



Age, growth and reproduction of *Cobitis paludica* in a seasonal stream

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In the Iberian endemic loach *Cobitis paludica*, in a small seasonal tributary of the Guadalquivir River, 65–70% of the total growth in length occurred in the first year of life. The maximum ages observed were 3+ years in males and 4+ years in females. Both sexes matured at the beginning of their second year of life. There was a significant difference from 1 : 1 in the overall sex ratio of 412 males to 674 females. Spawning began in late March and ended in July. *Cobitis paludica* is a multiple spawner that releases a minimum of two batches of eggs per female each year. Once spawning had started, however, there was no recruitment from the stock of transparent oocytes to the mature stock. The number of eggs decreased from the first batch to the second, but there was no significant difference in the mean egg diameter between batches. Compared with other populations of this species, the present population, from a low latitude, is characterized by a low number of age groups, fast growth, early maturity and high fecundity in multiple spawnings. These life-history characteristics are typical of species in unstable environments, where adult mortality is high, variable or unpredictable.

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Key words: *Cobitis paludica*; age; growth; reproduction; fecundity; life-history tactics.

INTRODUCTION

Cobitis paludica (De Buen) is an endemic loach distributed throughout the southern area of the Iberian Peninsula (Doadrio *et al.*, 1991; Perdices & Doadrio, 1997). There are some recent papers on its taxonomy, karyology, genetic variability and feeding (Madeira *et al.*, 1992; Vasil'eva *et al.*, 1992; Perdices *et al.*, 1995; Valladolid & Przybylski, 1996; Doadrio & Perdices, 1997). Few papers treat *C. paludica* exclusively, however, and only three describe some aspects of its life history (Lobón-Cervía & Zabala, 1984; Przybylski & Valladolid, 2000; Soriguer *et al.*, 2000).

This 2 year study examines the annual cycle of a population of *C. paludica* in a river basin at the southern limit of the species in Europe. It forms part of a wider study of the fish community of this river (Herrera *et al.*, 1988; Herrera & Fernández-Delgado, 1992, 1994; Fernández-Delgado & Herrera, 1994, 1995a,b). There is a need to increase knowledge of the life history characteristics of fishes under threat as a necessary tool for management action and conservation programmes (Wootton *et al.*, 2000).

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MATERIALS AND METHODS

The population inhabits an intermittent stream of the Guadalquivir River basin in southern Spain (38°0'N; 4°43'W), 5 km long, 1–4 m wide and 25–80 cm deep. In this locality *C. paludica* co-exists with *Chondrostoma willkommii* Steindachner, *Chondrostoma lemmingii* (Steindachner) (= *Rutilus lemmingii*), *Barbus sclateri* Günther, *Leuciscus pyrenaicus* Günther and *Squalius alburnoides* (Steindachner) (= *Tropidophoxinellus alburnoides*).

The hydrology of the study area is typical of Mediterranean intermittent streams. During the study period (November 1987 to October 1989) flow was maximum between October and March. The minimum temperature recorded was 5° C (January) and the maximum dissolved oxygen content was 10.1 mg l⁻¹ (December). From June–July until September–October flow ceased and the river consisted of isolated pools. During this period maximum temperatures (25° C in August) and minimum oxygen concentrations (2 mg l⁻¹ in July) occurred. Throughout the study period these parameters were measured once a month between 0800 and 1000 hours (Herrera *et al.*, 1988).

Electrofishing was used to collect fish between November 1987 and October 1989. A total of 1179 specimens was obtained (weekly during the reproductive period and monthly during the rest of the year). Fish were preserved in neutralized formaldehyde solution (4%) and transported to the laboratory, where their mass ($M \pm 0.1$ g) and total length (L_T , mm), were recorded. Sex (male, female or indeterminate) was determined by visual observation of the gonads and secondary morphological characteristics. Eviscerated fish and testes were dried (24 h) to constant mass (± 0.1 mg) in an oven at 80° C. Ovaries were examined to determine fecundity and ovary development and were then dried in an oven at 80° C. Drying time varied between 24 and 72 h, depending on ovary size.

AGE AND GROWTH

Age determination was carried out using two methods: based on bony structures (otoliths and scales) and based on length-frequency distributions. Otoliths for the validation study were examined after clearing (Smyly, 1955; Robotham, 1981). Scales below the first radius of the dorsal fin and above the lateral line were removed from a total of 567 females and 263 males. These were cleaned using 8% NaOH and placed on two slides for age determination. Finally, the modal distribution of samples was studied over a short period of time (month and seasonal periods) separately to reduce the effects of seasonal growth (Rosenberg & Beddington, 1988). Age validation was attempted using a length-frequency based method available in the FISAT software (FAO ICLARM Stock Assessment Tools, Ver. 1.01). Size groups presumed to represent age classes in the length-frequency seasonal samples were identified by the method described by Bhattacharya (1967). This was followed by application of modal class progression analysis, the value of separation index (I_s) must be >2 to provide meaningfully separated groups (Gayaniilo *et al.*, 1988).

Over a defined period of time, the specific growth rate (g) (Wootton, 1990) was calculated as: $g_L = (\log_e L_{Tf} \cdot L_{Ti}^{-1})t^{-1}$ and $g_M = (\log_e M_f \cdot M_i^{-1})t^{-1}$ where L_{Tf} and M_f are final L_T and final M respectively, L_{Ti} and M_i are initial L_T and initial M and t is time interval. Specific growth rate was expressed as % per unit time, that is: $G_L = 100 g_L$ and $G_M = 100 g_M$.

The relationships (log transformed data) between L_T and eviscerated carcass dry mass (M_{ED} mg) (dependent variable) were estimated separately for males, females and immature fish. To avoid the use of negative values, the variables were multiplied by 10⁴. This procedure (i.e. to multiply by a power of 10) is suitable when variables range from 0 to 1 (García-Berthou & Moreno-Amich, 1993). The somatic condition cycle was indexed by residuals from these regressions (Sutton *et al.*, 2000) so body length effects were removed.

