

Growth Pattern of Stream-Dwelling Brown Trout under Contrasting Thermal Conditions

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Abstract.—Growth of brown trout *Salmo trutta* was analyzed based on 3 years of simultaneous temperature and growth data from seven streams of contrasting chemical and biological character. A laboratory-based growth model was employed to examine geographical variation in growth performance among wild populations. A sensitivity analysis of model predictions was also performed based on simulated optimum temperatures for growth within the range of observed temperatures and on the optimum temperature used in the model. In spite of the diverse environmental conditions, the annual increment in body mass was not significantly different among most populations. However, the ratio of the actual growth rate to the maximum growth rate predicted by the model differed among rivers. A significant negative correlation was found between this ratio and mean annual water temperature. The growth model thus underestimated growth in the coldest rivers, suggesting that adaptations to local thermal conditions can occur at a small geographical scale. Seasonal changes in the fit to the growth model were also different among rivers. Our simulations showed that, in almost all rivers, the best fit to the model among age-1 trout was obtained at lower values of optimum temperature in both spring and summer. Our findings suggest that the parameters of the model may not be identical for all brown trout populations. The discrepancies between observed and predicted growth indicated that temperature alone did not account for all the spatial and temporal variation in growth rates.

The growth pattern is an important life history trait (Stearns 1992), especially in organisms with indefinite growth such as fish, since the energetic investment in somatic growth depends on and influences the allocation of resources into reproduction (Reznick 1983; Hutchings 1993). Furthermore, interpopulation variance in growth rate is a key factor for explaining variability in life history features among populations (Roff 1984; Stearns and Koella 1986). Moreover, body size is probably the most important life history trait influencing animal fitness, as many fitness-related aspects scale with size (Roff 1992; Jonsson et al. 2001).

Water temperature is the most pervasive environmental factor affecting fish growth (Wootton 1998), and in brown trout *Salmo trutta*, growth takes place within a limited thermal range (Elliott et al. 1995). Thus, the temperature regime determines the length of the growth season. Growth of

individual brown trout may also be affected by population density (Le Cren 1962, 1965; Crisp 1993; Newman 1993; Jenkins et al. 1999), but this effect is difficult to observe (Egglisshaw and Shackley 1977; Mortensen et al. 1988; Baglinière and Maise 1990; Weatherley et al. 1991), especially in stream-dwelling populations (Elliott 1994; Knapp et al. 1998).

Elliott et al. (1995) developed a predictive model for maximum growth in weight for brown trout when fed to satiation, expanding on his earlier growth model (Elliott 1975). The model provides a baseline from which the magnitude of the effects of factors other than water temperature and initial fish size on trout growth can be assessed. The model has been tested in almost 70 brown trout populations in Europe, mostly in northern latitudes (43–70°N; Mann et al. 1989; L'Abée-Lund et al. 1989; Crisp et al. 1990; Weatherley et al. 1991; Andersen et al. 1992; Jensen et al. 2000; Lagarrigue et al. 2001), as well as in four populations outside the native range of the species (Allen 1985; Preall and Ringler 1989).

The brown trout is one of the most important

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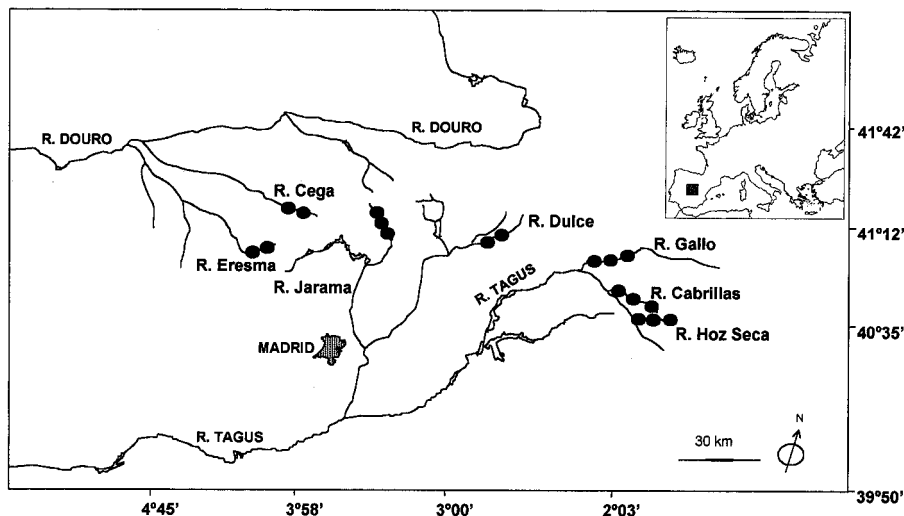


FIGURE 1.—Study area, showing the location of the 18 sampling sites (closed circles) in seven Spanish rivers surveyed for brown trout every third month from March 1996 to December 1998.

angling species in Spanish waters (Almodóvar and Nicola 1998; Almodóvar et al. 2002), and the analysis of geographical variation in growth may help improve the management of this species. Elliott (1994) pointed out the need for comparative work on contrasting populations of brown trout, so that intraspecific similarities and differences would be described and predicted. In spite of their genetic singularity (García-Marín et al. 1999; Machordom et al. 2000; Sanz et al. 2000; Suárez et al. 2001), southern populations of native brown trout (40–41°N) are less studied than their temperate conspecifics. Our purpose was to analyze the growth pattern of wild, resident brown trout subjected to contrasting environmental conditions, particularly temperature and other growth-governing factors such as food availability. Specifically, we hypothesized that the differences in thermal regime among rivers would produce stream-specific variation in growth. To test this prediction, simultaneous temperature and growth data from seven streams of contrasting chemical and biological character were used to assess the geographical variation in growth. Growth was expected to be slow in populations with low water temperature and low food abundance as compared to populations experiencing more optimal conditions for growth. The growth model developed by Elliott et al. (1995) was used to explore growth performance among these natural populations of brown trout and to determine the potential mechanisms controlling growth in the study area. By modeling performance under optimal experimental condi-

tions, we were able to explore whether trout growth was determined by ambient temperature regimes rather than by other environmental variables or by genetic factors.

Study Area

We studied brown trout from seven Spanish rivers (Figure 1). Five are tributaries to the River Tagus (Hoz Seca, Cabrillas, Gallo, Dulce, and Jarama) and two are tributaries to the River Douro (Cega and Eresma). Two or three sampling sites were selected in each river. The streams are significantly different in physical, chemical, and biological characteristics (multivariate analysis of variance [MANOVA], $F_{60,15} = 0.13$, $P < 0.001$; Nicola and Almodóvar 2002) (Table 1). However, they may be divided into two groups. Streams of the first type (Jarama, Cega, and Eresma) are soft-water streams arising from granite and gneiss watersheds at elevations between 1,100 and 1,300 m above sea level. The streams primarily originate from surface drainage, becoming torrential in their upper reaches as the snow melts in early spring. In these streams, the flow fluctuations throughout the year are pronounced, with a marked difference between winter and summer. The water temperature is close to 0°C in winter and 12–14°C in summer. The benthic fauna is quite sparse. Streams of the second type (Hoz Seca, Cabrillas, Gallo, and Dulce) have hard, fertile waters arising from limestone catchments at elevations from 850 to 1,400 m above sea level. The geology of the watersheds and the mild climate provide for an even flow re-

TABLE 1.—Selected environmental characteristics of the seven rivers from which brown trout were collected. Mean, mode, and range of annual water temperature (T_{ANNUAL} [°C]), frequency (%) of four annual temperature ranges, and mean water temperature in spring (T_{SPRING}), summer (T_{SUMMER}), and autumn (T_{AUTUMN}) are included. Flow data were obtained from a database maintained by the Spanish Ministry of Environment. Chemical variables were analyzed according to APHA (1985) methods from samples taken annually under wet and dry weather conditions during 1996–1998. Benthic macroinvertebrates were sampled every third month from March 1996 to December 1998 in each sampling point with a Neil cylinder sampler (250- μm -mesh net). Specimens were dried in an oven at 60°C for 24 h and weighed. Brown trout density was estimated by applying the three-catch removal method (Zippin 1956). More details about the methodology are given in Nicola and Almodóvar (2002).

