

A comprehensive assessment of the failure of *Barbus barbus* spawning migrations through a fish pass in the canalized River Meuse (Belgium)

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Abstract

This paper presents a comprehensive study of the impact of damming on the spawning migrations of *Barbus barbus* in the canalized River Meuse (Southern Belgium). A Denil fish pass on the Ampsin-Neuville dam was controlled 251 times in 1989-1993. The most striking feature is the almost complete absence of barbel in 1990-1993 (15 fishes in 4 years). Most captures of barbel in the fish pass in 1989 were clumped within a few days (mid-May) and related with spawning migrations. Stepwise multiple regression analyses revealed that attractivity was the major condition set allowing barbel to migrate successfully through the pass, while feasibility parameters (water velocity) were found not to be relevant. The variables involved in the attractivity condition set refer indirectly to the influence of water catchment by a hydroelectric plant and to the relative importance of the flow in the pass. The study concludes that this additional condition set significantly interferes with the natural environmental stimuli triggering spawning migrations in barbel and questions the effectiveness of the thermally-related reproductive strategy of the species in an environment with restricted longitudinal connectivity. This statement is discussed in parallel with the recent evolution of barbel populations in canalized rivers.

Keywords : *Barbus barbus*, Cyprinidae, migration, spawning season, River Meuse, fish pass, discharge attractivity, temperature effect.

Une étude d'impact des passes à poissons de la Meuse sur l'échec des migrations de reproduction de Barbus barbus.

Résumé

De 1989 à 1993, nous avons étudié l'impact de barrages sur les migrations de reproduction du barbeau fluviatile, *Barbus barbus*, dans le cours belge de la Meuse, via le contrôle d'une passe à poissons de type Denil. Les 251 contrôles (vidange des bassins intermédiaires) ont mis en évidence l'absence quasi complète de barbeaux dans la passe, en 1990-1993 (15 poissons en 4 ans). La majorité des captures en 1989 étaient regroupées en une décade (5-15 mai) et correspondaient à la migration de reproduction des géniteurs mâles et femelles. L'analyse de la périodicité des captures (régression multiple pas-à-pas, seuil d'entrée = 0,10) exclut l'influence de critères de faisabilité (franchissement de l'obstacle) mais met significativement en évidence le rôle déterminant d'un ensemble conditionnel d'attractivité, impliquant le débit dans la passe à poissons et le débit de fonctionnement de la centrale hydroélectrique établie sur le barrage. Cet ensemble conditionnel interfère considérablement avec les stimuli environnementaux déclenchant les migrations et les activités reproductrices chez le barbeau. En conséquence, la stratégie reproductrice de l'espèce, basée sur un déclenchement thermique des activités reproductrices s'avère peu adaptée à un environnement dont le gradient longitudinal est restreint. L'impact de cet échec des migrations de reproduction est discuté dans le contexte de la régression démographique du barbeau dans les fleuves canalisés.

Mots-clés : *Barbus barbus*, Cyprinidae, migration de reproduction, Meuse, passe à poissons, attractivité, effet de la température.

INTRODUCTION

The problems related to the behaviour of fish confronted with natural or man-made obstacles on their migration route have been extensively studied in anadromous salmonids and clupeids (e.g. Steinbach *et al.*, 1986; Nettles and Gloss, 1987; Travade *et al.*, 1989; Larinier and Boyerbernard, 1991; Gosset *et al.*, 1992). Comparatively less attention has been paid to their impact on the movements of the so-called "resident" coarse fish species. However, the considerable habitat modifications (dredging and deepening, bank rectification, canalization) in most large river ecosystems have resulted in a growing scarcity of optimal or at least suitable spawning grounds and nurseries for many fish species. This situation probably has imposed major environmental constraints on fish species that had to migrate to spawning grounds in the upper part of the rivers or in their tributaries, thus they faced the same problems as those encountered by migratory salmonids in the vicinity of dams and weirs.

