

Eco-ethological characteristics of two natural hybrids of *Abramis brama* (L.) from the River Meuse basin*

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ABSTRACT

Eco-ethology as expressed in migration patterns, abundance level, growth rates in river conditions, and reproductive behaviour in a controlled environment were investigated in natural common bream x roach and common bream x silver bream hybrids. From 2001 to 2003, hybrids and parental species were captured in a fish pass trap at the Lixhe dam on the Belgian Meuse river during their reproductive migration. The fish pass was checked 3 days a week and the water temperature was recorded hourly. The results showed that hybrids were less frequent but they had migrated during the same period and in the same environmental conditions as the

parental species. Scale readings showed that the growth of hybrids was intermediate to the two parent species growth. In reproductive experiments between hybrids under controlled conditions, the female hybrid mated with one to two hybrid males. In reproductive experiments with hybrids mixed with parental species males, the female hybrid mated with male hybrid and male roach or male silver bream, but not with the male common bream. The succession of spawning episodes in hybrids were those recognised in parental species. Aggressive and territorial acts were observed among the males of these hybrids in a territory including a spawning substrate. This study has proven that the natural hybrids are eco-ethologically viable.

INTRODUCTION

Roach *Rutilus rutilus* (L.), silver bream *Blicca bjoerkna* (L.), and common bream *Abramis brama* (L.) are three common cyprinid fish species in European waters (Philippart 1989; Volodin 1988; Vostradovsky 1973). These fish species usually live in sympatry in the same river, reproduce in spring from March to mid June, have the same spawning requirements (plant substratum at shallow depths and high water temperature), and release gametes on vegetation (Jurajda et al. 2004; Mills 1991; Nzau Matondo et al. 2008a; Poncin et al. 1996; Shestopalova 1978). Natural hybridisation between these species has already been reported by several authors in European waters in general (Cowx 1983; Demandt and Bergek 2009; Penczak 1978; Pethon 1978; Schwartz 1972; Slattenenko 1957; Swinney and Coles 1982; Wood and Jordan 1987) and in particular, in the Belgian Meuse river (Keulen et al. 1994).

Natural hybridisation in fish is facilitated by several factors, among which most important are the obstruction of fish movement (Balon 1992), the genetic affinity of species (Crivelli and Dupont 1987; Hubbs 1955), overlap of the spawning periods (Cowx 1983), interspecific competition for the same spawning grounds (Wheeler and Easton 1978), external fertilisation (Pitts et al. 1997), and the uniform karyotype in these species (Bianco et al. 2004).

The Belgian Meuse river at the Lixhe dam is a site with a high level of human interference caused by the construction of a dam, river banks, canalisation and deepening of the main river. This site is equipped with a fish pass, a good means of capturing fish for hybridisation studies.

From an ecological point of view, hybridisation is an indicator of habitat degradation (Didier 1997; Kestemont et al. 2002, 2004) and this process is not in congruence with biological species concepts. Hybridisation incorporates individuals with new biological characteristics into natural

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populations of parental species (Nzau Matondo et al. 2007, 2008b, 2008c), meaning that this phenomenon can alter the genetic integrity of parental species (Pitts et al. 1997; Thompson and Iliadou 1990). The genetic integrity is only altered if F1 hybrids are fertile and backcross with the parental species. Incorporation of genetic material from other species or hybrids into a focal species genetic material is called introgression. Hybridisation can thus modify the dynamics of natural populations (Wood and Jordan 1987).

In addition, the natural reproductive behaviour of parental species has already been studied. It has been described as polygamous (Diamond 1985; Shestopalova 1978; Spivak 1987) and that they are phytophilous spawners (Gillet 1989; Kozlovskij 1991). In common bream, males exhibit territorial and aggressive activity (Fabricius 1951; Poncin et al. 1996; Svårdson 1949) but in both silver bream and roach, males are nonaggressive and nonterritorial (Diamond 1985; Mills 1991; Nzau Matondo et al. 2009; Poncin et al. 2004). However, even though hybrids become more and more frequent in their natural environment, the reproductive behaviour of hybrids involving common bream has received little scientific attention and has only rarely been investigated.

Hence there is growing interest in knowing more about these hybrids in all aspects of their biology including their eco-ethology compared to parental species. Such studies could contribute to better understanding of hybridisation success and its impact on the wild populations of parental species. The hybrids involving common bream such as roach x common bream and silver bream x common bream were chosen because they are frequently captured in rivers (Demandt and Bergék 2009; Golubstov et al. 1990; Schwartz 1972, 1981; Wyatt et al. 2006) and are known to backcross with parental species (Cross and O'Rourke 1978; Nzau Matondo et al. 2008a; Pitts et al. 1997; Toscano et al. 2010; Wood and Jordan 1987).

The aim of this study was to further examine the viability of hybrids involving common bream in terms of: (i) migration patterns, abundance level and growth rates in river conditions, and (ii) reproductive behaviour under a controlled environment involving behavioural reproduction experiments between hybrids and behavioural reproduction experiments on hybrids mixed with parental species males.

