The life-history patterns of Barbus bocagei sclateri (Günther, 1868) in a tributary stream of the Guadalquivir River basin, southern Spain

Article *in* Ecology of Freshwater Fish · January 1992

2 authors:

Mercedes Herrera
University of Cordoba (Spain)
13 PUBLICATIONS 357 CITATIONS
SEE PROFILE

Carlos Fernandez-Delgado
University of Cordoba (Spain)
111 PUBLICATIONS 1,974 CITATIONS
SEE PROFILE

The life-history patterns of *Barbus bocagei sclateri* (Günther, 1868) in a tributary stream of the Guadalquivir River basin, southern Spain

Herrera M, Fernández-Delgado C. The life-history patterns of *Barbus bocagei sclateri* (Günther, 1868) in a tributary stream of the Guadalquivir River basin, southern Spain.
Ecology of Freshwater Fish 1992: 1: 42–51. © 1992 Munksgaard

Abstract – The age, growth and reproduction of *Barbus bocagei sclateri* (Günther, 1868) were studied from November 1987 to September 1989 in a tributary stream of the Guadalquivir River basin. The maximum ages observed were 8+ in males and 11+ in females. The seasonal growth began in April and lasted 4–6 months. The males matured during their third year of life (2+) and females during their fifth/sixth year (4+/5+). There was a significant difference in the overall sex ratio of 1.3:1 (961 males to 740 females). Reproductive activity started in April/May and lasted until June/July. The end of the reproduction period coincided with a fall in the percentage of oxygen saturation. During this reproductive period, females spawned 2 batches of eggs. The relationship between fecundity (Fec) and fork length (FL, mm) was: $\mathrm{Fec}=7.54\times10^{-4}\ \mathrm{FL}^{3.06}$. The maximum contribution to the fecundity of the population was observed in the 6+ female group. The reproductive effort was also maximum in this age. Compared with the rest of the European barbel populations studied, the life-history patterns of this stock are characterized by low annual growth, early maturity, reduced longevity and high fecundity.

M. Herrera,
C. Fernández-Delgado
Zoology Section, Department of Animal Biology, Science Faculty, University of Córdoba, Spain

Key words: *Barbus bocagei sclateri*; age; growth; reproduction; fecundity; life-history tactics

M. Herrera, Zoology Section, Department of Animal Biology, Science Faculty, University of Córdoba, San Alberto Magno Avenue, E-14004 Córdoba, Spain

Accepted for publication May 31, 1992

Un resumen en español se incluye debrás del texto principal de este articulo.

Introduction

Barbus bocagei sclateri Günther 1868 is an endemic species of the Iberian peninsula with a meridional distribution (Elvira 1990). Its biology is not well known (Lucena, Blasco & Camacho 1979; Castelló 1981; Lucena 1984; Herrera et al. 1988). The congeneric species, *Barbus barbus* (L., 1758) has been studied widely in other European areas, especially with respect to age structure and growth (Havlena 1964; Hunt & Jones 1975; Penaz 1977; Kraiem 1982) and intensive culture and reproduction in captivity (Hochman 1963; Poncin 1988). Nevertheless, there is little information about its reproductive biology in natural habitats (Hancock, Jones & Shaw 1976; Hancock 1979).

Most of information about life history in cyprinids is skewed towards northern latitudes, limiting the scope for broad geographical trends in life histories and reproductives styles in cyprinids (Mills, 1991). The aim of this article is to provide information on the annual cycles of growth, reproduction and population structure of a population of *B. b. sclateri* inhabiting a stream of southern latitude. The results form part of a more extensive investigation of the cyprinid community of this river (Herrera, 1991).

Material and methods

The study area was a stream of the Guadalquivir River basin (38° N, 4°43′ W) about 5 km long, 1–4 m wide and 25–80 cm deep. Here *Barbus b. sclateri* coexists with *Chondrostoma polylepis willkommi* Steindachner 1866; *Tropidophoxi nellus alburnoides* Steindachner 1866; *R. lemmingii* Steindachner 1866; *Leuciscus pyrenaicus* Günther 1868 and *Cobitis maroccana* Buen 1930.

During the study period (November 1987 to September 1989) the discharge peaked between October and March. At this time, the minimum values of temperature (5°C in January) and conductivity (200 μmhos in January) and maximum dissolved oxygen ($10.1\ \mathrm{mg\cdot l^{-1}}$ in December) were recorded.

From June/July until September/October, flow ceased and the river consisted of isolated pools. During this period, maximum values of temperature (25°C in August) and conductivity (750 μmhos in August) and minimum oxygen concentrations (2 $mg \cdot l^{-1}$ in July) occurred. These parameters were measured once a month between 0800 and 1000. For further information, see Herrera et al. (1988) and Herrera (1991).

The rainfall differed in the two years studied; 1988 was a normal year and 1989 was a dry year and some of the permanent pools disappeared.

Specimens were electrofished weekly (reproductive period) or monthly (rest of the year). The fish were preserved in neutralized formaldehyde (4%) and transported to the laboratory where their size (fork length, mm) and sex (male, female or immature) were recorded. Six to eight scales from the left side of the body, between the lateral line and dorsal fin, were removed and mounted dry between two slides to determine the age. A microfilm reader was used for age study. Growth was back-calculated as described by LeCren (1947). Von Bertalanffy growth parameters were calculated using a linear regression method (Stamatopoulos & Caddy 1989).

The testes were dried to constant weight (0.1 mg) (24 h) in an oven at 80°C. The ovaries were used to determine fecundity and ovary development (see below) and were then dried in the same way as the testes and weighed. Drying time varied between 36 h and 48 h depending on size.

After removal of gonads, the specimens were eviscerated and dried in an oven at 80°C. The drying time varied between 48 h and 72 h depending on the size.

To compare our results with those from other authors, we calculated the regression lines between fork length (FL, mm) and length at the end of the scaled body (SBL, mm); standard length to the hypural plate (StL, mm); and total length with caudal lobes closed (TL, mm). The following equations were obtained:

$\mathrm{SBL} = -1.23 + 0.94\ \mathrm{FL};\ R^2 = 99.98\%;\ n = 74$
$\mathrm{StL} = -0.97 + 0.86\ \mathrm{FL};\ R^2 = 99.96\%;\ n = 74$
$\mathrm{TL} = -0.06 + 1.11\ \mathrm{FL};\ R^2 = 99.95\%;\ n = 74$

Seasonal growth was studied using mean FL of 1986 to 1989 cohorts caught throughout the period of study.

