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Recruitment variability of resident brown trout in peripheral populations from southern Europe

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SUMMARY

1. Population regulation was studied for seven consecutive years (1992–98) in five rivers at the periphery of the distribution of *Salmo trutta*, where the fish were living under environmental constraints quite different from those of the main distribution area.
2. Recruitment is naturally highly variable and the populations had been earlier classified as overexploited. Thus we expected that densities of young trout in most populations would be too low for density-dependent mortality to operate. We tested this by fitting the abundance of recruits to egg densities over seven consecutive years (stock–recruitment relationship), and used the results to judge whether exploitation should be restricted in the interests of conserving the populations.
3. The density of 0+ trout in early September, as well as the initial density of eggs and parents, varied greatly among localities and years. The data for all populations fitted the Ricker stock–recruitment model. The proportion of variance explained by the population curves varied between 32% and 51%. However, in most cases the observations were in the density-independent part of the stock–recruitment curve, where densities of the recruits increased proportionally with egg densities.
4. Our findings suggest that recruitment densities in most rivers and years were below the carrying capacity of the habitats. Although density-dependent mechanisms seemed to regulate fish abundance in some cases, environmental factors and harvesting appeared generally to preclude populations from reaching densities high enough for negative feedbacks to operate. The findings thus lend support to Haldane's (1956) second hypothesis that changes in population density are primarily due to density-independent factors in unfavourable areas and areas with low density due to exploitation. Exploitation should be reduced to allow natural selection to operate more effectively.

Keywords: density-dependence, fisheries management, marginal populations, population abundance, population regulation

Introduction

Most ecologists agree that the persistence of animal populations is due to feedback mechanisms that actually or potentially regulate abundance (Turchin, 1999). However, other factors besides density affect growth rates of populations, and identifying them has been a long-standing issue in population ecology (Sibly & Hone, 2002; White, 2004). The dominating view is that internal and external forces contribute simultaneously to variation in population abundance (Berryman, 2004).

There is evidence that population dynamics vary across the range of a species in response to environmental changes (Lawton, 1993; Brown, Stevens & Kaufman, 1996; Case & Taper, 2000). Since population

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densities usually decrease from the centre to the margin of the distribution, the regulation of populations could switch from density-dependent processes at the centre to density-independent ones at the margin (Guo *et al.*, 2005; Antonovics, McKane & Newman, 2006). Moreover, there is growing evidence from some animal species that density-independent factors have a higher influence on demographic parameters and produce greater fluctuations in peripherally than centrally situated populations (Mehlman, 1997; Williams, Ives & Applegate, 2003; Giralt & Valera, 2006; Thingstad, Nyholm & Fjeldheim, 2006). Current climate change is aggravating the environmental constraints for population persistence at the southern range margins. Therefore, there has been increasing interest in the influence of edge effects on the ecology of individual species and the communities they form (e.g. Hoffmann & Blows, 1994; Peñuelas, Filella & Comás, 2002; Parmesan, 2006).

Brown trout (*Salmo trutta* L.) populations are influenced by a combination of density-dependent and density-independent processes, whose respective influence depends mainly on the life stage of the fish and on environmental conditions (Elliott, 2001). The main intrinsic demographic mechanism is usually competition for territories among young fry, which regulates populations during the post-emergence phase. Later in the life cycle, density of brown trout is seldom regulated, being chiefly influenced by density-independent factors (Elliott & Elliott, 2006). Among environmental variables, hydrological variability and drought are major factors shaping trout abundance (e.g. Jensen & Johnsen, 1999; Cattanéo *et al.*, 2002; Lobón-Cerviá & Rincón, 2004). Based on Haldane's (1956) second hypothesis, Elliott (1994) suggested that changes in brown trout density would be largely due to negative density-dependent factors in favourable areas with high density, and density-independent factors in unfavourable areas with low density as often seen at the edge of a species' range.