MATERIAL AND METHODS

Ecological observations

From 2001 to 2003, natural roach x common bream (RA) and common bream x silver bream (AB) hybrids and their parental species, the roach (R), the silver bream (B) and the common bream (A) were captured in a fish pass trap at the Lixhe dam of the Belgian Meuse River, 50°45'N; 5°40'E during their reproductive period. This dam has an 8m waterfall, a hydro-electric power plant and six spillways. On

the right shoreline, it is equipped with two fish passes consisting of a series of basins from the foot of the obstacle to the forebay in order to ensure the continuity of the river (Larinier and Travade 1992). The fish in the fish pass trap were collected three times a week from March to June. The water temperature was measured continuously using a temperature logger and dissolved oxygen was measured three times a week using a WTW OX 1330 oxymeter. Fish captured were systematically anesthetized with 2-phenoxyethanol (0.3ml·l⁻¹ of water), identified, and their fork lengths measured (in millimetres), and body mass weighed (in grams). The species and hybrids were identified according to morphological criteria accepted by Child and Solomon (1977); Klimczyk-Janikowska (1974); Nzau Matondo et al. (2008b); Spillman (1961), and Swinney and Coles (1982). The age of the fish was determined by counting annuli (Ombredane and Baglinière 1992) on scales (Katano and Hakoyama 1997; Philippart 1971) collected on the first two rows above the lateral line passing vertically from the anus (Philippart 1981). Abundance, water temperature, dissolved oxygen, the capture period and the growth of the hybrids compared to the parental species were analysed.

Behavioural analyses

Experiments were conducted in a 1.75·1.30·1.20m experimental aquarium equipped with a 1.05·0.89m synthetic spawning substrate simulating vegetation and positioned vertically. The water temperature was set at 20±0.1°C and the fish were placed in continuous lighting conditions throughout the entire experimental period. Dissolved oxygen was above 8mg·l⁻¹, pH 7.9±0.8 and nitrites and ammonium below 0.2 and 0.5mg·l⁻¹, respectively. A recirculation pump created an artificial water flow in the aquarium (21cm·s⁻¹). The fish were not fed. Spawning was induced by injection of Ovaprim, a synthetic hormone analogue to that of salmon GnRH and a dopamine inhibitor using two injections in the gravid females (0.5mg·kg⁻¹; time between injections, 8h) and a single injection in the males producing milt. Fish were injected the day after their capture at the Lixhe dam. According to Poncin et al. (1994) and Nzau Matondo et al. (2009), hormonal injection can be used to synchronise the spawning activity and to reduce the experimental time to 3 days only. All selected spawners were mature, females were gravid and males produced milt while checked by gentle pressure on the abdomen of fish. Behavioural experiments were conducted in two replicates. The fish used are presented in Table 1.

Hybrid mating and aggressive acts were studied in: (i) behavioural reproductive experiments between hybrids in which three female hybrids were placed to reproduce with nine corresponding hybrid males, and (ii) behavioural reproductive experiments of hybrids mixed with parental species males in which three female hybrids were mixed with three corresponding hybrid males and three males for each

Table 1. Description of behavioural experiments and spawners used: A-common bream, B-silver bream, R-roach, RA-natural hybrids of roach x common bream, AB-natural hybrids of common bream x silver bream; *n*-number of fish; mean±standard deviation values.

Experiment	Sex	<i>n</i>	Values of first/second replicate			
			Fork length (mm)	Weight (g)	Number of soft rays in anal fin	Age (years)
Reproduction between hybrids						
9♂RA x 3♀RA	♀	3	317±59/318±33	642±316/612±203	16±0.0/16±0.6	6±2/5±1
	♂	9	275±38/288±64	355±166/385±116	16±0.8/16±0.8	5±1/4±2
9♂B x 3♀AB	♀	3	305±15/310±10	610±168/570±66	24±0.6/24±1.0	5±0/5±1
	♂	9	302±31/345±43	510±185/804±257	24±0.9/24±0.9	5±1/5±1
Reproduction of hybrids mixed to parental species males						
3♂RA, 3♂A, 3♂R x♀RA						
RA	♀	3	273±65/339±71	391±249/731±381	16±0.6/16±0.6	5±2/6±2
RA	♂	3	287±76/335±20	405±245/644±126	16±0.6/17±0.6	5±2/6±1
R	♂	3	224±31/248±18	175±76/269±41	11±0.6/11±0.0	4±1/4±1
A	♂	3	392±19/363±20	960±123/856±178	25±0.6/26±1.0	7±1/5±1
3♂AB, 3♂A, 3♂B x♀AB						
AB	♀	3	267±11/366±25	378±46/1099±58	23±0.6/24±0.6	5±0/6±1
AB	♂	3	320±26/346±25	616±144/787±208	23±1.2/24±1.0	6±1/5±1
B	♂	3	250±14/265±14	273±29/353±17	22±0.6/22±0.6	5±1/5±1
A	♂	3	408±18/390±25	1150±93/1020±236	25±1.0/26±1.0	8±1/6±1

