Hydrobiologia 135, 81–94 (1986).

Reproductive ecology and growth of a population of brown trout (*Salmo trutta* L.) in an aquifer-fed stream of Old Castile (Spain)

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Keywords: *Salmo trutta*, density, demography, aquifer-fed stream, Spain

Abstract

In the River Lobos-Ucero and its tributary the River Avión-Milanos (Duero basin, Old Castile, Central Spain), two limestone streams fed by aquifers, the population of brown trout, as compared with the populations of other European streams, shows a high growth rate, high condition coefficients, short life-span and early age at first maturity. Gonad cycle was also studied. Size distributions of unshed eggs exhibit a dynamic activity with a bi-modal distribution from June onwards, spawning occurred in the last days of November. Fecundity (F) can be predicted from trout length (L, mm) according to the equation: $F = -646.47 + 5.6167 \cdot L$. Numbers and standing crop of trout range from 18 to 3903 ind. ha^{-1} and 3.6 to 452.9 Kg ha^{-1}, reaching higher values in the sites close to the aquifers. Egg production had values of 22.4 and 18.0 eggs m^{-2} in the Rivers Ucero and Avión-Milanos respectively. Some factors suggested as regulators of these demographical characteristics are discussed in the light of recent literature.

Introduction

The population ecology of brown trout (*Salmo trutta*) in European streams is well documented, but there is a dearth of information on the southern, Mediterranean populations. In order to understand the factors controlling the life history of both these populations, long term studies and comparisons between populations subjected to different environmental influence are needed.

Our paper investigates growth, reproductive cycle and density of a population of brown trout inhabiting a highly productive limestone stream fed by aquifers, a fairly unusual environment in Old Castile (Central Spain). Further information on the fish species distribution, diversity and production of these populations is given in Lobón-Cerviá, Montañés & Sostoa (1985, 1986).

The environment

The River Ucero is in the province of Soria (Old Castile, Spain) and is a tributary on the right of the River Duero, which flows into the Atlantic Ocean (Fig. 1). It is situated between 41°20′–42°00′ North and 3°00′ West. Its source is 1250 m above sea level and it flows into the River Duero at about 100 m asl. The River Ucero and its tributary, the Avión-Milanos, are limestone streams supplied by aquifers with continuous water-flows which spring up at a more or less constant temperature throughout the year. The maximum difference between the mean winter temperature (December-January) and the mean summer temperature (July-August) is no greater than 12 °C (Fig. 2). This temperature regime is similar to that of the chalk streams of southern England (Mann RHK, 1983). Unlike other Iberian rivers which are supplied by surface waters coming from mountains, here the water temperature is higher at the sources (springs) than in areas downstream. Water flow, measured on the River Ucero

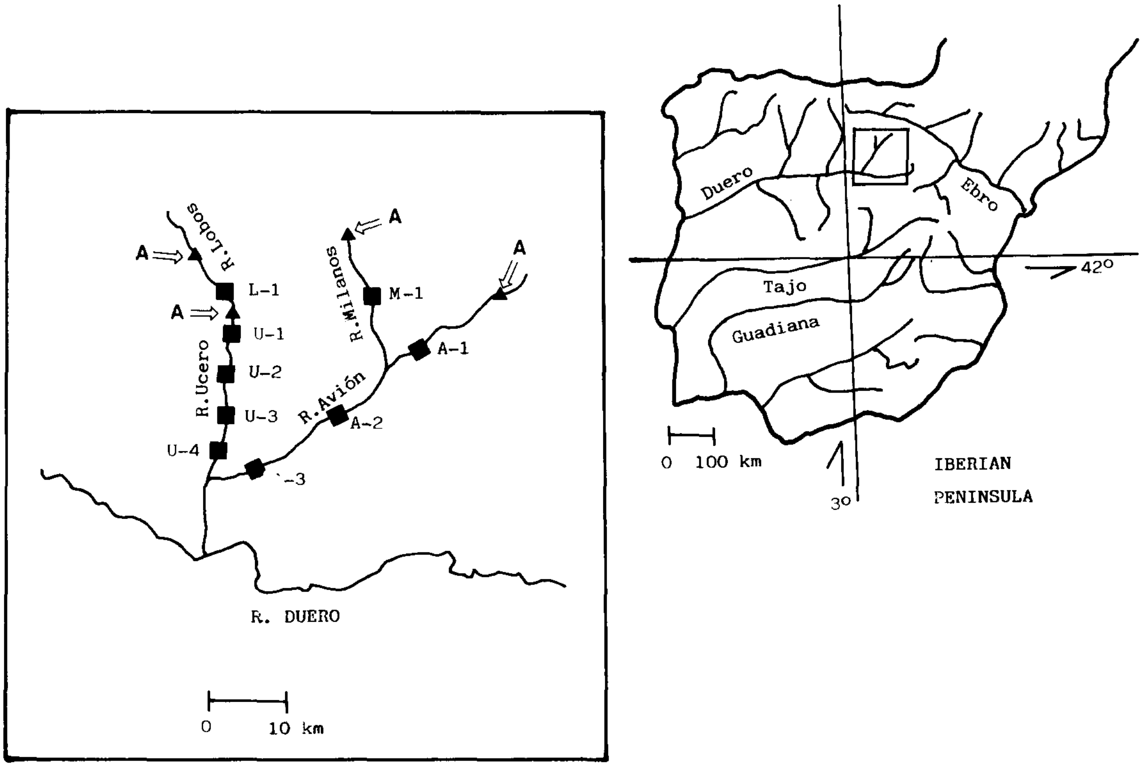

Fig. 1. Map of the Iberian Peninsula showing the geographical situation of the studied rivers and the sampling localities. A = Aquifers feeding the streams, L-1, U-1,... etc. localities sampled quantitatively.

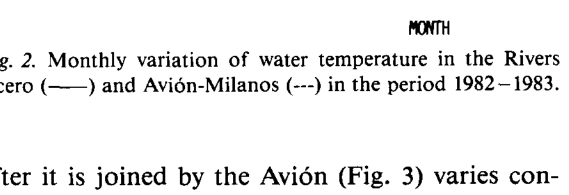

Fig. 2. Monthly variation of water temperature in the Rivers Ucero (——) and Avión-Milanos (---) in the period 1982–1983.

after it is joined by the Avión (Fig. 3) varies considerably throughout the year; it is at its maximum between January and February (minimum water temperatures) and at its minimum in August (maximum water temperature).