REPRODUCTION

The sex-ratio was analysed for the whole population by month, season and size. The degree of significance of the results obtained was established by χ^2 at value of $P < 0.05$.

TABLE I. Age structure as determined from scales in the population of *Cobitis paludica* sampled seasonally. (n =number of fish with a clear scale reading)

Season		n	Per cent of population in each age class per season				
			0+	1+	2+	3+	4+
Summer 1988	Females	77	12.99	53.25	28.57	3.89	1.30
	Males	41		48.78	46.34	4.88	
Autumn 1988	Females	30	26.67	40.00	26.67	6.66	
Winter 1988–1989	Females	57	45.61	24.56	17.54	18.77	3.51
Spring 1989	Females	118	26.25	31.36	21.19	16.96	4.24
	Males	101	30.00	53.64	13.64	2.72	
Summer 1989	Females	97	10.31	21.65	32.99	29.90	5.15

Gonadal development was studied using the standardized residuals from the least-squares regressions of gonad dry mass of fish (M_{DG} , ± 0.1 mg) on L_T . To determine whether values differed significantly between sexes and periods for a value of $P < 0.05$, ANCOVA, ANOVA and Kruskal–Wallis tests were carried out (Sokal & Rohlf, 1981).

Ovary development and fecundity were studied using the gravimetric method (Bagenal & Braum, 1978). There were no significant differences (ANOVA, $P > 0.05$) in egg diameter or egg number in relationship to their position in the gonad. Therefore, all eggs present in a sub-sample from the mid-portion of each preserved ovary were counted and measured under a stereomicroscope with an ocular micrometer.

Fecundity was determined in 105 mature females captured in April, May, June and July ($n=34$, reproductive period 1988; $n=71$, reproductive period 1989). ANCOVA was used to determine whether fecundity-length relationships changed between periods and residuals of these regressions were used to analyse the temporal variation.

RESULTS

AGE, GROWTH AND CONDITION

No patterns were apparent in otoliths, so they could not be used for ageing. Age determination by scales showed five age-groups (0+ to 4+ years) in females and four age-groups (0+ to 3+ years) in males (Table I). The maximum lengths observed were a 99 mm female caught in March (1988) and a 90 mm male caught in June (1989). Females were significantly (two-way ANOVA, $F_{1,1084} = 247.59$, $P < 0.001$) longer than males (females, $L_T = 71 \pm 0.99$ mm; males, $L_T = 59 \pm 0.67$ mm; mean \pm 95% CL).

The Bhattacharya method followed by the modal class progression analysis, using the length-frequency of the seasonal samples, identified probable distributions, with significant separation indices, of four cohorts in females and three in males, which were only detected in both summers (Fig. 1). Thus this method indicated one cohort fewer for each sex compared to scales. A comparison between mean L_T obtained by both methods (Table II) showed that there were no significant differences in the 0+ and 1+ year classes, but mean lengths of older fish did not always correspond.

Modal progression was examined in monthly and seasonal samples between December 1987 and August 1989 (sexes separately). Modal progression analysis

