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Population structure, growth and reproduction of *Tropidophoxinellus alburnoides* (STEINDACHNER 1866) in an intermittent stream of the Guadalquivir River basin (southern Spain)

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With 5 figures and 1 table in the text

Abstract

The age, growth and reproduction of *Tropidophoxinellus alburnoides* (STEINDACHNER 1866), an endemic cyprinid from the Iberian Peninsula, was studied for the first time for two years in a small seasonal tributary of the Guadalquivir River basin. Males reached a maximum age of 3+ yr (fork length, $L = 51$ mm) and females 6+ yr ($L = 100$ mm). Mean lengths of 3+ and 4+ age groups diminished during the summer. Both sexes matured during their second year of life. The overall sex ratio was dominated by females (319 males/2331 females) probably due to the effect of gynogenesis as the dominant reproductive strategy of the population. Reproduction began in March and lasted through June/July depending on the climatic conditions in each year. *T. alburnoides* is a multiple spawner that releases at least two batches of eggs per female each year. The number of ripe females in the population was maximum five times during the two reproductive seasons studied. The regression between fecundity (Fec) and fork length (mm) was represented in 1988 by the equation $Fec = 0.0167 L^{2.5717}$ and in 1989 by $Fec = 0.0041 L^{2.4701}$. Maximum contribution to the fecundity in the population was observed in intermediate ages.

Introduction

Tropidophoxinellus alburnoides (STEINDACHNER 1866) is an Iberian endemic cyprinid fish distributed along the Atlantic area of the Iberian Peninsula (ELVIRA 1990, DOADRIO et al. 1991). First described as *Leuciscus (Leucos) alburnoides* (STEINDACHNER, 1866), this species was assigned to the genus *Rutilus*, RAFINESQUE 1820 (BERG 1932), then to *Tropidophoxinellus* STEPHANIDIS 1974 (STEPHANIDIS 1974) and finally into *Pararutilus* BONAPARTE 1845 (LELEK 1980). According to COLLARES-PEREIRA (1984) and ELVIRA (1987) its inclusion in any of these genera is questionable. We have followed the latest taxonomic and bio-

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geographic studies which place the species within the genus *Tropidophoxinellus*.

Populations of *T. alburnoides* include both diploid ($2n = 50$) and triploid ($3n = 75$) genotypes, with gynogenesis occurring in the triploid group (COLLARES-PEREIRA 1985). This unusual reproduction is associated with the production of almost exclusively female populations (HUBBS & HUBBS 1932, CHERFAS 1981, COLLARES-PEREIRA 1985). A previous karyological study of 59 specimens from the same population on which we report here, found that 47 fish (80%) were triploids and that all but one of these were females (LOBILLO et al. 1989). Unfortunately diploid and triploid specimens have identical phenotypes (COLLARES-PEREIRA 1985). Because of the difficulty and the costs involved, we were unable to determine the karyology for all the specimens ($n = 3291$) in our study. Nevertheless, it is likely that our results refer to triploid females, owing to their high contribution to the population (80%), and diploid males.

The purpose of this paper is to provide the first data on the annual cycles of growth, reproduction and population structure in a population of *T. alburnoides* located in an intermittent stream typical of the Mediterranean area.

Materials and methods

The study area was a stream of the Guadalquivir River basin ($38^{\circ} 0' N$, $4^{\circ} 43' W$) about 5 km long, 1–4 m wide and 25–80 cm deep. Electrofishing was used to collect fish between November 1987 and October 1989. A total of 3291 specimens was obtained from weekly collections during the reproductive period (March–July) and monthly collections during the rest of the year. Fish were preserved in neutralized formaldehyde solution (4%) and transported to the laboratory where their size (fork length, mm) was recorded. Sex (male, female or immature) was determined by visual observation of the gonads. The testes were dried (24 h) to constant weight (± 0.1 mg) in an oven at $80^{\circ}C$. Ovaries were used to determine fecundity and ovary development, and were then dried in the same way as the testes and weighed. Drying time varied between 36 and 48 h depending on size. After removal of gonads, specimens were eviscerated and dried in an oven at $80^{\circ}C$. Drying time varied between 48 and 72 h depending on fish size. For further information about the physicochemical characteristics of the study area and fish manipulation both in the field and in the laboratory see HERRERA et al. (1988), HERRERA & FERNÁNDEZ-DELGADO (1992, 1993).