The regulation of brown trout populations has been the subject of many studies (e.g. Crisp, 1993; Langeland & Pedersen, 2000; Elliott & Elliott, 2006; Lobón-Cerviá, 2007), but most have been conducted within a limited range of stream types, chiefly in upstream river sections in central and northern Europe. Factors controlling the recruitment at the range margins are largely unknown, despite the fish facing ecological conditions quite different from those of the main distribution area. For instance, south European populations are subjected to a Mediterranean climate, characterized by seasonal flooding and drying and strong interannual flow variations. Furthermore, the stocks are currently threatened by habitat destruction, pollution, exotic species introductions, overexploitation and introgression of foreign genes as a result of artificial stocking (Elvira & Almodóvar, 2001; Almodóvar & Nicola, 2004; Almodóvar *et al.*, 2006a,b). Therefore, given the great social and economic value of brown trout, there is an urgent need for management plans aimed at protecting the species in southern Europe. To optimize management planning, it is essential to evaluate the importance of recruitment for population size and production.

The aim of this study was to test whether brown trout populations at the southern edge of the distribution area are regulated by density-dependence. Recruitment in this region is naturally highly variable and all populations are currently exploited by angling (Almodóvar, Nicola & Suárez, 2002; Almodóvar & Nicola, 2004). We hypothesized that the recruitment of most populations is too low for density-dependent mortality to operate, following the classical view of Haldane (1956) that density-independent processes would predominate in unfavourable areas with low density. We tested for evidence of density-dependent effects in five rivers supporting populations of brown trout by examining the relationship between the abundance of recruits and egg density over seven consecutive years (stock–recruitment relationships), and used the results to judge whether exploitation rate is too high and should be restricted.

Methods

Study area

We studied stock–recruitment relationships of brown trout populations in three tributaries of the River Tajo (Hoz Seca, Cabrillas and Dulce) and two tributaries of the River Duero (Cega and Eresma) (Table 1, Fig. 1). Two or three sampling sites with uniform habitat were selected in each river. The study reaches were in first-order streams and ranged from 39°50′N to 41°42′N latitude and from 2°03′W to 4°45′W longitude.

Mean altitude, drainage area, water temperature and flow regime vary among rivers (Table 1).

Table 1 Physical, chemical and biological characteristics of the rivers studied

	Hoz Seca	Cabrillas	Dulce	Cega	Eresma
River basin	Tajo	Tajo	Tajo	Duero	Duero
Elevation (m)	1360	1267	885	1250	1290
Lithology	Calcareous	Calcareous	Calcareous	Siliceous	Siliceous
Width (m)	8.6	4.3	4.9	5.8	6.3
Depth (cm)	38.4	31.9	46.1	28.7	21.8
Dominant substrate	Gravel	Cobble	Sand	Boulder	Boulder
Cover (%)	15.8	29.4	43.7	12.8	27.7
Submersed aquatic vegetation (%)	10.4	1.0	26.1	1.5	3.1
Annual discharge (min.–max., $m^3 s^{-1}$)	4.9 (0.9–19.7)	1.3 (0.4–4.1)	1.2 (0.5–3.5)	7.0 (0.4–14.9)	4.0 (0.4–11.2)
Annual temperature (min.–max., °C)	10.2 (8.4–12.0)	10.2 (4.7–16.0)	13.1 (7.6–18.6)	6.8 (0.3–15.4)	6.5 (0.3–13.3)
Conductivity ($\mu S\ cm^{-1}$)	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
Brown trout density (trout ha^{-1})	1567 ± 288	2379 ± 1499	5876 ± 1071	1957 ± 1027	4317 ± 2111

Mean (± SD) stream values of physical and chemical variables were calculated from seasonal measurements at each sampling point during the entire study period (1992–98). Density estimates (mean ± SD) of brown trout are detailed in Almodóvar *et al.* (2006b).