This problem is particularly relevant in the River Meuse Basin. Originally typical of the lower barbel zone (Huet, 1949), the Belgian stretch of the R. Meuse (182 km) has been dredged down to a depth of 5 m and banks have been canalized to provide navigation capacities up to 9 000 t (Micha, 1985; Verniers, 1988; Philippart *et al.*, 1988). Fourteen big dams – with a difference in level ranging from 4 to 6 m – have been built between the North Sea and Namur (Micha, 1985). These modifications have resulted in the extinction of the Atlantic salmon (*Salmo salar*) and other anadromous species (*Acipenser sturio*, *Alosa alosa*, *Petromyzon marinus*) in this ecosystem (Philippart, 1985, 1987b). Similarly, a major population decline was attended in several resident species in the R. Meuse Basin, specially amongst lithophilous and rheophilous cyprinids (Philippart and Vranken, 1983; Philippart *et al.*, 1988).

In a project aiming at the restoration of Atlantic salmon in the R. Meuse Basin (Philippart *et al.*, in press), in 1989, we started a research programme on the movements of fishes in this river, focusing on the interferences between genuine migratory tendencies and the condition sets allowing the passage through fish passes. These condition sets refer to the notions of attractivity and selectivity of fish passes documented by many authors (e.g.: Katopodis, 1981; Jens, 1982; Larinier, 1983; Beach, 1984; Slatick, 1985; Pelz, 1985; Larinier and Boyerbernard, 1991; Larinier, 1992). This study was conducted in 1989-1993 on the Ampsin-Neuville weir (between Namur and Liège), equipped with Denil fish passes (Denil, 1909) and with a hydroelectric plant, a situation representative of most obstacles on the R. Meuse (Philippart *et al.*, 1988). The barbel *Barbus barbus* L. was selected as an indicator in this investigation, based on its representativeness of the original R. Meuse ecosystem and on its recent decline in canalized rivers (Lelek,

1980; Banister, 1982; Philippart and Vranken, 1983). In addition, the development, during the last 20 years, of a multidisciplinary research programme on barbel population dynamics (Philippart, 1987a), physiology (Poncin, 1989) and behavioural ecology (Baras, 1992) should allow a better understanding of the migratory behaviours studied in a modified environment and a reliable assessment of the impact of obstacles on recruitment.

STUDY AREA

The weir of Ampsin-Neuville was constructed in 1958, 3.5 km downstream of Huy and 5.0 km downstream of the confluence with a valuable spawning tributary, the R. Méhaigne (*fig. 1A*). It is located 0.9 km downstream of a heated effluent from the Tihange nuclear power plant (2 600 MW), causing a 3-4°C water temperature increase in all seasons. The weir was initially equipped with a sluice (right bank) and two Denil fish passes were constructed on the sides of the spillway (*fig. 1B*). Each pass is composed of three successive Denil ladders (mean slope = 24%) equipped with 22 multiple-plane baffles spaced 35 cm apart and set at an angle of 45° to the axis of the channel (*fig. 1C, D*), in order to allow maximum energy dissipation (Denil, 1909). The ladders are separated by intermediate pools (upper, intermediate and lower). In 1964, the weir was fitted with a 10 000 kW hydroelectric plant on the left bank of the river. The 3 turbines of the plant catch a maximum 250 m³.s⁻¹ flow. The flow in the fish pass is mainly dependent on the water level upstream of the weir, which is constantly regulated for navigation purposes through modifications of the flow on the spillway, at least at flows ≥ 250 m³.s⁻¹.

MATERIAL AND METHODS

Fish migrations were assessed through regular control of the fish passes. Since the right fish pass was continually obstructed by debris and proved ineffective, we focused on the left fish pass, close to the hydroelectric plant. The upstream outlet of the pass was equipped with a steel grid and a 2 cm mesh net preventing fish from leaving the pass. The upper pool (30 m³) was emptied with a valve system and the intermediate and lower pools (7 m³) with an electric pump (30 l.s⁻¹). Fishes were captured with dipnets, anesthetized in a MS₂₂₂ solution (100 mg.l⁻¹), measured to the nearest mm (fork length) and weighed. Sex was determined by the release of milt or eggs when pressing the fish abdomen.

