Journal of Fish Biology (2009) **74**, 2355–2373
doi:10.1111/j.1095-8649.2009.02249.x, available online at www.interscience.wiley.com

Latitudinal and altitudinal growth patterns of brown trout *Salmo trutta* at different spatial scales

I. Parra*, A. Almodóvar*†, G. G. Nicola‡ and B. Elvira*

**Department of Zoology, Faculty of Biology, Complutense University of Madrid, E-28040 Madrid, Spain and ‡Department of Environmental Sciences, University of Castilla-La Mancha, E-45071 Toledo, Spain*

(Received 4 April 2008, Accepted 26 February 2009)

Spatial variation in growth of stream-dwelling brown trout *Salmo trutta* was explored in 13 populations using a long-term study (1993–2004) in the Bay of Biscay drainage, northern Spain. The high variability in fork length (L_F) of *S. trutta* in the study area was similar to the body-size range found in the entire European distribution of the species. Mean L_F at age varied: 0+ years, 57·4−100·7 mm; 1+ years, 111·6−176·0 mm; 2+ years, 155·6−248·4 mm and 3+ years, 194·3−290·9 mm. Average L_F at age was higher in main courses and lower reaches compared with small tributaries and upper reaches. Annual specific growth rates (G_L) were: 0+ to 1+ years, 0·634−0·825 mm mm^{-1} year^{-1}; 1+ to 2+ years, 0·243−0·342 mm mm^{-1} year^{-1}; 2+ to 3+ years, 0·166−0·222 mm mm^{-1} year^{-1}, showing a great homogeneity. Regression models showed that water temperature and altitude were the major determinants of L_F at age variability within the study area. A broader spatial analysis using available data from stream-dwelling *S. trutta* populations throughout Europe indicated a negative relationship between latitude and L_F of individuals and a negative interaction between latitude and altitude. These findings support previous evidence of the pervasive role of water temperature on the L_F of this species. Altitude appeared as the overall factor that includes the local variation of other variables, such as water temperature or food availability. At a larger scale, latitude was the factor that encompassed these environmental gradients and explained the differences in L_F of *S. trutta*. In summary, L_F at age in stream-dwelling *S. trutta* decreases with latitude in Europe, the converse of Bergmann's rule.

Key words: Europe; growth variation; latitude; altitude; temperature.

INTRODUCTION

Growth is a major life-history trait strongly linked to other features dependent on size, such as survival, longevity and reproduction (Wootton, 1998; Hendry & Stearns, 2004). Salmonids show a high interpopulation variability in mean body size, mainly as a response to different environmental conditions (Elliott, 1994; Lobón-Cerviá, 2000; Nislow, 2001; Nicola & Almodóvar, 2004).

Brown trout *Salmo trutta* L. is an important angling species in Spain, currently threatened by pollution, habitat destruction, introduction of exotic species, overfishing

†Author to whom correspondence should be addressed. Tel.: +34 913945135; fax: +34 913944947; email: aalmodovar@bio.ucm.es

and introgression of foreign genes caused by restocking (Elvira, 1995; Almodóvar & Nicola, 1998, 1999, 2004; Almodóvar *et al.*, 2001, 2002, 2006*a*; Elvira & Almodóvar, 2001). Moreover, it is a widespread species in Europe, showing large variations of its growth pattern among populations (L'Abée-Lund *et al.*, 1989; Elliott, 1994; Jonsson *et al.*, 2001; Klemetsen *et al.*, 2003). A wider knowledge of the factors that influence growth and produce this spatial variability could be a useful tool to achieve conservation and management plans, which involves comparative studies on contrasting populations at a large scale.

Water temperature is considered the most pervasive environmental factor affecting growth of *S. trutta* (Elliott, 1994). There have been various attempts to establish the optimum temperature for growth, but authors have found different values at diverse latitudes (Elliott, 1975*a*, *b*; Jensen, 1990; Forseth & Jonsson, 1994; Elliott *et al.*, 1995). Similarly, the thermal range that permits growth seems to vary between populations (Elliott *et al.*, 1995; Ojanguren *et al.*, 2001; Vøllestad *et al.*, 2002). This suggests that adaptations to local thermal conditions can occur, although there is still a lack of evidence of whether this variation has a genetic basis or is based on the phenotypic plasticity of the species (Forseth & Jonsson, 1994; Lobón-Cerviá & Rincón, 1998; Jensen *et al.*, 2000; Vøllestad *et al.*, 2002; Nicola & Almodóvar, 2004).

Along the Bay of Biscay drainage, *S. trutta* inhabit rivers with a wide variation of environmental conditions. This situation may be a favourable situation to identify factors affecting growth. The primary objective of this study was to describe the spatial variation in growth pattern of *S. trutta* in the Bay of Biscay drainage, and its relation to water temperature and altitude. The different thermal regimes of the streams were expected to affect growth, so growth would be slow in populations with lower water temperatures and shorter growing seasons, as compared with populations experiencing more optimal temperatures for growth. To test this prediction, mean fork length (L_F) at the end of the growing season as well as annual specific growth rate (G_L) were compared among 13 rivers, using a data set compiled over 12 years (1993–2004).

Finally, a broader study of L_F at age was used to compare available data for stream-dwelling *S. trutta* from European populations over the range of 37–70° N. This approach permitted an expansion of the spatial scale of the analysis and the understanding of factors influencing body size of *S. trutta* geographically.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in 13 rivers (Fig. 1), River Urumea and its tributary Zumarrezta, River Araxes and its tributary Errekagorri, River Leitzarán and its tributary Erasote, River Orabidea, and River Bidasoa and its tributaries Aranea, Zoko, Ezkurra, Arrata and Tximista. One sampling site was selected for each river, except for River Bidasoa, which is the longest, where four sampling sites were located (Bidasoa 1–4). The selection of sites was made to cover the range of environmental conditions within the area. Sampling sites corresponded to first to fifth-order streams and were located from 43°03′ to 43°16′ N and from 1°29′ to 2° W, at an altitude ranging from 40 to 490 m. Altitudes were measured directly from topographic maps. Mean altitude and other characteristics of rivers are shown in Table I. Water quality was in accordance with the limits proposed by the European Directive (EU, 2006). Ionic content was similar among the rivers, although the lowest values were found in River Urumea and its