parental species. More males than females corresponded to the situation commonly encountered in the wild during the spawning period of the parental species (Billard 1997; Breder and Rosen 1966; Diamond 1985; Poncin et al. 1996; Spivak 1987). Behavioural acts were analysed over 1 day from 8.00 to 18.00h, corresponding to the beginning and end of spawning activity (Nzau Matondo et al. 2009; Singh et al. 2010), using a remote-controlled video system. Mating was defined as sexual contact between fish of the opposite sex followed by expulsion of gametes indicated by trembling and violent splashing movements on the spawning substrate. Aggressive behaviour was defined as the attack of a fish by another fish of the same or different sex. For a territorial male, this attack consisted of rapid dashes towards the intruder followed by a quick retreat to the centre of the territory, with this pattern repeated until the intruder moved away. The numbers of mating and aggressive acts were counted hourly within the time period from 8.00 to 18.00h. Behavioural data were presented in mean values of two experimental replicates. Mating success, expressed as the percentage of eyed embryos 1 day after spawning, was evaluated from two samples of 100 eggs per experiment, using a microscope.

Statistical analysis

The mean performance of environmental conditions was analysed with the Kruskal-Wallis (KW) test. The Fisher exact probability (FEP) test was used to compare the relative abundance of hybrids and parental species, and the percentage of eyed embryos in behavioural experiments. The comparison of egg release and mating was statistically examined using the chi-square test. For all statistical tests, a probability level of $p < 0.05$ was considered significant.

RESULTS

Ecological observations

RA and AB hybrids were significantly less frequent (FEP test, $p < 0.0001$) than parental species (Figure 1). Their relative abundance did not reach the threshold of 1% of fish captured and no significant difference was found between these hybrids (FEP test, $p > 0.05$). Between species (relative abundance of 57.1, 37.6 and 4.1% for common bream, roach and silver bream, respectively), significant differences were found (FEP test, $p < 0.0001$).

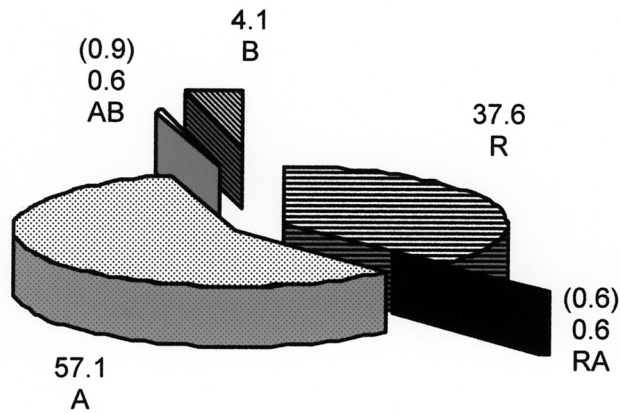


Figure 1. Relative abundance in percent of total capture of hybrids and species during their period of reproductive migration (March-June) from 2001 to 2003 in the Belgian Meuse River. Values in parenthesis indicate relative abundance of hybrids to their parental species (n-number of fish captured). A-common bream, $n=4961$; B-silver bream, $n=356$; AB-natural hybrids of common bream x silver bream, $n=53$; RA-natural hybrids of roach x common bream, $n=52$; R-roach, $n=3265$.

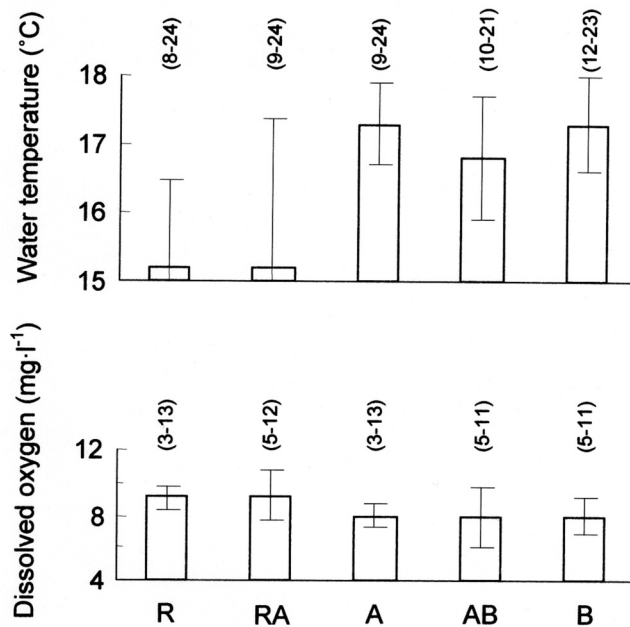


Figure 2. Water temperature and dissolved oxygen at the capture of hybrids and parental species during the period of reproductive migration (March-June) from 2001 to 2003 in the Belgian Meuse River. Mean values and error bars of annual values; values in parenthesis indicate extreme values of fish capture. A-common bream, B-silver bream, AB-natural hybrids of common bream x silver bream, RA-natural hybrids of roach x common bream, R-roach.

