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# Behavioural study of polyandrous spawning in *Blicca bjoerkna* under a controlled environment

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**Abstract.** This study describes the reproductive behaviour of silver bream, *Blicca bjoerkna*, in an aquarium environment with hormonal injection, constant temperature and natural photoperiod conditions. The results revealed that the reproductive behaviour of silver bream was polyandrous with courting tactics including a high level of tactile stimulation and following behaviour developed by the males, but without territorial or aggressive acts. The individual participation of males in mating acts showed a significant positive correlation with the individual participation of males in following a female. A successful spawning act included trembling movements and violent splashing while eggs and sperm were released on plants. The female mated with one to five males without an active inter- and intra-sexual selection.

**Key words:** reproductive activity, mating, silver bream, cyprinids

## Introduction

Silver bream *Blicca bjoerkna* is a common cyprinid fish species in European waters (Spillmann 1961, Wheeler 1969). For Lelek (1980) and Kottelat (1997), this species is widespread in stagnant waters of lakes and reservoirs, calm rivers and canals throughout central and northern Europe, from the east of England to the Caspian. This species is strictly a phytophilous fish species (Balon 1975, 1984, Philippart & Vranken 1983) and reproduces from May to July (Kottelat & Freyhof 2007). As it spawns at shallow depths, this species is highly sensitive to changes in water level; in the bays of the Kakhovka reservoir, Spivak (1987) has observed that the silver bream lays eggs along the shoreline at depths to 40 cm on willow roots, floating residues of the previous year‘s plants and stems of growing reed.

It is known in natural environments that this species is a gregarious fish (Muus & Dahlström 1968), exhibits polyandry during the breeding season with courting tactics developed by males, and releases eggs and sperm on plant substratum without providing parental care (Koli 1990, Kottelat 1997).

However, few studies have investigated the reproductive behaviour and mating tactics of silver bream in experimental and natural environments. Therefore, the spawning activity of silver bream has received little scientific attention and has only very rarely been investigated (Spivak 1987, Poncin et al. 2004). Investigating the reproductive behaviour of the silver bream would increase the knowledge on this poorly studied species in terms of its reproductive strategies and tactics. It is known that sexual behaviours are involved in the success of intra-species genetic diversity that are useful for the survival of the offspring in the wild (Becher & Magurran 2004, Barbosa & Magurran 2006, Nzau Matondo et al. 2007), and the hybridisation processes of silver bream with other sympatric cyprinid fish such as the roach *Rutilus rutilus* and the common bream *Abramis brama* (Nzau Matondo et al. 2009).

Therefore, this study aims (1) to describe the reproductive activity of the silver bream with precise data, including the behaviour of the male following a female and the mating patterns in an aquarium environment with hormonal injection, constant temperature and natural photoperiod conditions and (2) to test whether the female displays different mating preferences.

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## Material and Methods

Migrating breeders of silver bream were captured in the Meuse River in a fish pass during the reproductive period. Selected females were gravid and males produced milt. Behavioural experiments were conducted in two sets of conditions repeated twice (May and June of 2006 for the first and second repetition, respectively). In the first condition, two females were placed to reproduce with five males and in the second, one female was placed with five males. With this experimental procedure, it was possible to follow the individual reproductive activity for each fish. The fish were individually identified by morphological characteristics such as body size, the small tears on the fins caused in the river and by a slight cutting of the upper or lower lobe of the caudal fin. More males than females corresponded to the situation commonly encountered in the wild during the silver bream's spawning period (Breder & Rosen 1966, Spivak 1987, Koli 1990, Billard 1997). The fork length and weight of the fishes used are indicated in Table 1. Fish were held in aquaria measuring 3.5 × 1.3 × 1.2 m and 5 × 0.4 × 0.6 m for the first and second experimental conditions, respectively. They were maintained at a temperature of 18.5 ± 0.3°C and under natural photoperiod conditions (16L:8D in May; 16.5L:7.5D in June). Green plastic plants, imitating *Ceratophyllum demersum*, were either fixed in the gravel or floating on the surface (Poncin et al. 2005). Fish were fed daily with live or frozen chironomid larvae.

