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Reproductive strategies of two species of cyprinids in a stream with Mediterranean regimen (SW Spain)

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With 5 figures and 3 tables

Abstract: This paper describes and compares the different reproductive strategies of two cyprinid species, *Barbus sclateri* (GÜNTHER 1868), barbel, and *Leuciscus pyrenaicus* (GÜNTHER 1868), Iberian chub, in the Palancar Stream, SW Spain. *B. sclateri* only spawns once per year, during June. Intermediate age classes contribute most to the fecundity of the population, because of the decrease in numbers of individuals with increasing age. The male : female ratio is 3 : 1. Males and females mature at age classes 1+ and 4+, respectively. The females of *L. pyrenaicus* use a reproduction strategy not previously described in other populations of this genus: females of *L. pyrenaicus* with a total length greater than 101 mm (mean length of age class 5+) spawn twice whereas smaller individuals (<100 mm) of this species spawn only once per year. This behaviour increases the length of the spawning period and increases the fecundity of the population. The male : female ratio is 1 : 1. These conclusions are based on a detailed morphometric and histological study of the ovarian development in the populations.

Introduction

Sclarer's barbel (*Barbus sclateri,* GÜNTHER 1869) and the Iberian chub (*Leuciscus pyrenaicus*) are two endemic species from the central southern part of the Iberian Peninsula. These species co-exist in the Algarve, Guadiana and Guadalquivir river basins, in the south of Spain, and in that of the River Segura (HERNANDO & SORIGUER 1992), from their main courses up as far as the tributary streams that are subjected to seasonal variations in flow depending on rainfall.

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The Palancar stream is a typical affluent of Mediterranean regimen in the basin of the River Guadalquivir, which is characterised by wide variations in flow rate according to the rainfall regime (VIDAL-ABARCA et al. 1992). This makes its flow irregular, increasing strongly in winter but with very low water levels at other times (GUIDICELLI et al. 1985). Such unstable environmental conditions present difficulties for the aquatic species, given the effect on the physical, chemical and hydrological characteristics of the stream caused by unpredictable and often extreme fluctuations (MARGALEF 1983). The communities of fish that inhabit this type of stream become forced to adapt their life cycles to the hydrological fluctuations.

In this paper we study the reproductive strategies of two cyprinid species, Sclarer's barbel and Iberian chub, which coexist in Palancar stream. We identify the differences between them, and we provide new information regarding reproduction, adding to existing knowledge of the ecology of populations of cyprinids in Iberian rivers in the Mediterranean basin (HERRERA & FERNÁNDEZ-DELGADO 1992, RODRIGUEZ-RUIZ & GRANADO 1992, MAGALHÃES 1993, FERNÁNDEZ-DELGADO & HERRERA 1995, TORRALVA et al. 1997). Most previous studies have dealt with the species individually. To date, there have been no studies of the relationship between the two species in order to illustrate the mechanisms that have developed to facilitate their coexistence.

Material and methods

Study area

The Palancar stream is a small second order tributary of the central watercourse of the Guadalquivir River which crosses Andalusia from the NE to the SW, flowing into the Gulf of Cádiz. The study area is situated in the Natural Park of the Subbetic Sierra, (37° 27′ 46″ N, 4° 16′ 40″ W to 37° 27′ 59″ N, 4° 15′ 40″ W). Its geology consists of clays and marls with gypsum from the Trias. The stream originates at an elevation of 990 m and flows for 13 km from west to east. The fish assemblage in this river consists of the two cyprinid species and *Cobitis paludica* (BUEN 1930).

Field and laboratory methods

After examining the entire course of the stream, four sub-areas of 100 m length were selected as representative of the different types of habitat present in the stream (deeper pools, rapids, bank characteristics, etc.); the populations of cyprinids present also show well-defined structures. Measurements of the physical and chemical variables and samples of fish were taken at different points. To carry out the bathymetry, in each sub-area, transversal transects were made at 1 m intervals. At each transect, depth was measured at intervals of 25 cm. Maximum and mean depth and maximum, mean and minimum width of the watercourse are recorded in Table 1.

Table 1. Morphology and bathymetric characteristics of the watercourse at four sub-areas of the sample site.

Parameters	Unit	Sub-area 1	Sub-area 2	Sub-area 3	Sub-area 4
Mean width	cm	113	150	180	375
Maximum width	cm	150	175	375	475
Maximum depth[1]	cm	17	25	81	78
Mean depth	cm	10	7	18	37
Length	m	100			
Water velocity	m/s	1 (in winter)–0.1 (in summer)			
Morphology		Riffles	Riffles	Pools and Riffles	Pools
Substratum[2]		m = g > s	m >> s	m = g = s	m > g > s
Submerged plants		Abundant	Moderate	Few	Few
Trees along banks		Few	Moderate	Abundant	Abundant

[1] During the winter floods, the stream may burst its banks, reaching a depth of 2 m.
[2] m = mud, g = gravel, s = stones.