Fishes coming from the lower pool were not taken into account in the analyses on migration periodicity, based on both feasibility and significance criteria: on the one hand, since the outflow from the upper pool entered in this part of the fish pass directly, it

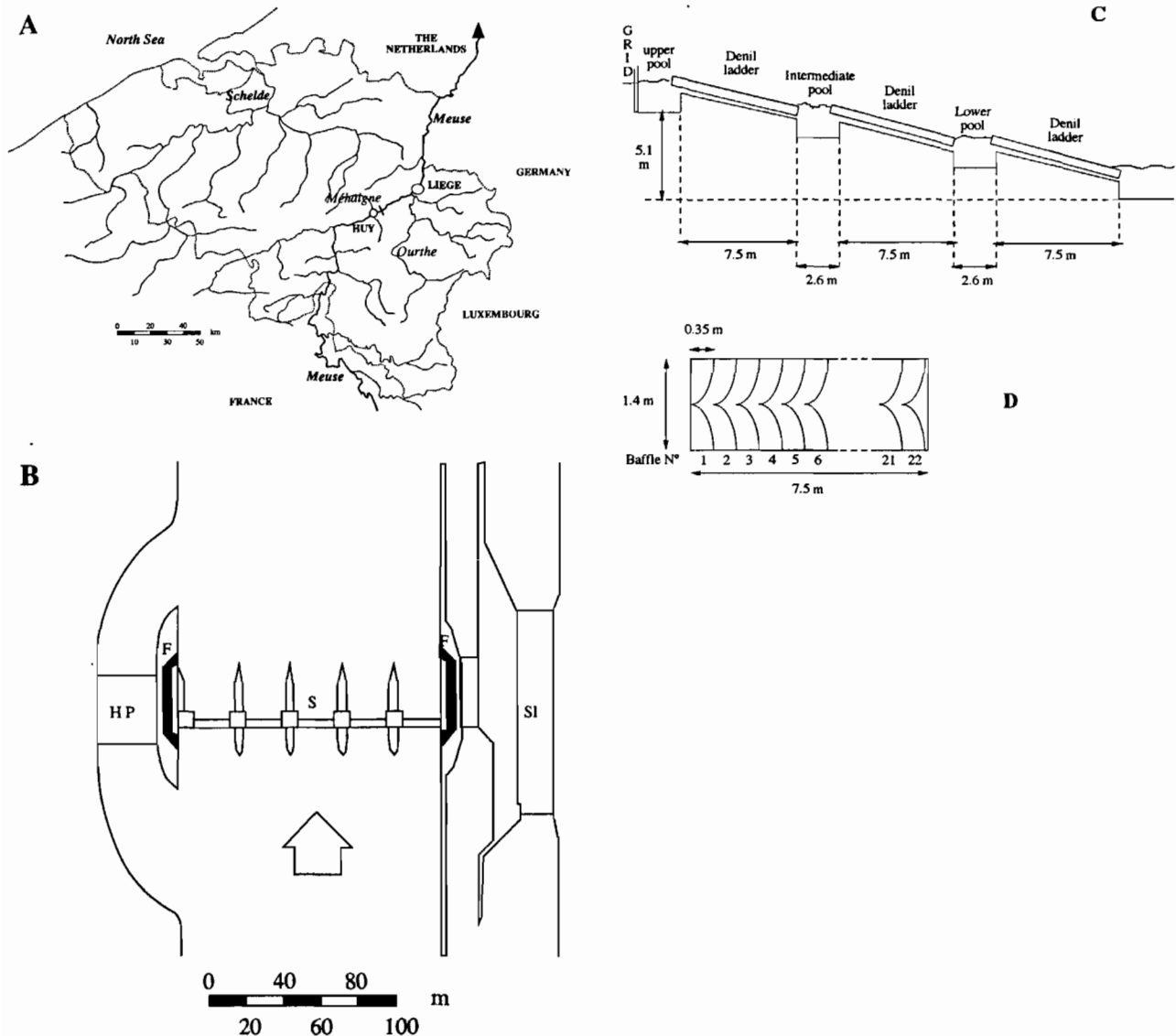


Figure 1. – Geographical situation (A) and description (B) of the study site, the Ampsin-Neuville weir (dark bar on map A, downstream of Huy), in the canalized River Meuse. HP=hydroelectric plant ($250 \text{ m}^3 \cdot \text{s}^{-1}$); SI=sluice; S=spillway; F=fish passes (Denil type). (C) Sagittal section of the fish pass. (D) Top view of a Denil ladder.

was impossible to empty this pool under high flow conditions; on the other hand, since the difference of level between the lower pool and the R. Meuse below the weir was reduced to 0.6 m, we thought that the presence of fish in the lower pool could not be considered as a reliable indicator of upstream tendencies.