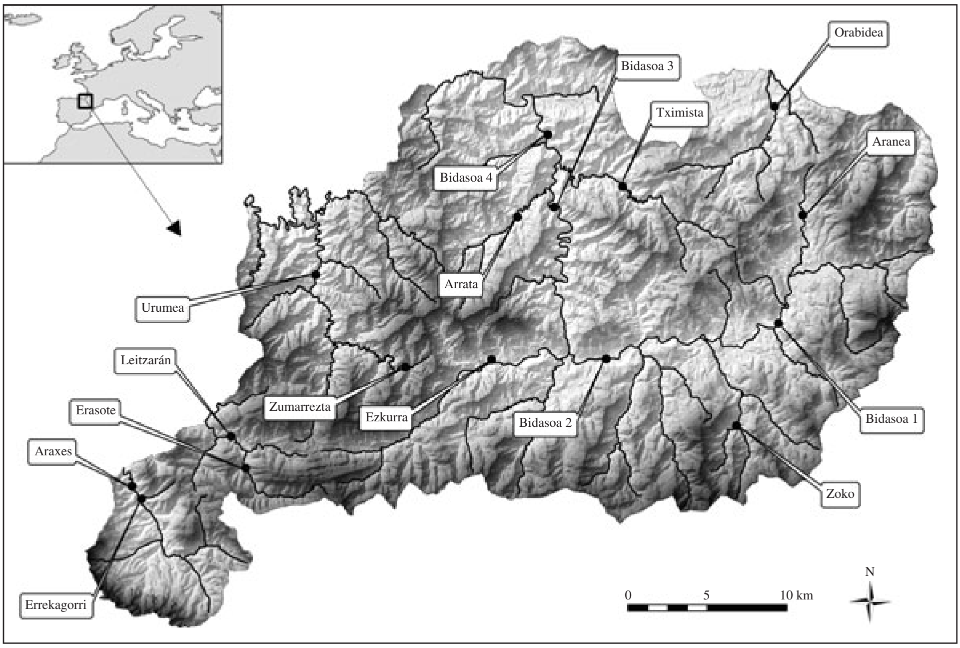

FIG. 1. Map of the study area in northern Spain, showing the location of the sampling sites.

tributary, River Zumarrezta, whereas the highest figures were found in River Araxes. Water mineral content has been considered as one of the factors affecting growth of *S. trutta* (Kelly-Quinn & Bracken, 1988; Mann *et al*., 1989; Nicola & Almodóvar, 2004). The rivers in the present study, however, flow in a small area and the differences in water mineral ionic content do not cover a range wide enough to induce differences in L_F. This meant that the present study was focused on other abiotic variables.

Salmo trutta is the prevailing fish species throughout the area and its populations only comprise freshwater resident individuals. Less common species are European eel *Anguilla anguilla* (L.), Pyrenean gudgeon *Gobio lozanoi* Doadrio & Madeira, Ebro nase *Parachondrostoma miegii* (Steindachner), Pyrenean minnow *Phoxinus bigerri* Kottelat, Pyrenean stoneloach *Barbatula quignardi* (Bacescu-Mester) and Atlantic salmon *Salmo salar* L., while Ebro barbel *Luciobarbus graellsii* (Steindachner), rainbow trout *Oncorhynchus mykis*s (Walbaum) and Adour sculpin *Cottus aturi* Freyhof, Kottelat & Nolte are rare. The streams are open to recreational angling except for some reaches, which are preserved sections. The scattered presence of power stations and dams on the lower reaches are the main anthropogenic pressures in the study area. In addition, industrial areas and alterations of the riparian habitat are found in Rivers Leitzarán and Bidasoa.

Water temperature was measured with data loggers (Minilog Vemco, Ltd; www.vemco.com) permanently placed in each river between July 2004 and October 2005. Mean daily temperature was the average of the maximum and the minimum readings in each 24 h period. Historical data series of temperatures were used. For other years, linear regression was used to estimate water temperature from air temperature readings at local meteorological stations (Elliott, 1984; Crisp, 1992). From the data, mean, minimum and maximum daily temperatures (T_M, T_{min} and T_{max}, respectively, in $^\circ$ C) were calculated. The values were typical of temperate rivers. Rivers Urumea, Araxes, Leitzarán and their tributaries (Rivers Zumarrezta, Errekagorri and Erasote, respectively) had lower temperatures, with mean annual values between 10·4 and 11·2° C and minimum and maximum annual temperatures between 4·6–5·3° and 15·6–16·3° C, respectively. Recorded values were higher for the remaining rivers, River Bidasoa and its tributaries Aranea, Zoko, Ezkurra, Arrata and Tximista, and

TABLE I. Location and some physico-chemical characteristics from the 16 sampling sites in 13 rivers from the Bay of Biscay drainage, Spain. Mean summer discharge was calculated for each sampling site during 1993–2004. Water temperature was measured with data loggers between July 2004 and October 2005 and these data together with historical data series were used to calculate annual water temperature (Annual T) and mean temperature during the growing season (T_{GS}, estimated for March to September) for the period 1993–2004. Conductivity data were obtained from databases held by the Northern Hydrographical Confederation (www.chn.es) and the Government of Navarre (www.navarra.es)

River	Latitude N	Longitude W	Altitude (m)	Width (m)	Depth (m)	Summer discharge (m^3 s^{-1})	Annual T (°C)	T_{GS} (°C)	Conductivity ($\mu S\,cm^{-1}$)
Urumea	43°10′57″	1°51′34″	145	8·7	0·292	1·883	11·20	12·61	103·5
Zumarrezta	43°07′45″	1°47′29″	470	4·8	0·227	0·094	—	—	71·2
Araxes	43°03′49″	2°00′14″	185	8·2	0·437	0·532	11·29	12·38	424·9
Errekagorri	43°03′23″	1°59′48″	210	2·5	0·123	0·053	—	—	304·0
Erasote	43°04′24″	1°54′57″	490	6·1	0·210	0·438	10·41	12·14	262·9
Leitzarán	43°05′29″	1°55′37″	440	7·6	0·302	1·238	10·39	12·08	262·9
Bidasoa 1	43°09′02″	1°30′05″	205	12·4	0·293	1·421	13·59	15·61	175·0
Bidasoa 2	43°07′56″	1°38′07″	130	16·7	0·353	2·769	13·61	15·59	237·5
Bidasoa 3	43°13′07″	1°40′26″	60	21·6	—	—	—	—	234·3
Bidasoa 4	43°15′36″	1°40′41″	40	22·2	0·251	3·539	—	—	234·3
Aranea	43°12′43″	1°28′52″	300	5·4	0·258	0·425	13·59	15·42	197·3
Zoko	43°05′35″	1°32′07″	340	4·5	0·170	0·170	13·36	15·78	192·8
Ezkurra	43°07′58″	1°43′28″	175	8·7	0·202	0·703	13·61	15·59	210·3
Arrata	43°12′48″	1°42′09″	115	6·1	0·218	0·329	14·03	16·06	242·0
Tximista	43°13′47″	1°37′14″	115	6·1	0·248	0·291	13·67	15·54	126·6
Orabidea	43°16′25″	1°30′06″	85	7·3	0·317	—	14·25	16·01	298·0

River Orabidea. They had mean annual temperatures oscillating between 13·4 and 14·3° C, whereas minimum and maximum values ranged 1·7–6·2° and 18·9–25·4° C, respectively.

SALMO TRUTTA POPULATIONS

Electrofishing with a 2200 W DC generator took place every year at the end of the growing period from 1993 to 2004. *Salmo trutta* individuals were anaesthetized with MS-222 (tricaine methanesulphonate), measured (L_F, to the nearest mm), and scales were taken for age determination. Then, the individuals were returned alive into the river. G_L was calculated as $G_L = (\ln L_{F2} - \ln L_{F1})(t_2 - t_1)^{-1}$, where L_{F1} and L_{F2} are mean L_F at age at times t_1 and t_2, that correspond to the month of September of 2 consecutive years, when the samplings took place.