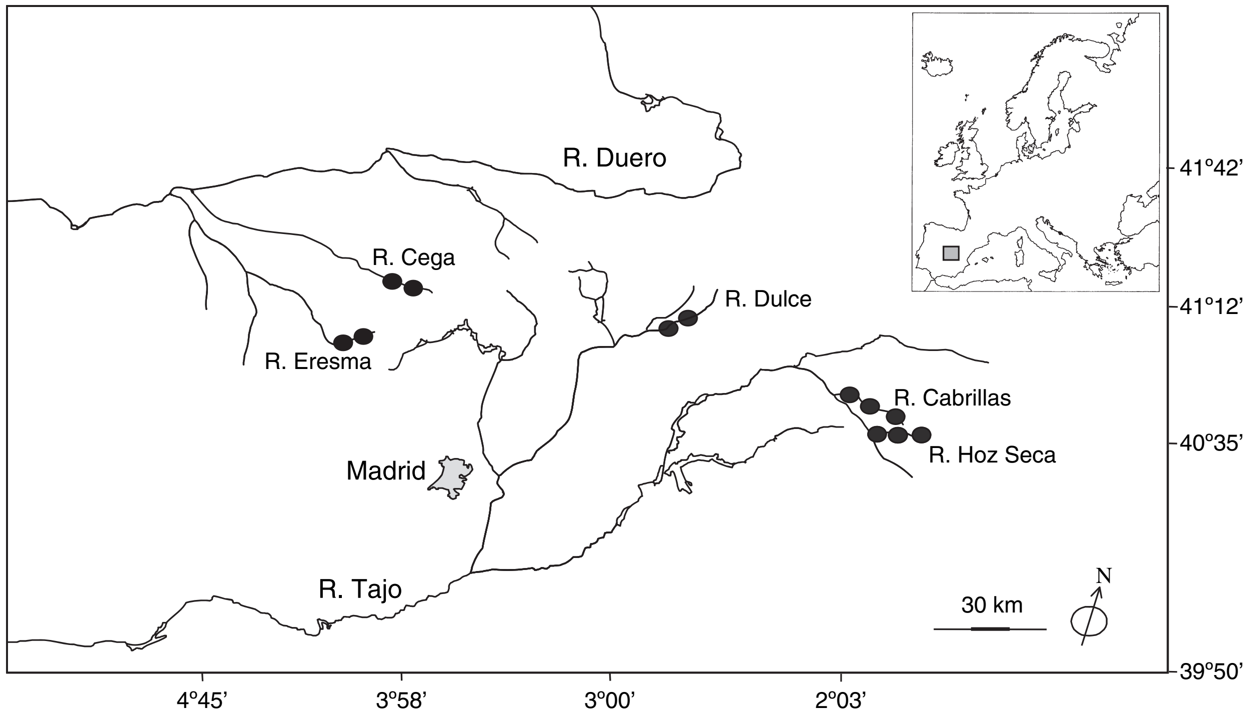

Fig. 1 Study area with locations of the sampling sites (filled circles) surveyed from 1992 to 1998.

However, they may be divided into two groups. The first type (Cega and Eresma) are softwater rivers arising from granite and gneiss catchments at elevations between 1100 and 1300 m. The river bed is mainly covered by boulders, most of their water comes from surface drainage and they become torrential in their upper reaches during snow melt in early spring. Flow fluctuations throughout the year are pronounced and characterized by frequent flow pulses of variable length and occasional freshets during winter and spring, as well as recurrent episodes of extremely low flow during summer. Water temperature is close to 0 °C in winter and reaches a maximum of about 13 °C in summer. The other three rivers (Hoz Seca, Cabrillas and Dulce) have hard, fertile waters arising from limestone catchments at elevations from 850 to

1400 m. The geology of the basins and the mild climate give an even flow regime throughout the year. The strength and frequency of high flow pulses and small floods during winter and spring were much lower in these rivers than in the Eresma and Cega. Extremely low flows during summer were only detected in the Cabrillas. The Cabrillas and Dulce exhibit a similar temperature regime, with winter means around 7 °C and summer means around 16 °C. The River Hoz Seca is somewhat different, being fed by limestone aquifers and with a water temperature that remains close to 10 °C year round. The rivers in the second group have a less coarse substrate than the Cega and Eresma.

Brown trout is the only, or the predominant, fish species present and the populations comprise resident individuals only. The rivers are not supplemented by hatchery fish 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. Further details of the study area are given in Almodóvar & Nicola (2004), Nicola & Almodóvar (2002, 2004) and Almodóvar, Nicola & Elvira (2006b).