Temperatures were recorded on a thermograph (Richard Instruments, S. A.) installed in the fish pass during the study period. The flow in the fish pass was obtained indirectly by measuring the time necessary for filling the intermediate pool. Flows in the R. Meuse and on the spillway were obtained from the Navigation Office and meteorological variables from the Belgian Royal Institute of Meteorology.

RESULTS

The pass was controlled 251 times during periods extending from mid-January to mid-July in 1989-1993, allowing the capture of 13693 fishes belonging to 21 species (table 1). The dominant species were chub (*Leuciscus cephalus*), bream (*Abramis brama*), bleak (*Alburnus alburnus*) and eel (*Anguilla anguilla*). All species, except barbel, trout and eel, were captured in larger numbers in the lower pool of the fish pass (99114 vs 4579 fish, table 1). Since the captures of barbel in 1990-1993 were dramatically low (15 fishes in 4 years) and could not be analysed statistically, we focused on 1989, when 115 barbel were captured in the upper and intermediate pools of the fish pass. The

Table 1. – List of species and captures in the Ampsin-Neuville Denil fish pass (upper and intermediate pools) in 1989-1993. Species are grouped in 7 categories of decreasing rheophilous tendencies, following the classification of Pelz (1985). Values between brackets refer to the captures in the lower pool and N to the number of controls.

Species	1989 (N = 53)		1990 (N = 52)		1991 (N = 41)		1992 (N = 43)		1993 (N = 62)		Species total	
1 Brown trout (<i>Salmo trutta fario</i>)	0	(0)	3	(0)	1	(0)	0	(0)	0	(1)	4	(1)
Sea trout (<i>Salmo trutta trutta</i>)	0	(0)	0	(0)	0	(0)	0	(0)	5	(2)	5	(2)
Barbel (<i>Barbus barbus</i>)	115	(4)	4	(3)	5	(1)	1	(1)	0	(0)	125	(9)
Nase (<i>Chondrostoma nasus</i>)	1	(0)	2	(5)	0	(0)	0	(0)	0	(0)	3	(5)
River bleak (<i>Alburnoides bipunctatus</i>)	0	(0)	0	(0)	0	(0)	0	(4)	0	(1)	0	(5)
2 Ide (<i>Leuciscus idus</i>)	0	(0)	4	(6)	0	(0)	0	(7)	3	(3)	7	(16)
3 Chub (<i>Leuciscus cephalus</i>)	390	(209)	321	(781)	57	(548)	79	(360)	48	(203)	895	(2 101)
Dace (<i>Leuciscus leuciscus</i>)	1	(1)	0	(0)	0	(0)	0	(0)	0	(0)	1	(1)
Bleak (<i>Alburnus alburnus</i>)	825	(597)	44	(1 591)	241	(200)	113	(60)	2	(762)	1 225	(3 210)
4 Roach (<i>Rutilus rutilus</i>)	46	(47)	19	(3)	29	(97)	36	(355)	20	(99)	150	(601)
Perch (<i>Perca fluviatilis</i>)	0	(3)	0	(0)	0	(0)	0	(0)	0	(3)	0	(6)
Pumpkinseed (<i>Lepomis gibbosus</i>)	0	(0)	0	(0)	0	(0)	0	(0)	0	(1)	0	(1)
5 Bream (<i>Abramis brama</i>)	181	(443)	140	(228)	44	(173)	31	(248)	16	(148)	412	(1 240)
White bream (<i>Blicca bjoerkna</i>)	3	(103)	0	(1)	0	(0)	0	(9)	0	(0)	3	(113)
Rudd (<i>Scardinius erythrophthalmus</i>)	0	(3)	0	(1)	0	(2)	0	(3)	1	(0)	1	(9)
6 Ruffe (<i>Acerina cernua</i>)	0	(0)	0	(0)	0	(0)	0	(0)	0	(2)	0	(2)
Pikeperch (<i>Stizostedion lucioperca</i>)	0	(0)	1	(0)	0	(0)	0	(0)	0	(0)	1	(0)
7 Carp (<i>Cyprinus carpio</i>)	0	(0)	0	(0)	0	(0)	0	(1)	0	(0)	0	(1)
Tench (<i>Tinca tinca</i>)	3	(2)	0	(0)	0	(0)	1	(0)	0	(0)	4	(2)
Tilapia (<i>Oreochromis aureus</i>)	0	(0)	0	(1)	0	(0)	0	(1)	0	(0)	0	(2)
Eel (<i>Anguilla anguilla</i>)	211	(36)	337	(398)	286	(168)	339	(277)	570	(908)	1.743	(1 787)
Annual total	1 776	(1 448)	875	(3 018)	663	(1 189)	600	(1 326)	665	(2 133)	4 579	(9 114)