DATA ANALYSIS

The total of individuals analysed was 36353. L_F at age and G_L were compared between populations using multifactor ANOVA, with subsequent Tukey's 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 α for all statistical tests was set at 0·05.

Pair-wise correlations (Pearson r) were used to explore relationships of L_F and G_L with environmental factors. Forward stepwise multiple regression analyses were performed with L_F and G_L as dependent variables, while those environmental variables significantly correlated with growth were employed as independent variables. Finally, a factorial multiple-regression analysis was employed to address the relationship between L_F and both altitude and latitude of *S. trutta* European populations. These linear regressions were selected applying an information–theoretic approach based on Akaike's information criteria (AIC; Burnham & Anderson, 2002; Motulsky & Christopoulos, 2003). In all cases, and in both small-scale and large-scale approaches, the lowest AIC values corresponded to the linear models compared to the values obtained with non-linear models ($y = ax^b$, $y = ae^{xb}$ and $y = a + bx + cx^2$). The obtained ΔAIC values indicated a 99·9% probability that linear models were the correct choice in overall analyses.

Statistical analyses were performed using the STATISTICA 6·1 computer package (StatSoft, Inc; www.statsoft.com).

RESULTS

SALMO TRUTTA POPULATIONS

Salmo trutta populations were long-lived, with a maximum longevity between 6 and 9 years and a clear dominance of age groups 0+ to 3+ years. These age classes were selected for the analyses because they were well represented in all the rivers.

There were marked differences between rivers in mean L_F of 0+ to 3+ year age classes at the end of the growing period, which were established in the first year of life (Table II). Populations from main streams and lower reaches had a higher mean L_F, whereas populations from small tributaries and upper reaches had a lower mean L_F. Thus, L_F defined a gradient where the highest values were found on the main course of River Bidasoa, then decreasing gradually in Rivers Leitzarán, Arrata, Orabidea, Tximista, Araxes, Ezkurra, Urumea, Aranea, Errekagorri, Zoko, Zumarrezta and Erasote.

Despite the wide differences found in mean L_F, the minimum size limit for angling is set at 200 or 230 mm, depending on the type of stream. Thus, *S. trutta* attains the recruitment age between 2+ and 3+ years. Taking into account that age at maturity

TABLE II. Fork length (L_F) at age (mean ± S.D.) of *Salmo trutta* from 16 sampling sites in 13 rivers from the Bay of Biscay drainage, Spain, during 1993–2004. The results of the one-way ANOVA tests are given and the significant differences are denoted as *** ($P < 0{\cdot}001$)

	Mean L_F 0+years (mm)	n	Mean L_F 1+years (mm)	n	Mean L_F 2+years (mm)	n	Mean L_F 3+years (mm)	n
Erasote	57·4 ± 9·1	2369	117·2 ± 10·6	1208	162·6 ± 13·3	1181	198·3 ± 9·5	303
Zumarrezta	57·9 ± 7·4	1298	111·6 ± 15·0	1330	155·6 ± 11·5	466	196·2 ± 12·6	107
Zoko	58·3 ± 9·0	1255	113·1 ± 17·4	1231	160·3 ± 11·2	335	201·5 ± 8·0	19
Errekagorri	60·4 ± 9·8	1468	114·1 ± 13·8	563	160·2 ± 11·1	185	194·3 ± 10·6	59
Aranea	66·9 ± 10·6	1634	131·5 ± 14·2	1668	179·2 ± 13·0	628	223·0 ± 11·7	105
Urumea	69·4 ± 10·6	1070	143·5 ± 12·9	574	159·5 ± 14·1	318	232·9 ± 13·2	81
Ezkurra	70·0 ± 10·3	1708	145·4 ± 14·9	757	190·8 ± 13·6	370	229·4 ± 11·3	92
Araxes	71·2 ± 10·7	1482	148·6 ± 14·7	568	191·6 ± 15·5	385	223·6 ± 21·8	227
Tximista	71·9 ± 9·3	333	153·4 ± 20·6	481	211·4 ± 12·7	77	259·4 ± 11·9	8
Orabidea	72·6 ± 11·1	1403	157·2 ± 19·3	813	216·4 ± 13·4	209	255·5 ± 11·5	51
Arrata	73·8 ± 10·5	778	156·4 ± 19·9	425	212·3 ± 11·6	62	254·7 ± 10·5	7
Leitzarán	76·8 ± 11·6	291	158·8 ± 20·1	658	223·4 ± 13·5	237	272·9 ± 12·8	129
Bidasoa 3	84·1 ± 13·2	47	176·0 ± 20·2	74	248·4 ± 26·0	13	290·9 ± 23·6	25
Bidasoa 1	84·5 ± 12·5	837	162·1 ± 19·3	1341	220·3 ± 11·9	239	265·6 ± 14·7	48
Bidasoa 4	92·6 ± 19·4	56	169·8 ± 19·7	476	239·7 ± 13·8	113	280·6 ± 12·4	42
Bidasoa 2	100·7 ± 13·9	627	166·4 ± 21·3	649	226·9 ± 13·4	155	272·6 ± 13·5	90
Mean	67·8 ± 14·3	16653	139·0 ± 26·5	12815	183·2 ± 27·7	4973	229·0 ± 33·0	1393
ANOVA	$F_{15,16637} = 1040{\cdot}11$	***	$F_{15,12799} = 1298{\cdot}33$	***	$F_{15,4957} = 1146{\cdot}61$	***	$F_{15,1377} = 414{\cdot}68$	***

(age at which 50% of a cohort is mature) of females varies in the studied rivers between 1+ and 2+ years, it is expected that some of the harvested females do not reproduce even once in their life.

Salmo trutta growth varied during the life span, reaching a peak in the first year of life, decreasing sharply in the second year and gradually diminishing thereafter. Populations showed little variation in G_L, in spite of the broad differences described in L_F. During the first annual interval (0+ to 1+ years), G_L was similar among the study sites, shaping a gradient where the only significant differences were observed between the extreme values (ANOVA, d.f. = 15, 161, $P < 0{\cdot}001$). Thus, the lowest rate found in River Errekagorri (0·634 mm mm^{-1} year^{-1}) contrasted with that of River Leitzarán (0·825 mm mm^{-1} year^{-1}). The trend of G_L during the second annual period (1+ to 2+ years) was similar to that described in the former interval, with significant differences among rivers (ANOVA, d.f. = 15, 161, $P < 0{\cdot}01$). Comparisons of means, however, only revealed significant differences between the highest values in River Zoko (0·333 mm mm^{-1} year^{-1}) and River Bidasoa at site 4 (0·342 mm mm^{-1} year^{-1}) and the remaining rivers. Conversely, the next annual period (2+ to 3+ years) had no significant differences in G_L among rivers (ANOVA, d.f. = 15, 143, $P > 0{\cdot}05$). The lowest value was found in River Bidasoa 4 (0·166 mm mm^{-1} year^{-1}), whereas the highest rate was found in River Zumarrezta (0·221 mm mm^{-1} year^{-1}).