Somatic condition (K) was estimated for male and female *B. b. sclateri* using the formula:

$$\mathrm{K} = \frac{10^5 \mathrm{DW}}{\mathrm{FL}^3}$$

where DW = dry weight of the eviscerated fish (0.1 mg) and FL = fork length (mm).

Gonal development was assessed using the gonadosomatic index (GSI):

$$\mathrm{GSI} = \frac{10^5 \mathrm{GDW}}{\mathrm{FL}^3}$$

where GDW = gonad dry weight (0.1 mg) and FL = fork length (mm).

Fecundity was studied using the gravimetric method (Bagenal & Braum 1978). Analysis of variance (ANOVA) showed differences ($P < 0.05$) between sizes of oocytes in the distal, middle and proximal zones of the ovaries (bigger diameter in the proximal zone), so all the oocytes in 3 subsamples of each ovary were counted and measured under a stereomicroscope with an ocular micrometer.

The total number of opaque oocytes (yellow/white eggs) and yolk-filled eggs (yellow/orange eggs) ($\Phi > 0.5$ mm) was used to determining the standard fecundity (StF):

$$\mathrm{StF} = \frac{\mathrm{Fec}\ 10^5}{\mathrm{FL}^3}$$

where Fec = fecundity (opaque + yolky eggs) and FL = fork length (mm) (Mils & Eloranta 1985a).

StF was independent of fork length in the 1988 reproductive period. In 1989 it was only independent for females ≤230 mm (FL), so StF was calculated in this particular year for specimens ≤230 mm (FL). There were no significant differences between the two reproductive periods in the mean age or length (*t*-test) of females. We also calculated StF using only yolky eggs. In the 1988 reproductive period, this was independent of the length; in 1989 it was independent for females ≥150 mm (FL), so calculations were carried out on specimens ≥150 mm (FL).

The percentage contribution of each age group to the total fedundity of the population was estimated according to the iterative method described by Pitcher & MacDonald (1973).

The reproductive effort (RE) was determined as the relative annual investment, by age group, in somatic growth and reproduction:

$$\mathrm{RE} = \frac{\mathrm{ODW}}{\mathrm{ODW} + \mathrm{SWI}}$$

where ODW = ovary dry weight (0.1 mg) and SWI = somatic weight increment (dry weight, 0.1 mg) in the last year of life (Mills & Eloranta 1985b).

Results

Age and growth

Nine age groups (0+ to 8+) in males and 12 (0+ to 11+) in females were detected in this population. The maximum lengths observed were 297 mm (FL) in one 8+ male and 413 mm (FL) in one 11+ female.

Annual rings were detected in three different forms: by the presence of one or two circuli that cut across several others (principally in the first annulus), by a braid-like structure between several circuli or by alternate bands with different degrees of circuli separation. The new annulus appeared in February and was evident in all the specimens caught in April, so we took 1 April as the birthdate, even though some specimens had not formed an annulus by this time.

The relationship between FL (mm) and the oral scale radius (SR, micrometer units, 1 mm = 68 MU) was:

$$\mathrm{FL} = 7.55\ \mathrm{SR}^{0.63};\ R^2 = 81.02\%;\ n = 293$$

There were no significant differences in the mean back-calculated lengths at age between the two winters (t-test), so data for the two years were combined, although male and female data were kept separate (Table 1).

There were significant differences in mean fork lengths between sexes (t-test, $P < 0.05$) in the 4+, 6+ and 8+ age groups. The males showed significant differences between observed and back-calculated mean lengths in the 3+ and 4+ age groups (Mann-Whitney test, $P < 0.05$) (3+ group: $\mathrm{FL}_{\mathrm{observed}} = 81 \pm 3.3$ mm, 95% confidence limits (CL); 4+ group: $\mathrm{FL}_{\mathrm{observed}} = 103 \pm 4.7$ mm, 95% CL) and in females in the 2+, 4+ and 8+ age groups (2+ group: $\mathrm{FL}_{\mathrm{observed}} = 60 \pm 6.6$ mm, 95% CL; 4+ group: $\mathrm{FL}_{\mathrm{observed}} = 106 \pm 6.2$ mm, 95% CL; 8+ group: $\mathrm{FL}_{\mathrm{observed}} = 180 \pm 15.8$ mm, 95% CL).

Von Bertalanffy growth parameters were estimated using mean winter lengths at age for males and females separately. The equations obtained were:

Males:

$$L_T = 440.424[1 - e^{-0.069(t+0.443)}]$$

Table 1. Mean back-calculated for lengths (mm) for males and females *B. b. sclateri* and for sexes combined when there were no significant differences. See text.

Age at capture	n	Length at age (years) I	II	III	IV	V	VI	VII	VIII
1+	25	40							
2+	64	42	64						
3+	43	42	65	86					
4+	29	41	66	88	110				
5+	11	45	66	92	116	137			
6+	9	42	68	93	116	136	153		
7+	3	38	72	94	114	134	148	165	
8+	4	40	64	93	111	126	137	151	164
Mean	188	42	65	89	112	135	148	157	164
±95% CL		1.1	1.6	2.3	3.8	6.9	9.0	10.7	13.1
Annual increment		23	24	23	23	13	9	7	
Males & females									
Mean		41	66	90		140		171	
±95% CL		0.8	1.3	2.0		4.9		8.7	

Age at capture	n	Length at age (years) I	II	III	IV	V	VI	VII	VIII	IX	X	XI
1+	9	41										
2+	29	41	68									
3+	31	40	65	88								
4+	20	39	65	91	119							
5+	12	46	67	94	121	143						
6+	14	45	73	97	123	147	168					
7+	10	41	62	88	112	135	151	163				
8+	5	37	58	82	111	137	158	183	201			
9+	2	45	83	119	145	173	191	210	227	237		
10+	1	34	54	110	129	148	161	194	211	223	236	
11+	1	50	77	120	150	168	179	196	208	230	249	270
Mean	134	41	67	92	120	144	163	177	208	231	243	270
±95% CL		1.3	2.1	3.3	4.9	6.6	8.5	11.1	13.1			
Annual increment		26	25	28	24	19	14	31				