The rivers studied are supplied mainly by four springs (F, Fig. 1). The first one is the middle reach of the River Lobos (Fig. 1). The second, which is

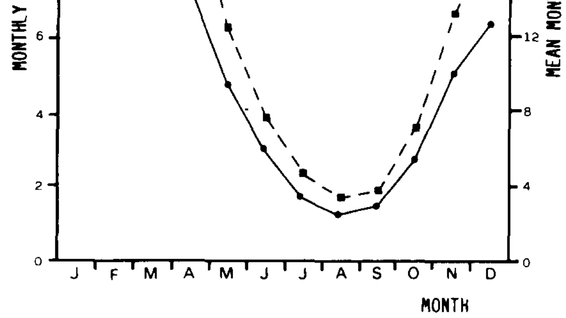

Fig. 3. Average monthly variations of water discharge (——) and water supplies (---) measured in the period 1970–1982 in the lower most part of the River Ucero after its confluence with the River Avión.

the most important, is situated 4 Km further downstream, and after this the river changes its name to the River Ucero. The third is the source of the River Avión and the fourth the source of the River Milanos.

The upper reaches of the Ucero, Avión and Milanos have stony bottoms with a vegetation cover; *Apium* and *Ranunculus* are the dominant species. The bank vegetation principally consists of *Alnus glutinosa* (L.) and *Salix* sp. In the middle and lower reaches of these rivers and in the River Lobos (above the Ucero) sandy bottoms predominate. Principal aquatic vegetation here is *Enea* and *Juncus*, and the water is transparent for ten or eleven months as against eleven to twelve for the uppest reaches of the Ucero, Avión and Milanos.

Apart from the brown trout, these rivers maintain seven species of fish. These are: *Chondrostoma polylepis* (Stein.,), *Barbus bocagei* (Stein.,), *Leuciscus cephalus* (L.), *Cobitis calderoni* (Bac.), *Rutilus arcasii* (Stein.,), *Gobio gobio* (L.) and *Phoxinus phoxinus* (L.). The last two of these species are not indigenous; the former may have been introduced into Spain in the late 19th or early 20th century (Lobón-Cerviá & Torres, 1983) and its presence in this river has been documented since 1951 (IFIE, 1952). The latter species has been cultivated in a fish farm, from which many have escaped during the last fifteen years.

The fish populations of these rivers have been trapped in the Ucero basin in the last years because of the considerable pollution amanating from the town of El Burgo de Osma just below the meeting point between the Ucero and the Avión (Fig. 1). Therefore, emigration and immigration between these populations and those of the River Duero is fairly unlikely.

Material and methods

A total of 450 specimens of all age classes were captured at monthly intervals (20–40 days) from April 1983 until August 1984. Electrofishing gear was used to sample at 200–400 V and 1.5–2.5 Amp D.C. During the months of December and January, we were unable to catch any fish due to the tremendous speed and force of the water (Fig. 3).

After being caught, the specimens were fixed in formol (7%) and taken to the laboratory. There they were measured (standard length, L, mm, used in cm when necessary), weighed (W, g) and sexed (except for those ≤ 50 mm). The gonads of the females were transferred into Gilson fluid (Bagenal & Braum, 1978) and the digestive systems were preserved whole in formol (5%). Scales were taken to age the fish.

Throughout this study, the following criteria have been used: age – class 0+ under 365 days age, 1+ between 365 days and 730 days old, and so on.

Monthly growth pattern was assessed by inspection of length frequency distributions. The annual growth pattern was analyzed by back-calculation and the equation:

$$L_t = L_\infty (1 - e^{-K(T-T_0)})$$

of Von Bertalanffy (1957) was used to smooth the data. Values of L_∞,K and T_0 were estimated from a Ford-Walford plot (Ford, 1933; Walford, 1947).

All the regression lines fitted in this study have been done so using the least squares method (LS), although we have sometimes followed Ricker (1973) by obtaining the regression using the geometric mean method (GM). A co-variance analysis (ANCOVA) was used to compare the slopes of these lines when necessary. In the case of the relation between the length of the fish (L) and the radius of the scales (S) which was established on the basis of the equation:

$$\text{Log } L = \text{Log } a + b \cdot \text{Log } S$$

the ANCOVA did not show any significant differences between the slopes (b) of the five regressions obtained for the fish captured in those areas of the rivers specified in Fig. 1. The same analysis did not show significant differences when comparing both sub-populations (Ucero as against Avión-Milanos). Therefore all the specimens wherever they came from were brought together into a single equation which took the form:

$$\text{Log } L = 0.8324 - 0.9406\ (\pm 0.048)\ \text{Log } S$$
$$R = 0.95,\ P \leq 0.001$$

this equation was then used to back-calculate lengths for age (Kipling, 1962).

The same method was used for the length (L, cm) to weight (W, g) regressions which were analyzed under the linear form: Log W=Log a+b·Log L. We compared these L–W relationships for four different alternatives, sexes (2 regressions), months (9), areas in each river (5) and between different rivers (2). The ANCOVA analysis for the slopes (b) did not either show significant differences in any case. Therefore all the specimens (350) with weights between 0.1 and 950 g were placed together to obtain one single equation with the formula:

$$\text{(LS)}\quad \text{Log W} = -1.6955 + 2.9355\ (\pm 0.066)\ \text{Log L}$$
$$\text{(GM)}\quad \text{Log W} = -1.7232 + 2.9586\ \text{Log L}$$
$$r = 0.9922,\ P \leq 0.001$$

Mean weights for age and related parameters were obtained using the equation (LS).

During the period before reproduction, between 28 September and 17 November 1983, the density of the brown trout was estimated in nine localities which were chosen so as to include the greatest possible variation in each particular area of the river. These nine localities were chosen in the five areas of the river shown in Fig. 1. The population ($\hat{N}$) was estimated according to Zippin's method (Seber, 1973), readjusted for three catches by Junge & Libosvarsky (1965): The initial number is obtained thus:

$$\hat{N} = \frac{6X^2 - 3XY - Y^2 + Y\sqrt{Y + 6XY - 3X^2}}{18(X-Y)}$$

catchability (p) is:

$$p = \frac{3X - Y - \sqrt{Y^2 + 6XY - 3X^2}}{2X}$$

where $X = 2C_1 + C_2$ and $Y = C_1 + C_2 + C_3$ (C_i each 'catch per unit effort'). The standard error (SE) is obtained from:

$$SE = \frac{\hat{N}\ (1-q^3)\ q^3}{(1-q^3) - 9\ p^2\ q^3} \quad (p+q=1)$$

An alternative solution for $X = 2C_1 + C_2$ and $Y = C_1 - C_3$, has been suggested by Lelek (1974). In any case, three catches method seems to be ideal for trout density estimates of the order of magnitude of those in our rivers (Bohlin, 1982) and it has the advantage that three is the minimum number for which the goodness of fit can be estimated. We have, therefore, obtained the goodness of fit with the T_1 statistic (Seber, 1973) which is distributed like a Chi-squared with one degree of liberty:

$$T_1 = \sum_{i=1}^{3} (C_i - E_i)^2 / E_i$$

where C_i is each catch per unit effort and $E = \hat{N}\ p$ ♀$^{i-1}$.