INFLUENCE OF ENVIRONMENTAL FACTORS ON L_F OF *SALMO TRUTTA*

The correlation analysis revealed significant relationships of L_F of *S. trutta* with water temperature and altitude. There was a positive relationship between L_F at age and maximum water temperature, whereas altitude was negatively related to L_F at age (Table III).

The L_F at age variability within the study area was determined by a combination of altitude and water temperature, whose respective influences seemed to depend on the life stage. Thus, altitude was the variable with the greatest effect on L_F at the beginning of life (0+ and 1+ year age classes, Fig. 2), accounting for 28–44% of the variance explained by the model (Table IV). Maximum water temperature, however, was the variable with the greatest effect on L_F variability of older individuals (2+ and 3+ year age classes), explaining between 33 and 37% of the variance (Table IV).

A wider spatial analysis was carried out based on the present data and a review of other European studies (Table V), showing a large L_F at age variability (L_F 0+ years, range: 25·0–107·5 mm; L_F 1+ years, range: 57·0–192·3 mm). L_F was negatively related to latitude in 0+ and 1+ year age classes (Fig. 3), whereas the interaction of latitude and altitude (latitude × altitude) had effects on L_F in their second year of life (1+ years, Table VI). The interaction term showed that the effect of latitude was magnified by altitude, *i.e.* the negative effect of latitude on L_F of *S. trutta* was more pronounced for high altitudes, whereas for low altitudes the slope of L_F related to latitude was lower.

TABLE III. Correlation coefficients (Pearson r) and their probabilities for comparisons of fork length (L_F) at age of *Salmo trutta* with altitude and variables measuring water temperature (mean, T_M; maximum, T_{max}; minimum, T_{min})

	L_F 0 + years	L_F 1 + years	L_F 2 + years	L_F 3 + years
Altitude	−0·57*	−0·69**	−0·63*	−0·59*
T_M	0·40	0·40	0·43	0·42
T_{max}	0·54*	0·58*	0·65*	0·62*
T_{min}	−0·39	−0·44	−0·53	−0·49

Significant correlations are shown as; $^{*}P < 0.05$ and $^{**}P < 0.01$

DISCUSSION

The present study shows that the variability in L_F of *S. trutta* in the study area is similar to that found in the entire European distribution of the species. For example, 0+ year individuals range from 25·0 mm in Iceland (Steingrímsson & Gíslason, 2002) to 107·5 mm in Spain (Braña *et al*., 1992), whereas in the study area, 0+ year individuals vary between 57·4 and 100·7 mm. Further, growth pattern was different even within the same river, as other authors have previously described (Otto, 1976; Nicola, 1999; Baglinière & Maisse, 2002; Hesthagen *et al*., 2004). An increase in L_F was found from tributaries to main courses (*e.g*. from River Erasote to River Leitzarán) and seawards within a main course (*e.g*. River Bidasoa).

The observed negative relationship between altitude and L_F at age may indicate a response of *S. trutta* to changes in environmental factors related to an altitudinal gradient, such as stream width, stream depth, water temperature, nutrients concentration or food abundance, which clearly influence growth of *S. trutta* and the availability of

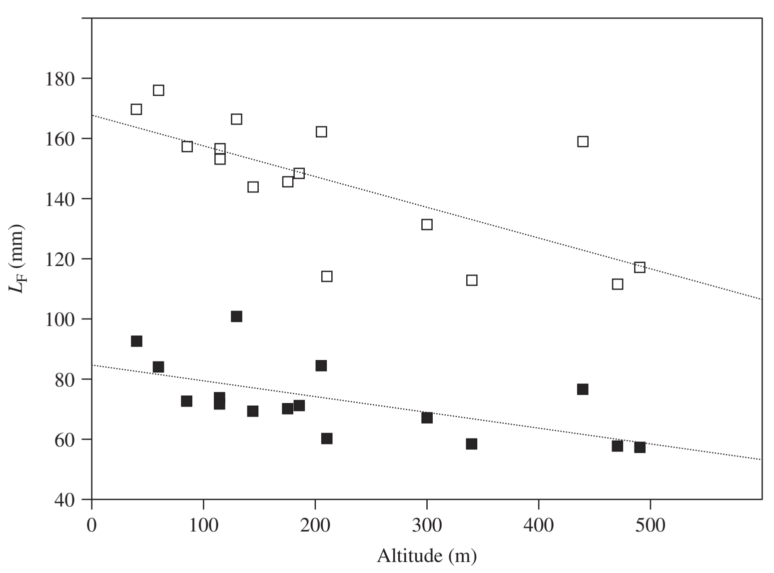

FIG. 2. Relationship between fork length (L_F) and altitude for populations of *Salmo trutta* in the studied rivers in northern Spain. Data are split into 0+ (■) and 1+ (□) year age classes (see Table IV).

TABLE IV. Results of regression analyses of fork length (L_F) at age in relation to maximum water temperature (T_{max}) and altitude of 16 sampling sites on 13 rivers discharging to the Bay of Biscay, Spain

Model	Dependent variables	Independent variables	Coefficient	(95% CI)	P
Adjusted $r^2 = 0·28$,	L_F 0+years	Altitude	−0·005	(−0·009 to −0·0009)	<0·001
d.f. = 1, 12; $P < 0·05$		Intercept	8·50	(7·42 to 9·58)	<0·05
Adjusted $r^2 = 0·44$,	L_F 1+years	Altitude	−0·009	(−0·015 to −0·003)	<0·001
d.f. = 1, 12; $P < 0·01$		Intercept	16·87	(15·52 to 18·21)	<0·01
Adjusted $r^2 = 0·37$,	L_F 2+years	T_{max}	0·559	(0·142 to 0·976)	<0·05
d.f. = 1, 12; $P < 0·05$		Intercept	9·48	(1·15 to 17·80)	< 0·05
Adjusted $r^2 = 0·33$,	L_F 3+years	T_{max}	0·583	(0·119 to 1·046)	<0·01
d.f. = 1, 12; $P < 0·05$		Intercept	13·21	(3·94 to 22·47)	<0·05

TABLE V. Summary of selected mean fork length (L_F) at age from the literature for European stream-dwelling populations of *Salmo trutta* at different altitudinal and latitudinal locations. The number of streams is indicated, and when data are given for different areas in a stream the number of sections is indicated in parentheses