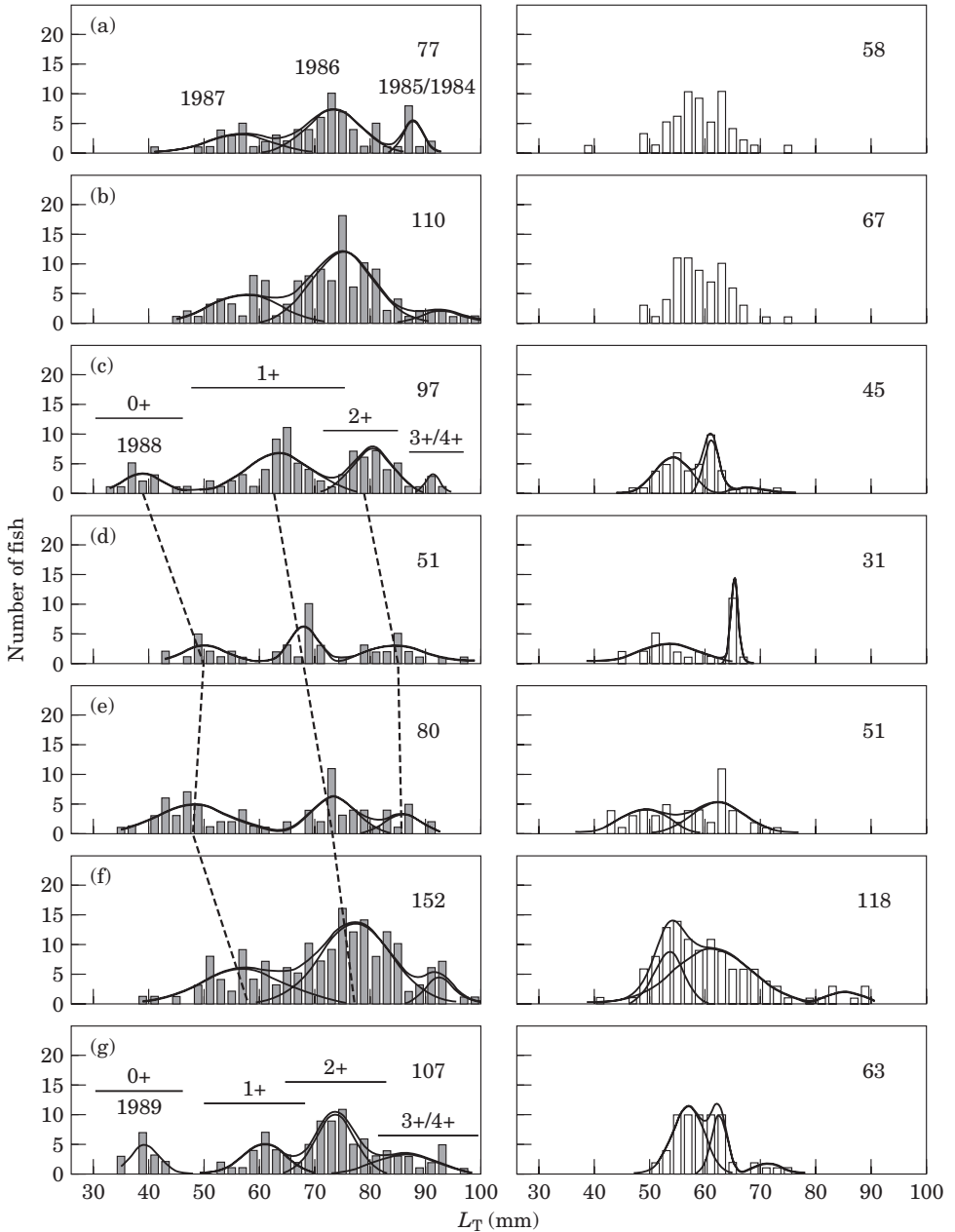


FIG. 1. Length-frequency modal progression of females (■) and males (□) of *Cobitis paludica* caught seasonally in the Mascatomiza Stream. Number of individuals per season is indicated. Means of females year classes (estimates that did not differ between FiSAT and scale analysis) are joined with broken lines. Year classes ages (0+ to 4+) and year of spawning are indicated. (a) Winter 1987–1988; (b) spring 1988; (c) summer 1988; (d) autumn 1988; (e) winter 1988–1989; (f) spring 1989; (g) summer 1989.

TABLE II. Comparison of fish length between age classes obtained from scales (L_T =mean L_T of each age class) and cohorts obtained by statistical methods (L_{T1} =mean L_T of each cohort)

		Comparison between L_T and L_{T1} in each age class per season				
		0+	1+	2+	3+	4+
Females	Summer 1988	$L_T=40.3$ $t=1.15$ $L_{T1}=38.8$ d.f.=9 $P=0.278$	$L_T=65.0$ $t=1.87$ $L_{T1}=63.5$ d.f.=40 $P=0.069$	$L_T=78.4$ $t=-1.74$ $L_{T1}=80.5$ d.f.=22 $P=0.096$	$L_T=85.7$ $t=-2.98$ $L_{T1}=91.2$ d.f.=2 $P=0.096$	$L_T=87.0$ **
	Autumn 1988	$L_T=50.9$ $t=1.00$ $L_{T1}=50.0$ d.f.=7 $P=0.351$	$L_T=67.6$ $t=-0.21$ $L_{T1}=68.0$ d.f.=11 $P=0.841$	$L_T=82.5$ $t=-1.66$ $L_{T1}=84.3$ d.f.=7 $P=0.141$	$L_T=88.0$ **	
	Winter 1988-1989	$L_T=48.7$ $t=1.43$ $L_{T1}=48.2$ d.f.=25 $P=0.671$	$L_T=71.6$ $t=-1.13$ $L_{T1}=73.7$ d.f.=13 $P=0.279$	$L_T=82.3$ $t=-2.93$ $L_{T1}=85.9$ d.f.=9 $P=0.017$	$L_T=86.0$ **	$L_T=91.0$ **
	Spring 1989	$L_T=54.8$ $t=-1.94$ $L_{T1}=57.4$ d.f.=30 $P=0.061$	$L_T=76.5$ $t=-2.00$ $L_{T1}=77.5$ d.f.=36 $P=0.053$	$L_T=84.3$ $t=-14.1$ $L_{T1}=92.5$ d.f.=24 $P=0.001$	$L_T=89.0$ **	$L_T=88.4$ **
	Summer 1989	$L_T=40.2$ $t=1.71$ $L_{T1}=39.1$ d.f.=9 $P=0.121$	$L_T=61.4$ $t=0.53$ $L_{T1}=60.8$ d.f.=20 $P=0.598$	$L_T=72.5$ $t=-1.80$ $L_{T1}=73.7$ d.f.=31 $P=0.081$	$L_T=83.7$ $t=-3.51$ $L_{T1}=86.4$ d.f.=28 $P=0.002$	$L_T=91.2$ **
	Males					
Summer 1988		$L_T=54.8$ $t=0.60$ $L_{T1}=54.3$ d.f.=19 $P=0.555$	$L_T=62.1$ $t=1.13$ $L_{T1}=61.1$ d.f.=18 $P=0.273$	$L_T=72.5$ $t=3.33$ $L_{T1}=67.5$ d.f.=1 $P=0.186$	$L_T=83.2$ **	
Spring 1989	$L_T=53.8$ $t=0.87$ $L_{T1}=53.3$ d.f.=32 $P=0.388$	$L_T=61.2$ $t=0.18$ $L_{T1}=61.3$ d.f.=58 $P=0.855$	$L_T=75.9$ $t=-5.40$ $L_{T1}=85.2$ d.f.=14 $P=0.001$			

* , Significant differences, t -test; ** , only results obtained by scales analysis.

TABLE III. Seasonal growth rates in length and mass of the female population cohorts of *Cobitis paludica* in the Mascatomiza Stream. Only growth rates with significant differences ($P < 0.05$) between seasons in the same cohort and between cohorts are presented

Cohort	Spring (1988)	Summer (1988)	Autumn (1988)	Winter (1988–1989)
G_L (%)				
1986	9.05	11.48	6.47	9.29
1987	11.59	16.94	14.97	13.07
1988			21.66	13.65
G_M (%)				
1986	29.82	37.84	21.34	30.65
1987	35.24	55.87	49.38	43.13
1988			71.41	45.00

was clear only in females (Fig. 1). Length-frequency histograms sampled in consecutive summers exhibited modes in similar positions, the modes representing consecutive age classes except the last mode which corresponded with two age classes. This age structure did not vary substantially between years. It was possible to follow the progression of the 1986–1988 age groups through all or part of the time series (Fig. 1). In this way, the seasonal growth rate was determined using mean length increments of the different cohorts caught during the study period (this analysis was restricted to 0+, 1+ and 2+ year fish, because, for these fish, the estimated mean lengths did not differ for age groups determined from scales and by length-frequency analysis) and extrapolating to eviscerated mass using length-mass relationships (Table III).