The environmental conditions such as water temperature (KW test: d.f.=4, $H=5.5$, $p>0.05$) and dissolved oxygen (KW test: d.f.=4, $H=2.308$, $p>0.05$) during the experimental period did not significantly affect the reproductive migration of hybrids and parental species (Figure 2). Hybrids of RA (range: 9–24°C and 5–12mg·l⁻¹ for water temperature and dissolved oxygen, respectively) and AB (10–21°C and 5–11mg·l⁻¹) had the same preference that parental species (8–24°C and 3–13mg·l⁻¹) when it came to water temperature and dissolved oxygen.

Hybrids and parental species migrated during the same period (March to June) (Figure 3). However, the highest capture of hybrids was observed in April and May for RA hybrids (40% of fish) and AB hybrids (64%). In the parental species, the highest capture was observed in March for roach (71%) and May for common bream and silver bream, accounting for 52 and 86%, respectively.

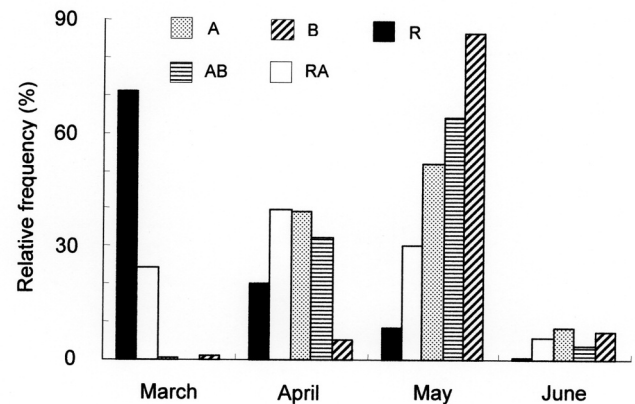


Figure 3. Monthly distribution of captures of hybrids and parental species in percent during the period of reproductive migration (March-June) from 2001 to 2003 in the Belgian Meuse River (n -number of fish captured). A-common bream, $n=4961$; B-silver bream, $n=356$; AB-natural hybrids of common bream x silver bream, $n=53$; RA-natural hybrids of roach x common bream, $n=52$; R-roach, $n=3265$.

The analysis of age structure (Figure 4) showed eight age groups for AB hybrids (range, 3–10 years) against nine for RA hybrids (2–10 years). The dominance of the 3-years group was observed in RA hybrids against the 3-years group in AB hybrids, accounting for 22% of fish in each type of hybrids. In the parental species, seven age groups were observed in silver bream (2–8 years) with the dominance of the 5-years group (25%) against eight age groups for roach (2–9 years) and common bream (3–10 years) with the dominance of age groups of 3-years (36%) and 5-years (24%), respectively.

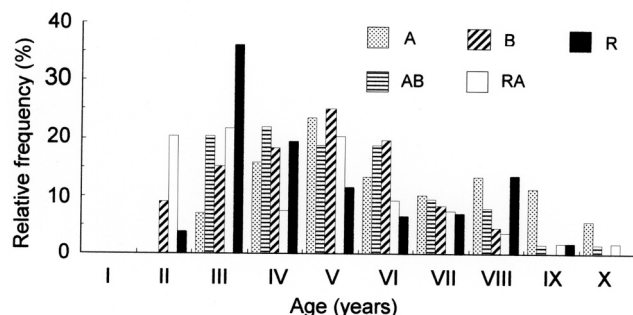


Figure 4. Age structure in hybrids and parental species during the period of reproductive migration (March-June) from 2001 to 2003 in the Belgian Meuse River (n -number of fish sampled). A-common bream, $n=196$; B-silver bream, $n=132$; AB-natural hybrids of common bream x silver bream, $n=53$; RA-natural hybrids of roach x common bream, $n=52$; R-roach, $n=155$.

The fork length of hybrids was intermediate to that of parent species (Figure 5). Between hybrids, AB hybrids showed higher fork length than RA hybrids. In the parental species, common bream showed higher fork length than roach.