Owing to the scarcity of males in this population, seasonal growth was studied only in females using mean fork lengths of the different cohorts caught throughout the period of study.

Somatic conditions (K) was calculated for male and female *T. alburnoides* using the formula:

$$K = \frac{10^4 W}{L^b}$$

where W = dry weight of the eviscerated fish (mg) and L = fork length (mm). The value of b was the length exponent in the length-weight relationship and was estimated separately for males, females and immatures. The exponent was significantly (t-test;

$p < 0.05$) greater than 3 in all cases: males ($b = 3.75 \pm 0.195$, 95 % C.L., $n = 242$), females ($b = 3.31 \pm 0.042$, 95 % C.L., $n = 1952$) and immatures ($b = 3.66 \pm 0.0193$, 95 % C.L., $n = 1095$).

Temporal patterns in gonad development were described using the Gonadosomatic Index (GSI) according to the formula:

$$\text{GSI} = \frac{10 \text{ GW}}{\text{W}}$$

where GW = gonad dry weight (mg).

Ovary development and fecundity were studied using the gravimetric method (BAGENAL & BRAUM 1978). There were no significant differences (ANOVA, $p > 0.05$) in either egg diameter or egg number in relationship to their position in the gonad, or between the two ovaries. Therefore, all eggs present in a sub-sample from the mid-portion of each preserved ovary were counted and measured under the stereomicroscope with an ocular micrometer. The percent contribution of each age-group to the total fecundity of the population was estimated using the iterative method of PITCHER & MACDONALD (1973).

Results

Age and growth

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 erosion on the lateral scale edge that sometimes caused annulus disappearance in that area of the scale complicated age determination. The new annulus appeared at the end of the winter and was evident in the specimens caught around the middle of March, so we designated the 15th of March as the birth date.

Age structure of specimens caught in winter was represented by two age groups (0+ and 1+) in males and five (0+ to 4+) in females. The age distribution of 382 specimens caught in winter included 41 % age 0+ (25 males, 131 females), 36 % 1+ (5 males, 134 females), 15 % age 2+, 7 % age 3+ and 1 % age 4+. Maximum lengths (L) and ages observed were a 51 mm male caught in August with three annuli on its scales (3+) and a 100 mm female belonging to the 6+ age group caught in June.

The estimated growth pattern was age-dependent (Fig. 1). Growth of age 0+ fish was evident for a 6 to 7 month period (June/July–December). However, mean length increments decreased with age and thus in 1988 the 1+ age group appeared to grow for only 3 months (mid March–mid June), the 3+ age group for 2 months (mid March–mid May) and the 4+ age group for 1.5 months (mid March–April).

Mean lengths increments of the 3+ and 4+ age groups appeared to be negative following the major reproductive period in the spring.

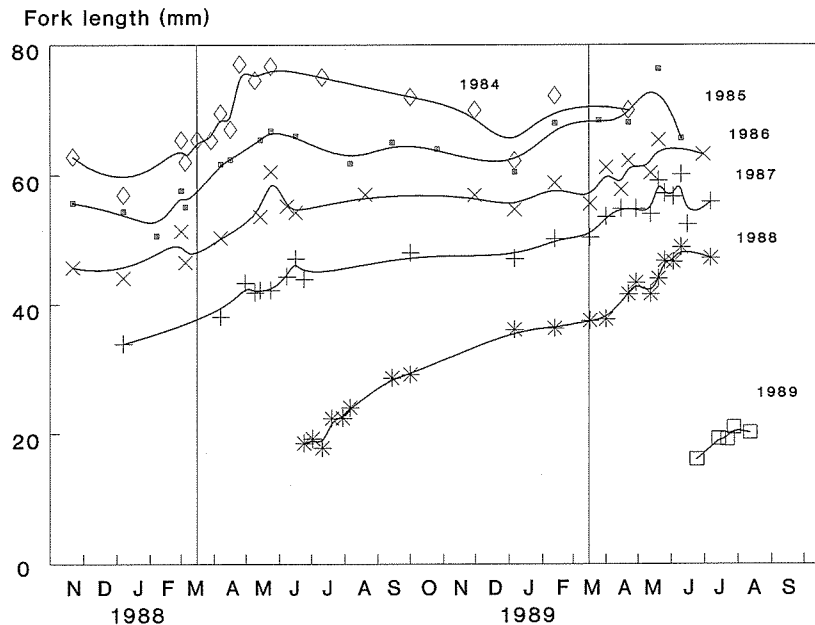


Fig. 1. Annual growth pattern of *T. alburnoides* for 1984–1989 female cohorts derived from the mean fork lengths (mm). 95 % Confidence Limits have been omitted for clarity. Vertical lines show birth date.