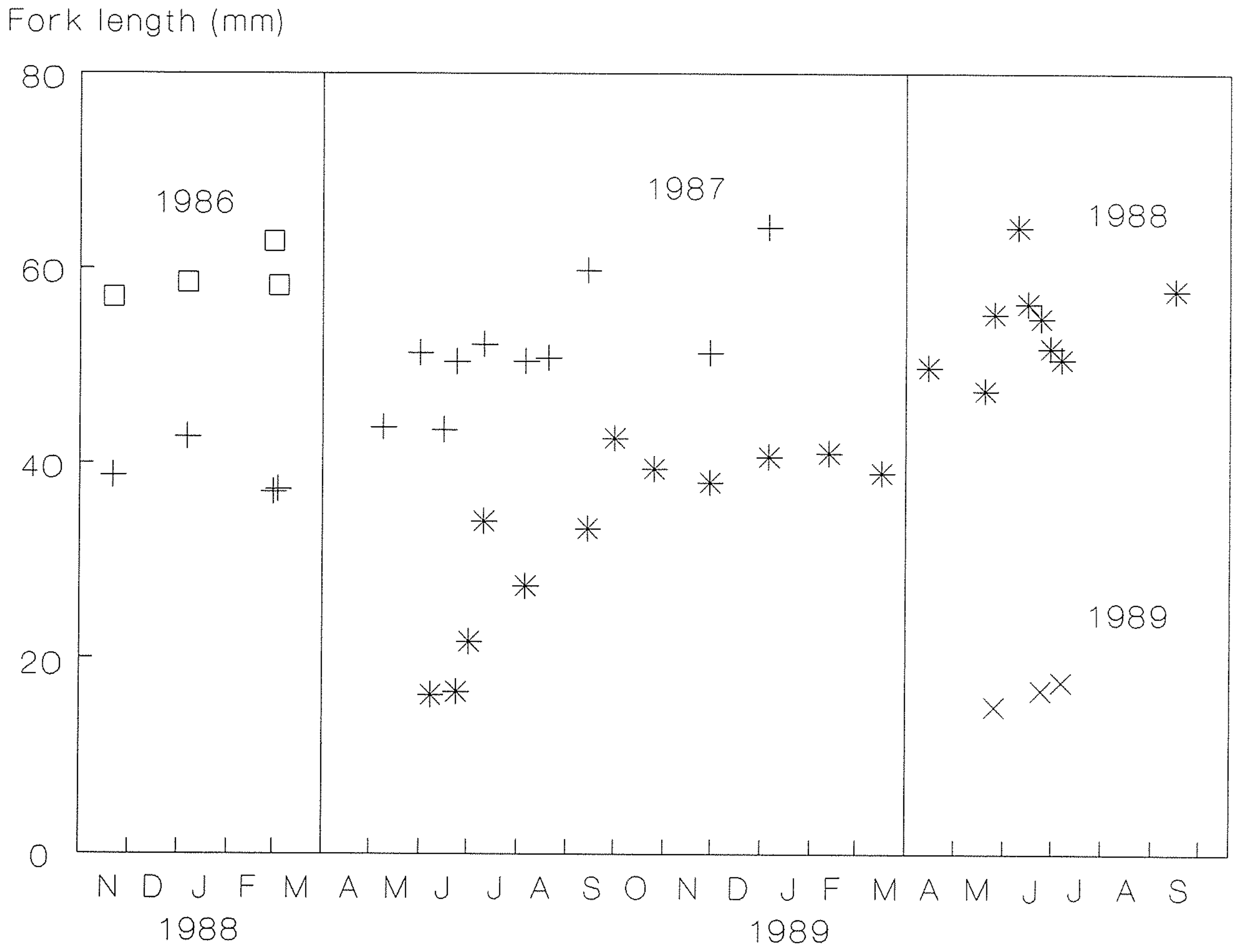

Fig. 1. Annual growth pattern of *B. b. sclateri* from 1986 to 1989 cohorts derived from the mean fork lengths (mm). 95% confidence limits have been omitted for clarity. Sexes combined. Vertical lines show birthdate.

95% CL:

$L_\infty = \pm 0.9099$ mm; $t_0 = \pm 0.0567$ years

Females:

$L_T = 436.391[1 - e^{-0.071(t+0.250)}]$

95% CL:

$L_\infty = \pm 0.6535$ mm; $t_0 = \pm 0.0905$ years

Fig. 1 shows the seasonal growth of the 1986–1989 cohorts calculated from the mean lengths of specimens caught during the study period; 1989 growth was lower than 1988. Thus, for example, in 1988, 1+ group grew during 6 months (April–September) but for only 4 months (April–July) in 1989. Nevertheless, at the end of the growth period, the mean increments were similar for both years.

Somatic condition

The annual values of condition during the year can be divided into 3 periods that are similar for males, females and immatures (Fig. 2). The mean maximum values were reached from March to June. In July, condition progressively decreased to reach a minimum in August/September. After the autumn rains, condition increased until March, when maximum values were reached again.

Reproduction

The males were mature in their third year of life (2+ group), between 60 mm and 90 mm (FL). In this age group there were significant differences (*t*-test; $P < 0.05$) between mean FL of mature (71 ± 3.3 mm, 95% CL) and immature (59 ± 5.5 mm, 95% CL) specimens.

Females mature between their fifth and sixth year of life (4+ and/or 5+ groups) from 130 mm (FL) onwards. Both groups showed significant differences (*t*-test, $P < 0.05$) between mean FL of mature and immature specimens (4+ group: $FL_{mature} = 164 \pm 4.8$ mm, 95% CL; $FL_{immature} = 133 \pm$