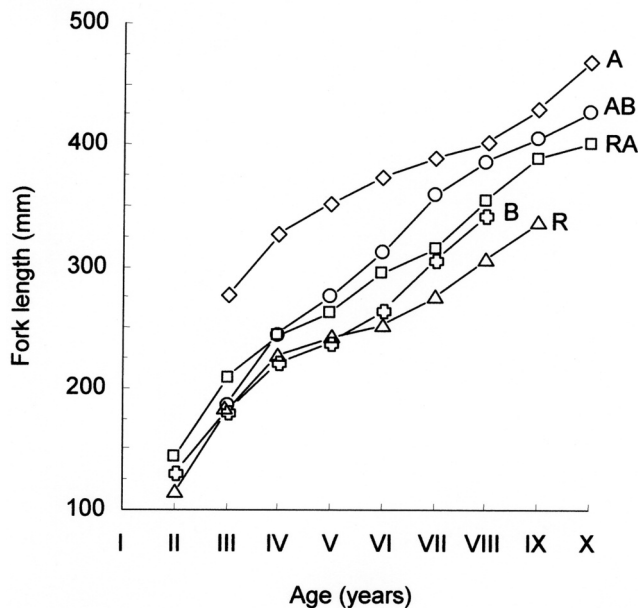


Figure 5. Fork length in different age classes in hybrids and parental species during the period of reproductive migration (March-June) from 2001 to 2003 in the Belgian Meuse River (n -number of fish sampled). A-common bream, $n=196$; B-silver bream, $n=132$; AB-natural hybrids of common bream x silver bream, $n=53$; RA-natural hybrids of roach x common bream, $n=52$; R-roach, $n=155$.

Behavioural analyses

Highly similar egg release and mating numbers (Figure 6a) were observed for both types of female hybrid in both reproductive experiments except in experiments with RA hybrids mixed with parental species males, in which the number of egg releases (mean, 17) was higher than the mating numbers (eight matings) but the difference was not significant (χ^2 test, $p>0.05$). Between reproductive experiments, egg release numbers were lower in experiments with hybrids mixed with parental species males (13 and 17 egg releases for AB and RA hybrids, respectively) than in reproduction experiments between hybrids (27 and 54 egg releases for AB and RA hybrids, respectively). The highest egg release activity was observed in RA hybrids.

The female hybrid mated with one to two males, including male hybrids, in reproductive experiments between hybrids; they mated with male hybrids and male roach or male silver bream but not with the male common bream in reproductive experiments with hybrids mixed with parental species males (Figure 6b). RA and AB hybrids shared two features: (i) the female hybrid mated more frequently with a male hybrid, and (ii) the male common bream did not participate in reproduction with female hybrids.

The mating success assessed 1 day after spawning (Figure 6c) revealed that the percentage of eyed embryos was lower in reproductive experiments with hybrids mixed with parental species males (mean, 10 and 17% for RA and AB hybrids, respectively) than in reproductive experiments between hybrids (25 and 31% for RA and AB hybrids, respectively) with both types of hybrid. No significant difference (FEP test, $p>0.05$) was found between RA and AB hybrids in similar reproductive experiments.

In reproductive experiments between hybrids (Figure 6d), a male hybrid defended a territory and attacked the other male hybrids. In reproductive experiments with hybrids mixed with parental species males, the male hybrid did not defend a territory, but it attacked the roach, common bream and silver bream males. Territoriality was acquired by a male common bream, which attacked conspecific males, the roach and silver bream males, and the male and female hybrids. The female hybrids were attacked by their corresponding hybrid male in both reproductive experiments between hybrids and in reproductive experiments with hybrids mixed with parental species males.

Spawning episodes

The succession of spawning episodes was similar in the two types of reproductive experiment in these two types of hybrids. The female hybrid, ready to release eggs, moved to the spawning ground composed of artificial vegetation by passing through a territory defended by a male. This male joined the female during an ascending movement towards the water surface (Figure 7A) along the vertically placed spawning ground.