There was little difference in the growth rates between seasons, although the highest growth rate was observed in summer. The growth period was long (9–10 months), with a suggestion of a short non-growing period during winter. There was a tendency towards a reduction in the seasonal growth rates with age (Table III).

Annual growth rates during the period from spring–summer 1988 to spring–summer 1989 decreased with age (1988 cohort (0+ years): $G_L = 44.8\%$ $G_M = 147.9\%$; 1987 cohort (or 1+ years): $G_L = 14.9\%$ $G_M = 49.1\%$).

The relationships between L_T and M_{ED} (dependent variable) were estimated separately for mature males, mature females and immature fish. There were no significant differences between mature fish (ANCOVA $F_{3,836} = 1.750$, $P = 0.155$, slope) but this relationship was different between mature and immature individuals (ANCOVA, $F_{3,1084} = 18004.4$, $P < 0.001$, slope). No group presented differences over time in these relationships (season as a factor; mature specimens ANCOVA, $F_{3,836} = 1.788$, $P = 0.148$ in the slope; immature specimens ANCOVA, $F_{3,248} = 1.071$, $P = 0.326$, slope). Therefore, the L_T – M_{ED} relationship was used for all mature individuals ($b = 3.10 \pm 0.11$, 95% CL, $r^2 = 0.928$, $F_{1,838} = 10776.6$, $P < 0.001$) and immature individuals ($b = 3.43 \pm 0.05$, 95% CL, $r^2 = 0.983$, $F_{1,250} = 19230.6$, $P < 0.001$) separately to obtain the standardized residuals.

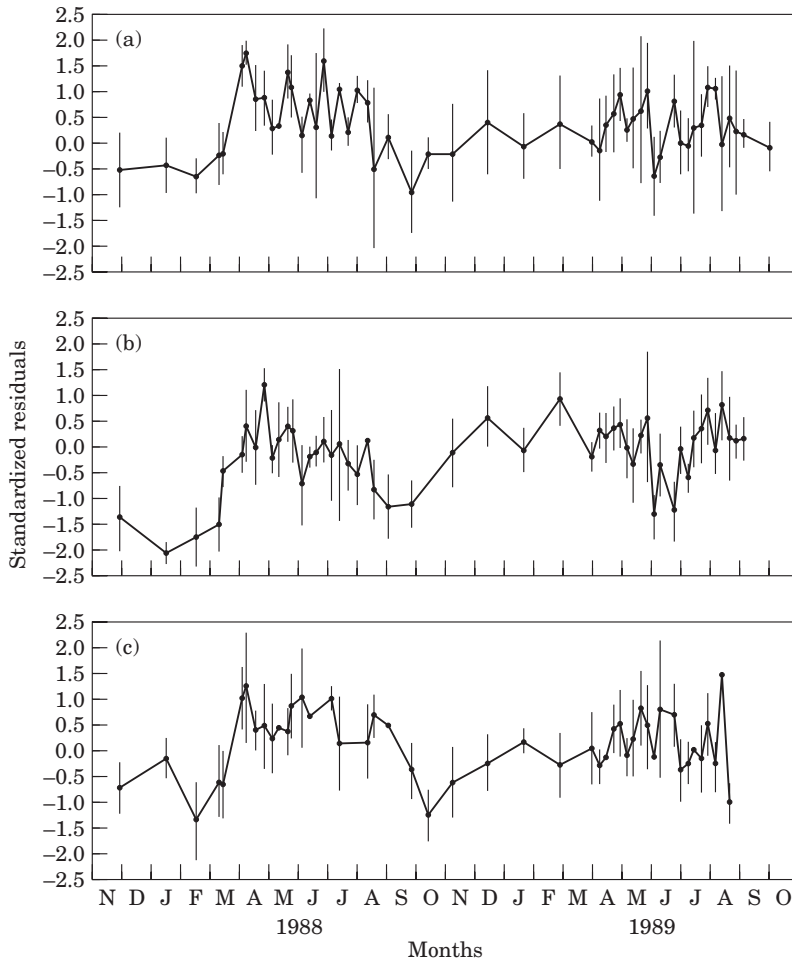


FIG. 2. Seasonal changes in somatic condition for (a) immature, (b) mature males and (c) mature females of *Cobitis paludica* populations located in the Mascatomiza Stream. Mean \pm 95% CL of L_T and M_{ED} relationship standardized residuals for samples of five or more fish.

Significant changes were obtained in the temporal variation of somatic condition (Kruskal–Wallis test; immature: $H=105.8$, d.f.=48; males $H=152.3$, d.f.=52; females $H=223.1$, d.f.=51; $P<0.001$). A similar somatic condition cycle was evident in both sexes and immature fish, although this was clearer in 1988 than in 1989 (Fig. 2). The mean maximum values were reached from April to late July. In August, the condition progressively decreased to reach minimum values for the cycle at the end of summer in mature specimens and 1 month later in immature fish. During the autumn, the condition increased until March (with greater increase in females), before maximum values were again reached.

Females had a similar somatic condition in the two breeding seasons (two-way ANOVA, $F_{1,368}=1.54$, $P=0.216$), while the condition of males was significantly lower for the second breeding season (two-way ANOVA, $F_{1,242}=5.60$, $P<0.05$).