The somatic condition of females tended to be higher than that of both males and immature fish (Fig. 2). Minima were observed from August to November in females, then *K* increased significantly (Tukey test, $p < 0.05$) during the winter and reached the highest values in spring, with maxima between March and July (1988) or June (1989). During the spring (when spawning began) a series of oscillations in this index were observed in mature specimens, possibly related to the transfer of energy to the formation of reproductive tissue. Males and immature specimens displayed very few oscillations with minima from June/July.

Reproduction

The sex ratio of the samples showed a preponderance of females (M:F; 1:7.3) in the population. The fish matured in their second year of life (1+) from 33 mm in males and 40–47 mm in females. There were significant differences (ANOVA, $p < 0.0001$) in the mean fork lengths of 1+ immature (36.37 ± 0.740 mm, 95 % C.L.; $n = 100$) and mature (44.79 ± 0.072 mm, 95 % C.L.; $n = 105$) females.

Three phases in gonad activity could be differentiated (Fig. 3), one of quiescence (August–January), another of gonad maturation (February–

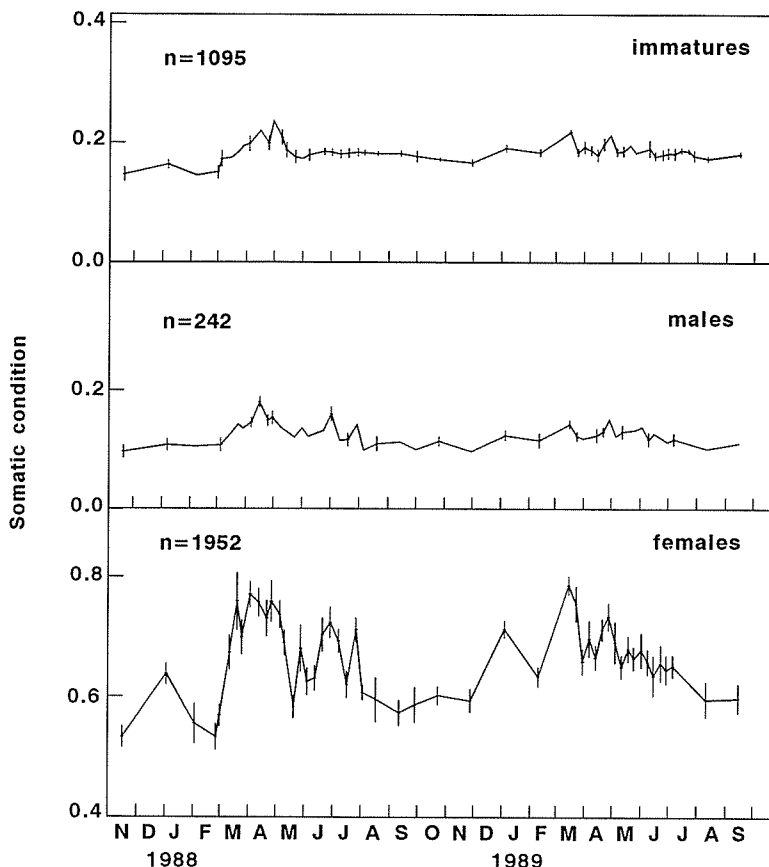


Fig. 2. Seasonal changes in somatic condition for immature, male and female *T. alburnoides*. Means and 95% C.L. for samples of 5 or more specimens.

March) and finally reproduction (April–July). Ovary weight increased steadily from February until the initiation of spawning (April). Weekly samplings, during the two reproductive periods, revealed five peaks in ovary activity.