Variable	Dulce	Gallo	Cabrillas
Mean T_{ANNUAL}	13.1	12.0	10.2
Mode T_{ANNUAL}	10.0	11.0	15.0
Range T_{ANNUAL}	8–19	5–18	5–16
0–5°C frequency (%)			2
5–10°C frequency (%)	20	32	50
10–15°C frequency (%)	50	43	38
15–20°C frequency (%)	30	25	11
Mean \pm SD T_{SPRING}	13.8 \pm 1.9	12.9 \pm 2.0	10.1 \pm 1.7
Mean \pm SD T_{SUMMER}	17.1 \pm 1.1	16.3 \pm 1.0	14.9 \pm 0.5
Mean \pm SD T_{AUTUMN}	11.7 \pm 1.6	10.0 \pm 2.5	9.3 \pm 2.5
Mean annual discharge and range (m^3/s)	1.2 (0.5–3.5)	1.4 (1.0–4.0)	1.3 (0.4–4.1)
Mean \pm SD conductivity ($\mu\text{S}/\text{cm}$)	602.0 \pm 76.7	967.0 \pm 97.0	606.1 \pm 135.4
Mean \pm SD alkalinity (CaCO_3 mg/L)	309.7 \pm 5.0	388.4 \pm 3.7	412.5 \pm 15.1
Mean \pm SD calcium (Ca^{2+} mg/L)	56.6 \pm 17.7	85.0 \pm 22.3	101.3 \pm 6.3
Mean \pm SD magnesium (Mg^{2+} mg/L)	22.0 \pm 2.9	26.4 \pm 2.8	33.4 \pm 4.9
Mean \pm SD benthos dry biomass (g/m^2)	2.75 \pm 1.16	6.15 \pm 1.31	1.72 \pm 0.42
Mean \pm SE brown trout density (fish/ha)	1,365.3 \pm 291.9	851.5 \pm 234.8	1,709 \pm 379.8

gime throughout the year. Particularly, the River Hoz Seca receives a substantial proportion of its flow from limestone springs, and therefore remains close to 10°C year-round. The rivers Cabrillas, Gallo, and Dulce show a similar temperature regime, with an annual mean between 10°C and 13°C. The seven streams differ markedly in concentrations of common ions (Table 1). Therefore, benthic macroinvertebrates are more abundant in the second group of rivers than the first group. Further details of the study area are given in Nicola and Almodóvar (2002). The brown trout is the only or the most abundant fish species present in all the rivers, and the populations differ significantly in fish density (Table 1).

Methods

Electrofishing with a 220-W DC generator took place at 18 localities every third month from March 1996 through December 1998. Fish caught were anesthetized with tricaine methanesulfonate (MS-222; SANDOZ), and their fork lengths (nearest mm) and weights (nearest g) were measured. Scales were taken for age determination. The instantaneous rate of growth in weight (G_{obs}) was estimated separately for the dominant year-classes (age 0 to age 2) as:

$$G_{\text{obs}} = 100 \cdot [(\log_e W_t - \log_e W_0)/t] \quad (1)$$

where W_0 and W_t are the mean weights (g) of each year-class at the beginning and the end of t days, respectively. G_{obs} was calculated for spring (March to June; mean, 92 \pm 10 d; range, 67–108 d), summer (June to September; mean, 87 \pm 5 d; range, 74–97 d), autumn (September to December; mean, 74 \pm 12 d; range, 57–105 d), and winter (December to March; mean, 113 \pm 18 d; range, 75–130 d) of every sampling year. The annual growth rate was calculated in September because growth in trout populations virtually ceases by this time of the year; we used equation (1) to calculate annual growth for the intervals age 0 to age 1 and age 1 to age 2.

The growth model given by Elliott et al. (1995) was employed to estimate the maximum growth of brown trout at excess food rations. According to this model, the maximum weight (W_t) after a period of t days is

$$W_t = [W_0^b + bc(T - T_{\text{LIM}}) \cdot t / \{100(T_M - T_{\text{LIM}})\}] \quad (2)$$

where T is the observed temperature, T_M is the optimum temperature for growth, and T_{LIM} is the temperature limit. T_{LIM} assumes the value of the lower or upper temperatures at which the growth rate is zero (T_L or T_U) depending on whether T is higher or lower than T_M (i.e., $T_{\text{LIM}} = T_L$ if $T <$

TABLE 1.—Extended.

Variable	Hoz Seca	Jarama	Cega	Eresma
Mean T_{ANNUAL}	10.2	8.6	6.3	6.5
Mode T_{ANNUAL}	10.0	6.0	3.0	3.0
Range T_{ANNUAL}	8–12	0–18	0–13	0–13
0–5°C frequency (%)		23	46	48
5–10°C frequency (%)	42	38	28	26
10–15°C frequency (%)	58	30	26	26
15–20°C frequency (%)		9		
Mean \pm SD T_{SPRING}	10.2 \pm 0.5	8.0 \pm 2.6	5.6 \pm 2.5	5.0 \pm 1.7
Mean \pm SD T_{SUMMER}	11.6 \pm 0.3	14.7 \pm 1.3	11.5 \pm 1.1	11.8 \pm 1.3
Mean \pm SD T_{AUTUMN}	9.9 \pm 0.6	6.7 \pm 3.2	6.0 \pm 3.1	7.2 \pm 3.3
Mean annual discharge and range (m ³ /s)	4.9 (0.9–19.7)	7.2 (0.5–27.2)	7.0 (0.4–14.9)	4.0 (0.4–11.2)
Mean \pm SD conductivity ($\mu\text{S}/\text{cm}$)	611.2 \pm 82.8	25.9 \pm 5.8	17.7 \pm 5.4	65.3 \pm 18.0
Mean \pm SD alkalinity (CaCO ₃ mg/L)	366.7 \pm 78.9	18.1 \pm 11.7	20.7 \pm 3.8	29.6 \pm 1.1
Mean \pm SD calcium (Ca ²⁺ mg/L)	84.4 \pm 4.6	1.2 \pm 0.3	2.8 \pm 1.0	3.1 \pm 0.3
Mean \pm SD magnesium (Mg ²⁺ mg/L)	25.7 \pm 4.1	1.3 \pm 1.1	0.9 \pm 0.5	0.9 \pm 0.1
Mean \pm SD benthos dry biomass (g/m ²)	1.76 \pm 0.65	0.49 \pm 0.03	0.56 \pm 0.05	0.47 \pm 0.13
Mean \pm SE brown trout density (fish/ha)	565.9 \pm 57.8	1,530.0 \pm 263.9	2,486.7 \pm 293.3	4,894.5 \pm 441.8