Latitude (°N)	Altitude (m)	L_F 0+years (mm)	L_F 1+years (mm)	Number of streams	Country	Reference
70·6	77	—	61	1	Norway	Power, 1973
69·8	57	43	—	1	Norway	Hesthagen, 1989
65·6	200	25	57	1	Iceland	Steingrímsson & Gíslason, 2002
63·1–66·2	45–380	41·4–60·5	86·6–111·1	3	Sweden	Näslund *et al*., 1998
61·9–62·0	450–720	35–43	76–78	1 (2)	Norway	Hesthagen *et al*., 2004
61·2–61·3	400–479	61·8	90·0–118·0	3	Norway	Jonsson & Sandlund, 1979
58·7	106	63·7	127·5	1	Norway	Bergheim & Hesthagen, 1990
56·3	400	49	97	1	Scotland	Egglishaw & Shackley, 1977
54·7–55·9	85–150	82·8–91·1	162·5–167·9	23	Lithuania	Skrupskelis *et al*., 2006
54·6–55·7	0–36	67–88	—	1 (2)	Sweden	Otto, 1976
54·7	460–550	52–69	86–110	17	England	Crisp *et al*., 1974
54·7	564	52–56	87–107	2	England	Crisp *et al*., 1975
54·6	430	61	102	1	England	Crisp & Cubby, 1978
53·5	125	72	142	1	Poland	Mortensen & Penczak, 1988
52·4–53·9	18–100	49–73	102–146	4 (13)	Ireland	Lobón-Cerviá & Fitzmaurice, 1988
53·3	46–167	55·5–76·0	114·4–130·5	1 (5)	Ireland	Kelly-Quinn & Bracken, 1988
52·1–52·4	130–360	75·2–82·6	128·6–148·2	4 (11)	Wales	Milner *et al*., 1978
51·9	200–250	63·5–65·0	117·5–122·8	3	Wales	Bembo *et al*., 1993
50·8	59	48	102	1	England	Elliott, 1988
48·33	125	96·3–96·5	183·5–192·3	2	France	Baglinière, 1981
43·9	40–150	70–90	117·5–175·0	3 (4)	France	Baglinière & Maisse, 1990
43·4	167–267	69–91	107–168	4	Spain	Lobón-Cerviá *et al*., 1997
43·1	460–1380	60–95	115–183	1 (5)	Spain	García & Braña, 1988
43·0	553–858	82·3–107·5	116·0–175·0	1 (6)	Spain	Braña *et al*., 1992

TABLE V. continued

Latitude (°N)	Altitude (m)	L_F 0+years (mm)	L_F 1+years (mm)	Number of streams	Country	Reference
42·2–42·9	695–1291	—	116·5–135·3	8 (19)	Spain	García de Jalón & Serrano, 1985
42·3	1000	72·0–82·1	133·0–157·3	2	Spain	García de Jalón *et al.*, 1986
42·1	1050–1400	—	84–101	1 (3)	Bulgaria	Jankov, 1986
41·7	40	66	120	1	Portugal	Valente, 1988
41·7	980	80	185	4 (9)	Spain	Lobón-Cerviá *et al.*, 1986
41·4–41·8	1010–1360	69·3–94·0	132·5–152·0	3	Spain	Almodóvar & Nicola, 2004
40·6–41·9	885–1340	57·4–99·3	107·2–176·6	7	Spain	Nicola & Almodóvar, 2002
40·8	770–810	80·3–85·0	164·5–175·6	1 (2)	Spain	Lobón-Cerviá & Penczak, 1984
39·7	946	79	121	1	Greece	Papageorgiou *et al.*, 1983–1984
37·8	1300	92·2	118·2	1	Turkey	Alp *et al.*, 2005

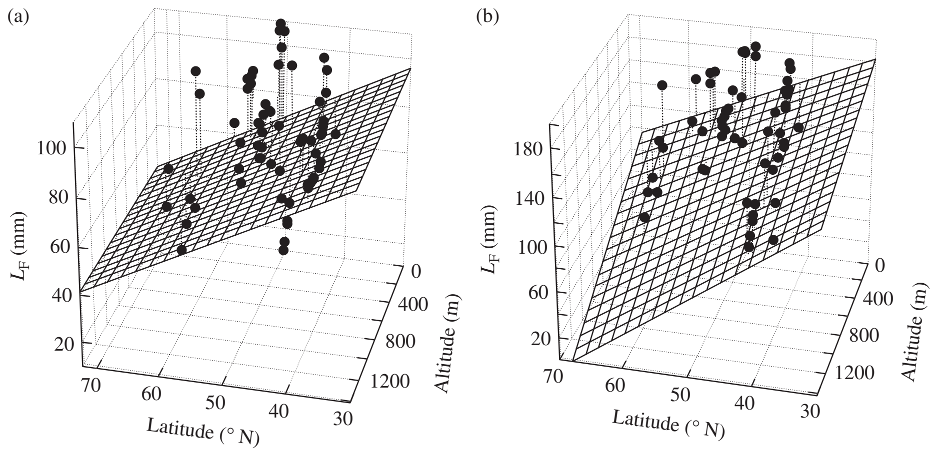

FIG. 3. Relationship between fork length (L_F; y) of (a) 0+ year and (b) 1+ year age classes with latitude (x) and altitude (z) for the studied European populations of *Salmo trutta*. The curves were fitted by: (a) $y = 13{\cdot}53 - 0{\cdot}130x$ and (b) $y = 25{\cdot}25 - 0{\cdot}230x - 0{\cdot}00006xz$.

suitable habitat for larger individuals (Reyes-Gavilán *et al*., 1995; Almodóvar *et al*., 2006*b*; Ayllón *et al*., 2009). Other life-history features related to growth have been found to differ with altitude. Vøllestad *et al*. (1993) found that altitude was a good descriptor of the variation in both length at maturity and estimated asymptotic length.

The local thermal regime was also observed to be positively related to L_F variability. Water temperature is known to have a strong effect on size of *S. trutta*. Growth is controlled by enzymatic activities, so *S. trutta* only grow at a given range of temperatures (3·6–19·5° C; Elliott *et al*., 1995). In addition, water temperature can exert an indirect influence on growth, affecting other features such as metabolic rate (Forseth & Jonsson, 1994; Wootton, 1998), embryonic development (Ojanguren & Braña, 2003), feeding activity (Elliott, 1989; Ojanguren *et al*., 2001) and food availability, as temperature increases reproduction, diversity and abundance of invertebrates (Egglishaw & Shackley, 1977; Baglinière & Maisse, 2002).

G_L decreased with age, as has been observed in other populations of this species (Jonsson, 1977, 1985; Mortensen, 1977, 1982; Papageorgiou *et al*., 1983–1984; Elliott, 1994; Forseth & Jonsson, 1994; Wootton, 1998; Baglinière & Maisse, 2002; Nicola & Almodóvar, 2002, 2004). Growth of fishes is indeterminate and asymptotic, and several factors influence this decrease in growth intensity, *e.g*. the relationship between stomach surface area and body size (Wootton, 1998) and the relative size of gill area (Forseth & Jonsson, 1994). Maturity, however, is considered the main cause of the growth reduction, since the energetic investment in reproduction depends on and influences the allocation of resources into somatic growth (Elliott, 1994; Jonsson *et al*., 2001; Lagarrigue *et al*., 2001; Baglinière & Maisse, 2002; Nicola & Almodóvar, 2002, 2004). On the other hand, G_L was homogeneous among the rivers studied, contrasting with the differences found in L_F at age. For instance, there were no differences in G_L between the main course of River Bidasoa and its tributaries, whereas wide differences were detected in L_F at age. There is a negative relationship between the date of fry emergence from the stream bed and water temperature (Elliott