Field sampling and analyses

Fish were sampled every third month from December 1992 to December 1998 at 12 localities by electrofishing using a 2200 W generator. Trout were anaesthetized with tricaine methane-sulphonate (MS-222) and their fork lengths (to the nearest mm) and masses (to the nearest g) were measured. Scales were used for age determination. The fish were placed in holding boxes to recover and then returned to the stream. Fish densities (trout ha^{-1}) with variance were estimated separately for each sampling point by the maximum likelihood method (Zippin, 1956) and the corresponding solution proposed by Seber (1982) for three-removals assuming constant-capture effort. Egg production of each cohort and density of the breeding stock were estimated from fecundity, trout density and percentages of sexually mature trout (Nicola & Almodóvar, 2002), according to Crisp (1994) and Almodóvar & Nicola (2004).

To evaluate the strength of density-dependence, we employed Ricker's stock–recruitment model (Ricker, 1954), following Elliott (1985), where the density of recruits to each year-class was related to the initial egg density by fitting the model:

$$R = a\,S\,\exp^{-b\,S}$$

where S and R are breeding stock and recruitment, respectively, and a and b are constants; a is the slope of the curve when S is very small and thus an index of the density-independent effect, b is an index of the density dependence (Pitcher & Hart, 1982). The Ricker model is a common density-dependent model that has been the basis for many marine fisheries and terrestrial studies (Elliott, 1994). In the absence of any density dependence, the number of offspring will be an increasing function of the abundance of the parental stock. If density-dependent effects on mortality are important, this should be reflected by loss-rate changes according to parental abundance. Elliott (1985) found the Ricker model to be the best stock–recruitment model for use with the different stages in the life cycle of brown trout.

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). The models tested were fitted by nonlinear least-squares, using a Gauss–Newton algorithm. Parameter standard errors and confidence limits for predicted curves were estimated by bootstrap methods. First, the density-dependence hypothesis was tested by exploring the amount of variation in recruitment accounted for by the density-independent relationship $R = a\ S$ (i.e. constant proportional survival), as well as by the null hypothesis of random variation of recruitment around its arithmetic mean (Bellows, 1981; Elliott, 1985; Lobón-Cerviá, 2006). Then, we tested for density dependence by fitting the data to the Ricker model. We used an information–theoretic approach to select the best-fitting model based on Akaike's information criteria corrected for small samples size ($\mathrm{AIC_c}$), which allows objective selection of the model most consistent with the data while balancing the trade-off between precision and bias (Burnham & Anderson, 2002; Motulsky & Christopoulos, 2003). The model with the lowest $\mathrm{AIC_c}$ was considered the best fit.

Differences between rivers in trout and egg densities were compared by one-way analyses of variance (ANOVA), with subsequent Scheffé tests for comparison of means. 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 $\alpha = 0.05$. Statistical analyses were performed using the STATISTICA 6.1 computer package (StatSoft, Inc., Tulsa, OK, U.S.A.).

Results

The brown trout in the rivers studied are short-lived and numerically dominated by age groups 0+ to 2+ (Hoz Seca, 0+ 36%, 1+ 23%, 2+ 26%; Cabrillas, 0+ 48%, 1+ 19%, 2+ 23%; Dulce, 0+ 40%, 1+ 26%, 2+ 27%; Cega, 0+ 30%, 1+ 36%, 2+ 23%; Eresma, 0+ 33%; 1+ 36%, 2+ 25%). Maximum longevity is between 4 and 5 years. Mean annual estimates of brown trout density during the period 1992–98 ranged from 1567 trout ha^{-1} in the Hoz Seca to 5876 trout ha^{-1} in the Dulce (Table 1).

The density of 0+ trout in early September, as well as the initial density of eggs and parentals, varied among rivers (Table 2, R, ANOVA, $F_{4,63} = 4.95$; $P < 0.01$; S_{eggs}, ANOVA, $F_{4,63} = 4.61$; $P < 0.01$; S_{parents}, ANOVA, $F_{4,63} = 7.94$; $P < 0.001$). Likewise, these variables showed an interannual variation within rivers during the study period, as reflected by the coefficients of variation (CV; Table 2, Fig. 2). At one extreme, egg density was lowest and most variable in the Cega (mean 67 236 eggs ha^{-1}, CV = 58%). It was highest and least variable in the Dulce (mean 238 927 eggs ha^{-1}, CV = 38%). The density of young trout was highest and most variable in the rivers Cega and Eresma, with mean values close to 1100 trout ha^{-1} and CV around 50%. The Eresma also showed the highest density of parents.