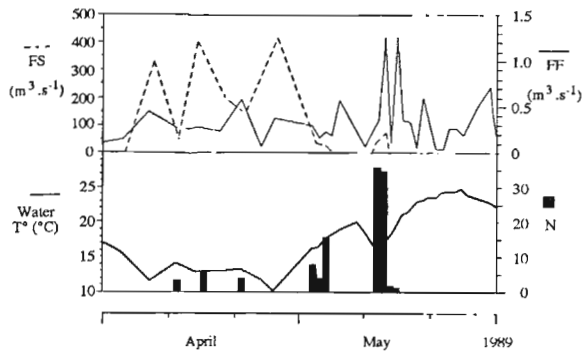


Figure 2. – Flows, temperature regimes of the River Meuse and corresponding captures of *B. barbus* in the Ampsin-Neuville fishpass in 1989. FS refers to the flow on the spillway and FF to the flow in the fish pass. This figure emphasizes the importance of a flow on the spillway in the attraction of *B. barbus* in the pass.

reasons for the near absence of barbel in the fish pass during these four years are discussed later.

Characteristics of the migrant population

The size distribution of the barbel captured in 1989 ranged between 356 and 740 mm (table 2). Fish averaged 493 mm (fork length (S.D.=55 mm) and 1520 g (S.D.=450 g). Forty-one fishes were identified as males, 38 as females and 36 as immature individuals. The mean sizes in these 3 categories were respectively 443, 544 and 481 mm and were statistically different (analysis of variance, ANOVA; $F=31.3$; $p<0.001$; 114 df). The sex ratio of the population migrating through the fish pass (1.08 male per female) was significantly different ($\chi^2=123.1$; $p<0.001$) from that observed in resident populations of barbel (R. Ourthe: 15 males: 1 mature female; Philippart, 1987a; Baras, in press).

Seasonal periodicity of migration (table 2, fig. 2).

No barbel was detected in the fish pass in late winter or early summer. All captures are clumped within a 5 week interval (April 11-May 15), with a major peak in mid-May, contrasting with the seasonal patterns of chub and bream, present in the fish pass throughout spring (table 2). The mid-May barbel peak is associated with a high proportion of mature individuals (61 out of 74 fishes), significantly higher (contingency table; $\chi^2=18.3$, $p<0.001$, 2 df) than in mid-April and in early-May (respectively 6 out of 13 and 12 out of 28 fish). The two latter periods differ as regards the sex ratio of the captures (<1.0 in mid-April and ≥ 1.0 in early May), although this difference is not statistically significant ($\chi^2=1.8$; $p=0.18$) owing to small numbers. These results suggest that the mid-May migration of barbel in the fish pass is related to reproductive activity while early captures are not.

Causal analysis

Barbel were captured in variable flood (229-677 $m^3.s^{-1}$) and temperature (12.8-19.3°C) regimes (table 2). No significant correlation was observed between these two variables and the number of barbel captured (respectively $R=0.21$ and $R=0.05$, 52 df). A permanent flow on the spillway (river flow \geq the maximum catchment of the hydroelectric plant, 250 $m^3.s^{-1}$) was identified as the major *sine qua non* condition for the presence of barbel in the fish pass (fig. 2). Indeed, only 1 barbel was captured in the absence of a flow on the spillway (May 15) while 114 individuals were captured on 9 of out of the 17 sampling days when this condition was fulfilled (χ^2 with correction of continuity = 15.8, $p<0.001$).