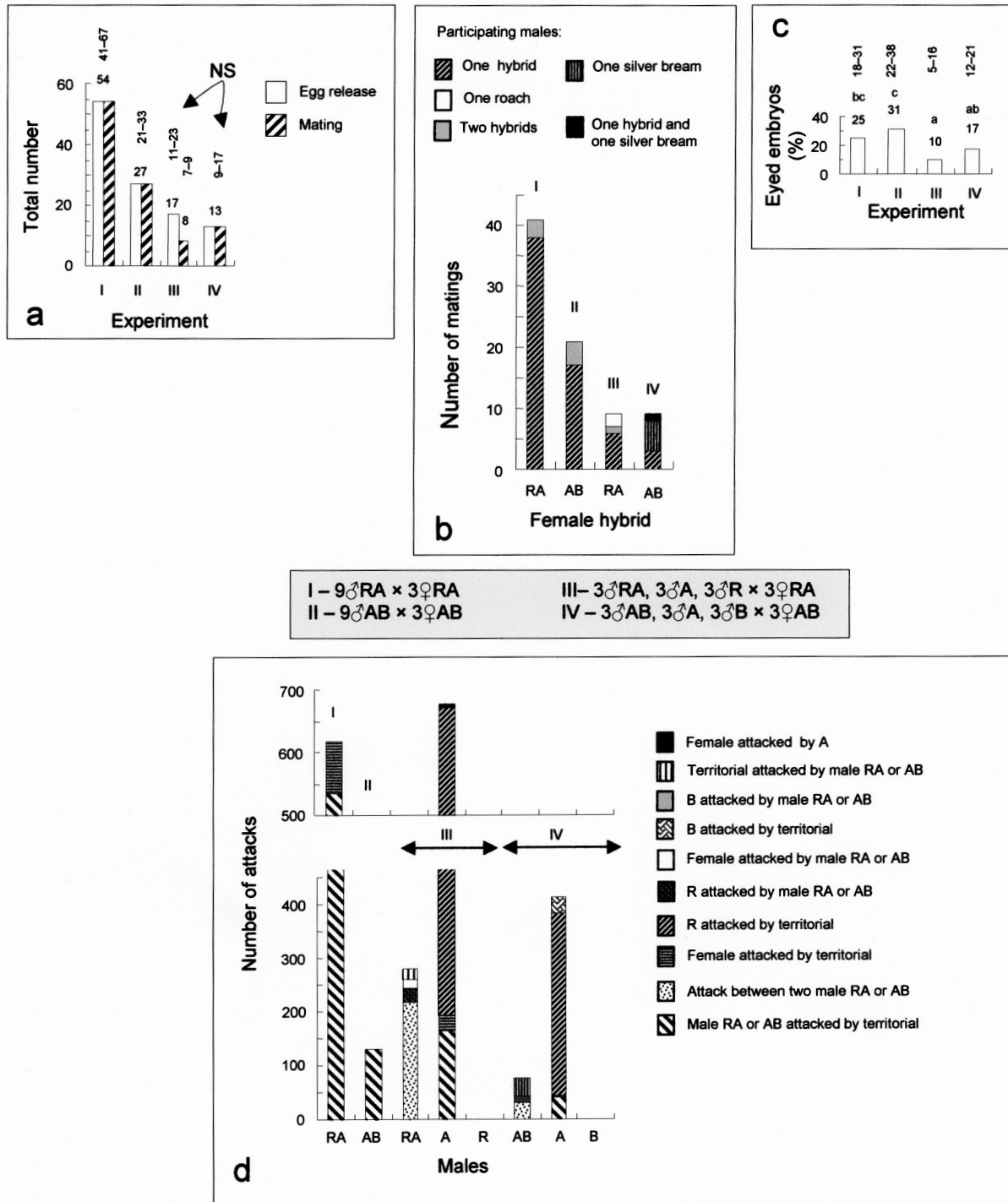


Figure 6. Egg release-mating comparison: (a) males participating in the mating, (b) mating success, (c) aggressive behaviour, (d) reproduction between hybrids and reproduction of hybrids mixed to parental species males from 8 to 18 hours. Shaded insert-number of fish per sex in experiment: A-common bream, B-silver bream, R-roach, RA-natural hybrids of roach x common bream, AB-natural hybrids of common bream x silver bream. Mean values of experimental duplicates; mean and range of values of experimental duplicates above vertical bars for egg release-mating comparison; range, extreme values of four observations in two replications in each experiments for eyed embryos; NS, no significant difference (χ^2 test, $p=0.252$); bars sharing at least one common script were not significantly different, whereas other comparisons differed at $p<0.05$ (FEP test); female attacked by A indicates the female hybrid was a victim of the aggression from the common bream male.

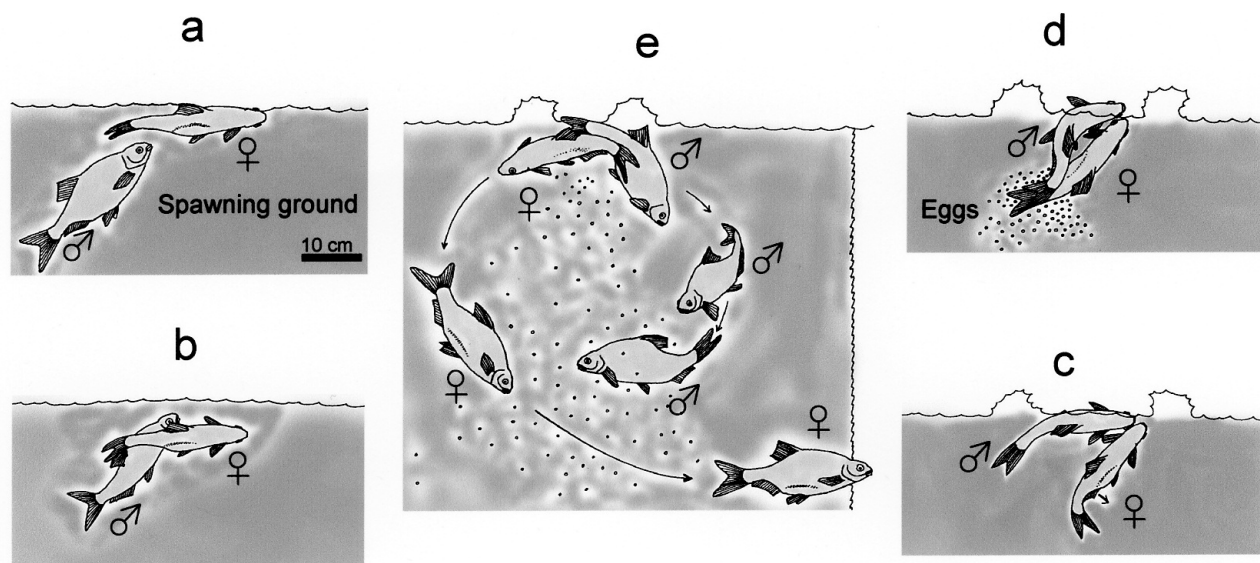


Figure 7. Scenarios type during the reproduction of hybrids. a-male joins female in ascent movement towards the water surface, b-pair formed, c-burrowing movements, d-spawning episode, e-returning movement toward the bottom (the spawning ground placed vertically).