Spawning was induced using two injections of carp pituitary extracts in the females (1 mg/kg and 10 mg/kg; time between injections, 24 h) and a single injection in the males (3 mg/kg), according to the method described by Woynarovich & Horvath (1981) that we used to study hybridisation in barbel species (Poncin et al. 1994). Fish were injected the day after their capture. According to Poncin et al. (1994) and Nzau Matondo et al. (2009), hormonal injection was used to synchronise the spawning activity and to reduce experimental time to 2 days only. The time between the hormonal treatment and the first spawning attempt varied between 190 and 330°h (number of hours × temperature in degrees).

The data on the behaviour were recorded with a video camera system over 2 days after hormonal treatment, corresponding to the spawning activities. Following behaviour (harassment) was expressed as the behaviour of one or more males aiming to be positioned as close to a female as possible (at its side or behind) for reproduction, and it was analysed for 10 min every hour. Mating was defined as sexual contact between fish of the opposite sex followed by release of eggs and sperm on spawning substrate, and it was quantified during the entire spawning period. Release of eggs and sperm was indicated by trembling movements and violent splashing on spawning substrate. In following and mating behaviours, the individual and collective participation of males was estimated. Fig. 4, illustrating the spawning behaviour, was drawn by hand from video camera images and visual observation of the fish.

The mean performance of individual participation of males in the following activity and mating act between experiments were analyzed with the Kruskal-Wallis KW test followed by multiple paired comparison tests using the Mann-Whitney U test. The Fisher exact probability FEP test was performed to compare the individual activity of males in following behaviour and the mating act in each experiment. Standard regression analysis was used to study the relations between the individual participation of males in following activity and the individual participation of males in the mating act. For all statistical tests, a probability level of $p < 0.05$ was considered significant.

## Results

During the reproductive period, a female silver bream was followed by all males in each experiment (Table 2). Following behaviour for each male was

***Table 1.*** *Individual values of fork length and weight of fish used in experiments. I and II, experiments with two females mixed with five males (2♀ × 5♂) ; III and IV, experiments with one female mixed with five males (1♀ × 5♂); male (♂); female (♀); arabic numerals indicate the number of fish per sex in each experiment.*

| | Females (first / second) | | | Males (first / second / third / fourth / fifth) | | |
|---|---|---|---|---|---|---|
| Experiments | *n* | Length (mm) | Weight (g) | *n* | Length (mm) | Weight (g) |
| I | 2 | 234 / 265 | 305 / 411 | 5 | 213 / 217 / 221 / 222 / 266 | 166 / 178 / 200 / 193 / 305 |
| II | 2 | 260 / 264 | 307 / 399 | 5 | 213 / 213 / 214 / 235 / 258 | 180 / 182 / 185 / 233 / 285 |
| III | 1 | 310 | 514 | 5 | 232 / 241 / 250 / 275 / 279 | 200 / 230 / 307 / 334 / 302 |
| IV | 1 | 297 | 555 | 5 | 235 / 258 / 265 / 268 / 290 | 230 / 285 / 305 / 309 / 488 |

significantly different between experiments (Kruskall-Wallis KW test, df = 3, H = 0.0299, $p$ = 0.0299). The paired comparison tests revealed no significant difference (Mann-Whitney U test, $p > 0.05$) between experiments with the same number of males and females. However, the highest number of following behaviours was observed in experiments with one female mixed with five males (mean value = 173 and 177, respectively, for experiments III and IV), and the smallest number in experiments with two females mixed with five males (115 and 167, respectively, for experiments II and I).

One to five males per female were counted for the following activity during silver bream reproduction in each experiment (Fig. 1a). Over 65% following behaviour in experiment I and 85% in experiments II, III and IV occurred with more than one male. However, experiments with two females mixed with five males (< 30%) showed a lower frequency of simultaneous participation of more than three males in following behaviour. Two major combinations of following behaviour were observed most frequently: (1) a female with a male in experiment I, accounting for 32%, and (2) a female with three males in experiments II, III and IV, accounting for 34%, 32% and 38%, respectively.