Stepwise multiple-regression analyses were used to isolate variables accounting for capture variability on the 17 sampling days when the flow on the spillway was above zero. Variables taken into account were photoperiod, mean daily water temperature (°C) and temperature variations at 1 to 7 day intervals, river flow (FR; $m^3.s^{-1}$) and its variations at 1 one to 7 day intervals, flow on the spillway (FS; $m^3.s^{-1}$), flow in the fish pass (FF; $m^3.s^{-1}$), the ratio of the two latter variables ($FF.FS^{-1}$) and sexual maturity (estimated by the percentage of mature individuals). The analysis resulted in a two-variable model with a R^2 of 0.795 ($F=27.1$, 16 df). The variables entering the model at the 0.1 level were (in decreasing order of importance): sexual maturity and $FF.FS^{-1}$. The significance of these relationships is debated below.

DISCUSSION

Seasonal periodicity of migration

The seasonal migratory pattern observed in the River Meuse fits the annual mobility cycle described in tracking studies of *B. barbus* in a tributary of the R. Meuse (R. Ourthe, Baras, 1992; 1993a) and emphasizing the hypermobility during the spawning period, when the probability for a fish to move from one locality to another between consecutive days is $\geq 50\%$. The absence of migrations during early summer confirms the result of tracking studies conducted in several rivers (Baras and Philippart, 1989; Pelz and Kästle, 1989; Baras and Cherry, 1990; Baras, 1993a) which have shown that summer is a major stability period, reflecting the fidelity to a defined activity area (Baras, 1993b).

The size distribution of barbel captured in 1989 was similar to that observed by Gillet (in Philippart *et al.*, 1990) controlling a fish pass on the navigation weir of Tailfer, in the upper R. Meuse. The first barbel captured in May in the fish pass were males and immature individuals, probably on their way to spawning grounds in an upstream tributary (R. Méhaigne). This interpretation is supported by

Table 2. - Dates of sampling, temperature, flow in the River Meuse and fish captured in the Ampsin-Neuville fish pass in 1989. Aa: *Anguilla anguilla*; Aal: *Alburnus alburnus*; Ab: *Abramis brama*; Eb: *Barbus barbus*; Lc: *Leuciscus cephalus*; Rr: *Rutilus rutilus*. M, I, F: numbers of Males, Immatures, Females.

