Multiyear homing and fidelity to residence areas by individual barbel (*Barbus barbus*)

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ABSTRACT. Nine barbels (*Barbus barbus*) from the River Ourthe (River Meuse basin) were equipped with transmitters programmed to switch ON during two consecutive spawning seasons in 1998 and 1999 (April to July). Six of the nine barbels tracked in 1998 were also tracked in 1999 during the same period. The length of the spawning migration ranged from 200 to 22700m. After the spawning activity observed from 12–16 May 1998 and 4–6 May 1999, the barbels homed to the site occupied before spawning. Each barbel used the same spawning area in 1998 and 1999, despite the presence of other spawning sites on their migratory route. These observations revealed the existence of strict reproductive homing in the barbel and a long-term fidelity to particular resting places.

KEY WORDS : migration, homing, reproduction, *Barbus barbus*, telemetry.

Fidélité inter annuelle aux sites de pontes et aux aires de résidences chez le barbeau fluviatile (*Barbus barbus*)

RÉSUMÉ. Neuf barbeaux fluviatiles de l'Ourthe (bassin de la Meuse) ont été équipés d'émetteurs radio programmés pour fonctionner durant deux saisons de reproduction consécutives (avril-juillet 1998 et 1999). Six des neufs poissons suivis en 1998 ont été retrouvés et suivis pendant la même période en 1999. L'ampleur des migrations de reproduction, unidirectionnelles vers l'amont, a varié de 200 à 22700m. Après le frai (12-16 mai 1998 ; 4-6 mai 1999), le retour direct et précis vers le gîte occupé avant la migration a été observé chez tous les individus. En 1999, aucun poisson n'a utilisé une frayère différente de celle fréquentée en 1998, et ce malgré la présence éventuelle d'autres sites de ponte sur son trajet migratoire. Ces observations traduisent l'existence d'un homing reproducteur assez strict chez les individus de *Barbus barbus* ainsi que d'une fidélité à long terme vis-à-vis d'un gîte de résidence particulier.

INTRODUCTION

The study of spawning homing in fish has long interested researchers and has been studied most in the different anadromous salmonid species (STABELL, 1984). Using marking-recapture techniques (YOUNGSON et al., 1994), experiments that moved migrating spawners (O'CONNOR & POWER, 1973) or released juveniles raised in hatcheries (POWER & McCLEAVE, 1980; PASCUAL et al., 1995) have demonstrated that most species of anadromous salmonids have a general fidelity to the birth river (PAPI, 1992; QUINN, 1993). This interest is warranted as much by the mystery surrounding this animal capability and the biological mechanisms involved as by the socioeconomic stakes at play in the intensive farming of migrating salmonid populations.

In freshwater-resident, non-anadromous fish species, interannual fidelity to a precise spawning area has also been observed. In these species, spawning activities are regularly observed on the same spawning sites from one year to the next (*Esox Masquinongy:* CROSSMAN, 1990; *Leuciscus leuciscus:* CLOUGH & LADLE, 1997; *Salvelinus alpinus*: FROST, 1962; *Salmo trutta*: OVIDIO, 1999; *Thymallus thymallus*: OVIDIO et al., 2004; PAVLOV et al., 1998; *Rutilus rutilus:* GOLDSPINK, 1977; L'ABBÉE-LUND & VOLLESTAD, 1985). Demonstrating this demecological characteristic has led to improvements in protective measures and restoration of spawning grounds and has contributed additional arguments in favour of maintaining free movements for fish in streams.

However, fidelity to a spawning site over several successive spawning seasons has rarely been observed at the individual scale. In Placentia Bay (Newfoundland, Canada) ROBICHAUD & ROSE (2001) observed that certain Atlantic cod, *Gadus morhua*, individuals used the same spawning site from one year to another. In freshwater species, similar observations are lacking in the scientific literature. Studying this fidelity in terms of spawning

ground requires tracking an individual over at least 2 years. This methodological requirement is difficult to satisfy using passive individual marking techniques. Yet recent technological progress in the field of aquatic telemetry has improved transmitters to extend their lifetime and to equip them with an internal clock to program the transmission period (duty cycle transmitters). This technical sophistication considerably expands the experimental range, notably in terms of the restrictions imposed by the transmitter's limited lifetime, particularly when the fish to study are low in weight. This type of study of individual behaviours over a protracted part of the life cycle can provide information on the fishes' life histories and behavioural choices, thus improving our understanding of population biology and the evolutionary consequences of life cycle modifications.