TABLE VI. Results of regression analyses of fork length (L_F) at age in relation to altitude and latitude from literature data on the European distribution of *Salmo trutta*

Model	Dependent variables	Independent variables	Coefficient	(95% CI)	*P*
Adjusted $r^2 = 0{\cdot}33$,	L_F 0+years	Latitude	−0·130	(−0·166 to −0·094)	<0·001
d.f. = 1, 99; $P < 0{\cdot}001$		Intercept	13·53	(11·80–15·26)	<0·001
Adjusted $r^2 = 0{\cdot}34$,	L_F 1+years	Latitude	−0·230	(−0·289 to −0·171)	<0·001
d.f. = 2, 119; $P < 0{\cdot}001$		Latitude × altitude	−0·00006	(−0·00009 to −0·00004)	<0·001
		Intercept	25·25	(22·19–28·31)	<0·001

& Hurley, 1998; Ojanguren & Braña, 2003). The thermal regime varied among the studied rivers and this probably led to interpopulation differences in emergence times. The date of emergence finally determines the length of the first growing period and therefore the L_F attained by 0+ year individuals (Ojanguren & Braña, 2003). The L_F variation among populations was therefore established in the first year of life and continued during following years due to similar G_L. The findings highlight the effect of growth of 0+ year individuals on their size at older ages.

Finally, G_L in the populations from the Bay of Biscay drainage showed higher values for the first growing period than observed in previous studies on *S. trutta* from the centre of the Iberian Peninsula (Almodóvar & Nicola, 1998; Nicola & Almodóvar, 2004). These differences in the intensity of growth could be due to the higher altitude in the centre of the Peninsula and the colder thermal regime, but at similar latitudes. A similar comparison with European populations of *S. trutta* could not be undertaken due to the scarcity of available data of G_L on stream-dwelling populations.

Altitude was the major factor affecting L_F at age of *S. trutta* at a local scale. When considering a broader scale with data from all over Europe, however, the differences among populations resulted from variations in latitude. Nevertheless, latitude determined a large part of the geographic variation in L_F of young individuals, whereas altitude only magnified the effect of latitude (*i.e.* the decrease in L_F with latitude was steeper for high altitudes). Some of the environmental factors previously mentioned to fluctuate with altitude are also highly correlated with latitude (Jensen *et al.*, 2000). When the spatial scale of the study became wider, latitude rather than altitude came out as the overall factor that encompassed those environmental gradients and would explain spatial differences in L_F of *S. trutta*.

One of the most well-known patterns of latitudinal variation in animal body size is Bergmann's rule (Belk & Houston, 2002). It holds that within endothermic animals, body size increases with increasing latitude (or decreasing temperature). Application of this rule in ectotherms is controversial. Belk & Houston (2002) and Millien *et al.* (2006) showed that, considering size at age, most North American freshwater fishes analysed followed the converse of Bergmann's rule.

Latitudinal trends in body size of *S. trutta* have been further studied in anadromous stocks of this species. *Salmo trutta* tend to be anadromous in northern regions and resident to the south, but migratory and resident individuals can occur even within a single population. Anadromous *S. trutta* grow faster and attain greater body size than resident fish (Jonsson, 1985; Klemetsen *et al.*, 2003). Moreover, an increase in longevity with latitude due to a later maturity has been described for anadromous populations. This higher longevity could imply a larger maximum size with latitude (Jonsson & L'Abée-Lund, 1993).

The results of the present study showed that stream-dwelling *S. trutta* populations follow the converse of Bergmann's rule, as reported in other European freshwater fishes including common dace *Leuciscus leuciscus* (L.) (Lobón-Cerviá *et al.*, 1996) and perch *Perca fluviatilis* L. (Heibo *et al.*, 2005). Temperature is perhaps the most important environmental factor for fishes growth. Since water temperature decreases with latitude, it would be expected that L_F at age is strongly negatively correlated with latitude.

The present study underscores several key points of interest to fishery managers, which could help in the sustainable exploitation of the populations. The minimum size limit established on the studied rivers does not ensure the reproduction of a proportion of the females at least once before being harvested. Besides, fast-growing populations have fewer potential chances for future spawning as a consequence of a higher adult mortality by angling (Almodóvar & Nicola, 2004). Thus, it is recommended to establish higher minimum size levels according to the situation of each population instead of using more generalized limits.

This study was supported by the Government of Navarre. I. Parra was funded by a postgraduate contract from the Government of Madrid and the European Social Fund (ESF). We would like to thank the comments of the assistant editor and two anonymous reviewers that considerably improved the manuscript.

References

Almodóvar, A. & Nicola, G. G. (1998). Assessment of a brown trout (*Salmo trutta* L.) population in the river Gallo (Central Spain): angling effects and management implications. *Italian Journal of Zoology* **65,** 539–544.

Almodóvar, A. & Nicola, G. G. (1999). Effects of a small hydropower station upon brown trout (*Salmo trutta* L.) and macrobenthos in the River Hoz Seca (Tagus River, Spain) one year after regulation. *Regulated Rivers, Research and Management* **15,** 477–484.

Almodóvar, A. & Nicola, G. G. (2004). Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology* **11,** 173–182. doi: 10.1111/j.1365-2400.2004.00402.x

Almodóvar, A., Suárez, J., Nicola, G. G. & Nuevo, M. (2001). Genetic introgression between wild and stocked brown trout in the Douro River basin, Spain. *Journal of Fish Biology* **59,** 68–74. doi: 10.1111/j.1095–8649.2001.tb01379.x

Almodóvar, A., Nicola, G. G. & Suárez, J. (2002). Effects of fishery management on populations of brown trout, *Salmo trutta*, in central Spain. In *Conservation of Freshwater Fishes: Options for the Future* (Collares-Pereira, M. J., Cowx, I. G. & Coelho, M. M., eds), pp. 337–345. Oxford: Blackwell Science Publications.

Almodóvar, A., Nicola, G. G., Elvira, B. & García-Marín, L. (2006*a*). Introgression variability among Iberian brown trout evolutionary significant units: the influence of local management and environmental features. *Freshwater Biology* **51,** 1175–1187. doi: 10.1111/j.1365–2427.2006.01556.x

Almodóvar, A., Nicola, G. G. & Elvira, B. (2006*b*). Spatial variation in brown trout production: the role of environmental factors. *Transactions of the American Fisheries Society* **135,** 1348–1360. doi: 10.1577/T05-189.1

Alp, A., Kara, C. & Buyukçapar, H. M. (2005). Age, growth and diet composition of the resident brown trout *Salmo trutta macrostigma* Dumeril 1858, in Firniz stream of the river Ceyhan, Turkey. *Turkish Journal of Veterinary and Animal Sciences* **29,** 285–295.

Ayllón, D., Almodóvar, A., Nicola, G. G. & Elvira, B. (2009). Interactive effects of cover and hydraulics on brown trout habitat selection patterns. *River Research and Applications.* doi: 10.1002/rra.1215 (in press).