The numbers and standing crops in each locality were calculated independently for each age class and for the total of the population. The uncaptured biomass or sampling error (corresponding to $\hat{N} - N$) was estimated assuming a direct proportion so that $\hat{B} = \hat{N}/N \cdot B$.

The monthly development cycle of the intraovarian ovules was analyzed by measuring the total number of ovules in the gonads of one female per month, the length of which was chosen to reflect the mean length of seasonal growth in that particular month. Fecundity, or the total number of mature ovules in the gonads before reproduction (Bagenal & Braum, 1978) was determined for a sample of 17 females between 170 and 270 mm in length. This sample includes the whole range of lengths and ages for the reproductive females in the population. The diameter of ovules was measured and the mean value for the diameter distributions obtained for the ovules fixed in Gilson fluid was taken as the mean diameter for each individual female.

Results

Growth and sex-ratio

The sex-ratio for the 450 specimens caught and the relationship between this and their length for the whole of the population (Ucero and Avión-Milanos Rivers) are shown in Fig. 4. All those fish over 350 mm were male. A Chi-square test showed that in the age classes 0+ to 3+ there was no significant difference between the expected ratio (parity 1:1) and the observed ratio. In age class 4+ the males predominate in both rivers (2:1 and 5:2 respectively) and the only specimen in class 5+, in

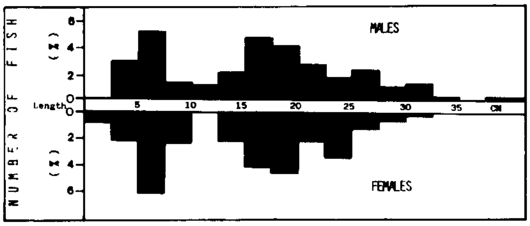

Fig. 4. Sex-ratio and its relation with length of brown trout of the Rivers Ucero and Avión-Milanos.

the Ucero, is a male. Therefore, in absolute number terms, there are more males than females in the population.

The seasonal growth pattern was studied with reference to the Ucero sub-population, using length distributions observed for each month in each age class. We estimated mean lengths and confidence limits to 95% (±2 SE). Fig. 5 shows this pattern observed for age classes 0+ and 1+. As it can be seen, there are two growth periods (April-November and March-April) and one of quiescence (November-March). The March-April growth takes place before the fish is 365 days old.

Monthly analysis of the scales in both sub-populations shows that the annual growth rings (annuli) are formed during a fairly long period of time between February and April. Unfortunately we have been unable to study scales from December and January, the months in which these rings must begin to form; scales of specimens captured in November show no trace of any annuli on the edges of the scales. Therefore it seems that, in general, the annuli are formed during the period of quiescence. The smallest specimens we managed to catch measured 42 mm in length and in these the scales were perfectly developed. These fish were captured in the first fortnight in May in both the years in which the study was undertaken (1983 and 1984). Taking the period of formation of the annuli as a basis, we could assume the population birthday at 15th April.

The mean back-calculated lengths for age and the means of the length frequency distributions observed for each age class were compared with each other with a t-student test in order to establish whether there were differences in growth between sexes, between different localities on the same river and between rivers. This test only indicated differences between rivers (Ucero and Avión-Milanos).

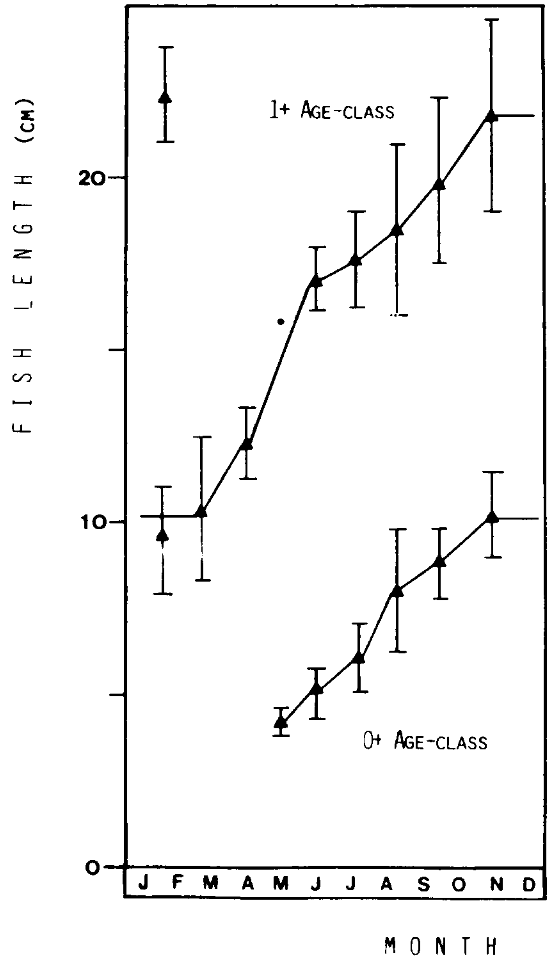

Fig. 5. Seasonal growth pattern of the 0+ and 1+ age-classes of brown trout of the Rivers Ucero and Avión-Milanos. ⫯ mean length and 95% C.L. obtained from monthly length frequency distributions observed in the population.

Therefore we can infer that both sexes grow equally, a common feature in this species, and that the same growth rate can be expected in any area of the same river. Lengths at each age are shown in Table 1. The sub-population of the Ucero has a greater growth rate than that of the Avión-Milanos. In both cases, the annual growth rate (L_{t-1}/L_t) is greater in the first year and decreases as age increases, and therefore it is appropriate to fit a von Bertalanffy equation. The constants for this, obtained for each sub-population are:

Ucero: $L_\infty = 65.9403$ and $K = 0.1831$
Avión-Milanos $L_\infty = 64.0374$ and $K = 0.1753$

Table 1. Back-calculated lengths (cm) for age of Ucero and Avión-Milanos brown trout, obtained from scale measurements.