The results of individual participation per male in following behaviour (Fig. 2a) showed a significant difference (Fisher exact probability FEP test, $p < 0.05$) between males in the same experiment. In each experiment, two to five males showed individual participation in following behaviour above 50%. Male 5 in experiments I, III and IV, accounting for 68%, 74% and 86%, respectively, and male 3 in experiment II (71%), displayed the highest proportion of following behaviour (FEP test, $p < 0.05$).

For the mating activity, no significant difference (KW test, df = 3, H = 5.426, $p$ = 0.1431) was found between experiments in terms of individual participation per male in mating acts (Table 2). In experimental conditions with two females mixed with five males, all the males present did not participate in mating. However, in experimental conditions with one female mixed with five males, each male participated in matings. Experiments with one female mixed with five males (mean values = 3 and 6 matings per male) displayed a higher number of individual participation in mating per male than experiments with two females mixed with five males (three and four matings per male).

A female silver bream mated with two to four males under experimental conditions with two females mixed with five males versus one to five males in experiments with one female mixed with five males (Fig. 1b). Two major combinations of matings were observed most frequently in each experimental condition: (1) a female mated with three males in experiments I and IV, accounting for 63% and 71% of matings, respectively, and (2) a female mated with two males in experiments II and III, accounting for 50% and 51%, respectively.

The results of individual participation per male in mating acts (Fig. 2b) revealed no significant difference between males (FEP test, $p > 0.05$) in each experiment except experiment IV in which male 5 showed a significantly higher participation in matings (FEP test, $p$ = 0.03) than male 2, but the difference was not significant with the three other males. In

***Table 2.*** *Numbers of individual participations of a male per reproductive activity. Total number of following behaviours or mating acts (n); mean values of five males in each experiment, range indicates extreme values of five males in each experiment; experiment number (no.); male (♂); female (♀); arabic numerals indicate the number of fish per sex in each experiment. Means with a common superscript in the column do not differ significantly (Mann-Whitney U test, p < 0.05).*

| | | Reproductive activity | | | | | |
|---|---|---|---|---|---|---|---|
| | | Following behaviour | | | Mating | | |
| | | | Individual participation per male (number) | | | Individual participation per male (number) | |
| Experiments | No. | *n* | Mean | Range | *n* | Mean | Range |
| 2♀ × 5♂ | I | 368 | 167[ab] | 85–250 | 8 | 4[a] | 0–7 |
| 2♀ × 5♂ | II | 205 | 115[a] | 76–146 | 6 | 3[a] | 0–4 |
| 1♀ × 5♂ | III | 266 | 173[b] | 149–197 | 7 | 3[a] | 1–5 |
| 1♀ × 5♂ | IV | 313 | 177[b] | 110–269 | 11 | 6[a] | 3–9 |

each experiment, three males showed a frequency of individual participation in matings of at least 50%. The highest frequency of individual participation in matings was observed in one male in experiments I, III and IV, accounting for 88% (male 5), 71% (male 4) and 85% (male 5), respectively, and in three males (males 2, 3