Three kinds of eggs were found in ovaries: (I) transparent recruitment eggs measuring less than 0.5 mm; (II) opaque eggs (yellow/white ≤ 1.0 mm) and (III) yolk-filled eggs (yellow/orange ≥ 1.0 mm). In Fig. 4, the ova size distribution of six specimens with the same length is shown. These have been selected to show the general pattern of egg development. *T. alburnoides* is a multiple spawner that released batches of eggs over a period of time (between April and July). As there was constant recruitment of ripe ova, total fecundity was difficult to assess and it is likely to be underestimated. The principal difficulty was

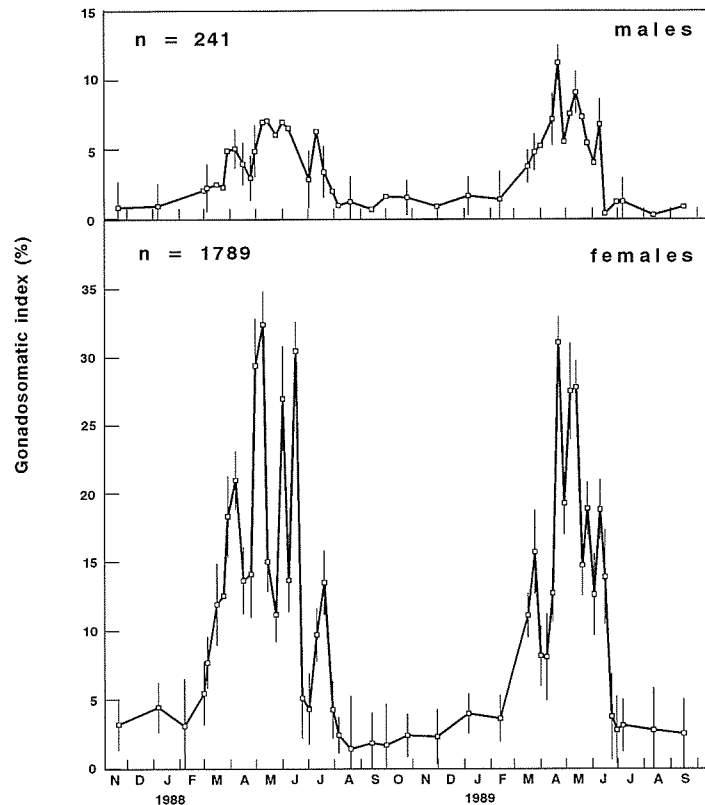


Fig. 3. Seasonal changes in gonadosomatic index for male and female *T. alburnoides*. Means and 95% C.L. for samples of 5 or more fish.

determination of the number of batches spawned per female, although the existence in the ovaries of yolky eggs at different maturation stages indicated a minimum of two batches of eggs per female.

The number of mature females with a mode of yolky eggs (Types d, e and f; Fig. 4) displayed five peaks during annual reproductive period even when spawning was a month shorter in 1989 (Fig. 5). These peaks coincided with those observed in the GSI (Fig. 3). Nevertheless, they represent the total female population, not individual specimens. There was a significant decrease (ANOVA, $p < 0.0001$) in the mean lengths and ages of reproducing females during the spawning period, which suggests death of larger and older specimens and/or continuous recruitment of mature females to the population during this period.

Number of yolky eggs was regressed against fork length using fish collected during reproductive peaks in both years. There were no significant differences in the five regressions obtained for each of the two spawning periods