T_M ; $T_{\text{LIM}} = T_U$ if $T > T_M$). The weight exponent b is the power transformation of weight that produces linear growth with time, and c is the growth rate of a 1-g trout at the optimum temperature. T_M was estimated at 13.11°C, and T_L and T_U were estimated at 3.56°C and 19.48°C, respectively (Elliott et al. 1995). The values of the constants b and c were 0.308 and 2.803, respectively (Elliott et al. 1995). Mean daily water temperatures were used to estimate growth. The mean daily water temperatures were estimated as the mean of all values recorded over 24 h by data loggers (Minilog; Vemco, Ltd.) placed in each river during 1997 and 1998. For the 1996 data, we used linear regression analysis to estimate the water temperature from the air temperatures measured at local meteorological stations (Elliott 1984; Crisp 1992). Water temperatures were closely related to air temperatures (mean $r^2 = 0.88$), as has been reported by other authors (Crisp and Howson 1982; Mohseni et al. 1998). More than 75% of predictions were within 1.0°C of the observed values. Estimates were checked occasionally by direct measurements, especially at low water temperatures.

Maximum growth rates (G_{max}) were calculated by inserting the weight estimates from equation (2) into equation (1). The ratio of the actual growth rate to the maximum growth rate predicted by the growth model ($[G_{\text{obs}}/G_{\text{max}}] \cdot 100$) was then cal-

culated. In order to assess the occurrence of size-selective mortality within a year-class, which could give an overestimation of the growth rates, the coefficient of variation (CV, defined as $100 \times \text{SD}/\text{mean}$) for lengths and weights was calculated. The CVs remained practically constant during the growth season, such that size-selective mortality seemed to be insignificant.

Additionally, a sensitivity analysis of the model (Brown and Rothery 1993) was carried out by adjusting T_M to equal the range of temperatures observed in each stream. The lower and upper temperatures for growth, as well as the constants b and c , were assumed to be the same as in Elliott et al. (1995). Growth was then simulated from observed data by computing predictions with varying T_M values that represented the range of observed temperatures in 1°C increments. The simulations were made for age-1 trout in spring, as well as age-0 and age-1 trout in summer of each sampling year.

Data were analyzed with multifactor analyses of variance (ANOVA), and subsequent Scheffé's tests were used for comparison of mean values. Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro-Wilk and Levene's tests, respectively. The significance level α for all statistical tests was set at 0.05.

Results

Brown trout growth varied during the year, peaking between March and September, gradually decreasing from September onwards, and culminating in a winter minimum (Figure 2). There were no significant differences among years in the mean age-specific weight of brown trout in each river. Therefore, data for the years 1996–1998 were pooled. The mean age-specific weight varied significantly among populations at the end of the growth period (two-way ANOVA, with age and river as classification factors; age \times river interaction: $F_{12, 2,874} = 7.22$, $P < 0.001$) (Table 2). Brown trout in the rivers Cega and Eresma were smaller than those in the other populations (Scheffé's test, $P < 0.001$). The highest mean weight at age was found in the River Gallo. However, during the first year of life (age 0 to age 1), there was no significant difference in the observed annual growth rate among populations (ANOVA, $F_{6,22} = 1.94$, $P > 0.05$). The mean observed growth rate in the first year ranged between 1.51 and 1.88, while the predicted growth rate varied between 1.62 and 2.75 (Table 2). The ratio between G_{obs} and the predicted G_{max} was significantly different among populations (ANOVA, $F_{6,20} = 5.54$, $P < 0.001$). The recorded growth rate in the first year was 60–104% of the corresponding growth rate estimated from the Elliott et al. (1995) model (Table 2). The lowest relative growth rates were found in the River Gallo and the highest mean ratios were observed in the rivers Cega and Eresma.

When mean observed and expected weights of age-0 trout throughout the year were compared, the best fit to the model was found in the coldest rivers, Cega and Eresma (Figure 2). However, these rivers had a presumed poor temperature profile for brown trout growth, since only 66% of mean daily temperatures were within the range 3.6–19.5°C. All mean daily temperatures in the remaining rivers fell within this range and suggested a potentially high growth rate for brown trout, but the fit to the model was worse.

During the second period of growth (age 1 to age 2), a significant difference was found in G_{obs} among populations (ANOVA, $F_{6,24} = 11.1$, $P < 0.001$), but subsequent comparisons only revealed significant differences between the River Hoz Seca and the rivers Gallo and Dulce (Scheffé's test, $P < 0.05$); the latter two streams showed the lowest growth rates among all populations (Table 2). Mean G_{obs} in the second year varied between 0.72/d and 1.17/d, whereas G_{max} ranged between 1.10

and 1.84/d. The ratio of G_{obs} and G_{max} was also significantly different among populations (ANOVA, $F_{6,16} = 10.91$, $P < 0.001$). The recorded growth rates constituted 45–88% of the corresponding growth rates computed from the model (Table 2). The lowest relative growth rate was found in the River Gallo, and the highest mean values were observed in the rivers Cega and Eresma. A significant negative correlation was found between the mean $G_{\text{obs}}/G_{\text{max}}$ and the mean annual water temperature for both periods of growth (age 0 to age 1, Pearson's $r = -0.55$, $P < 0.01$; age 1 to age 2, $r = -0.88$, $P < 0.001$).

During spring, G_{obs} in age-1 brown trout was significantly different among rivers (range 0.44–0.99/d; ANOVA, $F_{6,21} = 3.46$, $P < 0.05$), but subsequent comparisons of means only revealed significant differences (Scheffé's test, $P < 0.05$) between the low values of the River Dulce and the highest means of the rivers Cabrillas and Cega. The ratio of recorded and predicted growth rates was significantly different among rivers (ANOVA, $F_{6,21} = 6.35$, $P < 0.001$). G_{obs} was always higher than G_{max} in all the rivers except Dulce and Hoz Seca (Figure 3). The largest deviations were found in the rivers Cega and Eresma ($G_{\text{obs}}/G_{\text{max}} > 150$, Figure 3). G_{obs} was not significantly correlated with mean water temperature during spring ($r = -0.53$, $P > 0.05$).

In summer, G_{obs} of age-0 trout was significantly different among populations (range 0.94–2.25/d; ANOVA, $F_{5,16} = 4.84$, $P < 0.01$). G_{obs} of age-1 trout was also significantly different among rivers (range 0.18–0.67/d; ANOVA, $F_{6,26} = 3.45$, $P < 0.05$), but a posteriori comparisons only showed significant differences (Scheffé's test, $P < 0.05$) between the low values of River Gallo and the highest means of the rivers Eresma, Cega, and Jarama. G_{obs} was not significantly correlated with mean water temperature for age-0 brown trout during summer ($r = -0.40$, $P > 0.05$), but G_{obs} and mean temperature were correlated for age-1 trout ($r = -0.81$, $P < 0.05$). The ratio between G_{obs} and G_{max} was significantly different among rivers for both age-0 (ANOVA, $F_{5,16} = 4.50$, $P < 0.01$) and age-1 trout (ANOVA, $F_{6,26} = 3.28$, $P < 0.05$). G_{obs} of age-0 trout was higher than G_{max} in all rivers except in River Cega (Figure 3). G_{obs} of age-1 trout only equaled G_{max} in the River Dulce (Figure 3). In the remaining rivers, the mean values ranged from 39% in the River Gallo to 89% in the River Jarama.

