,46} = 1.07$, $P > 0.05$). Mean egg diameter was positive and significantly related to female length following the function:

$$\log_{10} \mathrm{D} = 0.15 + 0.35 \log_{10} \mathrm{FL}(r^2 = 0.25, \mathrm{d.f.} = 51, P < 0.001) \qquad (8)$$

Adjusted mean egg diameter varied significantly among populations (Table 4), but comparisons

Table 5 Mean ± SD content of protein (g), lipid (g) and energy (kJ) per 100 g wet weight of somatic and gonadal tissue from ripe females in the seven populations studied. Mean length ± SD of analysed specimens is given, as well as the results of the analysis of variance (ANOVA) among populations

		Somatic tissue			Gonadal tissue		
River	Length	Protein	Lipid	Energy	Protein	Lipid	Energy
Hoz Seca	21.3 ± 0.8	31.8 ± 4.2	0.05 ± 0.02	763.3 ± 102.3	50.1 ± 5.9	0.92 ± 0.12	1237.4 ± 137.3
Cabrillas	20.3 ± 2.9	31.6 ± 6.8	0.07 ± 0.03	760.0 ± 162.4	56.0 ± 9.9	0.60 ± 0.22	1366.6 ± 290.0
Gallo	22.6 ± 3.3	35.0 ± 1.0	0.05 ± 0.02	840.9 ± 24.4	43.7 ± 2.2	0.58 ± 0.07	1070.5 ± 49.7
Dulce	23.8 ± 2.3	27.9 ± 0.8	0.05 ± 0.01	670.9 ± 18.4	49.9 ± 5.1	0.65 ± 0.27	1222.4 ± 118.2
Jarama	17.8 ± 1.4	31.3 ± 3.7	0.05 ± 0.01	753.9 ± 90.3	55.9 ± 1.5	0.57 ± 0.11	1364.6 ± 39.2
Cega	19.9 ± 0.9	32.7 ± 6.6	0.08 ± 0.04	787.5 ± 159.3	47.8 ± 3.2	0.57 ± 0.15	1169.9 ± 73.1
Eresma	20.0 ± 2.5	29.7 ± 5.2	0.11 ± 0.07	717.8 ± 122.0	49.7 ± 6.3	0.74 ± 0.19	1223.2 ± 150.5
		$F_{6,19} = 0.88$ ns	$F_{6,19} = 1.27$ ns	$F_{6,19} = 0.94$ ns	$F_{6,19} = 1.60$ ns	$F_{6,19} = 2.01$ ns	$F_{6,19} = 1.80$ ns

ns = Not significant.

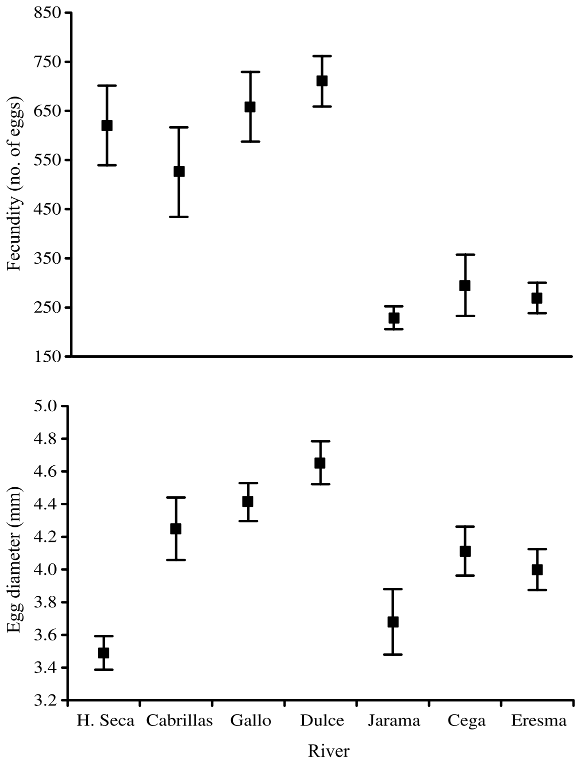

Fig. 2 Fecundity and egg diameter (mean ± SD) of mature female trout from the seven populations studied.