Long migrations towards spawning sites have been observed in different fish species residing in rivers. The barbel, which in Western Europe is often a good part of the fish biomass in medium-sized and large gravel bed streams, shows this migratory behaviour during the spawning period (BARAS, 1992). In the River Ourthe, a tributary of the Belgian River Meuse, which shelters the barbel population studied here, many spawners gather every spring on a few spawning grounds distributed along the river (BARAS, 1992). Observation of this behaviour has naturally raised the question of a possible interannual fidelity of the individual to a spawning site, a hypothesis that has been tested in the present study in the barbel, a

good study model because of its longevity and because it is highly representative in the river studied.

MATERIAL AND METHODS

Study site

The study took place in the River Ourthe, the main tributary of the River Meuse in Belgium (Fig. 1, in a 27km long stretch between the Chanxhe dam downstream and the Barvaux-sur-Ourthe dam upstream. At this spot, the river's slope is a mean of 1.5‰, for a width between 25 and 30m at the low water level and a mean annual flow rate of 22.9m^{3}s^{-1}. The water temperature was studied in a continuous manner using a thermograph (Richards Instrument, precision 0.1°C) situated at Hamoir-sur-Ourthe (50°25'36'' N, 5°32'25'' E). From 1989 to 1999, the water temperature varied from 0 to 26.8°C. The flow rate of the River Ourthe was recorded every hour at Durbuy (data from the D.G.R.N.E. Water Division). The ichthyofauna of the sector studied was dominated for the most part by *Barbus barbus* (up to 50% of the biomass observed; PHILIPPART, 1987; BARAS, 1992), mostly associated with *Rutilus rutilus* (L.), *Thymallus thymallus* (L.), *Salmo trutta* (L.), *Leuciscus cephalus* (L.), *L. leuciscus* (L.), *Chondrostoma nasus* (L.) and *Barbatula barbatula* (L.).
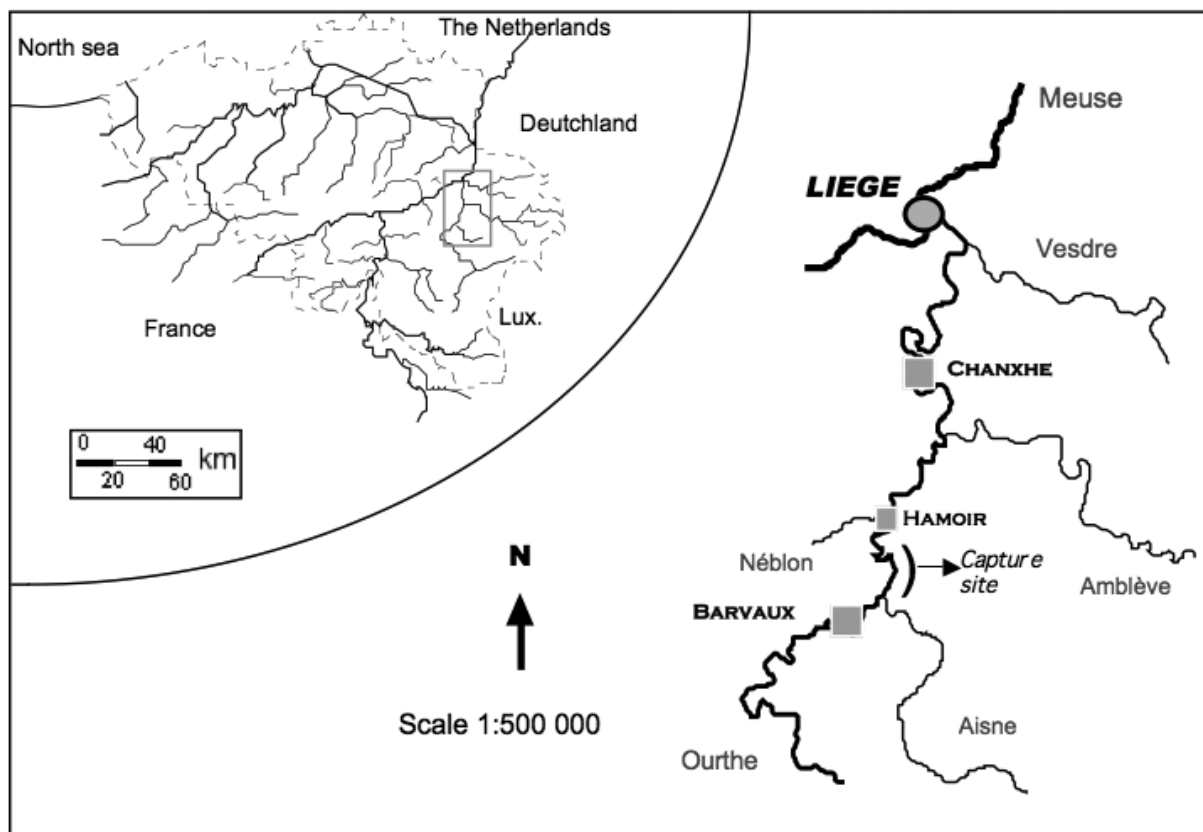