Samples were collected monthly for 30 min from August 1990 to July 1991, using electric shock pulsing equipment that consisted of an 800 W generator and a rectifier. Specimens captured were frozen to avoid the distorting effects of fixation and transported to the laboratory where the following parameters were measured for each specimen: total length (TL ± 1 mm), total weight (W ± 0.01 g) and somatic weight (SW ± 0.01 g) (corresponding to the fresh weight after removing the digestive tract and gonads). Scales from the left side of the body between the dorsal fin and lateral line, near the pectoral fin, were removed to determine the age, a technique that has been validated in many research studies of cyprinids in Iberian rivers (Lobón-Cervía 1982, Lobón-Cervía & Fernández-Delgado 1984, Herrera et al. 1988, Herrera 1991, Herrera & Fernández-Delgado 1992, Fernández-Delgado & Herrera 1995, Soriguer 1996, Torralva et al. 1997). The fish were sexed by inspection of gonads, and classified into one of three categories: mature male, mature female and immature. Ovary fresh weight was measured (OW ± 0.0001 g). After weighing, the ovaries were preserved whole in Gilson's fluid (Bagenal & Braun 1978). The number at oocytes in each gonad was calculated using a system of subsampling by area (Herrera et al. 1988). The diameter of the oocytes was measured (mm ± 0.001) with a profile projector and these were separated into vitelline (i.e. with yolk) and transparent or non-vitelline (i.e. without yolk). The mean diameter and the proportions of the different size classes present were calculated. Absolute fecundity was estimated as the number of mature eggs present in the ovary immediately prior to spawning. The relative abundance of each class in the samples was used to determine the percentage contribution of each age class to the total fecundity.

The individuals used for the histological study of reproduction were females of *B. sclateri* and *L. pyrenaicus* captured in July, November, January and May, corresponding to the four climatic seasons. Portions of the ovary of 1.5–2.5 cm length were taken after capture and were fixed in situ in an aqueous solution of formaldehyde, buffered with 10 % phosphate (0.1 M at pH 7.2). They were kept in this solution for a minimum of 24 h, after which time they were processed and put in paraffin at 56 °C melting point. The sections obtained were stained with haematoxalin-eosin and toluidine blue at pH 9.2, then observed by light microscopy.

Results

Barbus sclateri (GÜNTHER 1868)

A total of 559 specimens of this species were captured: 113 males, 37 females and 409 immatures. The sex ratio was 3 : 1. Captured mature males were from age class 1+ and older, and were larger than 60 mm total length, whereas the smallest mature females caught measured 90 mm and were age 4+ above, implying earlier maturation of the males. The mature males numerically dominated up to age class 7+ and after this age, populations were dominated by mature females. In age classes in which both sex-determined and immature fish coexisted, the former were always of larger size (Table 2).

The GSI (percentage of gonad weight/total weight) was calculated for mature females older than 4+, after this age all specimens were sexually fully developed. Seasonal development of this parameter (Fig. 1) shows a dormant period between August and November, after which time the gonads begin to grow slowly until April, when they represent about 6 % of total body weight. In May, gonad growth is substantial and the ovaries reach almost 17.5 % of the total body weight. High values are maintained in June and decrease sharply from July onwards.

Table 2. Total number of fish captured (N) in each age class, mean total lengths at capture (TL) and standard deviation (mm) of immatures, mature males and mature females in *B. sclateri* and *L. pyrenaicus*, in those age classes in which sex-determined and immature fish coexist.

Age	Immatures		Mature males		Mature females	
	N	TL	N	TL	N	TL
Barbus sclateri						
0+	259	36.51± 5.79				
1+	130	63.46± 6.90	3	70.77± 7.68		
2+	43	76.56± 6.90	33	87.63± 8.79		
3+	6	97.00± 4.5	23	110.5 ±11.33		
4+	1	115.0	41	132.8 ±13.61	8	132.9 ± 9.21
Leuciscus pyrenaicus						
0+	150	31.81± 5.73				
1+	102	49.88± 8.02				
2+	89	65.50± 9.07	10	70.67±13.91		
3+	39	78.81±10.07	21	86.00±12.20	20	90.67±10.66
4+	15	96.90± 7.34	17	104.21± 9.89	28	112.08±11.75