Age at capture	N_t	Length (cm) at age								
		I		II		III		IV		V
R. Ucero										
I+	101	11.0								
II+	84	10.7		20.1						
III+	25	11.0		20.0		27.8				
IV+	3	11.1		20.1		27.7		34.2		
V+	1	10.8		20.1		27.9		35.4		39.5
Length ($\bar{L}$, cm)		10.9		20.1		27.8		34.8		39.5
Length increment			9.2		7.7		7.0		4.7	
R. Avión-Milanos										
I+	57	9.3								
II+	43	10.7		18.7						
III+	19	11.7		18.7		25.3				
IV+	7	11.6		17.7		25.5		31.8		
Length ($\bar{L}$, cm)		10.3		18.6		25.3		31.8		
Length increment			8.3		6.7		6.5			

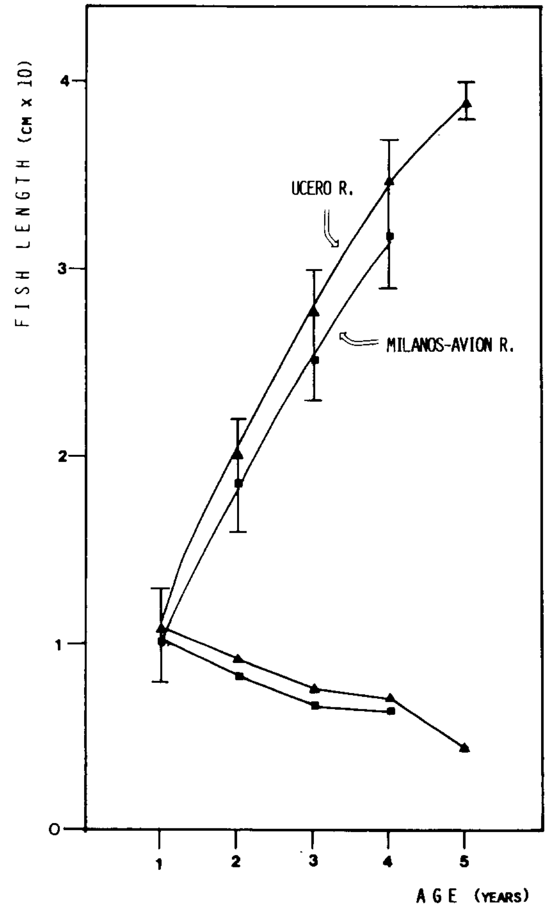

Fig. 6. Mean back-calculated lengths for age (95% C.L.) and mean annual length increment of the Ucero (▲) and Avión Milanos (■) brown trouts, obtained from scale measurements. Smoothed data from von Bertalanffy equations.

The graphic representation of these equations, together with the mean back-calculated length for age and the annual increase in length, are shown in Fig. 6.

The annual instantaneous growth rate (G): $G = \text{Ln}\ (W_{t-1}/W_t)$ was calculated for the time of birthday of both sub-populations. The values obtained in both cases, together with the corresponding mean weights ($\bar{W}$, g) are shown in Table 2.

The condition coefficients (K) or Fulton's index ($K = W/L^3 \cdot 100$) where W and L are defined in the

Table 2. Mean weights ($\bar{W}$) and instantaneous growth rates (G) of brown trout (sexes combined) of the Rivers Ucero and Avión-Milanos.

Age	R. Avión		R. Ucero	
	$\bar{W}$	G	$\bar{W}$	G
0	0.04*		0.04*	
		6.16		6.37
1	18.9		23.4	
		1.73		1.75
2	107.4		134.9	
		0.90		0.95
3	265.1		349.5	
		0.67		0.66
4	518.6		675.8	
				0.33
5			944.2	

* Mean weight of one egg estimated from a sample for all age-classes combined.

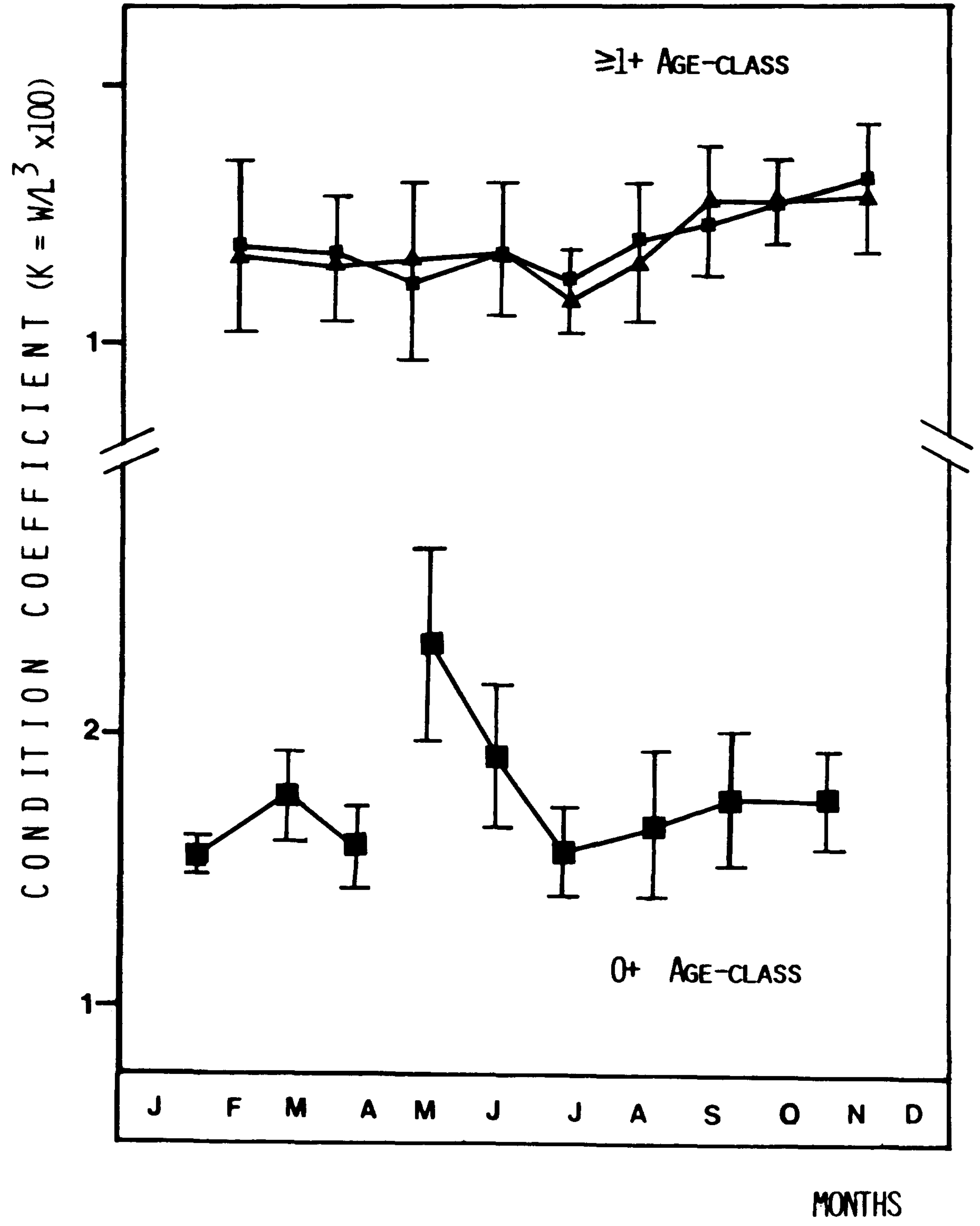

Fig. 7. Monthly variations in the condition of 0+ and ≥1+ trouts (sexes combined) of the Rivers Ucero and Avión-Milanos.