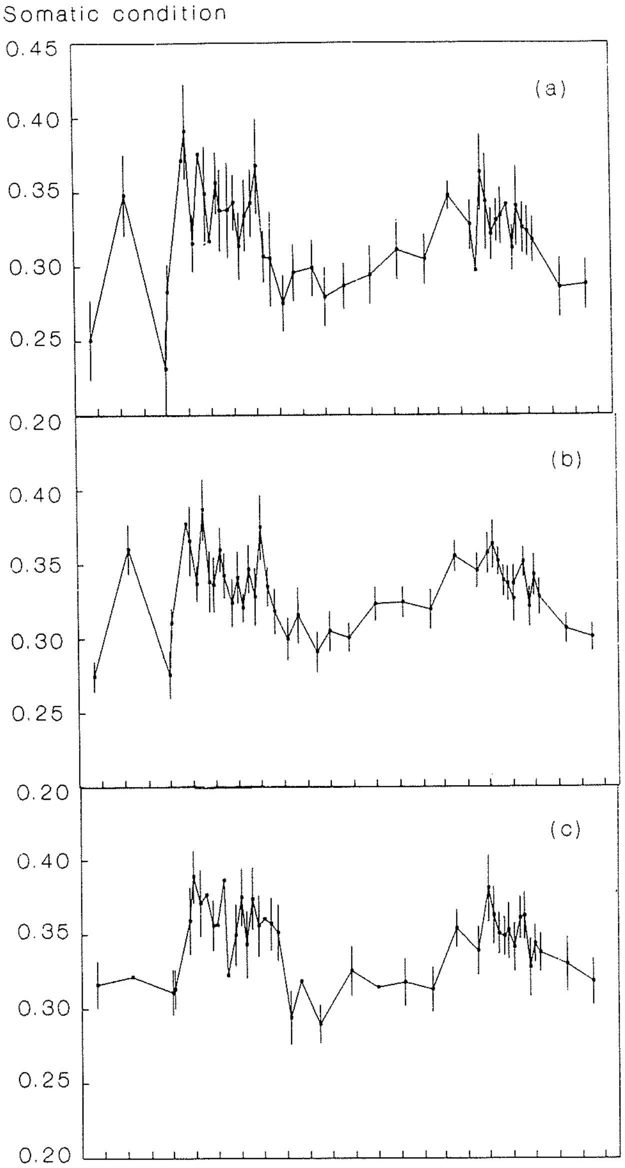

Fig. 2. Seasonal changes in somatic condition for (a) immatures, (b) males and (c) females of *B. b. sclateri.* Mean and 95% CL for samples of 5 or more fish

2.4 mm, 95% CL) and 5+ ($FL_{mature} = 174 \pm 5.6$ mm, 95% CL; $FL_{immature} = 136 \pm 4.6$ mm, 95% CL).

There were differences (binomial test with normal approximation, $P < 0.05$) in the overall sex ratio, 1.3:1, of 961 males to 740 females. However, females dominated significantly from 165 mm (FL) onwards (78 males/185 females).

Testes began to develop in January (Fig. 3) after a quiescent period of 6 months (July-December): The maximum increment occurred between March and May, and maximum values were reached in May 1988 ($\bar{X}_{GSI} = 0.032 \pm 0.0031$; 95% CL) and April 1989 ($\bar{X}_{GSI} = 0.029 \pm 0.0032$; 95% CL). Ovary development began in September (Fig. 4), but the largest increment was in April, at the beginning of spawning. The maximum GSI values were observed in May 1988 ($\bar{X}_{GSI} = 0.074$) or April 1989 ($\bar{X}_{GSI} = 0.061 \pm 0.0102$; 95% CL). Then GSI decreased progressively to the beginning of the quiescent period, which lasted for 2 months (June/July–August). The end of the reproductive period coincided with the decline in oxygen saturation (Fig. 4).

Not all fish were at the same stage of development at the same time, but the egg diameter frequency distribution in 6 gonads from females of similar length shows a representative sequence of events (Fig. 5). During the quiescent period ovaries only contained transparent recruitment eggs ($\Phi_{max} \leq 0.5$ mm). In September vitellogenesis started and the distribution veered towards the right (Fig. 5a). In February, most ovaries showed a bimodal distribution, one made up of transparent oocytes and the other with white, opaque eggs ($\Phi = 0.79 \pm 0.022$ mm, 95% CL). They probably constituted the egg stock to be spawned in that particular year (Fig. 5b). One month later, the mode with opaque eggs divided into two, and now ovaries contained a trimodal egg size distribution: transparent, opaque ($\Phi = 0.85 \pm 0.025$ mm, 95% CL) and yolky eggs ($\Phi = 1.26 \pm 0.017$ mm, 95% CL) (Fig. 5c). The eggs in this last mode continued growing to the maximum size ($\Phi = 2.03 \pm 0.017$ mm, 95% CL) (Fig. 5d). This development coincided with the maximum GSI and was the stage prior to the onset of reproduction. The beginning of spawning was represented by ovaries with 2 egg groups (transparent + opaque eggs) that had lost the third group of mature oocytes. In this period, some yolky eggs remained in the gonads and would probably have been reabsorbed. This type of ovary was common in May-June (Fig. 5e). Another batch of yolky eggs appear reaching a maximum diameter in July ($\Phi = 2.00 \pm 0.002$ mm, 95% CL) (Fig. 5f). Most of the ovaries examined at this period had some few opaque eggs that would not reach the mature stage and would probably have been reabsorbed.

Standard fecundity diminished (Kruskal-Wallis test, $P < 0.05$) as the spawning progressed (Fig. 6). This suggests that there was no recruitment from the stock of transparent eggs once spawning had started. StF calculated for yolky eggs did not vary significantly (Kruskal-Wallis test) during the spawning period, suggesting that the number of yolky eggs was identical in both egg batches.

The relationship between fecundity and fork length was determined according to the total number of oocytes differentiated immediately prior to spawning (March–April). As there were no signifi-

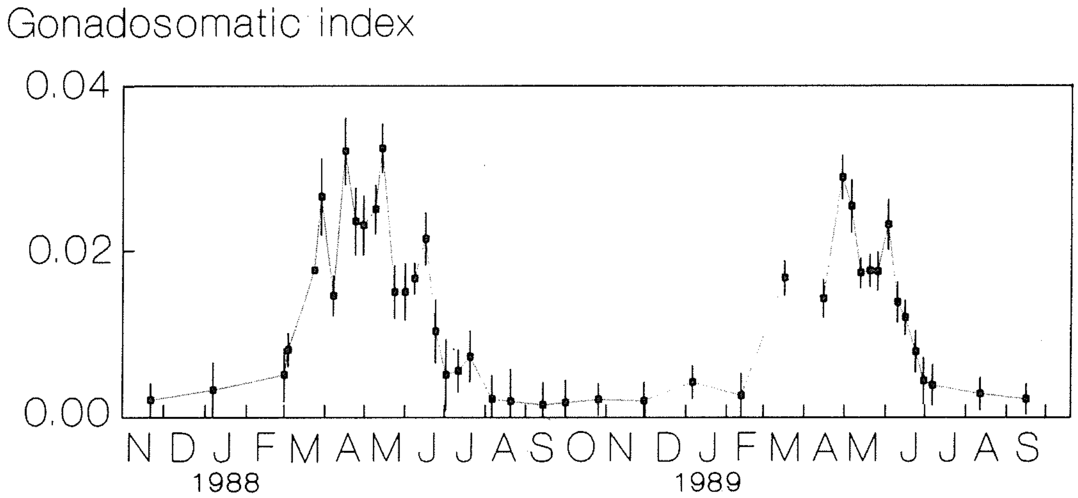

Fig. 3. Seasonal changes in gonadosomatic index for males of *B. b. sclateri*. Mean and 95% CL for samples of 5 or more fish

cant differences (analysis of covariance) between the regressions calculated for each of the two reproductive periods, the data were pooled and one regression was estimated:

$\mathrm{Fec} = 7.54\ 10^{-4}\ \mathrm{FL}^{3.06}$; $R^2 = 88.83\%$; $n = 41$

The mean egg diameter of yolky eggs showed significant differences (ANOVA, $P < 0.05$) with FL, although R^2 was very low:

$\Phi = 5.9574\ \mathrm{FL}^{0.3371}$; $R^2 = 15.68\%$; $n = 30$

The mean egg diameter of yolky eggs did not show

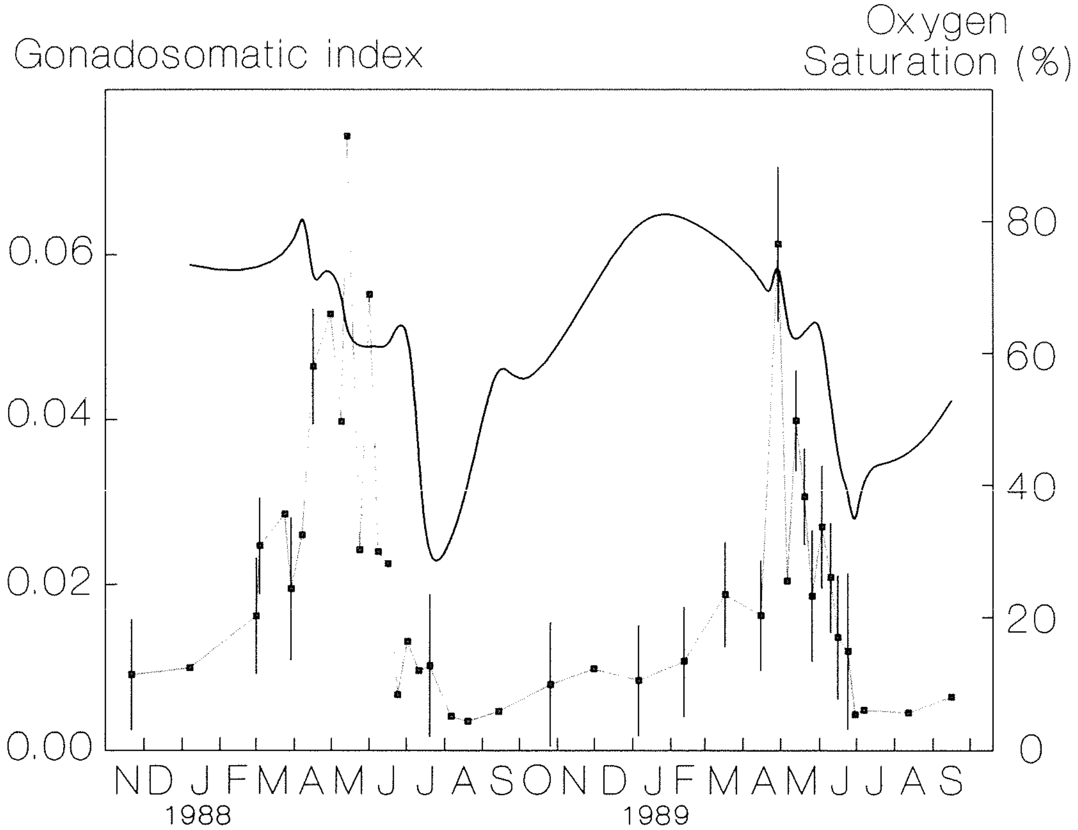

Fig. 4. Seasonal changes in gonadosomatic index for females of *B. b. sclateri* (mean and 95% CL for samples of 5 or more fish) and in the percentage of oxygen saturation (solid line)

significant differences (Mann-Whitney test) between the two batches in the same year.

The percentage contribution of each age group to the population fecundity was highest for females aged between 5+ and 8+ years (Table 2). In general, the decrease in number of fish as age increased was compensated by an increase of individual fecundity.

The reproductive effort was estimated for the total number of mature females caught in the two periods prior to the spawning (Table 3). The annual investment in reproductive tissue increased with age until a maximum RE=0.3419, at 6+ years, was reached.

Discussion

The annual growth increments of this population were similar to those found by Herrera et al. (1988) and, with the only exception of Lobón-Cerviá & de Diego (1988), were always lower than the rest of the European barbel populations studied (Hunt & Jones 1975; Penaz 1977; Kraiem 1982; Lobón-Cerviá & Fernández-Delgado 1984; Lucena 1984; Vitali & Braghieri, 1984 and others). Variations in fish growth can be explained as an adaptive response to different environmental conditions (Nikolsky 1963; Purdom 1979; Wootton, 1990). The population studied is located in a latitude where temperature allows for growth to occur for 6 months each year. Nevertheless, the ecological conditions of this river could limit the growth. The hydrological cycle of this small river is typical of the Mediterranean area, being at a maximum between autumn and the beginning of spring. In the summer, ecological conditions may become critical for fish because flow ceases and the river consists of isolated pools. During this period, all fish species living in the river are forced to live in these small pools. Hence, fish density increases, and competition for space and food is probably important. Moreover, pools are subject to plentiful sunshine (10–14 h), producing high water temperatures and the consequent oxygen depletion (particularly at night). These adverse ecological conditions could limit the growth of fish.