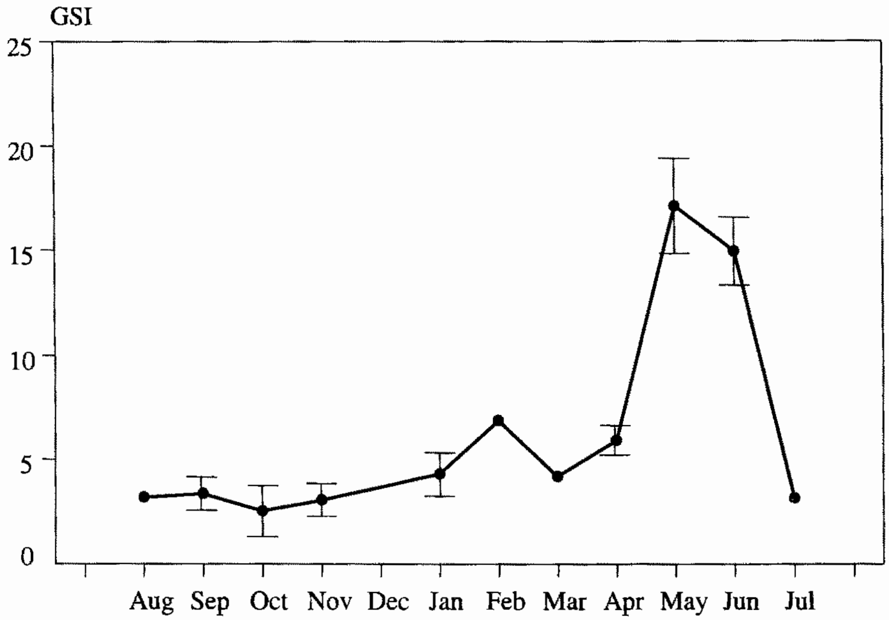

Fig. 1. Monthly changes (1990–1991) in gonadosomatic index (GSI) of *B. sclateri*, expressed by the ovary weight as a percentage of total weight. Vertical lines represent standard deviations.

The monthly variation of the frequency distribution of oocyte diameters (Fig. 2) confirms the existence of the cycle shown by changes in GSI. There is only one mode in the dormant period, August to November, which corresponds to vitelline oocytes with a diameter smaller than 0.5 mm. A second mode, corresponding to larger oocytes, is observed between December and April, becoming very marked in April. In May and June the third mode, comprised of oocytes between 1.6 and 2.0 mm diameter, can be clearly observed, which corresponds to a suitable size for spawning. This third mode disappears in July after spawning has taken place and part of the second mode still remains, formed by oocytes that have not spawned, which may possibly be reabsorbed.

The correlation coefficient between the mean monthly value of GSI and the mean oocyte diameter is $r = 0.90$, $R^2 = 0.817$ ($p < 0.001$). The increase in the percentage of vitelline oocytes each month follows the same temporal pattern as growth in oocyte diameter and GSI. The proportion of vitelline oocytes is very low in October and November but from December onwards begins to increase gradually until it reaches maximum values in April and May; it then begins to decrease until September.

Total fecundity was calculated from 15 females captured in the period prior to spawning, using the expression: $F = 7.317 * 10^{-4} * L^{2.967}$ ($r = 0.88$, $p < 0.05$).