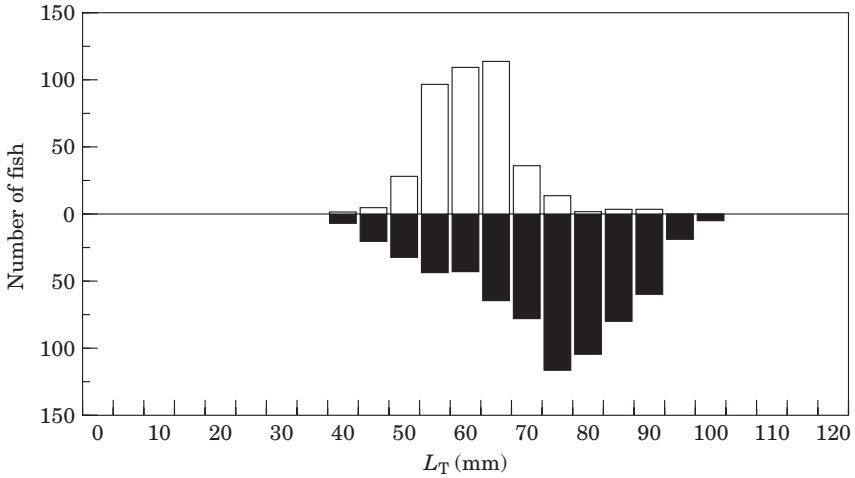


FIG. 3. Length frequencies of males and females of *Cobitis paludica* caught in the Mascatomiza Stream during the study period. (□), males ($n=412$); (■), females ($n=674$).

REPRODUCTION

Sex-ratio

There was a significant difference from 1 : 1 in the overall sex ratio (412 males to 674 females, $0.61 : 1$; $\chi^2=63.2$, $P<0.05$) (Fig. 3) and in mature specimens ($0.74 : 1$; $\chi^2=22.5$, $P<0.05$). Females were dominant significantly through the study period, except in February, May and October of 1988, when the proportion did not significantly differ from 1 : 1 (February, $\chi^2=0.06$; May, $\chi^2=0.39$; October $\chi^2=0.04$; $P<0.05$). The number of males was significantly higher ($1.65 : 1$; $\chi^2=308.6$, $P<0.01$), however, in the lower length classes ($L_T<65$ mm) (Fig. 3).

Length at maturity

Both sexes reached maturity at the beginning of their second year of life. All males were mature at 53 mm L_T and all females at 64 mm L_T . The smallest mature specimens caught in each sex were a male of 48 mm L_T and a female of 58 mm L_T .

Gonad development

The regression between L_T and M_{GD} (dependent variable) were estimated separately for sexually mature males ($L_T \geq 53$ mm) and females ($L_T \geq 64$ mm) and there were significant differences between these relationships (ANCOVA, $F_{3,836}=1085.9$, $P<0.001$, slope). There were no differences over time in these relationships for either sex (season as a factor; mature males ANCOVA, $F_{3,332}=0.747$, $P=0.625$, slope; mature females ANCOVA, $F_{3,491}=1.043$, $P=0.373$, slope). Therefore, the standardized residuals of female and male L_T and M_{GD} relationships (males: $b=4.76 \pm 0.62$, $\pm 95\%$ CL, $r^2=0.640$, $F_{1,334}=266.7$, $P<0.001$; females: $b=7.50 \pm 0.40$, $\pm 95\%$ CL, $r^2=0.823$, $F_{1,493}=1335.4$, $P<0.001$) were used separately.

Significant changes were obtained in the temporal variation of gonad activity (Kruskal–Wallis test; males $H=217.7$, d.f.=51; females $H=299.7$, d.f.=53;

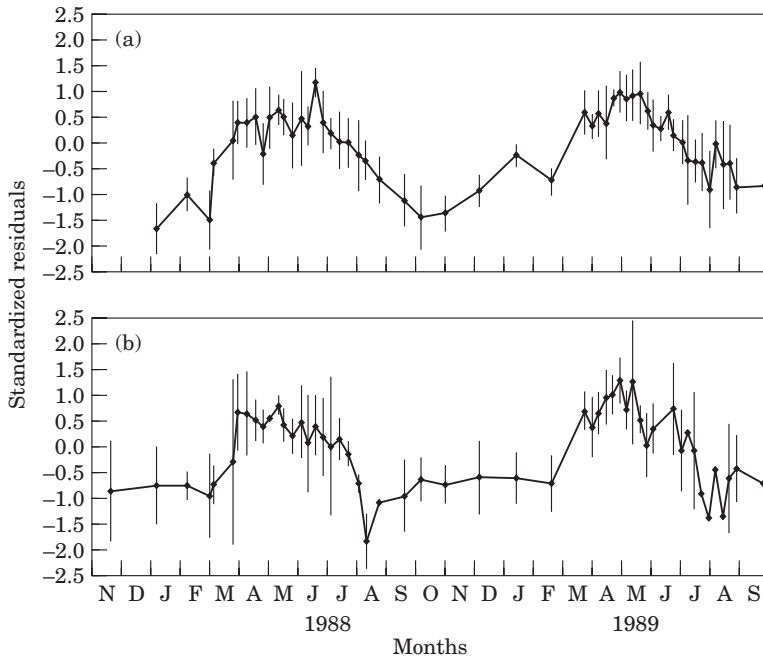


FIG. 4. Seasonal changes in gonad activity for mature (a) females and (b) males of *Cobitis paludica* populations located in the Mascatomiza Stream. Mean \pm 95% CL of L_T and M_{GD} relationship standardized residuals for samples of five or more fish.

$P < 0.001$). In both sexes, three phases were identified in gonad activity: quiescence, maturation and the reproduction phase (when the residual values were greatest). The ovary began to develop between December and January [Fig. 4(a)] after a quiescent period of 3 months (September–November), although the greatest increase was in late March and early April, at the beginning of spawning. Testes development began in early October [Fig. 4(b)] after a short quiescent period (August–September), while the greatest increase was in March. Both sexes had maximum residual values in spring (April–June) with the maximum monthly value in April 1989. These values represented 11.46 and 1.52% of the total mass for ovaries and testes, respectively. The index decreased sharply between July and the beginning of the quiescent period (August).

The pattern of gonad activity was similar in both study periods (Fig. 4). Weekly sampling, during the two reproduction periods, revealed five or six peaks in gonad activity. In males, however, the residual values of the second reproductive period were significantly higher (two-way ANOVA, $F_{1,223} = 8.70$, $P < 0.05$), females had similar values in the two reproductive periods (two-way ANOVA, $F_{1,358} = 0.814$, $P = 0.368$).