same way as in the length to weight relation, reaches fairly high values for our population, equal to or greater than, 1.5 in all age classes and in all four seasons (Fig. 7). The highest values are obtained in the youngest stages (1 month of life). After this K disminishes, stabilizing when the specimens reach about four months (August). For age classes $\geq 1+$, frequency distributions for monthly values of K do not show significant differences between sexes (Student's-t test). These mean values are constant during the period of quiescence ($\bar{K}=1.5$) increasing during the summer as length, somatic and gonad weight increase, reaching a maximum ($\bar{K}=1.8$) in November, just before egg-laying. Since after spawning $\bar{K}$ returns to its original value of 1.5, it can be assumed that this factor is more influenced by gonad development than by somatic growth. This suggestion is backed up by the fact that the condition coefficients do not increase as individual lengths or weights increase.

Density, population structure and mortality

The results of succesive fishings together with numbers and standing crops estimated in each locality are shown in Table 3. In six out of the nine cases, captures were absolutes ($C_3=0$). In seven cases the estimate of $\hat{N}$ was significant to at least $P \leq 0.05$ and in the two other cases the densities were only 1 and 3 specimens. The trout is the dominant species ($\geq 75\%$ of the standing crop) in five localities. The efficiency of fishing (C_1/C_t) is 72% (range 50–100%) for density and 75% (range 50–100%) for standing crop and it appears to depend more on the density of the brown trout themselves than on the number of accompanying species or the structural characteristics of the sites sampled. Numbers and standing crops in ind. ha^{-1} and kg ha^{-1} are shown for the nine localities in Table 4.

Independently of the accompanying species, the

Table 3. Numbers of brown trout (N, ind) and standing crop (B, kg) estimated in each studied locality. C_1 is the cath per unit effort and S the total number of fish species captured in each locality (for symbols see text).

Locality	S	C_1	C_2	C_3	N	B	$\hat{N}$	$\hat{N}_M$	$\hat{N}_m$	$\hat{B}$	$\hat{B}_M$	$\hat{N}_t$ (%)**	$\hat{B}_t$ (%)**
Lobos-1	8	1/ 0.2	0/0.0	0/0.0	1	0.2	1	1	1	0.2	0.2	0.2	2.8
Ucero-1	3	78/11.4	30/2.9	17/1.2	125	15.4	137*	150	125	15.9	16.3	79.2	99.1
Ucero-2	2	29/ 4.6	7/1.0	3/0.9	39	6.7	40*	43	37	6.9	7.4	83.3	85.5
Ucero-3	1	27/ 1.6	5/0.6	0/0.0	32	2.2	32*	33	30	2.2	2.3	100.0	100.0
Ucero-4	7	0/ 0.0	3/0.7	0/0.0	3	0.7	3	3	3	0.7	0.7	1.6	2.5
Milanos-1	1	18/ 1.8	6/0.5	0/0.0	24	2.2	24*	26	23	2.2	2.4	100.0	100.0
Avión-1	2	37/ 8.3	19/0.7	3/0.4	59	9.5	63*	69	56	10.1	11.1	80.0	89.6
Avión-2	6	6/ 0.7	3/0.3	0/0.0	9	1.0	9*	11	8	1.0	1.2	2.0	3.0
Avión-3	6	3/ 0.5	30.5	0/0.0	6	1.0	6*	9	4	1.0	1.5	2.2	3.6

* Significant in $P \leq 0.05$.

** Percentage of brown trout density ($\hat{N}_t$ %) and standing crop ($\hat{B}_t$ %) in all the fish taxocene.

Table 4. Density, maximum density ($\hat{N}$ and $\hat{N}_M$, ind. ha^{-1}), standing crop and maximum standing crop ($\hat{B}$ and $\hat{B}_M$, kg ha^{-1}) of brown trout, estimated in the 9 studied localities of the Rivers Ucero and Avión-Milanos.

Parameter	Localities								
	L-1	U-1	U-2	U-3	U-4	M-1	A-1	A-2	A-3
$\hat{N}$	18	3903	988	1052	44	1116	2000	150	130
$\hat{N}_M$	18	4273	1062	1118	44	1209	2190	183	195
$\hat{B}$	3.6	452.9	170.1	74.2	10.3	104.6	321.4	17.2	21.5
$\hat{B}_M$	3.6	465.8	182.8	76.5	10.3	113.3	352.0	21.0	32.3

density of trout is higher in the sites close to the aquifers, reaching values of 3903 ind. ha^{-1} (452.9 kg ha^{-1}) in locality U-1, 1116 ind. ha^{-1} (104.6 kg ha^{-1}) n M-1 and 2000 ind. ha^{-1} (321.4 kg ha^{-1}) in A-1. This contrast with the results obtained in mountain streams, where the density is greatest in the upper reaches. In the studied rivers, trout density is at a minimum in the upper reaches, as shown by the figure of 18 ind. ha^{-1} for the locality L-1 on the River Lobos.

On the basis of these densities, we structured both sub-populations with reference to areas 2 and 4 (Fig. 1), re-determining age from scales and from the age-length relation of Table 1.

The instantaneous mortality rate (Z) is calculated from the equation:

$$\mathrm{Ln}\ N_t = \mathrm{Ln}\ N_0 - ZT$$

a straight line whose slope Z represents mortality and where N_t is the number of individuals in a certain month, the age of which was established from the birthday. T is the age in months. The number of trout in a particular area, each month, was established on the basis on the electro-fishing efficiency, assuming a 70% efficiency any time we sample any locality (see Table 3).

Z was estimated for areas 2 and 4 which include localities U-1, U-2, U-3, M-1 and A-1, and the following values were determined:

Age (Months)	12		24		36		48		60
Ucero		1.50		1.36		1.86		1.09	
Avión-Milanos		0.97		0.93		1.38			

This mortality Z is not in fact a reflection of natural mortality, but also, apart from sampling bias, it includes mortality caused by angling and emigration and immigration for each particular locality.