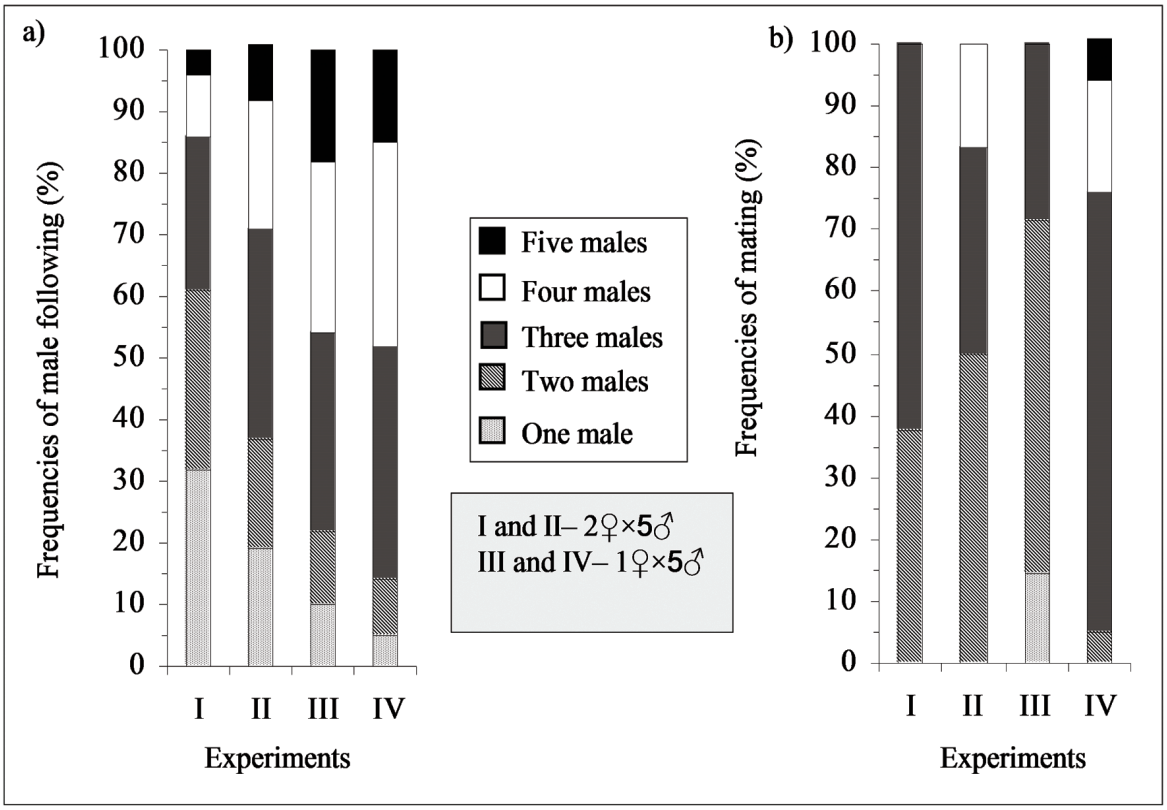


***Fig. 1.*** *Frequencies of occurrence of numbers of males participating in following (a) and mating (b) behaviours, in experimental conditions. Male (♂); female (♀); arabic numerals indicate the number of fish per sex in each experiment.*

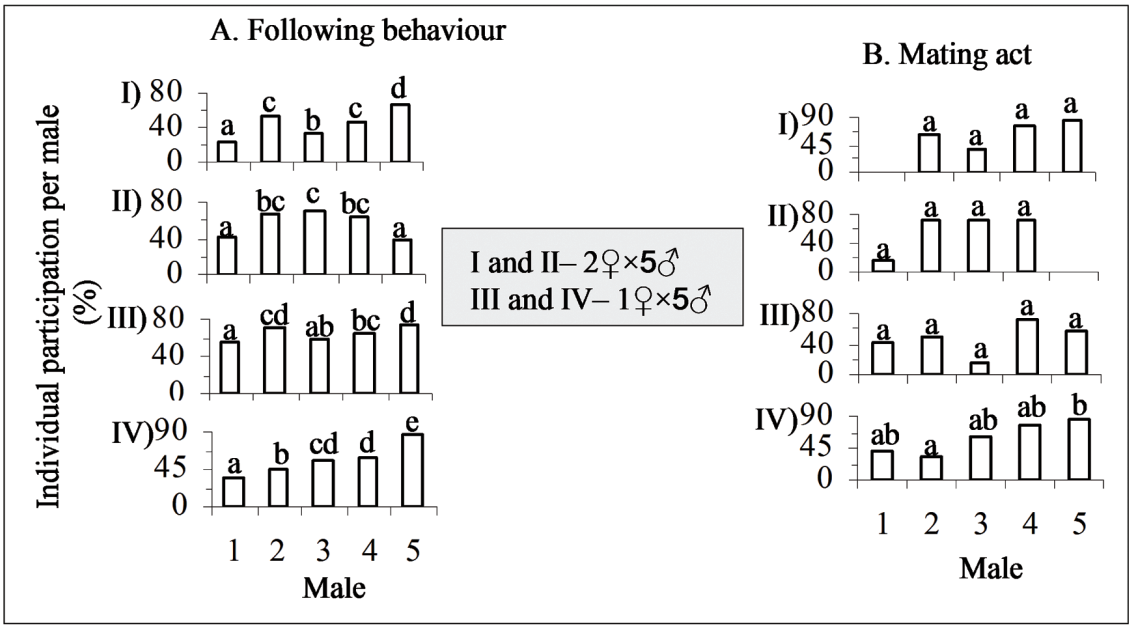


***Fig. 2.*** *Relative frequencies of individual participation per male in following behaviour and individual participation per male in mating acts. Bars sharing at least one common script are not significantly different, whereas other comparisons differ at $p < 0.05$ (Fisher exact probability FEP test, $p < 0.05$).*