With regard to autumn, G_{obs} of age-0 brown trout from rivers Gallo and Dulce were significantly dif-

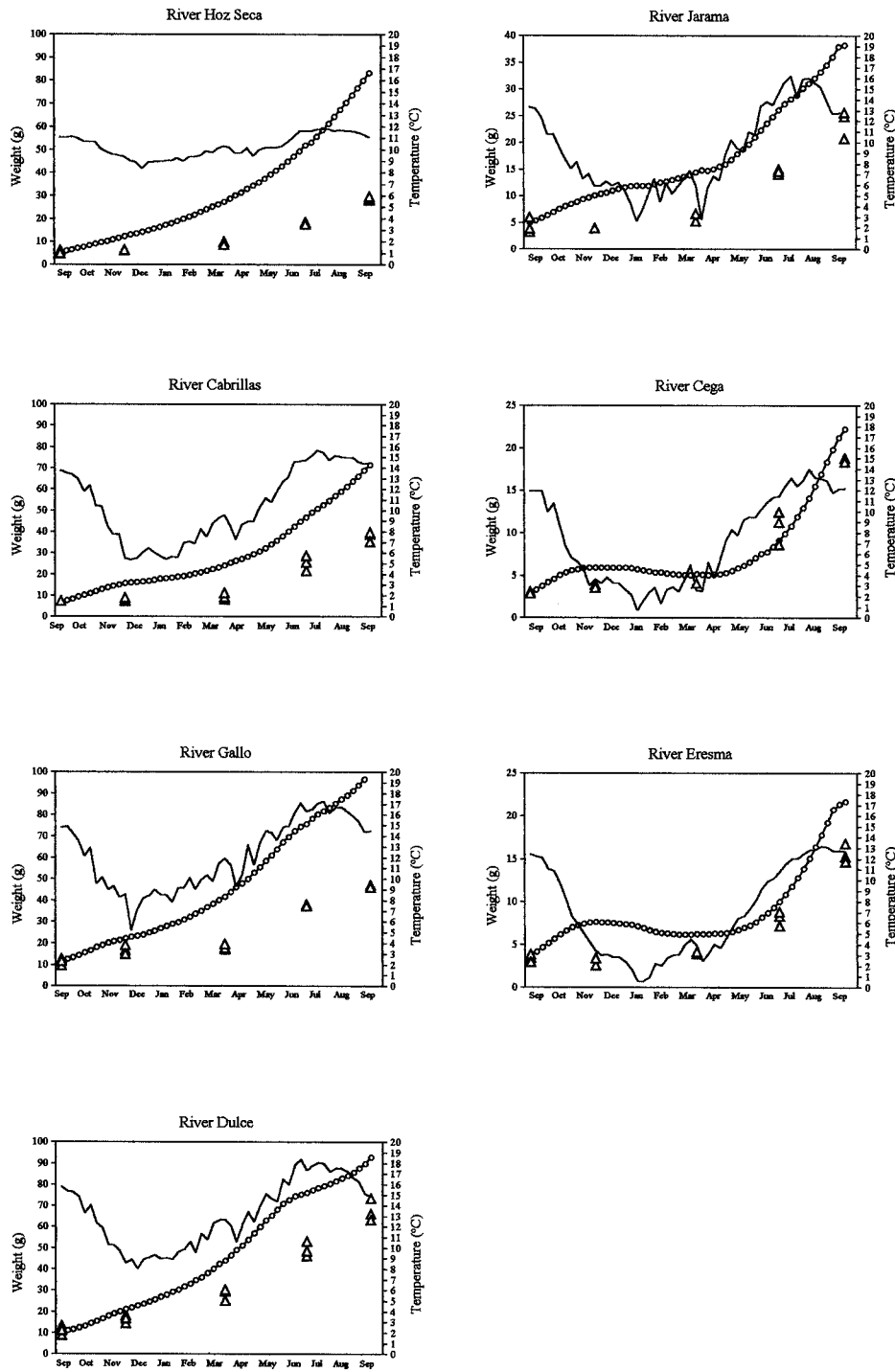


FIGURE 2.—Annual patterns in mean observed (triangles) and simulated (circles) weights of juvenile brown trout in each study river. The observed values started at age 0 in September and ended at age 1 in September during the three study years (1996–1998). The predicted growth curve starts in September, and the initial weight is estimated as the mean weight of age-0 fish during the sampling years (W_0 in Table 2). Mean daily temperature (°C; solid lines) during 1996–1998 is also given to show the annual patterns of temperature in each river.

TABLE 2.—Mean weight (W_0 , [g]) \pm SD of juvenile brown trout at the end of the growth season, sample size, and mean observed (G_{obs}) and predicted (G_{max}) annual growth rates in year⁻¹ \pm SD in the seven populations studied (1996–1998), during the first (age-0 to age-1) and second (age-1 to age-2) growth periods. The mean ratio and range (in parentheses) between observed and predicted growth are also given.

River	W_0	N	G_{obs}	G_{max}	$G_{\text{obs}}/G_{\text{max}}$ ratio (%)
Age 0 to Age 1					
Dulce	10.5 \pm 4.2	73	1.83 \pm 0.14	2.27 \pm 0.04	81 (74–88)
Gallo	11.8 \pm 5.0	57	1.36 \pm 0.33	2.26 \pm 0.23	60 (54–66)
Cabrillas	7.0 \pm 2.9	246	1.66 \pm 0.12	2.28 \pm 0.30	75 (59–84)
Hoz Seca	5.6 \pm 2.1	90	1.77 \pm 0.22	2.75 \pm 0.12	66 (61–73)
Jarama	5.1 \pm 3.1	191	1.64 \pm 0.23	2.17 \pm 0.24	75 (71–82)
Cega	3.7 \pm 1.4	179	1.88 \pm 0.32	1.81 \pm 0.17	104 (82–121)
Eresma	3.3 \pm 1.5	197	1.51 \pm 0.30	1.62 \pm 0.22	94 (72–117)
Age 1 to Age 2					
Dulce	65.8 \pm 20.9	73	0.72 \pm 0.11	1.57 \pm 0.03	46 (41–50)
Gallo	46.3 \pm 12.6	78	0.74 \pm 0.01	1.66 \pm 0.02	45 (44–45)
Cabrillas	35.4 \pm 10.1	79	0.91 \pm 0.04	1.58 \pm 0.22	58 (50–66)
Hoz Seca	29.7 \pm 9.9	59	1.17 \pm 0.11	1.84 \pm 0.04	62 (54–68)
Jarama	26.1 \pm 11.5	202	0.98 \pm 0.09	1.50 \pm 0.10	65 (61–72)
Cega	19.0 \pm 8.1	181	0.97 \pm 0.07	1.14 \pm 0.12	86 (76–104)
Eresma	15.5 \pm 5.2	344	0.95 \pm 0.06	1.10 \pm 0.13	88 (74–102)

ferent from the G_{obs} of the other populations (range 0.03–0.70/d; ANOVA, $F_{6,21} = 9.03$, $P < 0.001$; Scheffé's test, $P < 0.01$). G_{obs} of age-1 trout was not significantly different among rivers (range 0.02–0.21/d; ANOVA, $F_{6,15} = 2.29$, $P > 0.05$). G_{obs} was much lower than G_{max} in all the rivers (3–30%), except in age-0 trout from the rivers Gallo and Dulce (mean, 70%) (Figure 3). Some of these rivers showed water temperatures within the range 3.8–19.5°C, and temperatures were similar or even higher to those found in spring, although the growth pattern was markedly different during autumn. During winter, there was no growth in most cases.