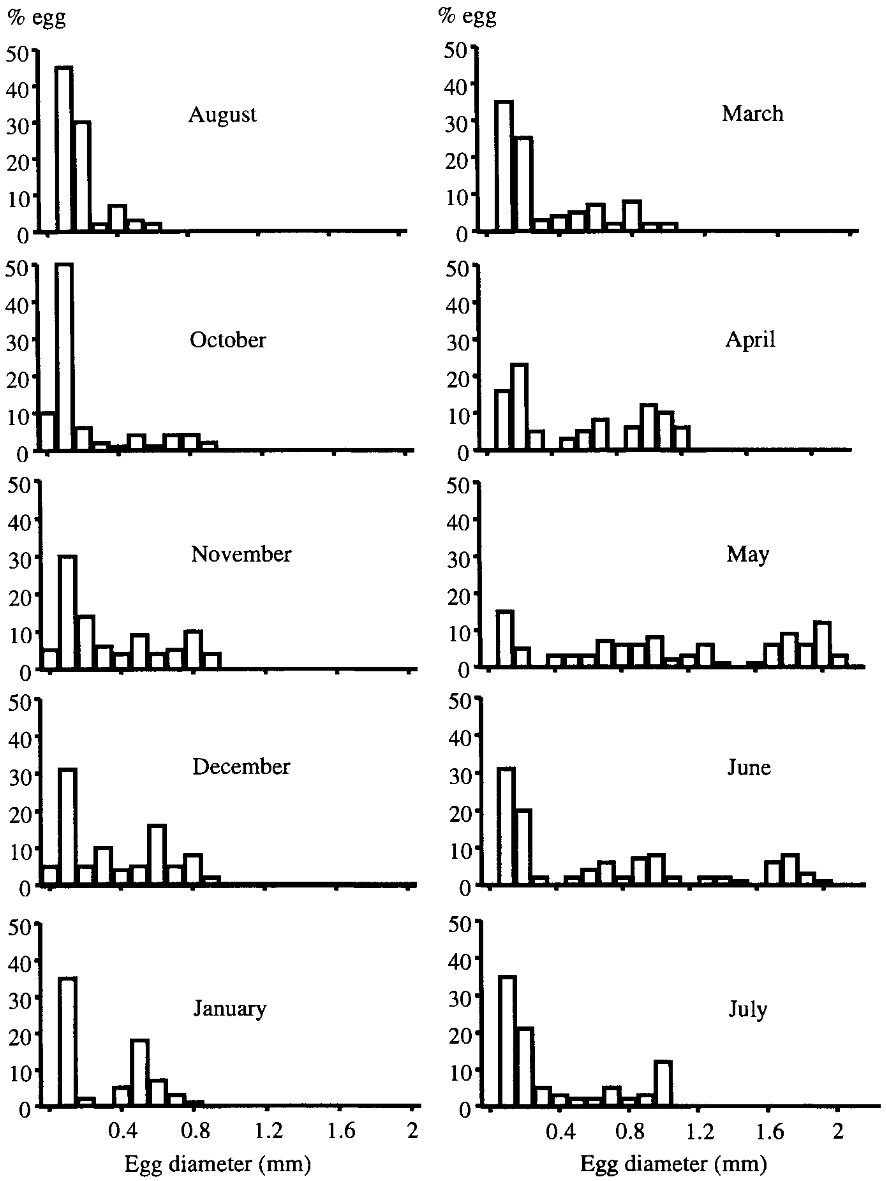

Fig. 2. Monthly (1990–1991) variation of frequency distribution of *B. sclateri* oocyte diameter.

The percentage contribution of each age class to the total fecundity (Table 3), calculated in the pre-spawning period, shows that the largest contribution is by the intermediate ages, mainly age 5+, after which it begins to decrease.

Table 3. Percentage of total fecundity contributed by age classes in *Barbus sclateri* (*B. s*) and *Leuciscus pyrenaicus* (*L. p*) populations.

Age class	3+		4+		5+		6+		7+		8+	
Species	*L. p*	*B. s*	*L. p*	*B. s*	*L. p*	*B. s*	*L. p*	*B. s*	*L. p*	*B. s*	*L. p*	*B. s*
Number of females	10	–	7	4	9	5	–	3	–	2	–	1
Contribution %	24	–	27	9	48	32	–	25	–	19	–	15

Leuciscus pyrenaicus (GÜNTHER 1868)

A total of 619 individuals of this species were captured, of which 395 were immatures. The proportions of mature males and mature females are almost equal, at 46.4 % and 53.6 %, respectively. As in other populations studied (LOBÓN-CERVÍA 1982), we found specimens which were of sufficient size to be sexed, but which were still not determinable (Table 2). The youngest mature female captured belonged to age class 3+ (TL = 75 mm) whereas the males mature by age class 2+, the smallest with TL = 65 mm. There were no males belonging to age class 7+.

The GSI of mature females smaller than 101 mm total length (mean TL, females ages class 5+) and of those longer than 101 mm showed similar behaviour trends during the dormant period until September and during the slow growth stage, which continues until March (Fig. 3). In the case of the group with TL <101 mm (a), rapid gonad growth takes place during May, is somewhat less in June and decreases from then on, whereas the start of accelerated growth of the ovaries in females with TL >101 mm (b) takes place earlier, in April. The GSI of the latter group decreases in May and increases again in June when the GSI in some females reaches 25 % of the body weight, after which time it begins to decrease again.

The frequency distribution of the diameters of oocytes in mature females captured throughout the year (Fig. 4) shows the existence of a single mode of transparent (non-vitelline) oocytes with a diameter less than 0.2 mm in September. This mode continues in October but then the diameter increases to around 0.4 mm. In November, a second mode of around 0.5 mm in diameter appears, which becomes the more predominant mode by March. In April, the oocytes of mature females <101 mm are not yet large enough for spawning, whereas in mature females >101 mm another mode appears of oocytes 1 mm in diameter. This situation is reversed in May, at which time the oocytes of the first group of females reach 1.2 mm diameter. In June all the captured females present a mode of oocytes of diameter greater than 1 mm that continues until July.

The relationship between fecundity (F) and total length (TL) in mm in this species is described by the expression: $F = 7.861 * 10^{-2} * TL^{2.10704}$ (r = 0.88,