Baglinière, J. L. (1981). Étude de la structure d'une population de truite commune (*Salmo trutta* L.) dans une zone à barbeau. *Bulletin Français de la Pêche et de la Pisciculture* **283,** 125–139.

Baglinière, J. L. & Maisse, G. (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.

Baglinière, J. L. & Maisse, G. (2002). La biologie de la truite commune (*Salmo trutta* L.) dans la rivière Scorff, Bretagne: une synthèse des études de 1972 à 1997. *INRA Productions Animales* **15,** 319–331.

Belk, M. C. & Houston, D. D. (2002). Bergmann's rule in ectotherms: a test using freshwater fishes. *The American Naturalist* **160,** 803–808. doi: 10.1086/343880

Bembo, D. G., Berverton, R. J. H., Weightman, A. J. & Cresswell, R. C. (1993). Distribution, growth and movement of River Usk brown trout (*Salmo trutta*). *Journal of Fish Biology* **43** (Suppl. A), 45–52.

Bergheim, A. & Hesthagen, T. (1990). Production of juvenile Atlantic salmon, *Salmo salar* L. and brown trout, *Salmo trutta* L. within different sections of a small enriched Norwegian river. *Journal of Fish Biology* **36,** 545–562. doi: 10.1111/j.1095–8649.1990.tb03556.x

Braña, F., Nicieza, A. G. & Toledo, M. M. (1992). Effects of angling on population structure of brown trout, *Salmo trutta* L., in mountain streams of Northern Spain. *Hydrobiologia* **237,** 61–66.

Burnham, K. P. & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information – Theoretic Approach.* New York, NY: Springer-Verlag.

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. & Cubby, P. R. (1978). The populations of fish in tributaries of the River Eden on the Moor House National Nature Reserve, northern England. *Hydrobiologia* **57,** 85–93.

Crisp, D. T., Mann, R. H. K. & McCormack, J. C. (1974). The populations of fish at Cow Green, Upper Teesdale, before impoundment. *Journal of Applied Ecology* **11,** 969–996.

Crisp, D. T., Mann, R. H. K. & McCormack, J. (1975). The populations of fish in the River Tees system on the Moor House National Nature Reserve, Westmorland. *Journal of Fish Biology* **7,** 573–593. doi: 10.1111/j.1095–8649.1975.tb04632.x

Egglishaw, H. J. & Shackley, P. E. (1977). Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966–1675. *Journal of Fish Biology* **11,** 647–672. doi: 10.1111/j.1095–8649.1977.tb05722.x

Elliott, J. M. (1975*a*). The growth rate of brown trout, *Salmo trutta* L. fed on maximum rations. *Journal of Animal Ecology* **44,** 805–821.

Elliott, J. M. (1975*b*). The growth rate of brown trout, *Salmo trutta* L. fed on reduced rations. *Journal of Animal Ecology* **44,** 823–842.

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. (1988). Growth, size, biomass and production in contrasting populations of trout *Salmo trutta* in two lake district streams. *Journal of Animal Ecology* **57,** 49–60.

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: Oxford University Press.

Elliott, J. M. & Hurley, M. A. (1998). An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. *Journal of Fish Biology* **53,** 414–433.

Elliott, J. M., Hurley, M. A. & Fryer, R. J. (1995). A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology* **9,** 290–298.

Elvira, B. (1995). Native and exotic freshwater fishes in Spanish river basins. *Freshwater Biology* **33,** 103–108. doi: 10.1111/j.1365–2427.1995.tb00390.x

Elvira, B. & Almodóvar, A. (2001). Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. *Journal of Fish Biology* **59,** 323–331. doi: 10.1006/jfbi.2001.1753

Forseth, T. & Jonsson, B. (1994). The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology* **8,** 171–177.

García, A. & Braña, F. (1988). Reproductive biology of brown trout (*Salmo trutta* L.) in the Aller River (Asturias, Northern Spain). *Polskie Archiwum Hydrobiologii* **35,** 361–373.

García de Jalón, D. & Serrano, J. (1985). Las poblaciones de truchas en los ríos de la cuenca del Duero. *Boletín de la Estación Central de Ecología* **28,** 47–56.

García de Jalón, D., Tolosana-Esteban, E. & Rodríguez-Alcalde, F. (1986). Estimación de algunos parámetros poblacionales de la trucha común (*Salmo trutta fario*) en los ríos pirenaicos. *Boletín de la Estación Central de Ecología* **29,** 51–58.

Heibo, E., Magnhagen, C. & Vøllestad, L. A. (2005). Latitudinal variation in life-history traits of Eurasian perch. *Ecology* **86,** 3377–3386. doi: 10.1890/04-1620

Hendry, A. P. & Stearns, S. C. (Eds). (2004). *Evolution Illuminated: Salmon and Their Relatives.* Oxford: Oxford University Press.

Hesthagen, T. (1989). Life history variables of resident Brown trout *Salmo trutta* L. in a coastal stream in northern Norway. *Fauna Norvegica Serie A* **10,** 25–32.

Hesthagen, T., Hegge, O., Skurdal, J. & Dervo, B. K. (2004). Age and growth of Siberian sculpin (*Cottus poecilopus*) and young brown trout (*Salmo trutta*) in a subalpine Norwegian river. *Hydrobiologia* **521,** 107–115.

Jankov, J. I. (1986). The production of the brown trout (*Salmo trutta fario L.*) in the Rilska river, Bulgaria. *Polskie Archiwum Hydrobiologii* **33,** 455–462.

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., Forseth, T. & Johnsen, B. O. (2000). Latitudinal variation in growth of young brown trout *Salmo trutta*. *Journal of Animal Ecology* **69,** 1010–1020. doi: 10.1046/j.1365–2656.2000.00457.x

Jonsson, B. (1977). Demographic strategy in a brown trout population in Western Norway. *Zoologica Scripta* **6,** 255–263.

Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society* **114,** 182–194.

Jonsson, B. & L'Abée-Lund, J. H. (1993). Latitudinal clines in life-history variables of anadromous brown trout in Europe. *Journal of Fish Biology* **43,** 1–16. doi: 10.1111/j.1095–8649.1993.tb01175.x

Jonsson, B. & Sandlund, O. T. (1979). Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta* m. *fario*) in Søre Osa river system, Norway. *Environmental Biology of Fishes* **4,** 43–54.

Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P. J. (2001). Life-history traits of brown trout vary with the size of small streams. *Functional Ecology* **15,** 310–317. doi: 10.1046/j.1365–2435.2001.00528.x

Kelly-Quinn, M. & Bracken, J. J. (1988). Brown trout, *Salmo trutta* L., production in an Irish coastal stream. *Aquaculture and Fisheries Management* **19,** 69–95.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12,** 1–59. doi: 10.1034/j.1600-0633.2003.00010.x

L'Abée-Lund, J. H., Jonsson, B., Jensen, A. J., Saettem, L. M., Heggberget, T. G., Johnsen, B.O. & Naesje, T.F. (1989). Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. *Journal of Animal Ecology* **58,** 525–542.