However the monthly sex-ratio and the length distributions suggest that the structure of the population is rather constant throughout the months, a finding which is uncommon among other known populations of this species. In these known populations, reproduction occurs up-stream causing continual structural changes owing to the immigration of young trout coming down-stream from the nurseries and the emigration of the adults up-stream in autumn and winter. The fact that this is not so in our river must be due to the fact that the lower reaches of the river show high structural diversity (a combination of gravel, stones and vegetation) allowing a certain slackening in the maintenance of individual and reproductive territories.

Reproduction

In the year studied, eggs were laid in the second fortnight in November. During the period September-November, direct observation of the gonads allowed us to discriminate between mature specimens which spawn and immature ones, so that we could determine the age at first maturity. None of the fish in the first age class (0+) matures for its first time in autumn. In class 1+, which are 19 months old in November, 36% of females and 28% of males are mature. 70% of females and 79% of males in class 2+ (31 months old) are mature, while all fish ≥3+ are reproductive (Table 5).

We have found no evidence to suggest that the fish die once they have reproduced for the first time (semelparity); in fact the data and direct observations suggest a certain amount of repetition in reproduction (iteroparity). However, the short-life-span in this population only allows a maximum iteroparity of 3-years for the females.

The monthly variations in the gonado-somatic index (I_g) for age classes 2+ and 3+ together are shown in Fig. 8. This is calculated thus: $I_g = (W_g/W_f) \cdot 100$ where W_g is the weight of the gonads and W_f the weight of the fish, both in grams. The mean values for this in males ($I_g = 0.4\%$) and in females ($I_g = 1.9\%$) are constant from December (after spawning) until July. After July the gonads begin to develop and they grow in weight until the next spawn. Although the development period of the gonads lasts about four months, the growth in weight is most rapid in the months of October and

Table 5. Age at maturity of females and males of the population of brown trout of the Rivers Ucero and Avión-Milanos. Nt = Number of specimens, I = Immatures, M = Matures.

Age	Male			Female		
	N_t	M	I	N_t	M	I
0+	5	0	5	8	0	8
1+	7	2	5	14	5	9
2+	14	11	3	10	7	3
≥3+	10	10	0	6	6	0

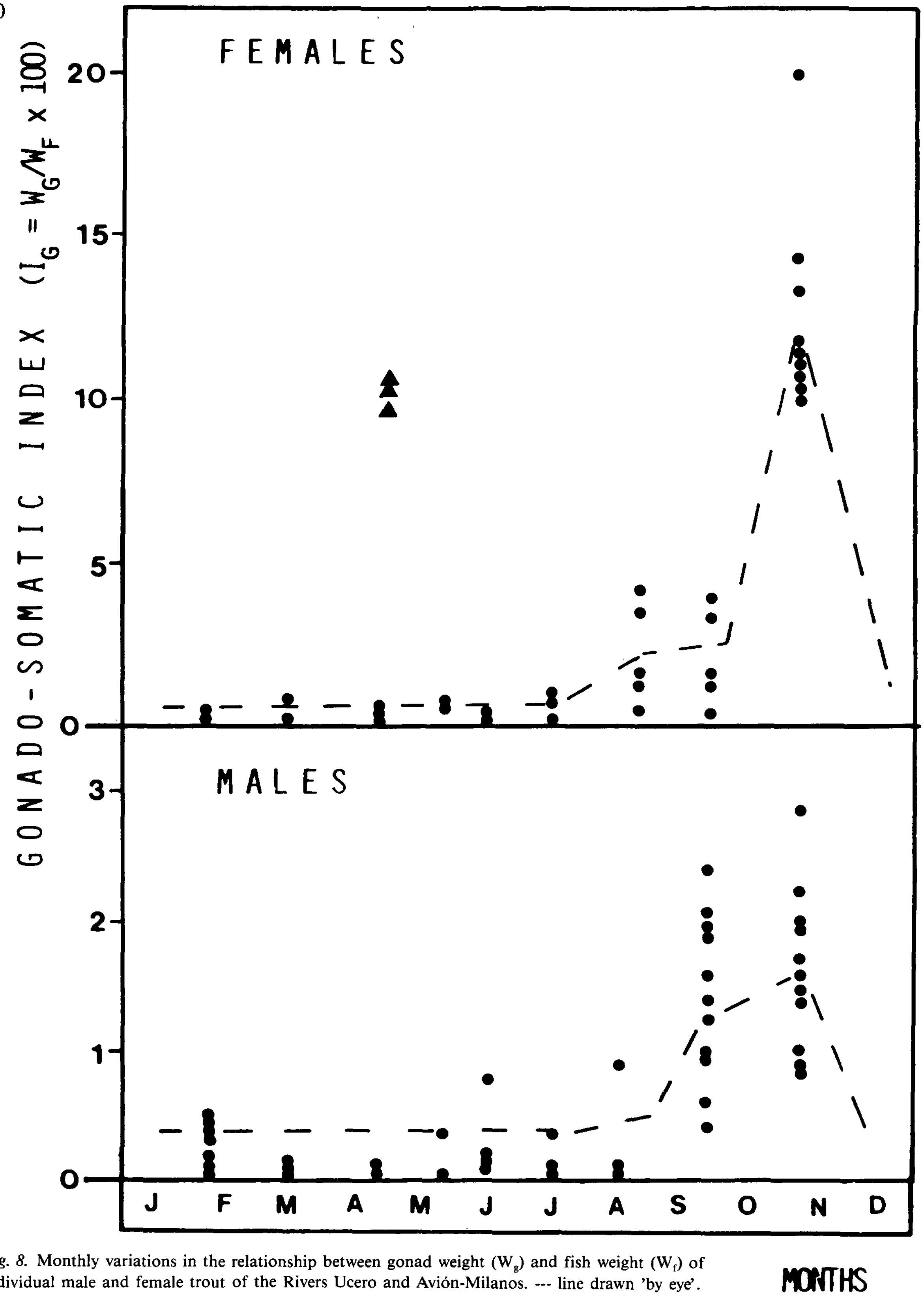

Fig. 8. Monthly variations in the relationship between gonad weight (W_g) and fish weight (W_f) of individual male and female trout of the Rivers Ucero and Avión-Milanos. --- line drawn 'by eye'.

November, above all in the females, which increases from $I_g = 2.5\%$ at the very end of September to $I_g = 12\%$ in mid November (i.e. a fivefold increase in this period).