The condition cycle shows the consequences of this seasonality, especially during the summer, when the index reaches its lowest values. With the arrival of the autumn rains, this index increases to reach its maximum values in the spring. This pattern is similar to that found by Herrera et al. (1988)

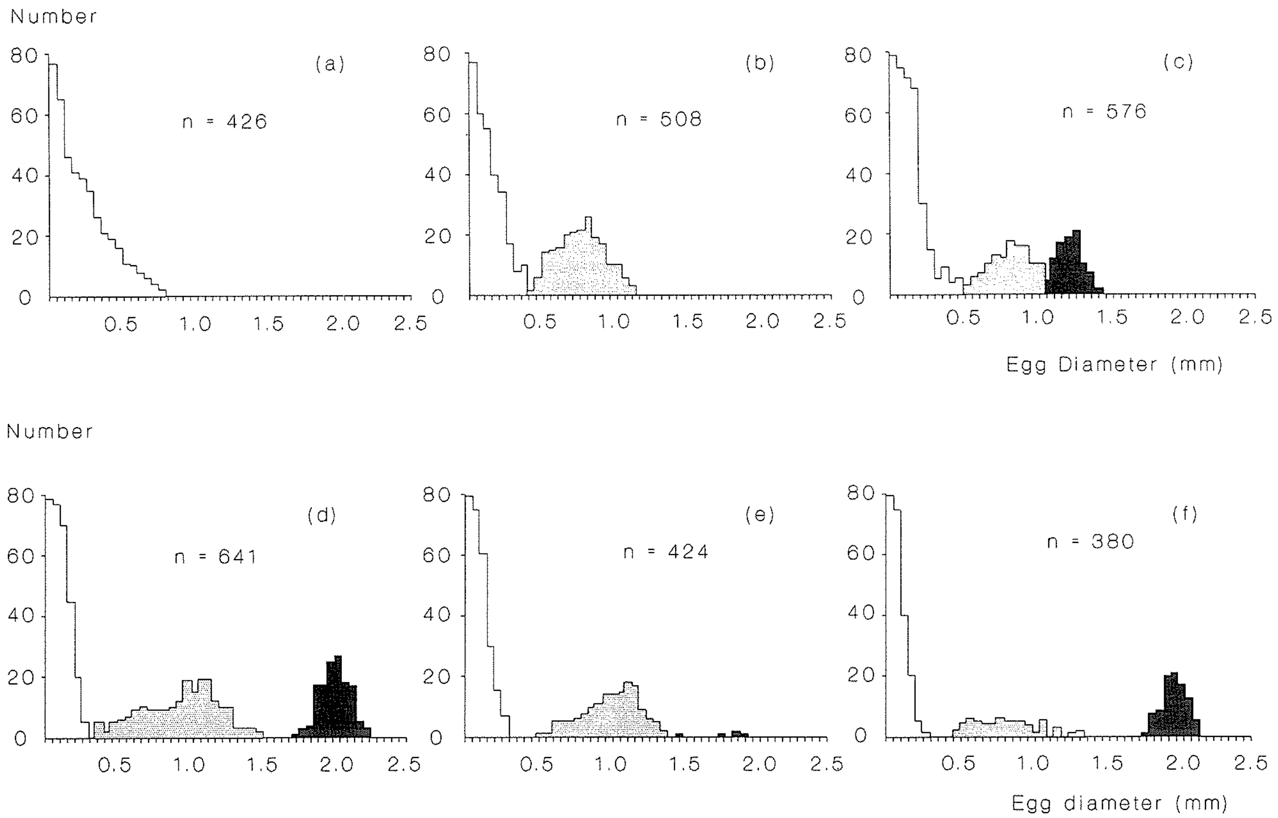

Fig. 5. Size frequency distribution of eggs from 6 *B. b. sclateri* females before, during and after the spawning period. White polygons represent immature oocytes; dotted polygons show oocytes in the maturation process and black polygons mature oocytes. See text for more explanation.

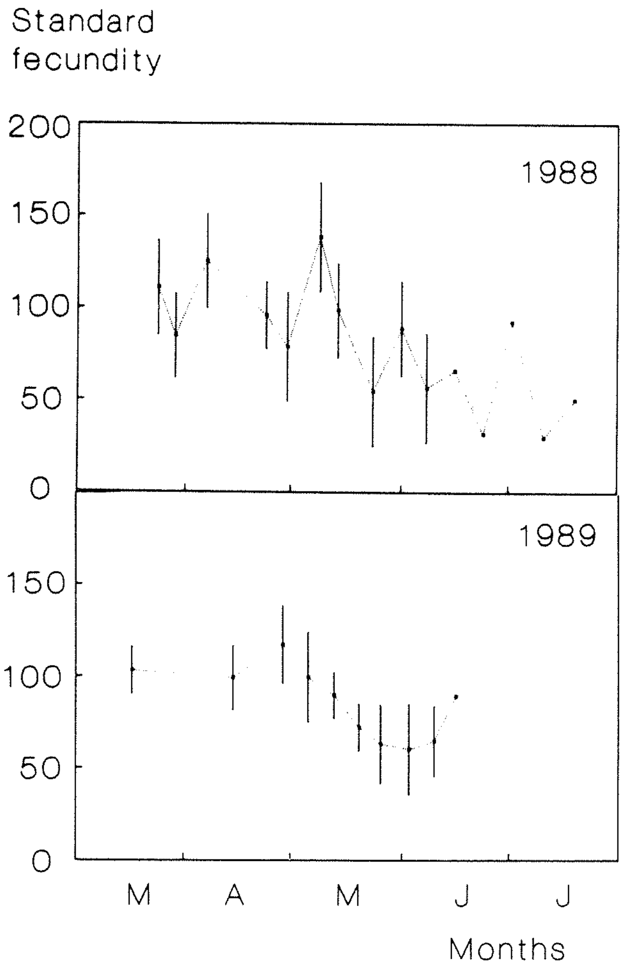

Fig. 6. Seasonal changes in the standard fecundity in *Barbus b. sclateri* during the 1988 and 1989 spawning periods. Mean values and 95% CL for samples of 5 or more fish

and Kraiem (1980), whereas Lobón-Cerviá & Fernández-Delgado (1984) did not find variations in this during their study period.