Table 2 Density (mean, range and coefficient of variation, CV) of 0+ trout in early September (R), initial egg input (S_{eggs}) and parental stock (S_{parents}) in the study rivers during the period 1992–98

	Mean	Min.	Max.	CV (%)
R (trout ha^{-1})				
Hoz Seca	302.2	170.7	467.9	36
Cabrillas	918.8	528.2	1224.9	28
Dulce	649.8	366.5	993.1	37
Cega	1029.3	320.2	1662.4	53
Eresma	1242.8	588.6	2232.1	55
S_{eggs} (eggs ha^{-1})				
Hoz Seca	137 543.8	60 668.9	323 536.4	71
Cabrillas	131 732.9	61 680.3	174 615.9	34
Dulce	238 926.5	112 034.5	327 525.4	38
Cega	67 235.5	12 534.7	126 238.7	58
Eresma	120 074.9	50 459.4	169 670.4	39
S_{parents} (trout ha^{-1})				
Hoz Seca	276.6	140.7	587.6	58
Cabrillas	347.1	160.6	467.7	34
Dulce	464.4	227.4	619.6	37
Cega	366.0	94.8	744.2	68
Eresma	813.8	381.2	1229.9	41

None of the populations exhibited a significant fit of data to the linear model (Hoz Seca, $r^2 = 0.23$, $P = 0.33$; Cabrillas, $r^2 = 0.52$, $P = 0.11$; Dulce, $r^2 = -0.30$, $P = 0.26$; Cega, $r^2 = 0.55$, $P = 0.09$; Eresma, $r^2 = 0.31$, $P = 0.25$). The null hypothesis of random variation of recruitment was not supported by the data (Hoz Seca, $r^2 = 0.92$, $P = 0.002$; Cabrillas, $r^2 = 0.95$, $P = 0.001$; Dulce, $r^2 = 0.94$, $P = 0.001$; Cega, $r^2 = 0.87$, $P = 0.006$; R. Eresma, $r^2 = 0.83$, $P = 0.012$). On the other hand, the Ricker model showed a significant fit to the data in all populations (Table 3, Fig. 2). Furthermore, our analyses indicated that the Ricker model fitted the data better (lower AIC$_c$ values) than the linear model in all populations. The differences between AIC$_c$ values of the two models were between 2.2 and 5.0 (mean ΔAIC$_c$ = 4.2), so that the Ricker models were between 74% and 92% more likely to be correct than the linear models. Coefficients of determination of the Ricker model indicated that variation in egg density between year-classes could account for more than 30% of the variation in 0+ trout density in September. Thus, between 32% (Eresma) and 51% (Dulce) of the variation in recruitment was explained by variation in initial egg density. This indicates that the abundance of the parental stock, measured as the eggs produced by females prior to spawning, was a good predictor of recruitment. The density-dependence hypothesis could not be rejected in any of the populations. Thus, it was concluded that density of 0+ trout in September was currently or potentially density-dependent based on egg density at the start of each year-class. However, in most cases the observations were in the density-independent part of the curve where the density of recruits increased almost proportionally with egg density (S is relatively small, Fig. 2).

The intensity and form of the stock–recruitment relationships, as well as the point where density-dependence begins to operate, showed some differences among populations. The relationships indicated that maximal densities in the first summer were produced by egg densities that varied from 14 eggs m^{-2} in the Dulce to 50 eggs m^{-2} in the Eresma,