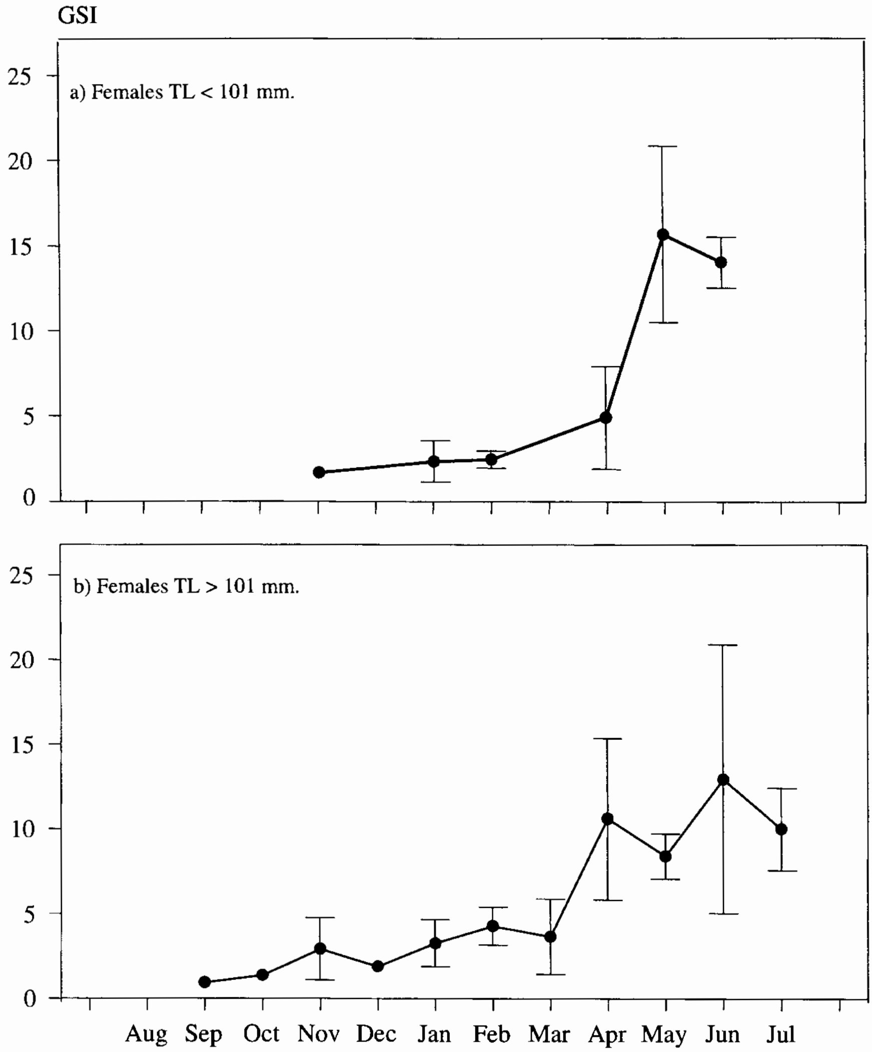

Fig. 3. Monthly (1990–1991) changes in gonadosomatic index (GSI) of *L. pyrenaicus* females: (**a**) Total length less than 101 mm and (**b**) total length more than 101 mm, expressed by the ovary weight as a percentage of total weight. Vertical lines represent the standard deviations.

$p<0.003$). The percentage contribution of age classes to total fecundity (Table 3) calculated from mature females captured in the pre-spawning period shows a predominance of age class 5+. There were practically no differences in the number of mature females of age classes 3+ to 5+ captured. Therefore, as the