Egg development

Not all the ovaries reached the same stage of development at the same time, although the frequency distribution of egg diameters in twelve females of similar length (Fig. 5) showed a representative sequence of events and illustrated the general pattern of egg development.

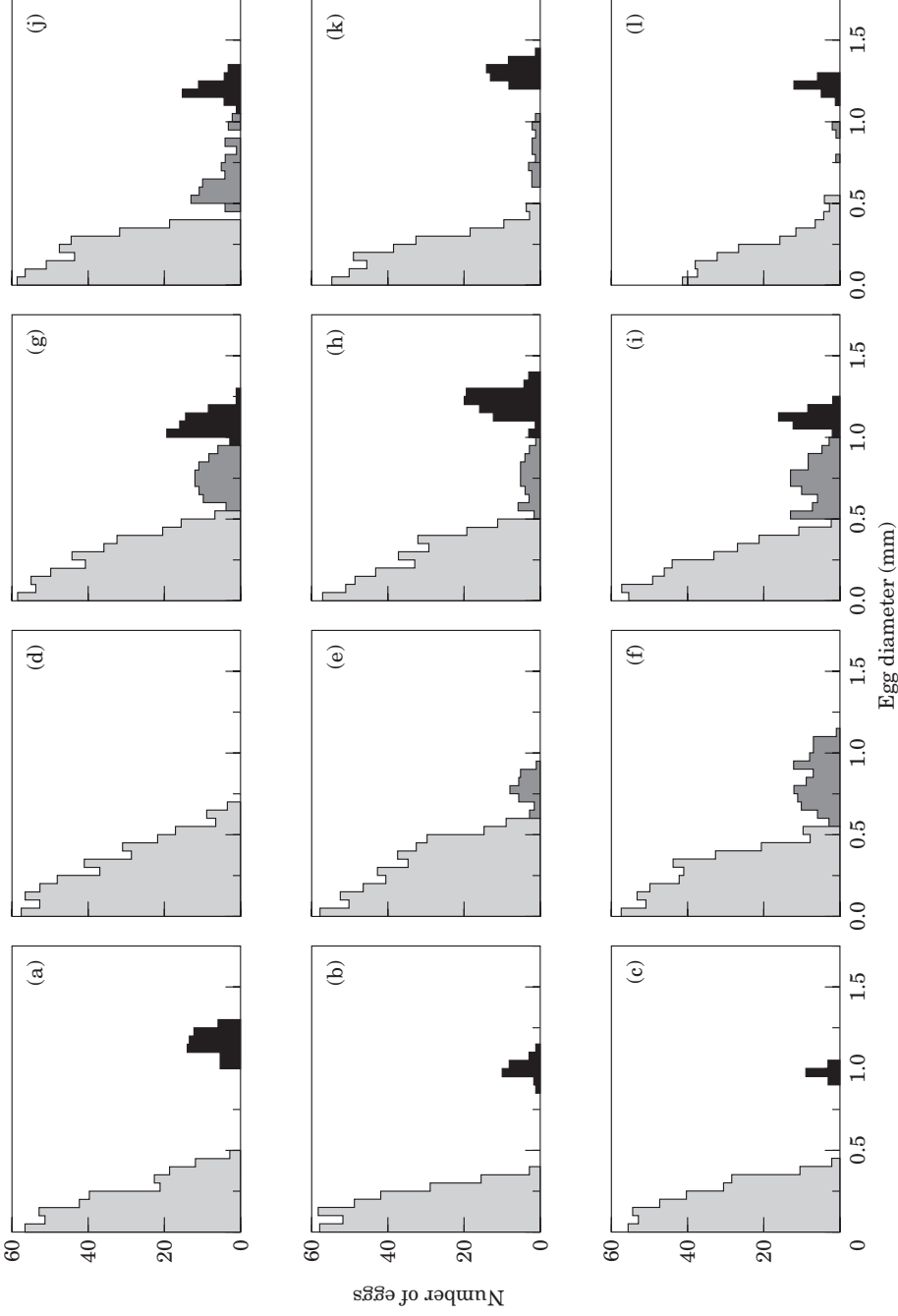


FIG. 5. Size-frequency distribution of eggs from 12 *Cobitis paludica* females (a)–(l), after the spawning period; (d)–(g), before the spawning period; (h)–(l), during the spawning period. □, Immature oocytes (transparent eggs); ■, oocytes in maturation process (opaque eggs); ■, mature oocytes (yolky eggs). (a) 19th August 1988, 379 eggs; (b) 13 September 1988, 332 eggs; (c) 29 November 1988, 338 eggs; (d) 5 January 1989, 493 eggs; (e) 11 February 1989, 502 eggs; (f) 16 March 1989, 545 eggs; (g) 31 March 1989, 595 eggs; (h) 14 April 1989, 478 eggs; (i) 21 April 1989, 499 eggs; (j) 25 May 1989, 516 eggs; (k) 9 June 1989, 369 eggs; (l) 21 July 1989, 253 eggs.

During the quiescent period the ovaries only contained transparent recruitment eggs (diameter <0.5 mm) and a small batch of yolky eggs (yellow and orange eggs), which decreased in number during this period [Fig. 5(a)–(c)]. In January vitellogenesis started [Fig. 5(d)], most of the ovaries at this time had no yolky eggs, which had probably been reabsorbed. In February and early March, most ovaries showed a bimodal distribution, one made up of transparent oocytes and the other of opaque eggs (yellow and white eggs; diameter = 0.738 ± 0.005 mm, mean \pm 95% CL). These probably constituted the eggs to be spawned in that year. In late March and early April, the mode representing opaque eggs divided into two, and ovaries now showed a trimodal egg size distribution: transparent, opaque and yolky eggs (diameter = 1.073 ± 0.009 mm, mean \pm 95% CL) [Fig. 5(g)]. The eggs in this last mode continued growing to the maximum size, coinciding with maximum gonad activity and prior to the onset of reproduction [Fig. 5(h)]. Ovaries during the spawning period had a group of opaque eggs which decreased in number during this period and another group of yolky eggs which reached maximum diameter in June (diameter = 1.278 ± 0.016 mm, mean \pm 95% CL) [Fig. 5(i), (j), (l)].