Sexual maturity was reached at ages lower than in other barbel populations (Lobón-Cerviá & Fernández-Delgado 1984). Theoretical studies on the patterns of life-history variation are based on predictions of age-specific mortality and fecundity rates and on the cost of reproduction (Stearns 1976). Increased fluctuation in the mortality of sexually mature stages favors an increase of reproductive effort and reduces lifespan (Murphy 1968; Schaffer 1974; Stearns 1976; Reznick 1985). *B. b. sclateri* may have opted for this strategy. The instability of the habitat of this population may cause unpredictable adult mortality rates, forcing this population to reproduce earlier with a higher reproductive effort. The organism benefits from producing more offspring earlier in life, since both factors contribute to a higher rate of population increase. The corresponding cost of reduced capacity for future reproduction is minimized because adult survival is low anyway.

The reproductive period of this population is similar to that found by Herrera et al. (1988) and longer than others previously studied (Hancock et al. 1976; Hancock 1979; Lobón-Cerviá & Fernández-Delgado 1984). The duration has a clear environmental influence and its decreased when percentage of oxygen saturation also decreased. According to Penaz (1973), low oxygen concentrations increase malformations in the embryo.

Prior to spawning, gonads show a trimodal distribution of egg sizes that was not detected by Herrera et al. (1988); Hancock (1979) observed the same overall egg size distribution, but only one batch of eggs, and the opaque oocytes remained in the gonads till the following spring. In our population, we observed two batches of eggs; higher values of the mean water temperature could cause this difference. According to the experiments carried out by Poncin et al. (Poncin 1984; Poncin, Philippart & Melard 1985; Poncin, Melard & Philippart 1987) an increase in water temperature induces several spawnings in barbel.

Multiple spawnings have indubitable advantages in fluctuating environments. They increase, for examle, individual fecundity (Nikolsky 1963). Compared with other barbel populations, the fish in our population have a higher fecundity; a 200-mm (FL) female has released 600 eggs in a population

Table 2. Age group contribution to total fecundity of the population in *B. b. sclateri*. *n*=number of specimens; F=fecundity.

Year 1988				Year 1989				Total	
Age	*n*	F	%	Age	*n*	F	%	F	%
4+	10	41286	11.3	4+	9	41253	9.0	83164	10.1
5+	7	36851	10.1	5+	21	99841	21.7	136433	16.6
6+	10	67456	18.5	6+	14	93841	20.4	160705	19.5
7+	9	55789	15.3	7+	10	79166	17.2	134553	16.4
8+	3	35225	9.4	8+	9	120260	26.2	155159	18.9
9+	4	65818	18.0	9+	2	24439	5.3	89414	10.9
10+	3	63125	17.3					63125	7.7

Table 3. Relative annual investment in somatic growth and reproduction in *B. b. sclateri.*

Age (years)	Number of specimens	Somatic weight (g)	Gonad weight (g) a	Somatic weight increment (g) b	a/a+b
4+	7	12.2555	0.7127	9.1129	0.0725
5+	14	17.2448	1.8323	4.9893	0.2686
6+	14	20.4975	1.6402	3.2527	0.3419
7+	10	29.9880	2.6237	9.4905	0.2166
8+	3	52.2205	2.8913	22.2325	0.1151

in Great Britain (Hancock 1979), 3000 in that of Lobón-Cerviá & Fernández-Delgado (1984), 7000 in that of Herrera et al. (1988) and 8000 in ours. With multiple spawnings, progeny are not risked in just one reproductive event and the optimum egg size can be selected, which avoids the possible conflict between egg number and egg quality (Miller 1979). Reproductive effort shows that the largest and oldest females are more fertile with less energetic investment than the smaller ones.

Compared with the rest of the European barbel populations studied, the life-history patterns of this stock are characterized by low annual growth, early maturity, reduced longevity and high fecundity in two batches of eggs.

Resumen

A largo de dos años (noviembre de 1987 a septiembre de 1989) se estudió la estructura de edades, crecimiento y reproducción de una población de *Barbus bocagei sclateri* (Günther 1868) localizada en el rio Mazcatomiza (cuenca del río Guadalquivir). Las edades máximas observadas fueron 8+ en machos y 11+ en hembras. El crecimiento estacional se inicia en abril prolongándose por espacio de cuatro a seis meses. Los machos maduran en su tercer año de vida (2+) y las hembras entre el quinto y sexo (4+/5+): En el total de las capturas, los machos dominaron significativamente (961 machos/740 hembras) respecto a las hembras. La actividad reproductora comienza en abril/mayo prolongándose hasta junio/julio. El final de la reproducción coincide con un descenso en el porcentaje de saturación de oxígeno. A lo largo del periodo reproductivo, las hembras desovan dos lotes de huevos. La relación entre fecundidad (Fec) y longitud furcal (LF, mm) fue: $Fec = 7.54\ 10^{-4}\ LF^{3.06}$. La máxima contribución a la fecundidad de la población fue para la clase de edad 6+. El esfuerzo reproductivo fue igualmente máximo en esta edad. El reducido volumen de agua de este río y las adversas condiciones ecológicas podrían incidir de forma esencial en el particular ciclo de vida de esta población caracterizada por un crecimiento anual bajo, madurez temprana, longevidad reducida y elevada fecundidad en dos puestas.

Acknowledgements

We thank Professor R. H. K. Mann for help in scale reading and Lourdes Lopera, Jesús Hidalgo and Francisco Martínez for their invaluable field and laboratory assistance. Three anonymous reviewers and the editors provided helpful suggestions for improvements of an earlier draft of the manuscript. Part of this work was done while one of the authors (C.F-D.) had a grant from the British Council in the Institute of Freshwater Ecology (Huntingdon, England).

References

Bagenal, T.B. & Braum, E. 1978. Eggs and early life history. In: Bagenal, T. B., ed. Methods for assessment of fish production in fresh waters. IBP Handbook No. 3. Oxford: Blackwell Scientific Publications, pp. 165–201.

Castelló, V. 1981. Relación longitud-peso y condición del barbo de Sclater (*Barbus barbus sclateri* G.) en el río Guadiato, Córdoba, España. Doñana, Acta Vertebrata 8: 5–13.

Elvira, B. 1990. Iberian endemic freshwater fishes and their conservation status in Spain. Journal of Fish Biology 37(A): 231–232.

Hancock, R.S. 1979. The annual cycle of intraovarian egg size and fecundity of the barbel *Barbus barbus* in the river Severn. Freshwater Biology 9: 535–542.

Hancock, R.S., Jones, J.W. & Shaw, R. 1976. A preliminary report on the spawning behaviour and nature of sexual selection in the barbel, *Barbus barbus* (L.). Journal of Fish Biology 9: 21–28.