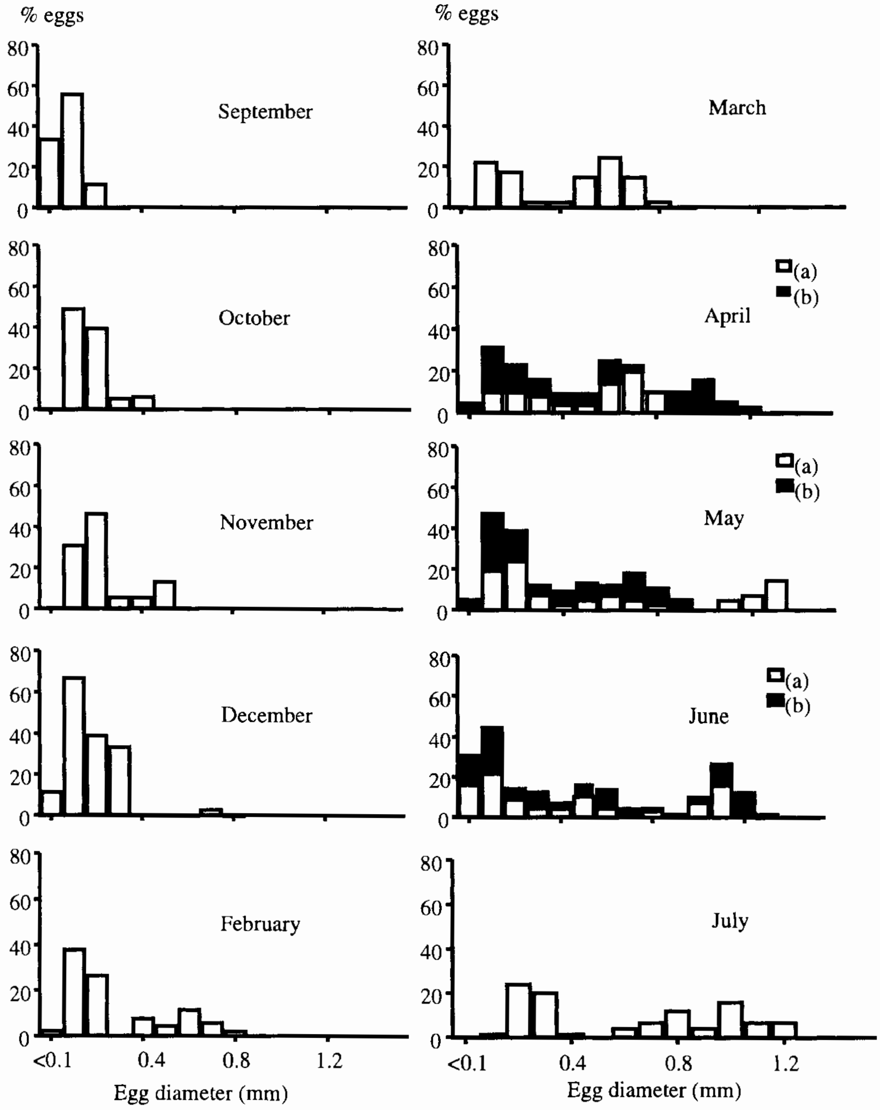

Fig. 4. Monthly variation (1990–1991) of frequency distributions of *L. pyrenaicus* oocyte diameter, where (**a**) corresponds to mature females of TL<101 mm and (**b**) TL>101 mm stacked bars.

fish length increases, the contribution to the fecundity of the population increases with age up to age class 5+.

Body size is the only morphological difference in the oocytes of these two species during their development. Therefore, in this paper, a sequence of four

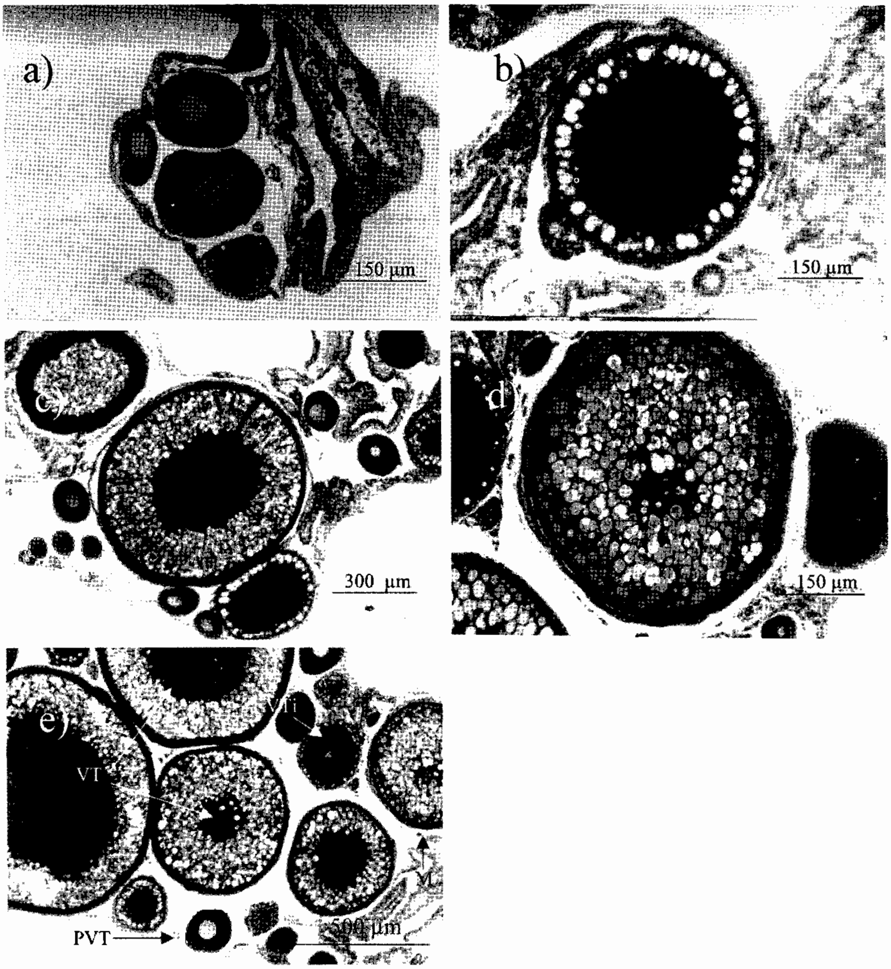

Fig. 5. Histological sections of ovaries of females of *B. sclateri,* at different stages of maturation. **a**) oocytes in pre-vitellogenesis; **b**) oocyte commencing vitellogenesis; **c**) oocyte in vitellogenesis; **d**) oocyte in the final stages of vitellogenesis, almost mature. **e**) section of ovary showing various oocytes present at different stages of maturation at the same time. PVT: in pre-vitellogenesis stage; Vti: in the initial stage of vitellogenesis; VT: in vitellogenesis stage; M: mature oocyte.

sections corresponding to *B. sclateri* is presented and one to *L. pyrenaicus,* which is representative of ovarian development during the course of the year. These results can be extrapolated to the ovarian development of *L. pyrenaicus.*

The first section (Fig. 5 a) corresponds to the period from the end of summer to the beginning of autumn. The oocytes are in the phase of pre-vitellogenesis, with clear nuclei in which fairly uniform nucleoli well-differentiated from the cytoplasm can be seen.