Fecundity

The number of eggs differentiated until the onset of the spawning period (March to early April) was plotted against L_T and using fish collected in both years. There were no significant differences in the regressions obtained for either of the two periods studied (ANCOVA, $F_{3,72}=1.057$, $P=0.373$, slope), so data were pooled and the best regression between ovarian fecundity per spawning (F_{OV}) and L_T was obtained: $F_{OV}=6.76 (10^{-5}) L_T^{3.82}$, $r=0.68$, $F_{1,70}=85.9$, $P<0.001$).

Relative fecundity measured as the residuals of the regression between $\log F_{OV}$ and $\log L_T$ changed significantly (ANOVA; 1988, $F_{4,29}=5.08$, $P=0.003$; 1989, $F_{5,68}=7.65$, $P<0.001$) and decreased significantly ($b_{1988} = -0.51 \pm 0.22$, \pm 95% CL, $r=0.64$, $F_{1,31}=22.18$, $P<0.001$; $b_{1989} = -0.29 \pm 0.10$, \pm 95% CL, $r=0.56$, $F_{1,69}=32.34$, $P<0.001$) as the spawning period progressed, which suggests that there was no recruitment from the stock of transparent oocytes to the mature stock once spawning had started.

The number of mature females whose ovaries contained a mode of yolky eggs displayed five or six peaks in both reproductive periods, coinciding with the peaks observed for gonad activity (Fig. 4). Nevertheless, the peaks refer to the total female population, not individual fish. By following increases in yolky egg diameter during the reproductive period (Fig. 6), it was possible to detect three maturation cycles in the population, although not in individual females. Moreover, relative fecundity calculated only for yolky eggs varied significantly (ANOVA; 1988, $F_{4,28}=3.77$, $P=0.014$; 1989, $F_{4,63}=2.60$, $P=0.044$) and diminished significantly ($b_{1988} = -0.45 \pm 0.24$, \pm 95% CL, $r=0.56$, $F_{1,31}=14.20$, $P=0.001$; $b_{1989} = -0.15 \pm 0.11$, \pm 95% CL, $r=0.31$, $F_{1,69}=6.98$, $P=0.01$) from the beginning to the end of the spawning period. This suggests that the number of yolky eggs decreased only slightly during this period, so that, while the number of oocytes developed in each of the batches differed, there were no significant differences in mean egg diameters between batches (ANOVA; 1988, $F_{2,30}=0.59$, $P=0.56$; 1989, $F_{2,65}=2.56$, $P=0.084$).

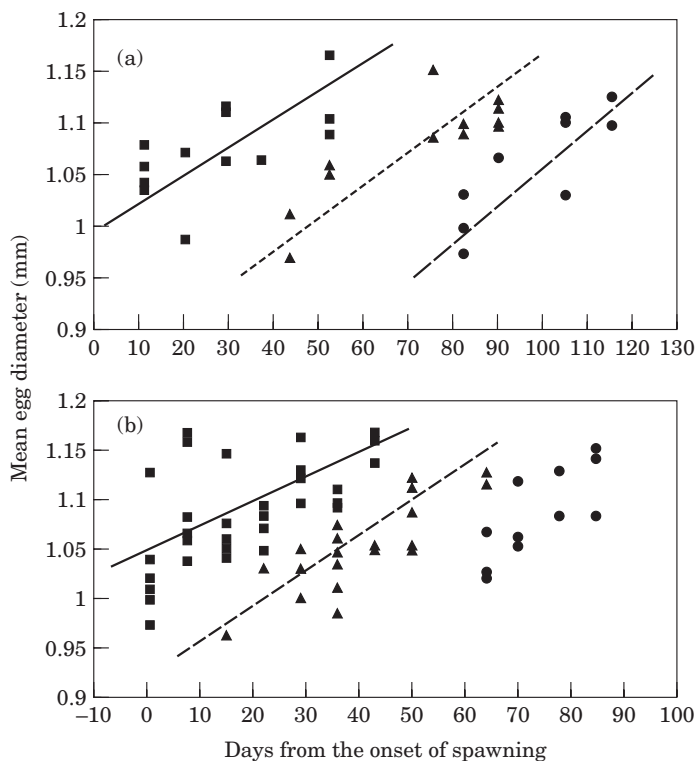


FIG. 6. Increase in the mean diameter of yolky eggs (mm) in *Cobitis paludica* during the (a) 1988 and (b) 1989 reproductive periods. CL have been omitted for clarity. ■, ▲, ●, Yolky eggs of the different maturation cycles.

Only in the 1989 reproductive period did the mean diameter of yolky eggs depend, but not strongly, on female L_T ($b_{1988}=0.00 \pm 0.002$, $\pm 95\%$ CL, $r=0.06$, $F_{1,31}=0.115$, $P=0.737$; $b_{1989}=0.0026 \pm 0.0015$, $\pm 95\%$ CL, $r=0.33$, $F_{1,69}=8.37$, $P=0.005$).