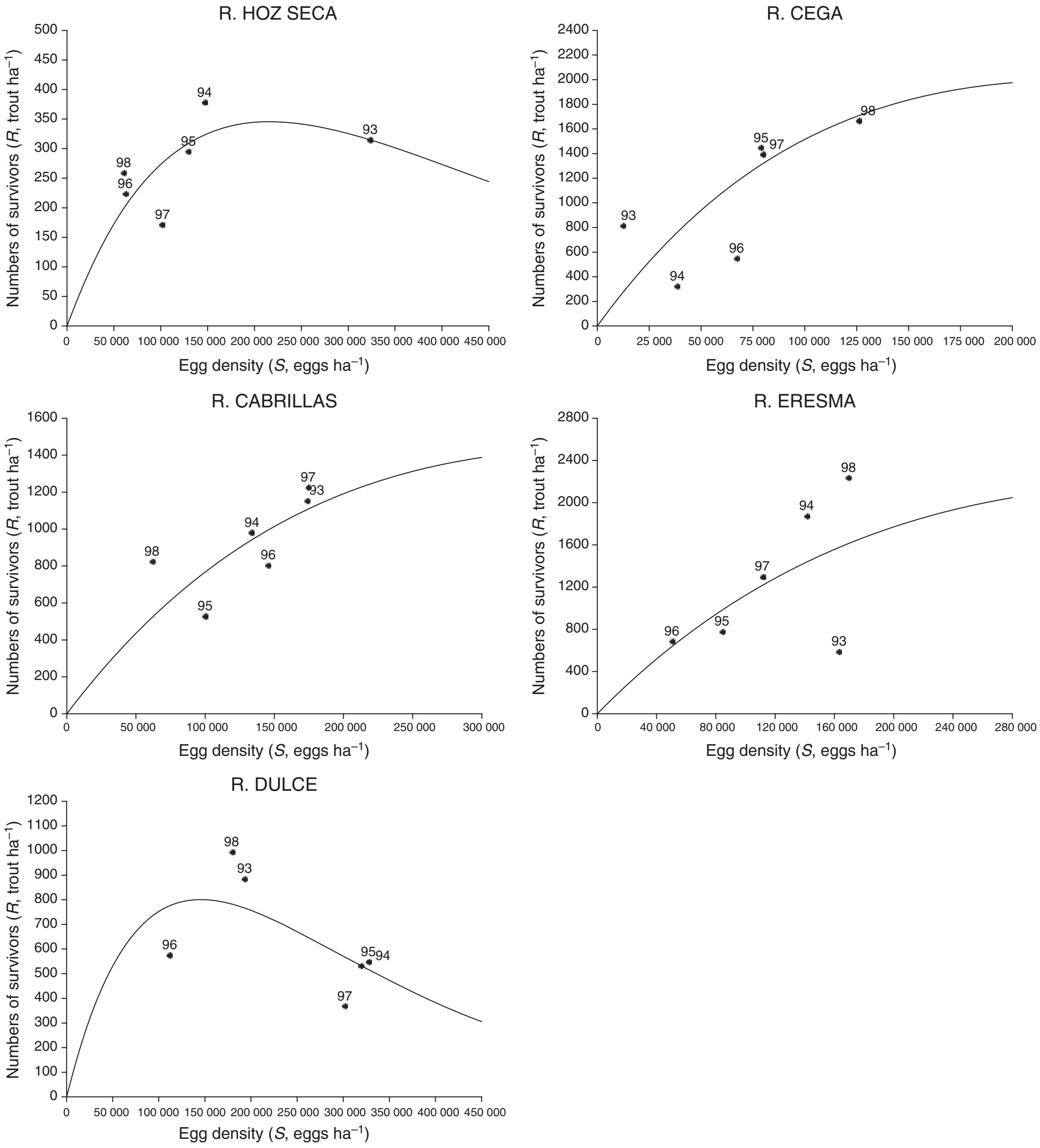

Fig. 2 Relationship between the number of recruits (R, trout ha^{-1}) and the initial egg density at the start of each year-class (S, eggs ha^{-1}) in five Spanish rivers from 1992 to 1998. Curves were estimated from Ricker's (1954) equation (see Methods for details). Parameter estimates for the Ricker model are given in Table 3.

which correspond to densities between 377 trout ha^{-1} in the Hoz Seca and 3053 trout ha^{-1} in the Cega (Fig. 2). In the Hoz Seca, egg density was above the estimated point only in 1 year, whereas the Dulce was the only river where mean egg densities were above the maximum point of the curve (i.e. exhibited negative density dependence). The egg densities in the remaining rivers were always below the maximum point of the stock–recruitment curves.