The second section (Fig. 5 b) corresponds to the end of autumn and the beginning of winter. The oocytes are commencing the vitellogenesis, with the appearance of vesicles of glycoprotein and vacuoles containing proteins and carbohydrates. The cytoplasm, until now still basophilic, becomes acidophilic as the oocyte grows. The follicular layer begins to be distinguishable.

The third section (Fig. 5 c) corresponds to the months of April and May. This is the period of vitellogenesis, characterised by the accumulation of yolk in the oocytes. There appear a large number of lipoprotein granules, circular in shape. The size of the oocytes increases notably in this period.

Lastly, in the fourth section (Fig. 5 d), corresponding to May and June, the vitellogenesis is complete, the granules have grouped together, the vesicles have joined together and the vacuoles have fused. The oocyte, now mature, has reached the optimum size for laying.

In fish which spawn more than once a year, like *L. pyrenaicus,* it is possible to differentiate a large number of oocytes at different stages of maturation, at the same time (Fig. 5 e). This is different from the development of *B. sclateri.*

Discussion

Changes in relative or absolute size of the ovaries throughout the reproductive cycle reflect growth of the oocytes and their accumulation of vitelline. The GSI of the females remains low during winter but grows rapidly during the month before spawning. This growth coincides with increasing day-length and temperature and is probably associated with an increase in food intake. Temperature and photo-period are considered to be the most important abiotic factors affecting temperate zone species (LAM 1982, BYE 1984, STACEY 1984, PONCIN et al. 1985, PONCIN & PHILLIPART 1986). WOOTTON (1979) casts doubt on whether temperature has a direct effect on the gonadal cycle. He suggests that the effect of temperature is indirect, due to its association with photo-period, food availability and the physiological requirements of individuals. The two cyprinid species coexisting in the Palancar Stream spawn between the end of spring and the beginning of summer. They have a prolonged dormant period until winter and rapid gonadal growth prior to spawning. In comparison with other populations in the Iberian Peninsula that have been studied, they have an early maturation in seasonal terms accompanied by decreased longevity and a drop in somatic growth (SORIGUER 1996).

In the *B. sclateri* population of the Palancar stream, females mature from age 4 onwards and the males mature from age 1+. These results are in accordance with those reported by HERRERA & FERNÁNDEZ-DELGADO (1992) for the populations in the Mascatomiza stream. However, this maturation is earlier than reported in other studies carried out in the Mascatomiza stream, in which maturation begins at age class 5+ and 2+, respectively (HERRERA et al. 1988), and in the *B. bocagei* population of the Jarama River, in which mature females and males belonging to age classes 6+ and 3+, respectively, were found (LOBÓN-CERVÍA 1982). The sex ratio of *B. sclateri* in the Palancar stream shows a clear predominance of mature males, as does the population of *B. barbus* studied by PENAZ (1977), while in other populations studied, the sex ratios are close to parity (LOBÓN-CERVÍA & FERNÁNDEZ-DELGADO 1984, HERRERA et al. 1988, HERRERA & FERNÁNDEZ-DELGADO 1992) or with mature female predominance (VITALI & BRAGHIERI 1984). In all the populations studied, mature females predominate in the older age classes. The GSI of mature females reaches values similar to those recorded for other populations at these latitudes in the same period of the year, in May (HUNT & JONES 1975, HANCOCK et al. 1976, LOBÓN-CERVÍA & FERNÁNDEZ-DELGADO 1984, VITALI & BRAGHIERI 1984, LUCENA et al. 1979, PONCIN et al. 1985, 1987, ENCINA 1991, HERRERA 1991). The frequency distribution of the oocyte diameter of this population shows one mode and coincides with the cycle described by HERRERA et al. (1988), and does not confirm the existence of two spawning periods as suggested by HERRERA & FERNÁNDEZ-DELGADO (1992). The fecundity found is greater than in European barbels (HANCOCK 1979, LOBÓN-CERVÍA & FERNÁNDEZ-DELGADO 1984) and is similar to that reported by HERRERA et al. (1988), but lower than that described by HERRERA & FERNÁNDEZ-DELGADO (1992).