For all the rivers, the best correlation between recorded and predicted growth of age-1 brown trout in spring was found when the optimum temperature for growth (T_M) was simulated to be smaller than that reported by Elliott et al. (1995), except for the River Hoz Seca, where the best fit was obtained at 13°C (Table 3). In summer, the best correlation between recorded and predicted growth of age-0 trout for the rivers Dulce, Gallo, and Cabrillas was found when the optimum temperature for growth was simulated to be higher than the value reported by Elliott et al. (1995), whereas the best correlation for the remaining rivers was found when the optimum temperature was simulated to be smaller (Table 3). For all the rivers, the best correlation for age-1 brown trout in summer was found when the optimum temperature for growth was simulated to be smaller than that reported by Elliott et al. (1995) (Table 3), except for

the River Dulce, where the best fit was obtained at around 13°C. The sensitivity of the model to simulated variations in T_M was different among rivers and between seasons. The change in T_M value seemed to affect the outcome of the model very much in some cases, which indicates that the model might need to be reconsidered.

Discussion

Brown trout growth in the study rivers followed the general pattern described for this species in several European populations (e.g., Egglisshaw and Shackley 1977; Mortensen 1982; Mann et al. 1989; Baglinière and Maisse 1990). In spite of the diverse environmental conditions, the annual increment in body mass was not significantly different among most populations. However, the ratio of observed to predicted growth significantly differed among rivers. The best fit to the model of Elliott et al. (1995) was found in rivers with low water temperature and low food availability (rivers Cega and Eresma), a finding that confirmed the pervasive role of temperature in trout growth in these rivers. In the rest of the populations, observed growth deviated from the model, equaling between 60% and 80% of predicted growth. Edwards et al. (1979) found similar results in 25 localities in Britain, ranging from limestone streams in southern England to mountainous Scottish rivers. These authors observed that the most temperate and productive rivers showed an observed growth equal to about 70% of predicted values, whereas in colder and less fertile rivers, growth was almost 80%

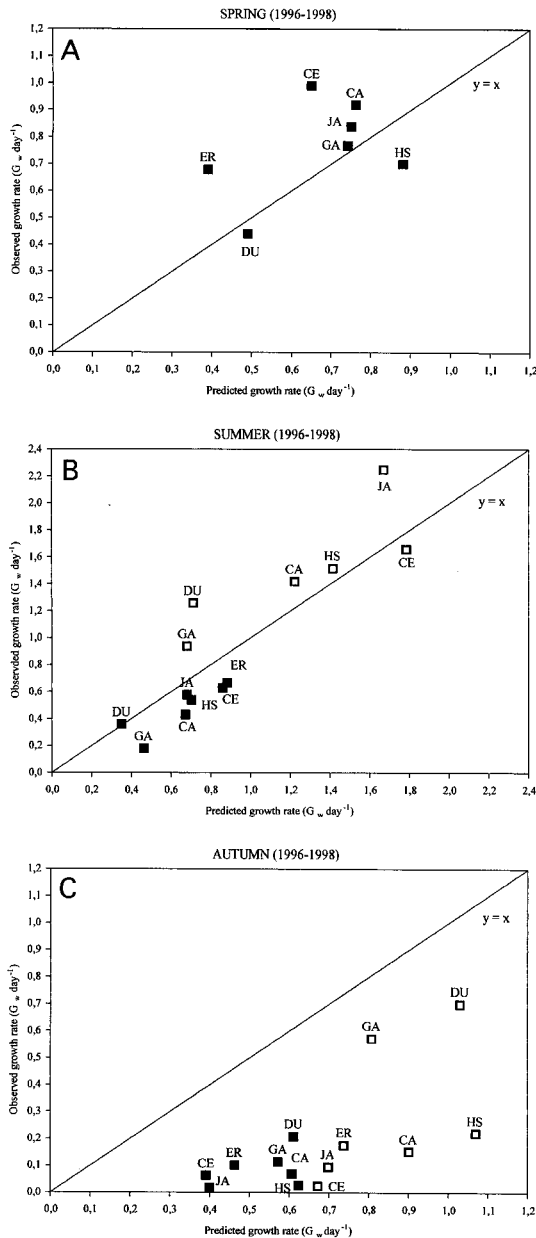


FIGURE 3.—Comparison between mean observed (G_{obs}) and mean maximum (G_{max}) instantaneous growth rates (d) of age-0 (open squares) and age-1 (closed squares) brown trout in the seven populations studied (rivers Dulce [DU], Gallo [GA], Cabrillas [CA], Hoz Seca [HS], Jarama [JA], Cega [CE], and Eresma [ER]) during (A) spring, (B) summer, and (C) autumn of 1996–1998.

of predicted values. Likewise, Jensen and Johnsen (1984) in Norway, Preall and Ringler (1989) in the USA, and Weatherley et al. (1991) in Wales obtained similar results to that of Edwards et al. (1979) and the present work. The most extensive use of Elliott's growth model is the recent study by Jensen et al. (2000), based on 42 European populations of brown trout. These authors found that most of the variation in annual growth rate (80%) was related to environmental variability. However, the model strongly underestimated growth in some of the coldest rivers, and a significant relationship was found between annual growth and temperature. The same findings have been obtained in the present work, albeit at a smaller geographical scale. At first, this suggests local thermal adaptations in the coldest rivers, but there are alternative explanations that we will discuss below.

A more detailed analysis of growth showed a marked effect of both season and river in the fit to the model. Thus, mean observed growth rate during spring equaled and even surpassed predicted values in most rivers, as has been reported for other populations (e.g., Mortensen et al. 1988; Jensen 1990; Elliott 1994; Lobón-Cerviá and Rincón 1998; Lagarrigue et al. 2001). Therefore, at temperatures below 13°C, brown trout in some populations were able to grow at least as fast or faster than British trout of the same size at the same temperature, fed to satiation under experimental conditions (Elliott et al. 1995). However, the ratio of recorded and predicted growth significantly varied among populations, although there were no significant differences in observed growth among most rivers. The actual growth considerably exceeded the maximum predicted growth in the rivers Cega and Eresma. However, during spring, mean water temperature in these rivers (~5°C) was lower than the optimum temperature for trout growth at excess rations (13.1°C; Elliott et al. 1995), and food abundance was low (mean dry biomass, 0.51 ± 0.01 g/m²). Allen (1985) also found a higher observed than predicted growth of trout (110–140%) with water temperatures below 13°C in the River Horokiwi in New Zealand. Likewise, Jensen (1990) found a significantly higher observed growth (115–172%) in four Norwegian rivers with low temperature and low water productivity. Previous studies on brown trout have shown that, if food consumption is reduced, the optimal temperature for growth also decreases (Elliott 1994). Certainly, the fit to the model in the rivers Cega and Eresma greatly improved during

TABLE 3.—Mean (\pm SD) ratio between observed and maximum growth ($G_{\text{obs}}/G_{\text{max}}$, expressed as a percent) found in the best fits to the model of Elliott et al. (1995) based on alternative values of optimum temperature for growth (T_M). Predictions of the model were computed with simulated values of optimum temperature covering the range of temperatures observed in each stream at intervals of 1°C. The mean $T_M \pm$ SD at which the best fit was found is also indicated.