a posteriori indicated that only the River Hoz Seca differed significantly from the other rivers (Table 4). The mean absolute egg size ranged from 3.49 ± 0.31 mm in the River Hoz Seca to 4.65 ± 0.42 mm in the River Dulce (Fig. 2). In an attempt to evaluate the resources invested by females in egg production, egg quality was also assessed by means of their protein, lipid and energy content. The protein and lipid contents of eggs did not exhibit significant differences among populations (Table 5), showing overall average values of 50.0 ± 6.8% g^{-1} wet weight and 0.67 ± 0.20% g^{-1} wet weight, respectively. The energetic content of eggs did not differ among populations (Table 5), attaining a mean value of 12.3 ± 1.6 kJ g^{-1} wet weight. Once the effect of length on both egg size and number was removed, a significant negative correlation was found between these two traits ($r = -0.62$, $P < 0.001$). At one extreme in this study was the River Hoz Seca population, which had relatively many, small eggs. At the other extreme were the populations from the Rivers Cega and Eresma, which had relatively few, large eggs. Fecundity (F) and egg diameter (D) were not significantly correlated with either benthic biomass (F, $r = 0.16$, $P > 0.05$; D, $r = 0.11$, $P > 0.05$) or mean water temperature during the growth season (F, Pearson $r = 0.39$, $P > 0.05$; D, Pearson $r = 0.21$, $P > 0.05$) (Fig. 3).

Discussion

The fish studied were short-lived and attained maturity at a young age, as is frequently observed in stream-dwelling brown trout (e.g. Jonsson & Sandlund, 1979; Maisse & Baglinière, 1990). After maturity, somatic growth ceases, as has been described for many salmonid populations (Jonsson, 1985; Myers *et al.*, 1986). Fishing pressure in these populations is high and decreases the longevity of the fish (Almodóvar & Nicola, 1998; Almodóvar, Nicola & Suárez, 2002). There is probably a relationship between maturation and longevity, because a short life span selects for maturity at a young age, as documented by Haugen (2000) for exploited grayling (*Thymallus thymallus* L.). A similar pattern has been reported for other exploited fish populations (Policansky, 1993; Reznick, 1993; Rochet, 1998) and for populations with high adult predation (Reznick, Bryga & Endler, 1990).

Maturity seemed to be attained at a given body size rather than at a definite age, as found in different age-structured European populations of brown trout from several geographical areas (e.g. Lobón-Cerviá *et al.*, 1997; Näslund, Degerman & Nordwall, 1998). In many salmonid species, maturation depends on the nutritional state of fish, which is frequently associated with feeding conditions (Thorpe, 1990; Tveiten, Johnsen & Jobling, 1996). The similarity in growth rate among the populations studied suggests that, despite the harsh environmental conditions, trout from the rivers Jarama, Cega and Eresma succeed in gaining sufficient resources to mature at a similar size, or even smaller, than in the other rivers analysed. The earlier maturity of females observed in Rivers Cega and Eresma could lead to an increased adult life span, perhaps compensating for low absolute fecundity at each spawning. These populations with comparatively smaller females would always produce fewer offspring in absolute terms, because female fecundity increases with body size (Jonsson & Jonsson, 1993).

Fish length was the major determinant of reproductive effort in females. The average reproductive effort did not seem to be affected by local environmental conditions after removing the effect of fish

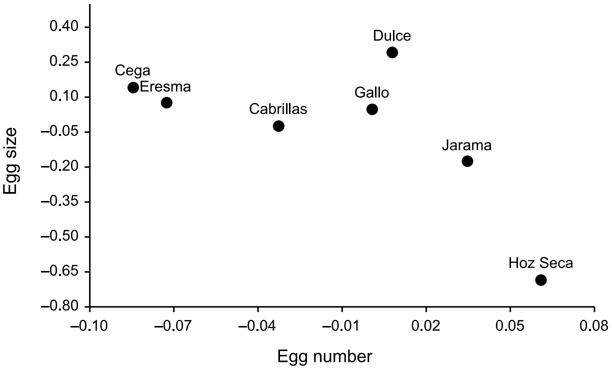

Fig. 3 Fecundity vs. egg size among rivers. Egg number and egg size are the mean relative fecundity and the mean relative egg size, respectively, in each population analysed once the female length effect was removed by means of residual analyses (see text for details).