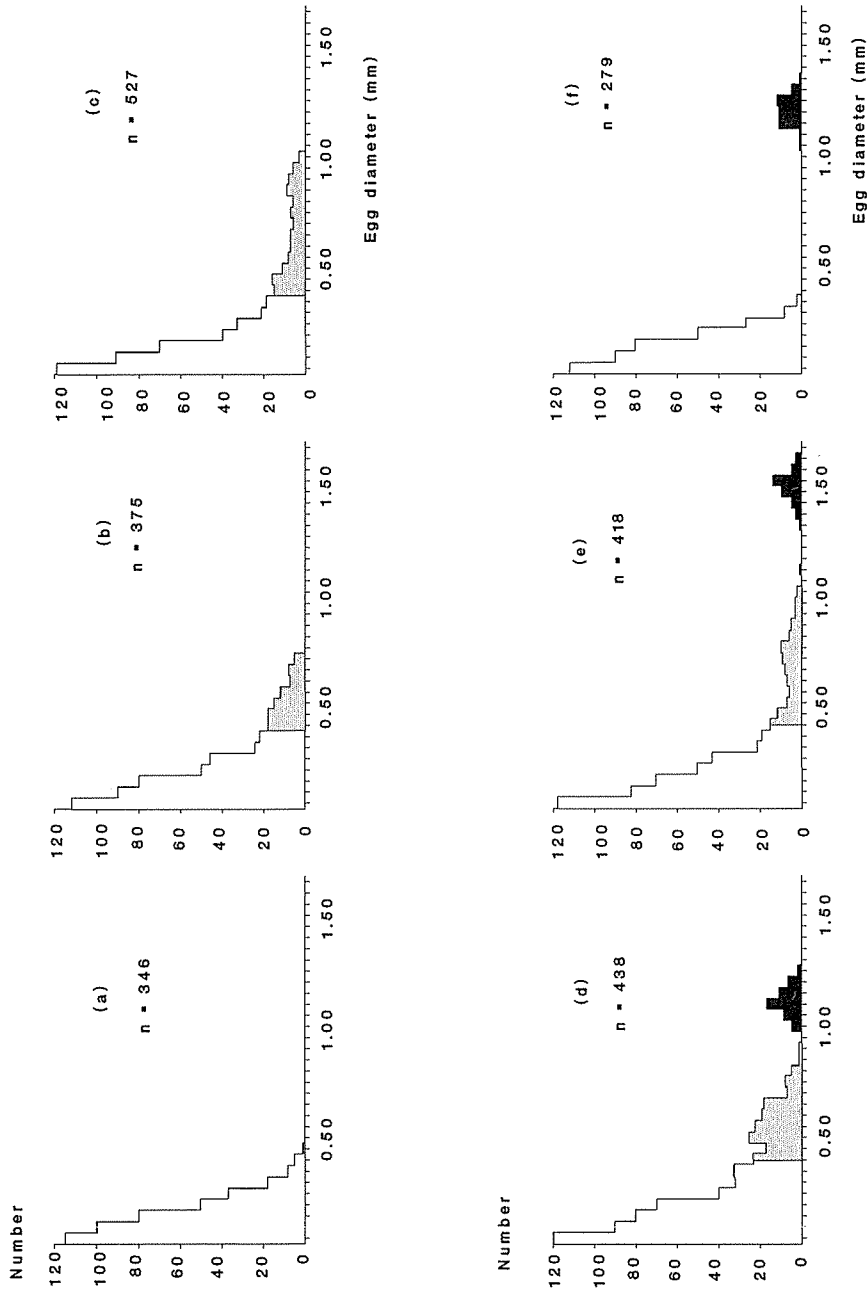


Fig. 4. Size frequency distribution of eggs from six *T. alburnoides* females before (a) and during (b–f, April–July) the spawning period. White areas represent immature oocytes; dotted areas show oocytes in maturation process and black areas represent mature oocytes.

Females in reproduction (%)

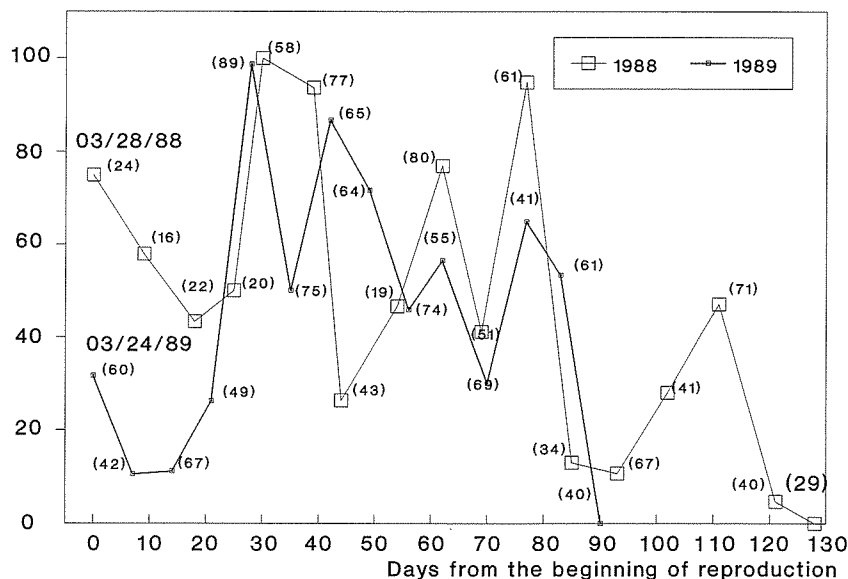


Fig. 5. Number of *T. alburnoides* females about to spawn during the two spawning periods studied. Samples sizes in parentheses.