Lagarrigue, T., Baran, P., Lascaux, J. M. & Belaud, A. (2001). Analyse de la variabilité de la croissance d'une pupulation de truite commune (*Salmo trutta* L.) dans un torrent pyrénéen. *Bulletin Français de la Pêche et de la Pisciculture* **357/360,** 573–594.

Lobón-Cerviá, J. (2000). Determinants of parr size variations within a population of brown trout *Salmo trutta* L. *Ecology of Freshwater Fish* **9,** 92–102. doi: 10.1034/j.1600-0633.2000.90111.x

Lobón-Cerviá, J. & Fitzmaurice, P. (1988). Stock assessment, production rates and food consumption in four contrasting Irish populations of brown trout (*Salmo trutta* L.). *Polskie Archiwum Hydrobiologii* **35,** 497–513.

Lobón-Cerviá, J. & Penczak, T. (1984). Fish production in the Jarama River, Central Spain. *Holarctic Ecology* **7,** 128–137.

Lobón-Cerviá, J. & Rincón, P. A. (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.

Lobón-Cerviá, J., Montañés, C. & De Sostoa, A. (1986). Reproductive ecology and growth of a population of brown trout (*Salmo trutta* L.) in an aquifer-fed stream of Old Castile (Spain). *Hydrobiologia* **135,** 81–94.

Lobón-Cerviá, J., Dgebuadze, Y., Utrilla, C. G., Rincón, P. & Granado-Lorencio, C. (1996). The reproductive tactics of dace in central Siberia: evidence for temperature regulation of the spatio-temporal variability of its life history. *Journal of Fish Biology* **48,** 1074–1087.

Lobón-Cerviá, J., Utrilla, C., Rincón, P. A. & Amezcúa, F. (1997). Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: trade-offs between egg size and number. *Freshwater Biology* **38,** 277–288.

Mann, R. H. K., Blackburn, J. H. & Beaumont, W. R. C. (1989). The ecology of brown trout *Salmo trutta* in English chalk streams. *Freshwater Biology* **21,** 57–70. doi: 10.1111/j.1365–2427.1989.tb01348.x

Millien, V., Lyons, S. K., Olson, L., Smith, F. A., Wilson, A. B. & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters* **9,** 853–869. doi: 10.1111/j.1461-0248.2006.00928.x

Milner, N. J., Gee, A. S. & Hemsworth, R. J. (1978). The production of brown trout, *Salmo trutta* in tributaries of the Upper Wye, Wales. *Journal of Fish Biology* **13,** 599–612.

Mortensen, E. (1977). Population, survival, growth and production of trout *Salmo trutta* in a small Danish stream. *Oikos* **28,** 9–15.

Mortensen, E. (1982). Production of trout, *Salmo trutta*, in a Danish stream. *Environmental Biology of Fishes* **7,** 349–356.

Mortensen, E. & Penczak, T. (1988). Populations, growth, biomass and production of fish in a small stream in north-west Poland. *Ekologia Polska* **36,** 445–458.

Motulsky, H. J. & Christopoulos, A. (2003). *Fitting Models to Biological Data Using Linear and Nonlinear Regression. A Practical Guide to Curve Fitting.* San Diego, CA: GraphPad Software Inc.

Näslund, I., Degerman, E. & Nordwall, F. (1998). Brown trout (*Salmo trutta*) habitat use and life history in Swedish streams: possible effects of biotic interactions. *Canadian Journal of Fisheries and Aquatic Sciences.* **55,** 1034–1042.

Nicola, G. G. (1999). Crecimiento y reproducción de la Trucha Común *Salmo trutta* en el centro de España. Doctoral Thesis, Department of Zoology, Complutense University of Madrid, Madrid, Spain.

Nicola, G. G. & Almodóvar, A. (2002). Reproductive traits of stream-dwelling brown trout *Salmo trutta* in contrasting neighbouring rivers of central Spain. *Freshwater Biology* **47,** 1353–1365. doi: 10.1046/j.1365–2427.2002.00866.x

Nicola, G. G. & Almodóvar, A. (2004). Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. *Transactions of the American Fisheries Society* **133,** 66–78.

Nislow, K. H. (2001). International symposium on the implications of salmonid growth variation. *Reviews in Fish Biology and Fisheries* **10,** 521–527.

Ojanguren, A. F. & Braña, F. (2003). Thermal dependence of embryonic growth and development in brown trout. *Journal of Fish Biology* **62,** 580–590. doi: 10.1046/j.0022–1112.2003.00049.x

Ojanguren, A. F., Reyes-Gavilán, F. G. & Braña, F. (2001). Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *Journal of Thermal Biology* **26,** 165–170.

Otto, C. (1976). Size, growth, population density and food of brown trout *Salmo trutta* L. in two sections of a south Swedish stream. *Journal of Fish Biology* **8,** 477–488. doi: 10.1111/j.1095–8649.1976.tb03991.x

Papageorgiou, N. C., Neophytou, C. N. & Vlachos, C. G. (1983–1984). The age, growth, and reproduction of brown trout (*Salmo trutta fario*) in the Aspropotamos stream. *Acta Hydrobiologica* **25/26,** 451–467.

Power, G. (1973). Estimates of age, growth, standing crop and production of Salmonids in some North Norwegian rivers and streams. *Report of the Institute of Freshwater Research Drottningholm* **53,** 78–112.

Reyes-Gavilán, F. G., Garrido, R., Nicieza, A. G., Toledo, M. M. & Braña, F. (1995). Variability in growth, density and age structure of brown trout populations under contrasting environmental and managerial conditions. In *The Ecological Basis for River Management* (Harper, D. M. & Ferguson, A. J. D., eds), pp. 389–403. Chichester: John Wiley & Sons.

Skrupskelis, K., Kesminas, V. & Stakenas, S. (2006). The growth of brown trout (*Salmo trutta fario* L.) in different climatic regions of Lithuania. *Acta Zoologica Lituanica* **16,** 286–292.

Steingrímsson, S. O. & Gíslason, G. M. (2002). Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxá, North-East Iceland. *Environmental Biology of Fishes* **63,** 417–426.

Valente, A. C. N. (1988). The trout population of a Portuguese river. *Publicaçoes do Instituto de Zoologia 'Dr. Augusto Nobre' Facultade de Ciências do Porto* **204**.

Vøllestad, L. A., L'Abée-Lund, J. H. & Sægrov, H. (1993). Dimensionless numbers and life history variation in brown trout. *Evolutionary Ecology* **7,** 207–218.

Vøllestad, L. A., Olsen, E. M. & Forseth, T. (2002). Growth rate variation in brown trout in small neighbouring streams: evidence for density-dependence? *Journal of Fish Biology* **61,** 1513–1527. doi: 10.1111/j.1095–8649.2002.tb02494.x

Wootton, R. (1998). *Ecology of Teleost Fishes.* London: Chapman & Hall.

Electronic Reference

EU (2006). Directive 2006/44/EC of the European Parliament and of the Council : on the quality of fresh waters needing protection or improvement in order to support fish life. *Official Journal of the European Union* **L 264**, 20–31. http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2006:264:0020:0031:EN:pdf