and 4) in experiment II, accounting for 71%.

The study of the relations between individual participation of males in following behaviour and the mating act (Fig. 3) revealed a significant correlation between these two reproductive activities in experiments with two females mixed with five males. In experiments with one female mixed with five males, no significant correlation was found in one experiment. Experiments with two females placed to reproduce with five males ($R^2 = 0.893$, $p = 0.0153$ and $R^2 = 0.966$, $p = 0.0027$ for experiments I and II, respectively) showed higher correlations than in experiments with one female mixed with five males ($R^2 = 0.248$, $p = 0.3929$ and $R^2 = 0.782$, $p = 0.0465$ for experiments III and IV, respectively).

In the study of spawning behaviour of silver bream, neither territoriality nor aggressive acts were observed in each experiment. Males were covered with small breeding tubercles mainly located on the operculum and the anterior part of the back (Fig. 4A). In pairs (Fig. 4B), these males exhibited forehead swimming followed by rapid swimming head against head (Fig. 4C), indicating that spawning was approaching. Subsequently, one female and a few males formed a spawning aggregate (Fig. 4D) in which males showed a courting tactic, stimulating by a tactile tactic the female's sides and abdomen (Fig. 4E and 4F). The male touched her on the tip of the snout and in most cases, the protraction of the mouth of the male on the female's body was observed. The female often rested on the bottom (Fig. 4F) after intense reproductive activity. Before each mating act, males conducted a high level of following and stimulating behaviours towards a female (Fig. 4G). The female, ready to release eggs, moved to the spawning substrate composed of artificial aquatic plants (Fig. 4H) on which she performed a few burrowing movements while moving towards the water's surface (Fig. 4I). In a successful spawning act (Fig. 4J), the female and one to five males released eggs and sperm in a twisting movement of the body, signaled by trembling movements and violent splashing on the spawning substrate. At this time, the arrival of opportunistic non-courting males attempting to participate in the mating or to fertilise eggs was observed. These fish, driven in reproductive movements, were subsequently observed in a horizontal position with a part of their body out of the water (Fig. 4K). After mating, the female swam away towards the bottom of the aquarium (Fig. 4L), while the males continued to follow her or to move away from her.