Havlena, F. 1964. Contribution to the study of the age and growth in the barb, *Barbus barbus* (L.) in the drainage area of the Orava river dam basin. Folia Zoologica 13(4): 321–326.

Herrera, M., Hernando, J.A., Fernández-Delgado, C. & Bellido, M. 1988. Age, growth and reproduction of the barbel, *Barbus sclateri* (Günther 1868), in a first-order stream in southern Spain. Journal of Fish Biology 33: 371–381.

Herrera, M. 1991. Modelos en los ciclos de vida de una comunidad de ciprínidos en un arroyo de primer orden de la cuenca del río Guadalquivir. Ph.D. thesis. Córdoba: University of Córdoba.

Hochman, L. 1963. [Let us try to obtain the own fry of the barb.] Ceskoslovenske Ribarstri 2: 23–24.

Hunt, P.C. & Jones, J.W. 1975. A population study of *Barbus barbus* (L.) in the river Severn, England. III. Growth. Journal of Fish Biology 7: 361–376.

Kraiem, M.M. 1980. Etude comparative de la condition physique du barbeau (*Barbus barbus* L.) (Poissons, Cyprinidae) dans deux rivères françaises: Le Rhône et l'Allier. Bulletin Naturelle Pêche Tunisie 4(1): 67–81.

Kraiem, M.M. 1982. Etude comparative de l'âge et de la croissance du Barbeau, *Barbus barbus* (L.), (Poissons, Cyprinidés) dans deux rivères françaises, le Rhône et l'Allier. Archiv für Hydrobiologie 96(1): 73–96.

LeCren, E.D. 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. Journal of Animal Ecology 16: 188–204.

Lobón-Cerviá, J. & Fernández-Delgado, C. 1984. On the biology of the barbel (*Barbus barbus bocagei*) in the Jarama river. Folia Zoologica 33(4): 371–384.

Lobón-Cerviá, J. & de Diego, A. 1988. Feeding strategy of the barbel (*Barbus bocagei* Steind.) with relation to benthos composition. Archiv für Hydrobiologie 114(1): 83–95.

Lucena, J. 1984. Etude comparative entre les peuplements de Barbeaux des barrages de Bermejales et Cubillas (Granada, Espagne). Vie Milieu 34(2/3): 105–108.

Lucena, J, Blasco, M. & Camacho, I. 1979. Estudio del crecimiento en peso y longitud del *Barbus barbus sclateri* Gthr. del embalse de Cubillas. Boletín de la Real Sociedad Española de Historia Natural 77: 479–488.

Miller, P.J. 1979. Adaptiveness and implications of small size in teleosts. In: Miller, P.J., ed. Fish phenology: anabolic adaptiveness in teleosts. Symposium of the Zoological Society of London, 44. London: Academic Press. pp. 263–306.

Mills, C.A. 1991. Reproduction and life history. In: Winfield, I.J. & Nelson, J.S., ed. Cyprinid fishes: systematics, biology and exploitation. London: Chapman & Hall. pp. 483–508.

Mills, C.A. & Eloranta, A. 1985a. The biology of *Phoxinus phoxinus* (L.) and other littoral zone fishes in lake Konnevesi, central Finland. Annales Zoologici Fennici 22: 1–12.

Mills, C.A. & Eloranta, A. 1985b. Reproductive strategies in the stone loach *Noemacheilus barbatulus*. Oikos 44: 341–349.

Murphy, G.I. 1968. Patterns in life history and the environment. American Naturalist 102: 390–404.

Nikolsky, G.V. 1963. The ecology of fishes. London: Academic Press. 352 pp.

Penaz, M. 1973. Embrionic development of the barb, *Barbus barbus* (Linnaeus 1758). Folia Zoologica 22(4): 363–374.

Penaz, M. 1877. Population analysis of the barb, *Barbus barbus*, from some moravian rivers (Czechoslovakia). Acta Scientarum Bohemoslovace Brno 11(7): 1–30.

Pitcher, T.J. & MacDonald, P.D.M. 1973. A numerical integration method for fish population fecundity. Journal of Fish Biology 5: 549–553.

Poncin, P. 1984. Observations sur le contrôle environmental de la reproduction du barbeau fluviatile *Barbus barbus* (L.) en captivité. Effets de la température et de la photopériode. Cahiers d'Ethologie Appliquée 4(4): 357–358.

Poncin, P. 1988. Le contrôle environmental et hormonal de la reproduction du barbeau, *Barbus barbus* (L.) et du chevaine *Leuciscus cephalus* (L.) (Pisces cyprinidae), en captivité. Cahiers d'Ethologie Appliquée 8(2): 1–330.

Poncin, P., Philippart, J.C. & Melard, C. 1985. Induction of repeated spawnings in female barbel, *Barbus barbus* (L.) (Pisces, Cyprinidae) reared in heated water. Abstracts of the 7th (Fish Culture) Conference of the European Society for Comparative Physiology and Biochemistry. Barcelona 3 pp.

Poncin, P., Melard, Ch. & Philippart, J.C. 1987. Utilisation de la température et de la photopériode pour controler la maturation sexuelle en captivité de trois espèces de poissons cyprinidés européens, *Barbus barbus* (L.), *Leuciscus cephalus* (L.) et *Tinca tinca* (L.). Résultats préliminaires. Bulletin Français Pêche Pisciculture 304: 1–12.

Purdom, C.E. 1979. Genetics of growth and reproduction in teleosts. In: Miller, P.J., ed. Fish phenology: anabolic adaptiveness in teleosts. Symposium of the Zoological Society of London, 44. London: Academic Press. pp. 207–217.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 4: 257–267.

Schaffer, W.M. 1974. Optimal reproduction in fluctuating environments. American Naturalist 108: 783–790.

Stamatopoulos, C. & Caddy, J.F. 1989. Estimation of von Bertalanffy growth parameters. A versatile linear regression approach. Journal du Conseil Internationale Exploration de la Mer 45: 200–208.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51(3): 3–47.

Vitali, R. & Braghieri, L. 1984. Population dynamics of *Barbus barbus plebejus* (Valenciennes) and *Leuciscus cephalus cabeda* (Risso) in the middle River Po (Italy). Hydrobiologia 109: 105–124.

Wootton, R.J. 1990. Ecology of teleost fishes. London: Chapman & Hall. 404 pp.