size. However, this finding does not agree with McFadden *et al*. (1965), who found that brown trout in productive streams produced a greater weight of eggs than those in unproductive waters. Similarly, a lower energy allocation to gonadal development because of low food supply has been observed in other populations of brown trout (e.g. Jonsson & Jonsson, 1997) and other salmonids (e.g. Scott, 1962; Tamate & Maekawa, 2000). On the other hand, the body condition of ripe females was not related to stream productivity or water temperature, but seemed to be related to reproductive effort. At one extreme in this study was the River Hoz Seca, showing the lowest relative mean of reproductive effort and one of the highest mean body condition. On the other extreme, females from River Dulce invested so much energy in their gonads that their body condition was the poorest among the study rivers. This trend apparently reflects a physiological trade-off (Stearns, 1992) between reproduction and condition.

The results showed a significant relationship between female length and the number and size of eggs produced. A large part of the variation in absolute fecundity among populations resulted from interpopulation variation in body length. However, female length explained only 25% of the interpopulation variation in egg size. A negative relationship between egg size and number was found among populations, so that part of the interpopulation variation in egg size can be attributed to local environmental factors. Thus, the populations with relatively fewer and larger eggs were found in rivers characterised by frequent spates, low temperature and food shortage (Rivers Eresma and Cega). This trade-off between egg size and number has been addressed by other comparative studies of brown trout (L'Abée-Lund & Hindar, 1990; Lobón-Cerviá *et al*., 1997; Jonsson & Jonsson, 1999) and a number of empirical studies on fish (e.g. Duarte & Alcaraz, 1989; Elgar, 1990; Fleming & Gross, 1990; Hutchings, 1991; Jonsson *et al*., 1996), where egg size has been found to be favoured over egg number in resource-poor habitats. The most remarkable finding was the significantly higher number of smaller eggs produced in the River Hoz Seca. The augmentation of egg number at the expense of egg size in this river could be related to an environmental perturbation. This river is regulated in its lower reaches by a hydropower station, which has caused a gradual loss of recruitment (Almodóvar & Nicola, 1999). The River Hoz Seca has homogeneous and stable environmental conditions throughout the year. Under these favourable conditions, females should produce more and smaller eggs to optimise fitness (Einum & Fleming, 1999). Such a rapid response to an environmental perturbation has been observed in a brown trout population from a regulated English stream. Thus, Crisp (1994) observed that females in tributaries laid on average three times as many eggs as females in the reservoir after few years of regulation.

To sum up, these populations had a similar reproductive performance, showing little variation in reproductive features in spite of being subjected to a wide range of environmental conditions. Neither a lower reproductive investment, nor higher physiological costs, were detected for those populations that were subjected to a poorer environmental quality, as in the Rivers Jarama, Cega and Eresma. Adjusted values of both fecundity and egg size did not seem to be affected by the environment in these rivers. The brown trout is a flexible species, being able to cope with different environments. Thus, trout from these populations succeed in gaining sufficient resources for maintenance, growth and reproduction. The earlier maturity observed in the Rivers Eresma and Cega, and the pattern of egg production found in River Hoz Seca, suggest that adaptations to local conditions occur on a small geographical scale, and are either genetically determined or based on the phenotypic plasticity of the species.

Acknowledgments

This research was supported by the Spanish INIA through a research project SC-95/005 and a postgraduate fellowship (to G.G.N). We are grateful to M. Díaz and B. Elvira for their helpful advice and comments on the manuscript. The valuable suggestions made by N. Jonsson substantially improved an earlier version of the manuscript. The Department of Animal Biology II, from the Complutense University of Madrid, kindly helped us with biochemical analyses. We also acknowledge the very constructive criticism of B. Jonsson, an anonymous referee and the editor, Alan Hildrew.

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(Manuscript accepted 2 October 2001)