The males and females of the Palancar Stream population of *L. pyrenaicus* mature early, at 2+ and 3+, respectively, as in other populations of this species in the Iberian Peninsula (LOBÓN-CERVÍA 1982, FERNÁNDEZ-DELGADO & HERRERA 1995). HARTLEY (1947), in a study of two populations of *L. leuciscus,* found that those females with a faster growth rate mature early, at 2+, whereas those with a slower growth rate mature at 3+. With respect to the GSI of *L. pyrenaicus,* FERNÁNDEZ-DELGADO & HERRERA (1995) showed that the highest value is reached in April and not at the end of spring or beginning of summer, as reported by ENCINA (1991). This study of the Palancar Stream population, separated into two size groups, shows a sequential maturation and the probable existence of two spawning periods in the larger females. Ovular development also seems to indicate the existence of two spawning periods in females larger than 100 mm TL. The existence of several spawnings or partial spawnings has already been suggested by FERNÁNDEZ-DELGADO & HERRERA (1995) for *L. pyrenaicus* and other cyprinids (HERRERA 1991) of the Mascatomiza stream. As in other studies carried out in rivers in the south of the Iberian Peninsula (ENCINA 1991, HERRERA 1991), reproductive cycles of fish at these latitudes are such that the spawning period coincides with the most productive season of the habitat, when the most food resources are available, in order to be able to satisfy the increased energy requirements associated with these processes (WOOTTON 1979, HIRSHFIELD 1980) and to assure increased larval and juvenile survival rates (STACEY 1984, BYE 1984).

The existence of at least two spawning periods has been demonstrated by HERRERA (1991) in *B. sclateri, Chondrostoma polylepis willcommi* and *L. pyrenaicus* in the Mascatomiza stream. In the Palancar stream, *L. pyrenaicus* shows a slower growth rate than other populations of the Iberian Peninsula, but successfully becomes the most abundant species in the river and is the only species with two spawning periods. The timing of the spawning periods of this species appears to be somewhat delayed compared to that of *B. sclateri.*

Multiple spawning is considered to be an adaptation to unfavourable and highly fluctuating conditions (CAMBRAY & BRUTON 1984), which is the main characteristic of Mediterranean rivers. It is very difficult to correlate environmental variables and changes in the reproductive strategies employed by species, and even more so to compare these strategies with those of other species when data on these environmental variables are not included in articles published on studies carried out.

In spite of this, we consider that the existence of two annual spawnings by *L. pyrenaicus* in the Palancar stream is a strategy imposed by the environmental conditions, since these are the only clear differences compared with other populations of this species studied in European rivers. Moreover, such a strategy has only been suggested before for this species in another population in a stream of Mediterranean characteristics.

A clear difference from the reproductive strategy in the Mascatomiza stream (FERNÁNDEZ-DELGADO & HERRERA 1995) is that in the Palancar stream not only double spawning is exhibited, but also the normal strategy of single spawning is modified depending on the rate of growth of the fish, i.e., mature females <101 mm spawn once in May, coinciding with that of *B. sclateri.* This spawning corresponds to mature females of ages 3+ and 4+, which show a smaller percentage contribution to the spawning, and it represents direct competition with the other species. In addition, the females >101 mm, among which are those contributing a greater percentage to total fecundity, perform this double spawning just before and just after the spawning of *B. sclateri.* In this way, *L. pyrenaicus* obtains advantages in reproduction. On the one hand, it competes with *B. sclateri* in the May spawning, and on the other hand, the reproductive success of its more fecund females is enhanced by the double spawning.

Between the months of March and June, the stream shows its most favourable environmental conditions, with continuous flow, high temperature and high concentration of dissolved oxygen in the water. The diversity and abundance of macroinvertebrates are thus maximised in this period (SORIGUER 1996, BRAVO 1998). This is the most suitable period for spawning, because later, from June until the end of October, the environmental conditions of the stream deteriorate considerably, and the flow is occasionally interrupted downstream, which leaves the fish stranded in pools.

The spawning of *B. sclateri* and of some of the *L. pyrenaicus* females takes place when there is greater availability of resources in the medium, and this coincides in time with the maximum overlap in the diet of the two species of cyprinids (SORIGUER 1996).

The two spawnings of *L. pyrenaicus* increase the fecundity of the population by extending the length of spawning time and by reducing the competition for resources. This phenomenon thus increases the probability of survival of the youngest age class of this species, which is the most abundant species of the assemblage of the Palancar stream (BRAVO 1998).

At the histological level, the presence of oocytes in various phases of maturation in the ovary of *L. pyrenaicus* with a trimodal distribution of the oocytes, has confirmed multiple spawning. This phenomenon has been observed in many species, and has been studied in depth in one species of cyprinids, *Barbus barbus* (L.), (LIBOSVÁRSKÝ & ŠTÊRBA 1981, PONCIN et al. 1996). The structure of the ovary of *B. barbus* has been described as quatrimodal in captivity (PONCIN et al. 1996) and as trimodal in individuals from the natural environment (PHILIPPART 1977, HANCOCK 1979). In the population of *B. sclateri* in the Palancar stream, as with *B. barbus* (HANCOCK 1979), a trimodal distribution of the oocytes during the ovarian development and a bimodal distribution after spawning was observed, with no oocytes in vitellogenesis.

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