Discussion

To understand the processes that regulate the abundance and persistence of wild populations is a

Table 3 Stock–recruitment relationships ($R = a\ S\ \exp^{-b\ S}$) in the five populations studied from 1992 to 1998

River	*a* (SE)	*b* (SE)	*F*	*P*-value	r^2
Hoz Seca	0.005130 (0.001303)	0.000005 (0.000001)	31.26	<0.01	0.38
Cabrillas	0.009878 (0.004620)	0.000003 (0.000001)	51.41	<0.01	0.38
Dulce	0.014958 (0.004942)	0.000007 (0.000001)	38.19	<0.01	0.51
Cega	0.016598 (0.009646)	0.000002 (0.000001)	17.76	<0.01	0.46
Eresma	0.014244 (0.012344)	0.000002 (0.000001)	12.52	<0.05	0.32

The estimates of the parameters *a* and *b*, the coefficients of determination (r^2) and significance levels for *F*-values are shown.

prerequisite for the management of living resources (Minto, Myers & Blanchard, 2008). Theoretically, density-dependence provides the obvious mechanism for population regulation (Sinclair, 1989). By using a mathematical model for density-dependence, such as the Ricker stock–recruitment model, one can test for a possible density-dependent effect (May *et al.*, 1974). Unfortunately, it is very time consuming to monitor vertebrate populations for a long enough time period to apply this theory, and variable abundance data make the demonstration of regulation processes challenging. This may be a prime reason why relatively few scientists have undertaken this effort. However, this method has high applicability in applied ecology and conservation biology as it gives an ecological basis for sustainable harvesting and management (e.g. Pöyasä *et al.*, 2004; Mills, 2006), and we found it useful when studying brown trout for the purpose of conserving marginal populations of the species in Spain.

In the present study, most of the egg densities of the studied populations were below the point of maximum recruitment. According to the Ricker model, they were chiefly in the density-independent section of the curve where offspring density increased almost proportionally with egg density. According to Haldane's (1956) hypothesis, density-independent processes dominate in unfavourable areas with low population densities such as those often found in marginal and heavily exploited populations. A study by Elliott (1987) supported this idea. He did not find any signs of density-dependent regulation in the juvenile stages in a low density freshwater resident brown trout population in the English Lake District, and later found evidence for density-dependent regulation in the adult resident trout (Elliott & Hurley, 1998). On the other hand, he found evidence of density-dependent regulation in a nearby high density population of anadromous brown trout. Haldane's (1956) hypothesis was also supported by Daufresne & Renault (2006) who studied the dynamics of a stream-living population of brown trout.

Mean egg densities in our study stocks were between 13 and 33 eggs m^{-2} across rivers and cohorts. According to Elliott & Elliott (2006), density-dependent mortality comes into play at values above 17 eggs m^{-2} in the anadromous trout population mentioned above. Crisp (1993) set this point around 6 eggs m^{-2} in lake-run brown trout from northern England, whereas Euzenat, Fournel & Fagard (2006) found a value close to 9 eggs m^{-2} in a sea trout population from northern France. In our study populations, this threshold was as high as between 14 and 50 eggs m^{-2}, but the observed variation across rivers may simply reflect differences in available food and space, which determine the carrying capacity of streams for young trout. In some years, egg input would be appreciable but survival of the intra-gravel or post-emergence stages would be too low for density-dependent mortality to operate.

In the Spanish rivers studied, brown trout recruitment appeared largely dependent on egg density and thereby adult abundance in the previous autumn. The populations are strongly affected by angling, as shown by previous studies (Almodóvar *et al.*, 2002; Almodóvar & Nicola, 2004). Human exploitation may thus be a main factor decreasing density, biomass and production of legal-sized trout, and depleting the breeding stock and fecundity of the populations beneath the point of maximum production according to the Ricker model. According to Almodóvar *et al.* (2002), legal-sized trout make the greatest contribution to population fecundity and to the breeding stock, but their average proportion is low in all populations (mean 11%). By concentrating exploitation on large trout, the reproductive age-classes are seriously reduced. Further restrictions on angling would enhance the parental stock and egg density and increase intraspecific competition among the fry. Johnston *et al.* (2007) observed that an overexploited population of bull trout *Salvelinus confluentus* (Suckley) started to be regulated by density-dependence soon after the implementation of a zero-harvest regulation and subsequent population recovery, and we expect that the same would occur in the rivers we studied if fishing was terminated.