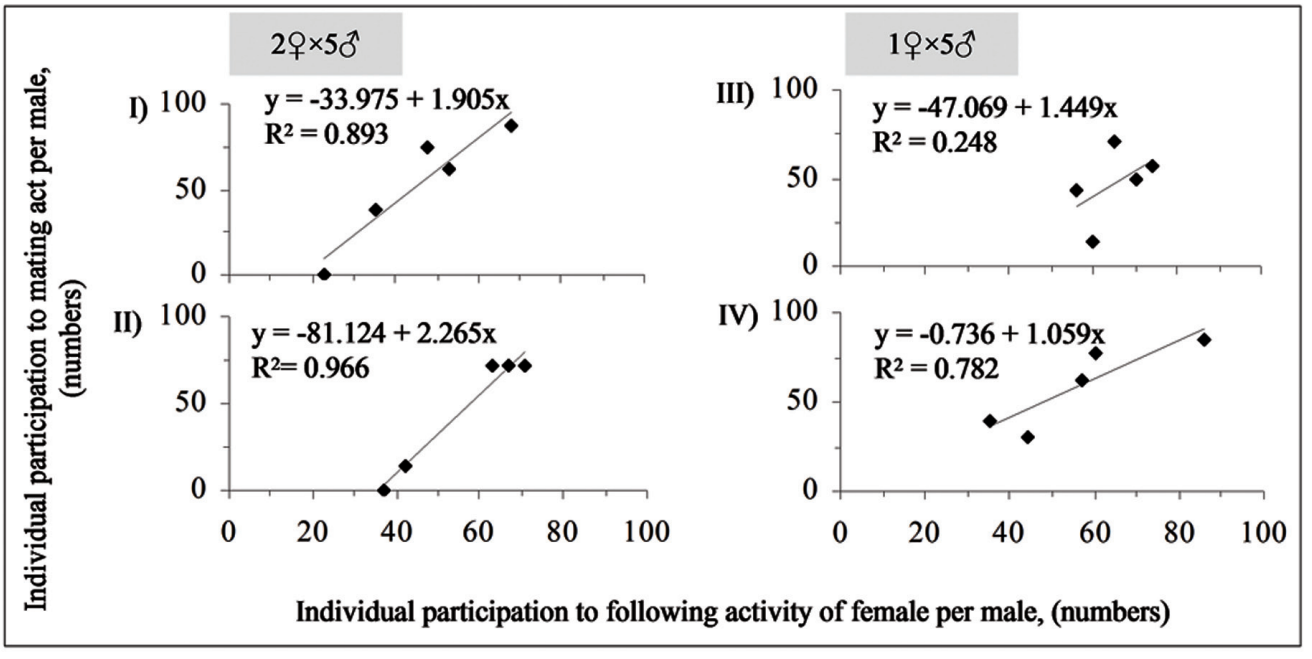


***Fig. 3.*** *Positive correlations between the individual participation per male in following behaviours and the individual participation per male in mating acts.*

## Discussion

The higher number of following behaviours per male observed in experiments with one female placed to reproduce with five males was associated with the males not being able to choose another female. A male's following behaviour to this single

experimental female could have a group effect, drive other males towards the same female, and therefore influence the high frequency of this activity per male. In experiments with two females mixed with five males, the male had a choice to follow one of two females, which resulted in the group separating into subgroups. This could also explain the low frequency of simultaneous participation of more than three males in the following behaviour and the predominance of following behaviour by one and three males observed in experiments I and II, respectively. The participation of all males individually or in groups in following behaviour of a female and their high frequency prove how this activity is important and characteristic for the species during the breeding season.

One male did not participate in matings in the experiments with two females mixed with five males. This situation could be explained by this group's having the lowest frequency of individual participation in the following behaviour. This is quite normal because the more the male harasses a female, the more he has the chance to mate with her. The high level of following behaviour in experiments with one female mixed with five males could contribute to the participation of all males in mating.

The predominance of matings between a female and more than one male in each experiment confirms that polyandry is a common mating system in the silver bream species. As in other animal groups, polyandry is very common among freshwater fish species (Gotto 1987, Dalton 1991, Vila-Gispert & Moreno-Amich 2002). Barbosa & Magurran (2006) reported that 60% of the species they examined demonstrate this type of mating system. In polyandry, a female mates with more than one male during a spawning season.

Polyandry was not always entirely a female decision in our experiments, as already reported by Barbosa & Magurran (2006), particularly in systems where females are constantly harassed by males. In this study, the female silver bream mated with males who harassed her to varying degrees, and the male mated with the female who was ready to release eggs, which reflects the absence of an active inter- and intra-sexual selection in this species. In contrary, in Midas Cichlidae *Cichlasoma citrinellum*, the male does not choose, but rather the female chooses her male sexual partner that is larger in size, a defender of the territory and more aggressive in order to better protect the young (Barlow 1992), and other fish species, other morphological selection criteria such as a large dorsal fin, a large tail fin, and large and symmetrical pelvic fins, are used by females to make a deliberate choice of their sexual partners among conspecific males (Bischoff et al. 1985, Karino 1997, Sekiya & Karino 2004). The difference in rates of following behaviour or harassment between males could explain the nonparticipation of some males in mating. Also, the highest frequency of following behaviour expressed by male 5 could be associated with its high growth, indicating more available energy for reproductive activity, but this male showed no significant difference compared to other males in terms of individual participation in matings. This could indicate that the males sampled and the morphological criteria used to identify each male do not seem to influence mating activity. Polyandry seems to be a mechanism used to avoid inbreeding and represents a benefit for the survival of the offspring by increasing intra-species genetic diversity in a natural population in which the future environmental conditions are unpredictable (Becher & Magurran 2004, Barbosa & Magurran 2006, Nzau Matondo et al. 2007). Indeed, polyandry can also be a favourable factor in hybridisation when heterospecific males are involved.