Table 1. Percent contribution per age group and cohort to total number of released eggs in *T. alburnoides*.

Year 1988			Year 1989				By ages		
Age	n	Fec (%)	Age	n	Fec (%)	Cohort	Age	n	Fec (%)
1+	97	13.2	1+	54	7.8	1988	1+	151	9.9
2+	149	33.7	2+	153	31.5	1987	2+	302	32.4
3+	80	26.8	3+	129	35.5	1986	3+	209	31.7
4+	49	21.7	4+	46	17.3	1985	4+	95	19.2
5+	8	4.7	5+	16	7.4	1984	5+	24	6.1
			6+	2	1.2	1983	6+	2	0.7

Fec = Total Fecundity.

studied (Bartlett's test, $p > 0.05$; ANCOVA, $p > 0.05$), so data were pooled and a common regression was obtained for each year: 1988, $Fec = 0.0167L^{2.5717}$ ($n = 81$); 1989, $Fec = 0.0041L^{2.4701}$ ($n = 106$). Mean egg diameter was independent of fork length (slope = 0, ANOVA; $p > 0.05$).

In the 1988 spawning period, the 2+ age group contributed a high percentage (33.7%) to total population fecundity, whereas in 1989 the 3+ group gave the highest contribution (35.5%) (Table 1). The 1+ and 5+ age groups contributed an approximately similar percentage to total fecundity, despite there

being a larger number of 1+ than 5+ fish. In general, the major contribution to population fecundity was by the intermediate ages.

Discussion

The decline observed in mean length of older cohorts after the reproductive period suggests size-selective mortality in larger individuals. A weakness of using changes in the mean size of fish to assess growth is that the loss of the largest individuals in a cohort may mask the actual growth rate of the survivors. It was unlikely that migration affected the growth estimates because the fish were living in isolated pools. This size-selective mortality could be related both to reproductive stress and to adverse ecological conditions. The hydrological cycle of this stream is typical of the Mediterranean area, where flow rates are maximum between autumn and early spring. In the summer, flow ceases and the river consists of isolated pools. During this period, all fish species living in the river (*T. alburnoides*, *Chondrostoma polylepis willkommi* STEINDACHNER 1866; *Barbus sclateri* GÜNTHER 1868; *Rutilus lemmingii* STEINDACHNER, 1866; *Leuciscus pyrenaicus* GÜNTHER 1868 and *Cobitis paludica* BUEN, 1930) become concentrated in these small pools. Hence, fish density increases, and competition for space and food may become important. Moreover, the pools are subject to thermal effects of insolation ($10-14 \text{ h d}^{-1}$), resulting in water temperatures up to $30-32^\circ\text{C}$ and low oxygen conditions (particularly at night). These adverse physical conditions, in addition to the somatic costs of reproduction, could have led to the death of the largest specimens within an age group.

Drought reduced the length of the spawning period by one month in 1989. In spite of the shorter season, the fish exhibited the same number of spawning peaks as in the previous year. Each female *T. alburnoides* released a minimum of two batches of eggs, the maximum number was impossible to estimate from the present data even with weekly samples. Multiple spawning has indubitable advantages in fluctuating environments. Progeny are not risked in just one reproductive event where a climatic catastrophe could destroy the whole spawning in a particular year. Also, individual fecundity is increased, which evades the trade-off between volume of body cavity and fecundity (NIKOLSKY 1963) and may allow for selection of optimum egg size avoiding the possible conflict between egg number and egg quality (MILLER 1979).

The presence of both diploid and triploid specimens in this population suggests the existence of two reproductive strategies, one asexual and another sexual. The high number of females captured suggests that asexual reproduction dominates because this strategy should produce triploid females almost exclusively. In general, the development of eggs produced by gynogenetic females must be activated by the sperm from a sexual species, normally a closely-

related sexually reproducing species. The sperm contributes neither genotypically nor phenotypically to the offspring (VRJENHOEK 1984). In this population most individuals may reproduce gynogenetically (producing only triploid specimens) using the sperm of the species reproducing during the same period, that is *L. pyrenaicus*, *R. lemmingii* or *B. sclateri*. These unusual species provide rich material for studying the ecological and evolutionary consequences of asexual and sexual reproduction and hybridation (WOOTTON 1990).

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