Date 1989	Water T° (°C)	Flow (m ³ .s ⁻¹)	Captures (all species)	Dominant species	<i>Barbus barbus</i> Size (mm)	M, I, F	Sex ratio
January 30	10.3	122	11	-	-	-	-
February 13	11.1	127	1	Ab	-	-	-
February 20	13.1	170	17	Ab	-	-	-
February 28	12.8	424	2	-	-	-	-
March 15	12.6	288	31	Lc	-	-	-
March 17	10.7	509	4	Lc	-	-	-
March 21	10.7	318	0	-	-	-	-
March 23	12.2	200	7	Lc	-	-	-
March 29	15.4	265	13	Lc, Ab	-	-	-
March 31	17.1	230	62	Lc, Ab	-	-	-
April 03	15.7	202	52	Lc, Ab	-	-	-
April 07	11.6	604	0	-	-	-	-
April 11	14.3	316	6	Eb	440-505	1, 0, 2	1:2
April 14	12.8	677	14	Eb, Lc	453-562	1, 3, 2	1:2
April 18	13.0	472	2	-	-	-	-
April 21	13.3	410	4	Eb	485-521	0, 4, 0	-
April 24	11.8	534	16	Ab	-	-	-
April 26	10.1	683	0	-	-	-	-
May 02	16.5	325	26	Lc, Ab, Eb	385-586	3, 2, 3	1:1
May 03	16.4	271	47	Lc, Ab	356-547	1, 3, 0	1:0
May 04	17.8	272	35	Lc, Eb	386-543	4, 11, 1	4:1
May 05	18.5	254	87	Lc, Ab	-	-	-
May 05	19.0	231	0	-	-	-	-
May 09	20.1	205	2	-	-	-	-
May 10	18.9	203	4	Ab	-	-	-
May 11	17.5	202	1	-	-	-	-
May 12	16.0	337	55	Eb, Lc	415-740	15, 10, 11	1.4:1
May 13	16.9	327	39	Eb	378-627	16, 2, 17	0.9:1
May 14	18.1	236	444	Aal, Ab	547-584	0, 0, 2	0:1
May 15	19.3	229	7	Lc, Aa	450	0, 1, 0	-
May 16	21.1	203	2	-	-	-	-
May 17	21.6	197	0	-	-	-	-
May 18	22.8	171	185	Aal, Aa	-	-	-
May 19	23.4	151	20	Aal	-	-	-
May 21	23.6	175	133	Aal, Aa, Lc	-	-	-
May 22	24.2	173	24	Lc, Rr, Ab	-	-	-
May 23	24.4	152	1	-	-	-	-
May 24	24.4	143	0	-	-	-	-
May 25	24.8	142	3	Aa	-	-	-
May 26	23.9	130	4	Aa	-	-	-
May 29	23.0	142	3	Lc	-	-	-
May 30	22.2	132	34	Aal	-	-	-
June 01	20.5	156	5	Aa	-	-	-
June 02	20.1	101	0	-	-	-	-
June 05	17.4	136	9	Lc	-	-	-
June 07	19.1	127	0	-	-	-	-
June 03	19.2	127	0	-	-	-	-
June 13	22.8	91	47	Lc, Rr	-	-	-
June 14	23.0	50	2	Lc	-	-	-
June 16	23.2	85	65	Aal	-	-	-
June 22	23.4	75	143	Aa	-	-	-
June 26	24.6	82	92	Aal	-	-	-
June 30	22.3	87	13	Aa, Lc	-	-	-

results of electrofishing surveys revealing that males start to gather in the vicinity of spawning grounds at least 1 week before the beginning of spawning

activities (Baras, 1992). The migration peak itself is characterized by a marked synchronisation of mature individuals (71 out of 115 barbel were captured in two

consecutive days) and by a short time lag between males and females (sex ratio < 1 on 13-14 May). This pattern corresponds to the observations of Hancock *et al.* (1976) and Baras (in press), revealing that males already occupy the spawning grounds - or their vicinity - when mature females reach these sites. The earlier migration and occupation of spawning grounds by males is probably related to demographic constraints imposed by the sex ratio of the population (see Baras, in press). As noted above, the sex ratio of the migratory population in the fish pass was almost balanced and significantly different from that of natural populations (Philippart, 1987a). This difference can be accounted for by the higher mobility of females during this period, as evidenced by telemetry studies in the R. Ourthe (daily journeys of ± 10 -15 km in females vs ≤ 0.6 km in males; Baras, 1993a).

The presence of barbel in the fish pass in mid-April was probably not related with spawning activities since most fishes were immature. Since these captures followed high flow conditions ($> 600 \text{ m}^3 \cdot \text{s}^{-1}$), they may be regarded as compensatory upstream movements of individuals flushed downstream during the flow increase taking place on the previous days. Langford (1981) tracked bream (*Abramis brama*) in the vicinity of dams in the R. Witham and observed similar behaviour in fish swept downstream when sluices were open and migrating up back to their original position. Tracking studies conducted on barbel in the R. Ourthe came to similar conclusions (Baras and Cherry, 1990).

Interference between migratory tendencies and feasibility parameters

The mechanisms controlling the seasonality and timing of reproduction in *B. barbus* have been investigated recently, both in controlled and natural environments, and emphasize the inhibitory action of decreasing photoperiods (Poncin, 1989) and the role of a thermal threshold in triggering and synchronizing spawners (Baras, 1992). The advantages and constraints of these reproductive strategies are detailed elsewhere (Poncin, 1988; Baras, 1993c). If most captures of barbel in the fish pass took place while the temperature was steady or slightly increasing, the major peak corresponded to a temperature decrease (May 12-13). This seeming paradox arises from problems related to the attractivity of the fish pass or to its selectivity. The latter condition set probably has a minimal influence. Indeed, the maximum current speeds measured in the fish pass under high flow conditions (1.2 - $1.5 \text{ m} \cdot \text{s}^{-1}$) were always far below the swimming capacities of large barbel ($4 \text{ body length} \cdot \text{s}^{-1}$; Kreitmann, 1932; Katopodis, 1981). Besides, the presence in the fish pass of species with lesser swimming capacities (rheophobic breams or ubiquitous chubs) on days when no barbel was captured suggests that the selectivity condition set is not relevant to account for the absence

of barbel in the pass. This interpretation is supported by the captures in 1990-1993 (table 1).