No significant correlation observed between following activity and the mating act in experiment III (one female mixed with five males) could be attributed to clustering of individual frequencies of following behaviour in all males. Significant positive correlations obtained in other experiments demonstrate that when the difference between males is high in the frequency of individual participation in following activity, there is also a greater chance of observing different levels of mating in the male. The main trend shown was greater mating activity observed in conjunction with greater following behaviour.

The absence of aggressiveness and territoriality in silver bream males observed during these reproduction experiments is consistent with the behaviour of the species and the results of Poncin et al. (2004) and Nzau Matondo et al. (2008, 2009) obtained in experimental environments. Between males, interactions consisted of the fact that when the males do not follow a female, they are resting or swimming one behind the other calmly and ready to rush toward her at the slightest movement. At rest, males were side by side without any interaction. When several males courting a female, each trying to stand by his side without express aggressive behaviour toward others. Males have developed courting and/or sneaking tactics. In contrast, in other species such as common bream, males display a lek-like reproductive system involving territorial males and nonterritorial sneaking males in which territorial males defend bank areas that include

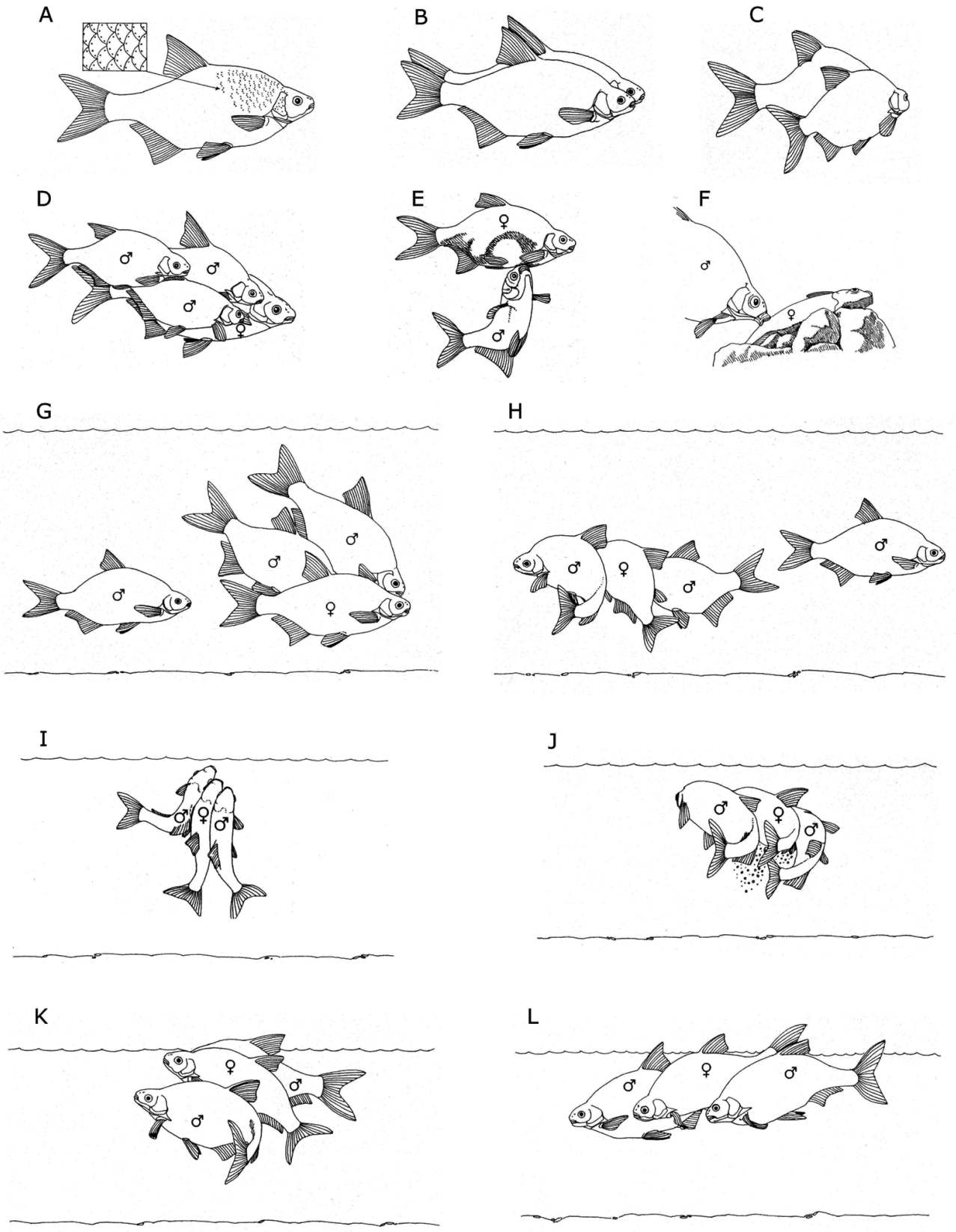


***Fig. 4.*** *Illustrations of spawning behaviours in silver bream. Nuptial tubercles on male (A); forehead swimming between males (B, C); spawning aggregate (D); tactile stimulation (E, F); following and stimulating behaviours (G); movement toward spawning ground (H); burrowing movements (I); spawning (J); part of fish body out of the water (K); returning movement toward the bottom (L).*

spawning substratum (Fabricius 1951, Kozlovskij 1991, Poncin et al. 1996).

Tactile stimulation and numerous following behaviours by males observed in silver bream during female rest or swimming demonstrates that these males are able to express a high level of courtship approach to the female during the reproductive activity.