In both years when we sampled the rivers (1983 and 1984) it is interesting to note that in April females were captured (two each year) with the gonads developed ($I_g = 10\%$) and with ovules of the same diameter as those of the females in November (spawning time). These four females were in age 1+ (two years old that April) and were somewhat shorter in length compared with others in the same age class. We concluded that these females had not reproduced successfully, among other reasons because we have found females but not males in this state. As far as we know, this phenomenon has not been mentioned in the literature; but it is known for anglers, and we have personally observed it in some rivers (mainly limestone streams). The similarity of accumulated temperatures (in degree-days) when spring begins with respect to the previous autumn (specially in these warm water streams) and the trout growth noted between march and April may explain this phenomenon.

The analysis of the frequency distributions of the diameters of the intraovarian ovules studied in the same age class is shown in Fig. 9. Mono-modal distribution of the diameters of the ovules after spawning remains constant until February. After this, differential growth of the ovules leads to a bimodal distribution in June and July (Fig. 9). The greater mean for this distribution correspond to those ovules which are to be laid in that year, while the smaller mean correspond to the stock of ovules which will be developed in the following year. This bi-modal distribution is clearly seen from July onwards although the increase observed in ovule diameter is not reflected in the gonado-somatic index (i.e. the weight of the gonads) (Fig. 8 and 9). After July there is a large increase in ovule diameter which is reflected in the weight of the gonads, and a bimodal distribution gives way to two monomodal distributions with no overlap.

As a measurement of the reproductive capacity of the population, we determined the fecundity of 17 females between 170–270 mm in length, counting the total number of developed ovules present in the gonads before laying. In the length range selected, this number varies between 350 and 1220 eggs per female. The diameter of the ovules ($\varnothing$, mean diameter distribution) vary between 26 and 38 mm. Both these variables are positively correlated with trout length (Szczerbowsky, 1966) and the appropriate linear regressions are:

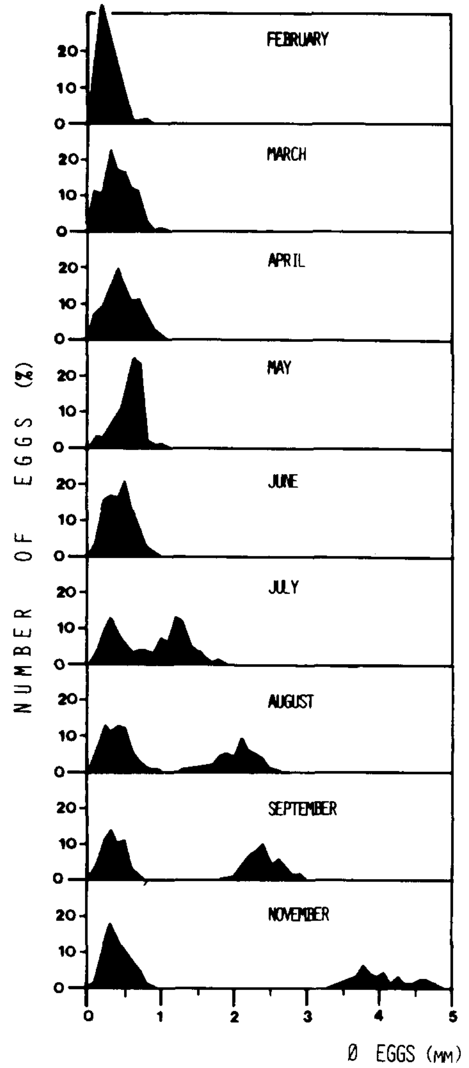

Fig. 9. Monthly size frequency distributions of unshed eggs of brown trout of the Rivers Ucero.

$$F = -646.47 + 5.6167\ (\pm 0.5766) \cdot L$$
$$(r = 0.8923,\ P \leq 0.01)$$
$$\varnothing = 1.2009 + 0.0887\ (\pm 0.0031) \cdot L$$
$$(r = 0.9486,\ P \leq 0.01)$$

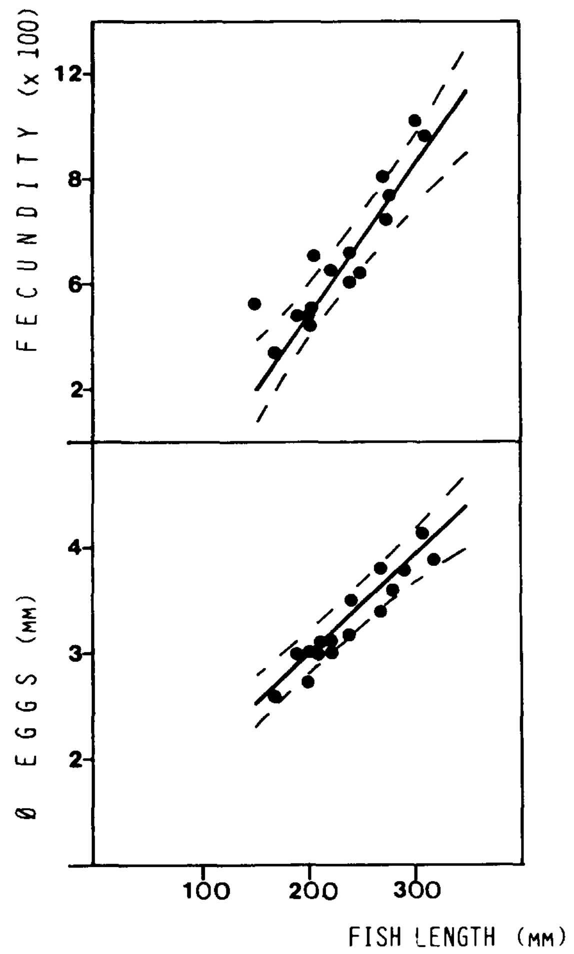

Fig. 10. Relationships between female trout length, fecundity and egg diameters. ● represent individual observations, —— line fitted by least square method (see text for regressions) and --- 95% C.L. of the regressions.

The larger and therefore the older the females, the more eggs they lay, and the larger the eggs are. This relationships are shown in graphic form in Fig. 10.

The total egg production estimated for areas 2 and 4 (Fig. 1) is based on the population structure and the mean density of the combined sites which go to make up each area. For all these sites mortality Z, sex-ratio (Fig. 4), age at first maturity (Fig. 5) and length (age) – fecundity relationships have been taken into account. On this basis, egg production in the Ucero sub-population varies between 9.7 (max. 10.3) and 34.8 (max. 38.2) eggs m^{-2}, the mean being 22.4 eggs m^{-2}. Production of eggs for the Avión-Milanos sub-population is lower, owing to a lower density and varies between 14 (max. 15) and 22 (max. 24) eggs m^{-2} with a mean of 18 eggs m^{-2}.