Since barbels are rheophilous, they are probably attracted by the strongest flow (Jens, 1982), thus by the outflow of the hydroelectric plant ($\leq 250 \text{ m}^3 \cdot \text{s}^{-1}$). In order to find the entrance of the fish pass, they should be driven away from the hydroelectric plant by the presence of another major flow, such as a flow on the spillway (FS). This consideration explains the nature of the *sine qua non* condition, which could be considered as the first component of the attractivity condition set (attracting fish in the suitable area). The non-significant correlation between the flow on the spillway and the number of barbel captured in the fish pass reflects the existence of a second component of the attractivity condition set, the attractivity of the fish pass itself, which will be directly dependent on the flow in the fish pass (FF) and to its relative importance ($\text{FF} \cdot \text{FS}^{-1}$) vs the flow on the spillway. Consequently, we suggest that the migratory tendencies of barbel were indeed stimulated by the increase of water temperature but that the fishes could not be attracted by the fish pass since no flow was recorded on the spillway from May 5 to 11. They climbed up the fish pass on the first day when the *sine qua non* condition was fulfilled (May, 12) owing to an increase of river flow following rainfalls that also caused a decrease of water temperature, explaining the seeming paradox mentioned above. This interpretation would also account for the virtual absence of barbel in the pass in 1990-1993 since river flows $\geq 250 \text{ m}^3 \cdot \text{s}^{-1}$ were exceptional during the period when barbel have upstream tendencies: the fish could not be driven away from the "dead end" represented by the main outflow of the hydroelectric plant to find the entrance of the fish pass. This functional interpretation tends to be supported by the observation of numerous barbel at the outflow of the hydroelectric plant while none was captured in the pass. Ubiquitous or rheophobic species would be less attracted by this outflow, have a more erratic behaviour and more easily find the entrance of the fish pass, these elements explaining the more regular distribution of their captures during the study period.

CONCLUSION

The precision of thermal mechanisms triggering spawning was presented as a major advantage of *B. barbus* strategies in a non-modified environment (Baras, 1992), since it allows a synchronization of spawners at a time of the year when environmental conditions are favourable for maximizing the survival of progeny and subsequent stock recruitment. This study clearly demonstrates how the existence of additional and often incompatible conditions (simultaneous temperature increase and high flow) - resulting from the installation of an hydroelectric plant - may cause this strategy to prove inefficient

in a modified environment (migration only significant in 1 out of 5 years). Besides, since barbel eggs can survive a maximum 48 h after the gonadic maturity is completed (Poncin, 1988), a time lag caused by the absence of favourable conditions allowing ripe females to climb up fish passes may also result in a partial or total failure of the reproductive effort.

This interpretation from a strategic point of view may partly explain, in parallel with acute pollution problems (van Hoof et al., 1984) and the growing scarcity of spawning habitats (Philippart et al., 1988), the demographic decline of barbel populations during the last 30 years in the R. Meuse and in many other modified large river ecosystems (Philippart, 1993). Similar considerations are most probably relevant for

salmonids and other rheophilous cyprinids. Indirectly, this study raises the problem of instream flows in regulated rivers with impoundments for hydroelectric facilities: reducing the flow of the Ampsin-Neuville hydroelectric plant during the migration period of *B. barbus* would allow higher flows on the spillway, better attractivity of the fish pass and better chances for recruitment. If a management policy were undertaken to restore the free circulation of spawners, the interference with the activities of the hydroelectric plant (i.e. reduction of the flow) would be extremely limited over the daily cycle, given the typical crepuscular activity rhythm pattern of *B. barbus* at temperatures $\geq 10^\circ\text{C}$ (Baras, 1992).

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