The ascending movements of fish for spawning at the water's surface and the returning movements in deeper water after spawning are consistent with the reproductive behavior of species in rivers in which they release gametes, usually in shallow areas with herbaceous vegetation warming more rapidly than other areas (Spivak 1987) useful for egg development. For Molls (1999), in the Rhine River, silver bream prefer the main river outside spawning periods, move from the river into the oxbows with their spawning sites and return to the river after spawning. The main river provides better feeding for adults, whereas oxbows are rich in vegetation and provide optimal habitats for spawning and larva and juvenile growth.

During the silver bream reproduction period, each male can successively mate with several females and each female may mate with several males simultaneously or successively. This system maximises the opportunities for mating with several individuals and consequently maximises the genetic diversity of offspring. As phytophilous spawners, silver bream exhibit no parental care, which also contributes to the polygamous nature of their breeding system (Bruch & Binkowski 2002).

The spawning behaviour observed in this study is consistent with the typical behaviour patterns recognised in the silver bream and has some similarities to the behaviour patterns observed in other cyprinid fish species such as roach *Rutilus rutilus*, rudd *Scardinius erythrophtalmus*, carp *Cyprinus carpio* and goldfish *Carassius carassius* (Svärdson 1949, 1952, Diamond 1985, Fahy et al. 1988, Cowx 1990). This reproductive behaviour, involving no territoriality, is also close to that of small common bream *Abramis brama* adults (nonterritorial males, 3–4 years old) adopting opportunistic tactics during reproduction (Poncin et al. 1996). Thus, the influence of the hormonal injection of spawning in the silver bream seems not to have modified its reproductive behaviours, as already observed in barbels *Barbus barbus* and *B. Meridionalis* (Poncin et al. 1994). Moreover, behavioral similarities are factors promoting natural hybridisation between these species.

In conclusion, the results of this study have demonstrated that the reproductive behaviour of silver bream was polyandrous, with courting tactics including a high level of tactile stimulation and following behaviour developed by the males, but without territorial or aggressive acts. A successful spawning act included trembling movements and violent splashing, while eggs and sperm were released on plants. Male participation in mating acts was positively correlated with following behaviours. Polyandry and other behavioural similarities could explain the hybridisation process observed in rivers between this species and other cyprinid species.

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