Our study rivers are characterized by seasonal events of flooding and drying, as well as marked interannual variation in flow, typical for the Mediterranean climate. This environmental variability may be an additional reason why offspring densities were in most cases below the point of maximum recruitment, as egg density accounted for <50% of the observed variation. Functional links between recruitment and hydrological factors have been described for some brown trout populations (e.g. Cattanéo *et al.*, 2002; Lobón-Cerviá & Rincón, 2004; Lobón-Cerviá & Mortensen, 2005; Elliott & Elliott, 2006), emphasizing that density-independent factors such as flooding and droughts are important driving forces for trout dynamics. Among biotic factors, some studies (e.g. Titus & Mosegaard, 1992; Nordwall, Näslund & Degerman, 2001; Cattanéo *et al.*, 2002) have indicated that intercohort competition can significantly influence recruitment. Furthermore, a dispersed nest distribution in the river may decrease intracohort competition and increase offspring survival, as found by Einum *et al.* (2008) for Atlantic salmon (*Salmo salar* L).

In our systems, only the fish in the River Dulce revealed strong signs of density-dependent mortality. Like the others rivers, it is subjected to wide variations in environmental conditions. Nevertheless, egg density is high enough to allow intraspecific competition in emergent fry in some years (i.e. when egg density passed the point of maximum recruitment). The reason may be limited availability of suitable microhabitats for young trout soon after emergence. The habitat surveys (see Table 1) showed there are few shallow gravel areas with low water velocity, the habitat preferred by young fry (Heggenes, Bagliniere & Cunjak, 1999).

In our study populations, 30–50% of variance of 0+ trout density in early September was explained by variations in initial egg densities. These values are similar to those of Euzenat *et al.* (2006) from a French sea trout population (39%). Langeland & Pedersen (2000) explained 29% of the variation in 1-year-old trout in a Norwegian lake using the same model. Elliott & Elliott (2006) explained as much as 72% of the variation in 0+ trout in August/September based on egg density, using the Ricker model. In addition, Mortensen (1977) documented density-dependent mortality in brown trout fry during the first 3 months of life in lake-run brown trout in Danish streams, and Crisp (1993) observed density-dependent fry mortality in two English streams experimentally stocked for 9 years. But neither Mortensen (1977) nor Crisp (1993) fitted Ricker curves to their data.

Studies on population control of resident brown trout are few and the results contradictory. Elliott (1987) found no sign of density-dependent early mortality and, similarly, Lobón-Cerviá (2007) and Lobón-Cerviá & Rincón (2004) found no indication of density dependence when analysing stock–recruitment relationships, but found strong effects of water discharge on juvenile production. However, Einum (2005) re-analysed Lobón-Cerviá & Rincón's (2004) data and found support for the presence of endogenous regulation. Einum (2005) suggested that probably internal and external forces are so closely related that the distinction between density-dependent and density-independent factors may be indiscernable. In contrast to these studies, Carline (2006) found that annual recruitment of introduced brown trout in Pennsylvania (measured as 1+ trout in June) was inversely related to spawner abundance. Most of the annual variation in recruitment was due to the interactive effects of discharge and density. On the other hand, Zorn & Nuhfer (2007) reported that egg density was one of the most influential variables explaining the variation of 0+ brown trout in a Michigan river. Although comparable studies on peripheral populations of resident brown trout are lacking, the studies of Lobón-Cerviá (2007) and Lobón-Cerviá & Rincón (2004) in northwest Spain suggest that population size is environmentally driven, which is in agreement with the present results.

Although density-dependent mechanisms sometimes appear to regulate abundance in the studied populations, environmental factors and harvesting appear to preclude populations from reaching densities high enough for negative feedbacks to operate. As García de Leaniz *et al.* (2007) suggested, maladaptation often results from a phenotype–environment mismatch. To avoid this, one should act as if all populations are locally adapted. This means that one should allow for population size to extend beyond the carrying capacity of the habitat to maintain genetic diversity and encourage competition and other sources of natural mortality required for natural or stabilizing selection. To maintain strong natural selection among the young trout in the studied habitats, the populations should be allowed to increase above the point of maximum recruitment. Population fecundity appears to be a key factor in the dynamics of these marginal populations, and managers should protect spawning stocks through appropriate angling regulations. The Ricker model is useful in setting reference points for population management and for predicting the effects of some natural and human induced actions on populations.

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