River	Summer					
	Spring (age-1)		Age-0		Age-1	
	$G_{\text{obs}}/G_{\text{max}}$	T_M	$G_{\text{obs}}/G_{\text{max}}$	T_M	$G_{\text{obs}}/G_{\text{max}}$	T_M
Dulce	100.7 \pm 1.4	11.6 \pm 0.7	107.3 \pm 7.3	17.0 \pm 1.5	102.6 \pm 2.1	12.6 \pm 2.8
Gallo	103.7 \pm 0.8	10.6 \pm 1.8	105.9 \pm 8.1	14.9 \pm 1.9	82.2 \pm 18.5	5.2 \pm 0.3
Cabrillas	108.1 \pm 10.8	8.7 \pm 1.8	103.6 \pm 4.6	14.4 \pm 1.0	90.0 \pm 16.6	8.3 \pm 3.5
Hoz Seca	86.2 \pm 15.1	13.0 \pm 0.3	100.8 \pm 0.8	12.4 \pm 0.4	89.7 \pm 17.7	8.3 \pm 0.3
Jarama	99.0 \pm 1.5	10.7 \pm 1.9	110.9 \pm 8.5	12.4 \pm 1.9	99.7 \pm 2.8	11.4 \pm 3.3
Cega	106.7 \pm 14.0	8.4 \pm 1.8	99.9 \pm 1.1	12.1 \pm 0.7	84.4 \pm 18.9	6.1 \pm 1.5
Eresma	100.1 \pm 0.7	8.1 \pm 1.8	—	—	94.2 \pm 9.9	5.9 \pm 1.0

spring at a simulated T_M of approximately 8°C. In contrast, the fit to the model in the other rivers was hardly enhanced when varying T_M , though the best fits were obtained when T_M was simulated to be smaller. Alternatively, Allen (1985) pointed out that trout used in experiments may not reach their maximum growth scope, and Forseth and Jonsson (1994) suggested that food rations could be higher in the wild than that considered by Elliott (1975) as maximum. In addition, Spigarelli et al. (1982) observed better feeding and higher growth in a thermocyclic regime than at a constant temperature, which agrees with observations by Hokanson et al. (1977) and Biette and Green (1980) in other salmonid species. However, Elliott (1975) tested the viability of the model in the wild, finding a similar growth than that of trout in captivity. Additionally, fish from the coldest rivers may have a compensatory growth response during spring, as has been broadly described in salmonids (e.g., Miglavs and Jobling 1989; Reimers et al. 1993; Nicieza and Metcalfe 1997). This would lead to annual growth rates similar to the other rivers and sometimes higher than predicted from the model.

During summer, mean observed growth rates of age-1 trout were lower than predicted values in most rivers, as reported for other populations (Preall and Ringler 1989; Jensen 1990; Lagarrigue et al. 2001). It is important to emphasize the decrease of this ratio in the rivers Cega and Eresma, although mean water temperature was higher than in spring (11–12°C). In the rivers Cabrillas, Gallo, Dulce, and Jarama, the mean water temperature exceeded 13°C in summer (14.4–16.7°C). In almost all study rivers, the best fit to the model among age-1 trout was found when T_M was simulated to be smaller ($T_M = 5$ –11°C). Higher summer temperatures may be responsible for the decrease in summer growth rates through increasing

metabolic rates (Elliott 1994), but variations in stream temperature are accounted for in the model. Growth during summer may also decrease due to limited food availability, as the model assumes no food limitation and does not take into account changes in food availability (Elliott and Hurley 2001). However, mean dry biomass of bottom fauna during summer (1.99 g/m², range 0.51–6.45 g/m²) was similar to that found during spring (2.14 g/m², range 0.44–7.49 g/m²). A more likely explanation is given by the onset of gonad maturation during summer (Nicola 1999), provided there is a tradeoff between maturity and growth (Stearns 1992). However, in all rivers, females matured at age 2 as opposed to age 1 or 2 for males (Nicola and Almodóvar 2002). Therefore, other factors are likely limiting summer growth in age-1 trout in the studied rivers.

A widespread reduction in growth took place during autumn in all the populations, even though mean water temperature in the rivers was suitable for brown trout growth. Hence, observed values were much smaller than predicted, except for age-0 brown trout in the rivers Dulce and Gallo, which supported approximately 70% of predicted growth. This means that food may be a limiting factor within this period, as suggested by Mortensen (1985) and Mortensen et al. (1988) in Denmark, and Elliott (1985) and Mann et al. (1989) in Britain, all of whom found comparable patterns. However, Elliott (1989) obtained a similar result with age-0 trout under experimental conditions with unlimited food. Furthermore, the mean biomass of benthic invertebrates during autumn in the rivers studied (1.96 g/m², range 0.48–5.84 g/m²) was similar to that found during the growth period. Elliott (1989) suggested that this pattern could be related to seasonal rhythms in feeding motivation, with a loss of appetite as autumn begins and water tempera-

tures start to decrease, similar to the phenomenon observed in Atlantic salmon *Salmo salar* (e.g., Metcalfe et al. 1986; Metcalfe and Thorpe 1992; Simpson et al. 1996). Besides the change in feeding activity, the observed seasonal changes could also be influenced by photoperiod. The progressive increment of day length may stimulate growth in spring, whereas the shortening of days in autumn may diminish growth (see Boeuf and Le Bail [1999] for a review). Consequently, although the fit to the model was considerably high during the growing season in the rivers studied, the retarded growth in autumn and winter resulted in annual growth rates usually below the estimated growth.