Discussion

Growth in length, and specially in weight, is high and is accompanied by a fairly high physical condition. Various studies of trout growth in European waters can be seen in Kirka (1969), Kennedy & Fitzmaurice (1971) and Edwards *et al.* (1979). The high growth rates found in this study are comparable with those for populations in warm water streams supplied by aquifers such as the chalk streams of southern England. In these the growth of the populations is greater than in those streams fed by surface water. The average annual temperature close to 13 °C, ideal for the growth of this species (Elliot, 1975), their homothermic nature (Edwards *et al.*, 1979) and the high rate of secondary production (i.e. food) more than explain these growth rates. It is quite possible that the differences in temperature observed between the two rivers (Ucero and Avión-Milanos) (Fig. 2) also explain the higher growth rate observed in the sub-population of the River Ucero.

The individual fecundity for each age class in the studied streams easily surpasses that of other European populations such as some in Czechoslovakia (Kirka, 1969), those of northern England (F=0.0892 L exp 2.642 and F=0.399 L exp 2.092 for the populations of Upper Teesdale (Crisp, Mann & McCormack, 1974) and F=0.440 L exp. 2.0366 for the population of trout beck (Crisp *et al.*, 1975)) or for the Søra Øsa River in Norway (F=27 L−273) (Jonsson & Sandlund, 1979).

The amount of variation observed in the demographic characteristics of freshwater fish seems to be a phenetic adaptation to the ecological conditions. This has been shown in the experiment undertaken by Mann, Mills & Crisp (1983) transplanting specimens of bullhead (*Cottus gobio* L.) from cold rivers in northern England to the warmest and most productive rivers in the south.

Various species of freshwater fish from families which are relatively distant in evolutionary terms such as gudgeon (*Gobio gobio* L.), bullhead (*C. gobio*) and stone loach (*Noemacheilus barbatulus* L.) show demographic changes in their European populations. They show, among other things, that in warm water rivers with high production rates, the growth rate is high with several egg batches a year, reproduction beginning at an early stage, together with a short lifespan (LS); whereas in colder, less productive rivers the opposite is true (longer LS, fewer batches or one, later age at first maturity (AFM), etc.) (Mann *et al.*, 1983). Given the fact that the warm, productive rivers tend to be more 'predictible' systems, at least in terms of temperature, water flow and food availability, the results obtained are in direct conflict with the predictions of the theory of strategies r and K (MacArthur & Wilson, 1964; Pianka, 1983).

In populations of brown trout (*S. trutta*) the problem is certainly more complex because of the capacity this species has for adapting itself to life in all macro-environments (brooks, rivers, lakes, etc.). In any case, if we compare the population examined in this study, which comes from a fairly predictable warm stream with a high production – at least in those terms stated above – and we compare it with other populations of trout included in the same taxonomic group (*S. trutta m. fario*) living in rivers which are structurally similar but subject to different ecological influence, such as those in the north of England studied by Crisp *et al.*, (1974, 1975), the River Søra Øsa in Norway (Johnson & Sandlund, 1979) or the Brodska Brook in Czechoslovakia (Libosvarsky & Lusk, 1974), we can see that the differences observed coincide with the results obtained by Mann *et al.* (1983).

In fact, in our population, sexual maturity is achieved at 2+ years, when 75% of the population reproduce, while in the various tributaries of the River Tees this age is 3–4 years. A similar situation prevails in the River Søra Øsa (4 years), the growth rate and fecundity being lower in these rivers, while LS is higher. That is, these populations show r strategy characteristics in the most predictable systems and K strategy characteristics in the least predictable ones.

There are two sources of evidence in the literature to support the extension of this demographic tendency to populations of trout in general, and it can be included in what Stearns (1976) calls 'bet-hedging'. The first of these is in McFadden, Cooper & Anderson (1965) in a study of various stocks of North American trout. They found that in more fertile (i.e. productive) rivers the fish spawn more and heavier eggs than those of similar lengths in infertile (i.e. unproductive) rivers, showing that even populations which have been introduced, as the trout has been in North America, tend to respond in a similar way to high productivity conditions. The second piece of evidence is experimental (Bagenal, 1969). This author, experimenting in conditions where feeding was controlled, observed that trout reproduce earlier when food was more abundant.

This author also succeeded in showing a definite relationship between the survival of the larvae and the diameters of the ovules from which they come. From this evidence and the relationship between length and fecundity (Fig. 10), it can be assumed that high growth rates, greater lengths of particular specimens in the population and individual high growth within each reproductive age class, must be favoured by natural selection, so that each of these specimens has a greater chance of its descendants surviving.

Although little observation of this demographic phenomenon is available, we think there are enough to suggest that this type of response in trout populations is due as much to a direct relationship between production (i.e. food), temperature and age at first maturity (AFM), as to a negative relationship between energy expenditure in reproduction (cf. gonado-somatic index, I_g) and life-span. This idea is borne out by two facts. The first is that both the population of the River Ucero and the Brodska Brook reach their AFM before the population in the Rivers Tees and the Søra Øsa, and that the LS is lower; in the Søra Øsa the AFM is not reached until age 5 for the whole of the population and it is here oldest specimens can be found. The River Tees populations show intermediate characteristics. The second fact is that the males, whose gonado-somatic index is usually no greater that 2.5% (Fig. 8) tend to have a greater LS than the females, they are certainly dominant in the sex-ratio for the older age classes, although numbers of each sex are fairly equal for the younger specimens showing that the mortality of the females is higher.

This fact also seems to be confirmed in other species of freshwater fish belonging to families which are very distant in evolutionary terms. An example of this is Iberian Barbel (*Barbus bocagei* Stein.,). The males reproduce from age 2–3, their gonado-somatic index is greater than 10% and they do not live longer than eight years; while the females, whose gonado-somatic index is very similar; do not reproduce until 6–7 years and survive until age 11 (Lobón-Cerviá & Fernandez-Delgado, 1984).

The data presented here are certainly not conclusive, among other things because, as Stearns (1976) points out, an unlimited number of theoretical hypotheses can be proposed for a collection of relationships which have been observed. However, we believe that the data are sufficient to indicate certain demographic responses, that seem to be valid for trout populations of streams in general, and they confirm observations made in other species of fish which are very different, both in phylogenetic and evolutionary terms from brown trout, as those studied by Mann *et al.* (1983).

Acknowledgements

Teófilo Fernandez and Pablo Colomo together with José Antonio del Riego from ICONA helped as much as possible. R. H. K. Mann (F.R.A., England) read a first draft of this paper. This research has been partially supported by the CSIC subproject N. 211.

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