DISCUSSION

The age structure of *C. paludica* specimens caught in Mascatomiza Stream differs from that observed in the Jarama River (Lobón-Cerviá & Penczak, 1984) and in the Lozoya River (Przybylski & Valladolid, 2000), both sites located in the Tajo River basin, at a more northern latitude than the present study site. It also differs, however, from the population of Palancar Stream (Soriguer *et al.*, 2000) located at the same latitude. There were fewer age groups in Mascatomiza Stream population than in the Lozoya River and Palancar Stream populations (Table IV), while the maximum lengths observed in the Lozoya River (83 mm for females; 57 mm for males) and in Palancar Stream (90 mm for females; 85 mm for males) were smaller than those observed in the present study (99 mm for females; 90 mm for an exceptional male). The study area on the Lozoya River was a regulated stretch with high and unpredictable flow variations (Valladolid & Przybylski, 1996), characteristics which might have determined the greater

TABLE IV. Age structure in different European populations of *Cobitis*

Species	Locality	Age groups	References
<i>C. paludica</i>	Mascatomiza Stream (Spain)	4+ (f) 3+ (m)	This study
<i>C. paludica</i>	Palancar Stream (Spain)	5+ (f) 4+ (m)	Soriguer <i>et al.</i> (2000)
<i>C. paludica</i>	Lozoya River (Spain)	5+ (f) 3+ (m)	Przybylski & Valladolid (2000)
<i>C. paludica</i>	Jarama River (Spain)	3+ (*)	Lobón-Cervía & Penczak (1984)
<i>C. taenia</i>	Psovka River (Czech Republic)	4+ (f) 3+ (m)	Slavík & Ráb (1995, 1996)
<i>C. taenia</i>	Timonchio River (Italy)	4+ (f) 3+ (m)	Marconato & Rasotto (1989)
<i>C. taenia</i>	Great Ouse River (England)	3+ (f) 2+ (m)	Robotham (1981)
<i>C. aurata</i>	Syr Darya River (Tadzhikistan)	3+ (*)	Maksunov (1969)

f, Females; m, males; *, sexes were not separated.

longevity, which would be a feasible mechanism to counteract the mortality of fish larvae and juveniles caused by changing water velocity (Keckeis & Schiemer, 1992; Torralva *et al.*, 1997). In general, European populations of *Cobitis* show two main characteristics in their age structures: a low number of age-groups and greater life expectancy in females (Table IV).

Cobitis paludica grows rapidly during the year before first spawning (females $L_T = 50.0 \pm 2.1$ by the first autumn). For the population studied 65–70% of the total potential growth in length occurred during the first year of life (females $L_T = 57.4 \pm 2.0$), meaning that the annual increase in growth diminishes markedly after sexual maturity. The length reached in the first year of life is similar to the 41.8 mm (L_S) and 53 mm observed in the Lozoya and Jarama Rivers, respectively, but higher than 37.43 mm (males) and 36.00 mm (females) proposed from von Bertalanffy's model for the Palancar Stream population.

A high growth rate during the first year has been observed in other small fish species living in the same stream (Fernández-Delgado & Herrera, 1994, 1995b). The hydrological cycle of the Mascatomiza Stream is typical of the Mediterranean area, where flow ceases in the summer and the river consists of small isolated pools. During this period, all fishes living in the river become concentrated in these habitats. Hence, fish density increases and competition for space and food may become important. Associated with these changes in environmental conditions, basic changes may occur in life history attributes (Schlosser, 1991). In the Mascatomiza Stream a high growth rate in the first year of life may be an adaptation to increase fitness rapidly.

The somatic condition cycle reflects this seasonality, especially at the end of summer, when the index reaches its lowest values. With the arrival of the autumn rains, this index increases to reach maximum values in spring. At the end of spring and in early summer (when spawning begins) variations in this index were observed, particularly in mature specimens, possibly related to the

transfer of energy to the gonads. This pattern is similar to those found in other species in the same stream (Herrera *et al.*, 1988; Herrera & Fernández-Delgado, 1992; Fernández-Delgado & Herrera, 1994).

The proportion of males to females in the present samples of *C. paludica* differed significantly from parity (in overall specimens 0.61 : 1; in mature specimens 0.74 : 1) and was unlike that found by Lobón-Cerviá & Zabala (1984). Bohlen & Ritterbusch (2000) proposed the dominance of polyploid sperm parasite as the main reason for the observed unbalanced sex ratio in genus *Cobitis*. A single electrofishing carried out per sample, however, may mean the number of females could have been overestimated (Marconato & Rasotto, 1989).

Sexual maturity was reached between the end of the first year of life and the beginning of the second year. Although no data on the age of maturity in other populations of this fish species are available, according to the life history theory, the cost of early maturity entails a reduction of life span (Roff, 1992).

The spawning period in females agrees with that proposed by Soriguer *et al.* (2000), but was longer than that proposed by Lobón-Cerviá & Zabala (1984) although the maximum values of the gonad activity were similar in both populations. Unlike these authors, seasonal changes in gonad activity in males were also detected.

The population of *C. paludica* in the Mascatomiza Stream is a multiple spawner (Mills, 1991) or batch spawner (Wootton, 1990) that releases batches of eggs between April and July–August, the same spawning period as in the Palancar Stream (Soriguer *et al.*, 2000) and 1 month earlier than in the Jarama population (Lobón-Cerviá & Zabala, 1984). Multiple spawning has also been suggested for *Cobitis taenia* L. (Marconato & Rasotto, 1989). This tactic has advantages in fluctuating environments, since progeny are not at risk in just one reproductive event when a climatic catastrophe could destroy the whole spawning in a particular year (Cambray & Bruton, 1984). Although the ovary is asynchronous, with oocytes in different stages of vitellogenesis, three maturation cycles of yolky eggs in the population were detected. Thus, a female may be able to spawn at least two hatches of eggs per breeding season. An estimation of fecundity suggests 1986 eggs for a 90 mm L_T female, which is higher than the 1400 eggs per female proposed by Lobón-Cerviá & Zabala (1984) and 1235 eggs proposed by Soriguer *et al.* (2000).

Because there is also a slight correlation between egg size and female size, it might be deduced that small *C. paludica* females in the Mascatomiza Stream need to maximize the number of eggs they produce as their fecundity is relatively low. Large females may be able to sacrifice some fecundity in favour of increasing the size of their eggs, which implies an increase in quality. Maximization of maternal fitness by sacrificing offspring survival (Einum & Fleming, 2000), however, may be an important phenomenon in this population.

The life-history pattern of this stock, located in a small and seasonal stream of southern latitude, is characterized by a low number of age groups, a high growth rate during the first year of life, early maturity, a short life-span and high egg production from multiple spawnings (at least two batches per female).

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