The ratio of observed to predicted growth showed no clear pattern among streams when T_M was 13.11°C. However, when alternative values of optimal temperature were used in our simulations, the fit to the model was similar among populations, although the simulated T_M value that gave the best fit varied considerably. Our results suggest that the parameters of the model may not be identical for all brown trout populations, as noted by other authors (Allen 1985; Crisp et al. 1990; Lobón-Cerviá and Rincón 1998). Accordingly, in experiments that use alternative mathematical functions, the estimated optimal temperature for growth of brown trout was found to be between 14°C and 17°C in Norway (Forseth and Jonsson 1994) and 16.9°C in Spain (Ojanguren et al. 2001). Further, Jensen (1990) found a better fit to the original model of Elliott (1975) at T_M values equal to 14.9°C in a Norwegian population of brown trout. Allen (1985) and L'Abèe-Lund et al. (1989) also noted that the temperature for optimal growth in wild populations of brown trout seemed to be higher than that recorded by Elliott (1975) for experimental fish. Therefore, the thermal responses of brown trout populations seem to be different from those used to develop the model. There is still little support for the hypothesis of adaptation to local thermal conditions proposed by several authors (e.g., Allen 1985; Weatherley et al. 1991; Lobón-Cerviá and Rincón 1998; Jensen et al. 2000). However, the geographical variability in the fit to the model observed in the present work could be related to genetic differences among populations. Further, Nicieza et al. (1994) found genetically-based differences in the digestive performance of Atlantic salmon in a high-latitude population, suggesting that this population may have developed certain mechanisms to compensate for presumably more restricted conditions for growth. Further, several workers have pointed out the relationship be-

tween the genetic variability of some metabolic enzymes of salmonids and the growth rate (e.g., Jordan and Youngson 1991; Torrisen et al. 1994). Another factor that might be partially responsible for the observed discrepancies is the feeding regime. Recently, Elliott and Hurley (2000) have demonstrated that a change in diet from invertebrates to fish, and hence in the energy available for growth, can increase the optimum temperature for trout growth to 17°C. Finally, recent studies indicate that intraspecific competition is an important factor for explaining variation in growth in stream-dwelling brown trout (Jenkins et al. 1999; Nordwall et al. 2001; Bohlin et al. 2002; Vøllestad et al. 2002). However, in the study rivers, density-dependent effects on growth rate may be minimal, as a significant positive correlation was found between the ratio $G_{\text{obs}}/G_{\text{max}}$ and mean brown trout density (Spearman's $r = 0.82$, $P < 0.05$).

In summary, the populations studied showed little variation in growth rate, in spite of being subjected to a wide range of environmental conditions. However, some discrepancies were found between observed and predicted growth, which indicates that temperature alone did not account for all the spatial and temporal variation in growth rates. In addition, the ratio of observed to predicted growth increased with decreasing water temperature. The growth model thus underestimated growth in the coldest rivers, suggesting that adaptations to local thermal conditions can occur. The studied populations show genetic differences, especially between the Tagus and Douro river basins (Machordom et al. 1999, 2000; Suárez et al. 2001), but common-environment or reciprocal transplant experiments are required in order to find some support for the local thermal adaptation hypothesis. Some other factors, such as feeding behavior, could also cause the observed discrepancies. Finally, controlled experiments are needed to estimate the parameters critical to the model for the study populations before alternative explanations can be suggested.

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References

- Allen, K. R. 1985. Comparison of the growth rate of brown trout (*Salmo trutta*) in a New Zealand stream with experimental fish in Britain. *Journal of Animal Ecology* 54:487–495.
- Almodóvar, A., and G. G. Nicola. 1998. Assessment of a brown trout population in the River Gallo (central Spain): angling effects and management implications. *Italian Journal of Zoology* 65:539–543.
- Almodóvar, A., G. G. Nicola, and J. Suárez. 2002. Effects of fishery management on populations of brown trout, *Salmo trutta*, in central Spain. Pages 337–345 in M. J. Collares-Pereira, I. Cowx, and M. M. Coelho, editors. *Conservation of freshwater fishes: options for the future*. Fishing News Books, Oxford, UK.
- APHA, American Water Works Association, and Water Pollution Control Federation. 1985. *Standard methods for the examination of water and wastewater*, 16th edition. APHA, Washington, D.C.
- Andersen, T. H., H. O. Hansen, T. M. Iversen, D. Jacobsen, L. Krojgaard, and N. Poulsen. 1992. Growth and feeding of 0+ brown trout (*Salmo trutta* L.) introduced to small Danish streams. *Archiv für Hydrobiologie* 125:339–346.
- Baglinière, J. L., and G. Maisse. 1990. La croissance de la truite commune (*Salmo trutta* L.) sur le bassin du Scorff. *Bulletin Français de la Pêche et de la Pisciculture* 318:89–101.
- Biette, R. M., and G. H. Green. 1980. Growth of under-yearling sockeye salmon (*Oncorhynchus nerka*) under constant and cyclic temperatures in relation to live zooplankton ration size. *Canadian Journal of Fisheries and Aquatic Sciences* 37:203–210.
- Boeuf, G., and P. Le Bail. 1999. Does light have an influence on fish growth? *Aquaculture* 177:129–152.
- Bohlin, T., L. F. Sundström, J. I. Johnsson, J. Höjesjö, and J. Pettersson. 2002. Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. *Journal of Animal Ecology* 71:683–692.
- Brown, D., and P. Rothery. 1993. *Models in biology: mathematics, statistics and computing*. Wiley, Chichester, UK.
- Crisp, D. T. 1992. Measurement of stream water temperature and biological applications to salmonid fishes, grayling and dace. *Freshwater Biological Association, Occasional Publication* 29.
- Crisp, D. T. 1993. Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *Journal of Applied Ecology* 30:759–771.
- Crisp, D. T., and G. Howson. 1982. Effect of air temperature upon mean water temperature in streams in the north Pennines and English Lake District. *Freshwater Biology* 12:359–367.
- Crisp, D. T., R. H. K. Mann, P. R. Cubby, and S. Robson. 1990. Effects of impoundment upon trout (*Salmo trutta* L.) in the basin of Cow Green reservoir. *Journal of Applied Ecology* 27:1020–1041.
- Edwards, R. W., J. W. Densem, and P. A. Russell. 1979. An assessment of the importance of temperature as a factor controlling the growth rate of brown trout in streams. *Journal of Animal Ecology* 48:501–507.
- Egglisshaw, H. J., and P. E. Shackley. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966–75. *Journal of Fish Biology* 11:647–672.
- Elliott, J. M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. *Journal of Animal Ecology* 44:805–821.
- Elliott, J. M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *Journal of Animal Ecology* 53:327–350.
- Elliott, J. M. 1985. Growth, size, biomass and production for different life stages of migratory trout *Salmo trutta* in a Lake District stream, 1966–83. *Journal of Animal Ecology* 54:985–1001.
- Elliott, J. M. 1989. Growth and size variation in contrasting populations of trout *Salmo trutta*: an experimental study on the role of natural selection. *Journal of Animal Ecology* 58:45–58.
- Elliott, J. M. 1994. *Quantitative ecology and the brown trout*. Oxford series in ecology and evolution. Oxford University Press, Oxford, UK.
- Elliott, J. M., and M. A. Hurley. 2000. Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. *Freshwater Biology* 44:237–245.
- Elliott, J. M., and M. A. Hurley. 2001. Modelling growth of brown trout, *Salmo trutta*, in terms of weight and energy units. *Freshwater Biology* 46:679–692.
- Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology* 9:290–298.
- Forseth, T., and B. Jonsson. 1994. The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology* 8:171–177.
- García-Marín, J. L., F. M. Utter, and C. Pla. 1999. Post-glacial colonization of brown trout in Europe based on distribution of allozyme variants. *Heredity* 82:46–56.
- Hokanson, K. E., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 34:639–648.
- Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology* 74:673–684.
- Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* 80:941–956.
- Jensen, A. J. 1990. Growth of young migratory brown