During spawning, the pair formed side by side (Figure 7B), with the male showing a courting tactic. The male and female performed burrowing movements (Figure 7C) while moving towards the water surface. In a successful spawning act (Figure 7D), they released eggs and sperm on plants in a quick twisting movement of the body, indicated by trembling movements and violent splashing. The scattered eggs were found glued in the “synthetic plants” of the substrate, on part of the aquarium walls and on its bottom. Fertilised eggs were observed 1 day post spawning and larvae were observed 4 days after spawning. In post-spawning (Figure 7E), the male territorial hybrid followed the female who left the territory immediately.

Under reproductive experiments with hybrids mixed with parental species males, these spawning episodes were observed very quickly without the participation of common bream male. They occurred in the male bream's territory when it removed it or it attacked another male conspecific or hybrid attempting to enter the territory.

DISCUSSION

Ecological observations

Our ecological results revealed that the hybrids were less abundant compared to the record captures obtained from other water systems such as the Irish reservoir in England, where RA hybrids accounted for 37–90% of fish in the parental populations (Fahy et al. 1988). In a lake in Ireland, Kennedy and Fitzmaurice (1973) observed 42 and 68% of RA hybrids in two samples taken using fishing nets. However, the proportion of hybrids found in this study corresponded to that commonly encountered in many other continental

European fish communities (Sindilariu et al. 2002). These hybrids were identified according to morphological criteria without screening combination of molecular markers, and therefore, the identification of post-F1 hybrids is limited. Thus, the exact status of hybridisation is yet to be established with precision. The presence of RA and AB hybrids in the investigated site is nevertheless a sign of the existence of the hybridisation process between parental species in natural populations; hence there is increasing interest in gaining better knowledge of these hybrids ecologically and in all aspects of biology compared to the parental species.

In hybrids as in the parental species, the water temperature played a dominant role in triggering fish spawning and migration (Baras et al. 1994; Berg and Berg 1989; Jensen et al. 1986; Olla et al. 1980; Santos et al. 2002). Indeed, a slow increase in water temperature at the beginning of the year led to late spawning migration, switching to early spawning migration when the temperature increased rapidly. In the parental species, reproductive movements were observed within the periods and environmental conditions observed in European rivers for the roach (Billard 1997; Gulidov and Popova 1981; Herzig and Winkler 1986; Kokurewicz 1970), the silver bream (Keith and Allardi 2001; Koli 1990; Spivak 1987) and the common bream species (Shestopalova 1978; Spratte and Hartmann 1997; Vostradovsky 1973) but with some early migration starting dates. The early migration observed in our experimental site could be explained by a faster rise in temperature caused by thermal effluents discharged into the Meuse by several nuclear power plants upstream. This clearly shows that the frequency of migration is not rigid but flexible, depending on the environmental conditions, most particularly on water temperature.

No fish of hybrids or parental origin belonging to the 1-year group were caught. Sexual immaturity at this age could explain this finding. The low number of young and old fish observed might be related to the high mortality rate due to the stress they undergo during the sexual maturation and reproductive period. In contrast, the predominant age groups could be correlated with: (i) the years of very good recruitment of fish attributable to high summer temperatures, encouraging rapid growth, and (ii) the variations in size between hybrids and their parents within the sample size analysed.

The intermediate growth observed in these hybrids is consistent with the results reported by Pethon (1978), Purdom (1979), Bianco (1982), Fahy et al. (1988), and Bracewell (1994). However, faster growth compared to parents (heterosis) has already been observed in chub (*Leuciscus cephalus*) x bleak (*Alburnus alburnus*) hybrids (Kanno 1968) and in bleak x roach hybrids (Crivelli and Dupont 1987), but the heterosis phenomenon has not been observed in all hybridisation studies.

At 4 years of age, RA hybrids measured 243mm in this study versus 194mm in the River Exe (Cowx 1983), which showed better growth for fish in the Belgian Meuse, as also found in the parent species such as the roach: 226mm in this study versus 170mm in the River Lugg (Hellowell 1972); the silver bream: 221mm versus 130mm in Lake Balaton (Specziár et al. 1997); and common bream: 326mm versus 205mm in Lake Tjeukemeer (Mooij et al. 1996). This very good growth rate in the Belgian Meuse could be explained by the impact of relatively high river temperatures, due to the thermal effluents that it receives. Indeed, temperature acts directly on the growth rate through its effect on the metabolism and general activity of poikilotherms but also indirectly on the production of nutrients for fish (Eppley 1972; Gabillard et al. 2005; Lares and McClintock 1991; Perin et al. 1996).