- trout *Salmo trutta* correlated with water temperature in Norwegian rivers. *Journal of Animal Ecology* 59: 603–614.
- Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. *Journal of Animal Ecology* 69:1010–1020.
- Jensen, A. J., and B. O. Johnsen. 1984. Size-dependent survival of juvenile Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* from the cold river Beirelva, northern Norway. *Fauna Norvegica, Series A* 5:42–45.
- Jonsson, B., N. Jonsson, E. Brodtkorb, and P. J. Ingebrigtsen. 2001. Life history traits of brown trout vary with the size of small stream. *Functional Ecology* 15:310–317.
- Jordan, W. C., and A. F. Youngson. 1991. Genetic protein variation and natural selection in Atlantic salmon (*Salmo salar*, L.) parr. *Journal of Fish Biology* 39:185–192.
- Knapp, R. A., V. T. Vredenburg, and K. R. Matthews. 1998. Effects of stream channel morphology on golden trout spawning habitat and recruitment. *Ecological Applications* 8:1104–1117.
- L'Abée-Lund, J. H., B. Jonsson, A. J. Jensen, L. M. Sættlem, T. G. Heggberget, B. O. Johnsen, and T. F. Naesje. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Ecology* 58:525–542.
- Lagarrigue, T., P. Baran, J. M. Lascaux, and A. Belaud. 2001. Growth variability analysis of a brown trout (*Salmo trutta* L.) population in a Pyrenean mountain stream. *Bulletin Français de la Pêche et de la Pisciculture* 357/360:573–594.
- Le Cren, E. 1962. The efficiency of reproduction and recruitment in freshwater fish. Pages 283–296 in E. D. Le Cren and M. W. Holdgate, editors. *The exploitation of natural animal populations*. Blackwell Scientific Publications, Oxford, UK.
- Le Cren, E. D. 1965. Some factors regulating the size of populations of freshwater fish. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 13:88–105.
- Lobón-Cerviá, J., and P. A. Rincón. 1998. Field assessment of the influence of temperature on growth rate in a brown trout population. *Transactions of the American Fisheries Society* 127:718–728.
- Machordom, A., J. L. García-Marín, N. Sanz, A. Almodóvar, and C. Pla. 1999. Allozyme diversity in brown trout (*Salmo trutta*) from central Spain: genetic consequences of restocking. *Freshwater Biology* 41:707–717.
- Machordom, A., J. Suárez, A. Almodóvar, and J. M. Bautista. 2000. Mitochondrial haplotype variation and phylogeography of Iberian brown trout populations. *Molecular Ecology* 9:1325–1338.
- Mann, R. H. K., J. H. Blackburn, and W. R. C. Beaumont. 1989. The ecology of brown trout *Salmo trutta* in English chalk streams. *Freshwater Biology* 21: 57–70.
- Metcalfe, N. B., and J. E. Thorpe. 1992. Anorexia and defended energy levels in overwintering juvenile salmon. *Journal of Animal Ecology* 61:175–181.
- Metcalfe, N. B., F. A. Huntingford, and J. E. Thorpe. 1986. Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology* 64:2439–2446.
- Miglav, I., and M. Jobling. 1989. Effects of feeding regime on food consumption, growth rates and tissue nucleic acids in juvenile Arctic charr, *Salvelinus alpinus*, with particular respect to compensatory growth. *Journal of Fish Biology* 34:947–957.
- Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. *Water Resources Research* 34:2685–2692.
- Mortensen, E. 1982. Production of trout, *Salmo trutta*, in a Danish stream. *Environmental Biology of Fishes* 7:349–356.
- Mortensen, E. 1985. Population and energy dynamics of trout *Salmo trutta* in a small Danish stream. *Journal of Animal Ecology* 54:869–882.
- Mortensen, E., P. Geertz-Hansen, and E. Marcus. 1988. The significance of temperature and food as factors affecting the growth of brown trout, *Salmo trutta* L., in four Danish streams. *Polskie Archiwum Hydrobiologii* 35:533–544.
- Newman, R. M. 1993. A conceptual model for examining density dependence in the growth of stream trout. *Ecology of Freshwater Fish* 2:121–131.
- Nicieza, A. G., and N. B. Metcalfe. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology* 78:2385–2400.
- Nicieza, A. G., L. Reiriz, and F. Braña. 1994. Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. *Oecologia* 99:243–251.
- Nicola, G. G. 1999. Crecimiento y reproducción de la trucha común *Salmo trutta* en el centro de España [Growth and reproduction of brown trout *Salmo trutta* in central Spain]. Doctoral dissertation. Complutense University of Madrid, Madrid.
- Nicola, G. G., and A. Almodóvar. 2002. Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. *Freshwater Biology* 47:1353–1365.
- Nordwall, F., I. Näslund, and E. Degerman. 2001. Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2298–2308.
- Ojanguren, A. F., F. G. Reyes-Gavilán, and F. Braña. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *Journal of Thermal Biology* 26:165–170.
- Preall, R. J., and N. H. Ringler. 1989. Comparison of actual and potential growth rates of brown trout (*Salmo trutta*) in natural streams based on bioenergetic models. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1067–1076.
- Reimers, E., A. G. Kjørrefjord, and S. M. Stavøstrand.

1993. Compensatory growth and reduced maturation in second sea winter farmed Atlantic salmon following starvation in February and March. *Journal of Fish Biology* 43:805–810.
- Reznick, D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. *Ecology* 64:862–873.
- Roff, D. A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* 41:989–1000.
- Roff, D. A. 1992. The evolution of life histories. Theory and analysis. Chapman and Hall, New York.
- Sanz, N., J. L. García-Marín, and C. Pla. 2000. Divergence of brown trout (*Salmo trutta*) within glacial refugia. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2201–2210.
- Simpson, A. L., N. B. Metcalfe, F. A. Huntingford, and J. E. Thorpe. 1996. Pronounced seasonal differences in appetite of Atlantic salmon parr, *Salmo salar*: effects of nutritional state and life-history strategy. *Functional Ecology* 10:760–767.
- Spigarelli, S. A., M. M. Thommes, and W. Prepejchal. 1982. Feeding, growth, and fat deposition by brown trout in constant and fluctuating temperatures. *Transactions of the American Fisheries Society* 111:199–209.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
- Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40:893–913.
- Suárez, J., J. M. Bautista, A. Almodóvar, and A. Marchordom. 2001. Evolution of the mitochondrial control region in Palaearctic brown trout (*Salmo trutta*) populations: the biogeographical role of the Iberian Peninsula. *Heredity* 87:198–206.
- Torrissen, K. R., E. Lied, and M. Espe. 1994. Differences in digestion and absorption of dietary protein in Atlantic salmon (*Salmo salar*) with genetically different trypsin isozymes. *Journal of Fish Biology* 45:1087–1104.
- Vøllestad, L. A., E. M. Olsen, and T. Forseth. 2002. Growth-rate variation in brown trout in small neighbouring streams: evidence for density-dependence? *Journal of Fish Biology* 61:1513–1527.
- Weatherley, N. S., E. Campbell-Lendrum, and S. J. Ormerod. 1991. The growth of brown trout (*Salmo trutta*) in mild winters and summer droughts in upland Wales: model validation and preliminary predictions. *Freshwater Biology* 26:121–131.
- Wootton, R. J. 1998. Ecology of teleost fishes. Fish and fisheries series 24, 2nd edition. Chapman and Hall, London.
- Zippin, C. 1956. An evaluation of the removal method of estimating animal population. *Biometrics* 12:163–189.