Behavioural analyses

The observations from the reproductive experiments both among hybrids and of hybrids with parental species revealed that hybrids participated actively in reproduction under natural conditions. Hybrids were fertile, reproduced and produced F2 progeny.

These hybrids had in common the nonparticipation of male common bream, which might mean that backcrosses between female hybrids and male common bream had a very little chance of taking place in rivers. The most convincing alternative of backcrossing may be the cross between female common bream and male natural RA or AB hybrids, a hypothesis which deserves to be confirmed or more thoroughly studied. Moreover, the dominance of female common bream in heterospecific matings has already been demonstrated in the study of hybridisation direction from natural RA hybrids by molecular analysis (Wyatt et al. 2006), natural AB hybrids using mitochondrial ATP synthase subunit 6 and 8 region (Demandt and Bergek 2009), and in a behavioural study of hybridisation

between silver bream and common bream in a controlled environment (Nzau Matondo et al. 2009).

The territoriality and aggressive acts observed in the males of the two hybrid types may reflect the nature of interactions existing among hybrids and with their parental species in rivers. They also showed that the hybrids can acquire parental traits such as aggressiveness and territoriality recognised in the parental species, the common bream (Fabricius 1951; Kozlovskij 1991; Poncin et al. 1996; Svårdson 1949). As in common bream, the territorial activity observed in these hybrid males under reproductive experiments between hybrids was used to establish a spawning site in which all rivals were vigorously excluded. The similar success of male hybrids in terms of their aggressive behaviour has already been observed in male *Cyprinodon pecosensis* x *C. variegatus* hybrids (Rosenfield and Kodric-Brown 2003). From a behavioural point of view, our results proved that those hybrids were very active in nature. Under reproductive experiments of hybrids mixed with parental species males, the common bream male exhibited a high territoriality level with establishment of a spawning site but without his participation in mating. In these experiments, mating occurred between female hybrid and male hybrids or parental species: roach or silver bream. In contrary to the common bream species in rivers, the territorial male establishes a spawning site in which it mates with the female conspecific (Poncin et al. 1996).

The survival of embryos observed in post-spawning in reproductive experiments between hybrids and reproductive experiments of hybrids mixed with parental species revealed that those hybrids (male and female) were fertile. This means that the next generations may be available by intracross or backcross from hybrids, and repeated backcrosses may provide a means to transport certain characteristics from one species to another. The reproductive success of hybrids is not only limited to these hybrids, but it has already been observed for other hybrids such as cultured AB hybrids (Nzau Matondo et al. 2008a) and roach x silver bream hybrids (Nzau Matondo et al. 2008b).

Spawning episodes involving following the female and courting tactics, and the release of eggs and sperm on the shallow depths of the spawning ground without providing parental care observed in these hybrids were consistent with the spawning patterns recognised in the parental species (Billard 1997; Diamond 1985; Koli 1990; Kottelat 1997; Poncin et al. 1996, 2004; Nzau Matondo et al. 2008a, 2009; Vostradovsky 1973) and in other phytophilous cyprinid fish species such as common carp (*Cyprinus carpio*) and goldfish (*Carassius carassius*) (Cowx 1990; Fahy et al. 1988; Svårdson 1949).

CONCLUSION

The results of this study have demonstrated that natural RA and AB hybrids were less abundant but eco-ethologically viable. In terms of evolutionary biology, hybrids may be a sign of adaptation to environmental change and a source of genetic

variability (Carvalho 2005; Forsman et al. 2008). However, from the point of view of the conservation of wild populations of parental species and the management of habitats in rivers, hybrids may be regarded as indicators of degradation of the aquatic environment (Didier 1997; Kestemont et al. 2002, 2004). Indeed, hybridisations are favoured by the concentration of spawner fish downstream from impenetrable or difficult-to-penetrate barriers and by the concentration of fish in small spawning areas (often aquatic plants or roots of trees extending from a shoreline). Especially when considering that males of many species can be ready to release milt over several weeks facilitating the heterospecific crosses. These situations occur in artificial environments such as canals and channelled streams. The restoration of free fish movement, the preservation of spawning grounds of phytophilous species and their restoration in highly degraded environments (Philippart 2007) are the main lines of intervention in aquatic habitats that are likely to slow unwanted hybridisation processes. Beall et al. (1997) have advocated limiting hybridisation between Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), recommending that river managers in Western Europe ensure the quality and quantity of spawning areas to maintain the balance of spawner populations and to limit the restocking of non-native fish. The field of aquarium fish with its practices such as fish imports and local production of fish in ponds, the voluntary release into rivers of coloured varieties of fish from breeding and the release into water of the fish used as bait also contributes to the dispersion into the environment of non-native species of various origins, which then can hybridise with native species and cause the genetic and morpho-ecological alterations of protected species with a high heritage value (De Wolf 2004; Hänfling et al. 2005).

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