Fig. 1. – Localization of the study site in Belgium, between Barvaux and Chanxhe on the main reach of the River Ourthe.

TABLE 1

Characteristics of the barbels radiotracked in the Ourthe at the time they were captured in April–May 1998.

Fish	FL (mm)	Weight (g)	Sex	Date de capture	Transmitter weight (g)	Tag ratio* (%)
1	462	1172	Female	6 May 1998	18.5	1.58
2	429	957	Female	6 May 1998	18.4	1.92
3	427	935	Female	6 May 1998	18.5	1.98
4	430	961	Female	6 May 1998	18.8	1.96
5	420	927	Male	6 May 1998	18.4	1.98
6	481	1404	Female	5 May 1998	18.5	1.32
7	438	944	Female	6 May 1998	18.8	1.99
8	428	1063	Female	5 May 1998	18.5	1.74
9	415	874	Female	28 April 1998	18.6	2.12

* ratio between the weight of the transmitters and the weight of the fish

METHODS

Nine barbels (B1–B9; Table 1) were captured using electric fishing (Deka 5000), from 28 April to 6 May 1998, in the sector between Hamoir and the confluence of the Ourthe with the Aisne. The fish were anaesthetised with 2-phenoxyethanol (0.4mL l–1) and a radiotransmitter (40MHz, internal antenna, 18.5g in the air, 68×16mm in diameter, ATS, Inc.) was inserted in the intraperitoneal cavity through a midventral incision between the ano-genital papilla and the insertion of the pelvic fins. The incision was closed with three suture stitches (resorbable 3/0 catgut on a 16mm needle). The transmitters used were programmed to only function (emit a signal) during a period of 70 days between 28 April and 7 July, and to remain inactive during the 295 days completing the annual cycle, with this procedure repeated until the transmitter's battery ran out, which allowed us to follow six of the nine barbels over two consecutive spawning seasons (1998–1999). After tagging, the fish were released at their capture site, immediately after they recuperated their swimming and orientation capacities. The transmitter to marked fish weight ratio remained less than 2% (except for barbel no. 9: 2.12%; Table 1), which is considered a very comfortable mass ratio (WINTER, 1996; JEPSEN et al., 2002).

The fish were localized during the day (diamond directional antenna, Fieldmaster receiver, ATS, inc.). In 1998, fish were localized every day from 28 April to 22 May and every 2 days from 23 May to 5 July. From 28 April to 6 July 1999, the fish were positioned three times a week. Movements were calculated with a precision of 10–15m based on field markers or using topographic maps. The main spawning sites (whether or not they were used by the barbels tracked in 1998 and 1999) were identified along the entire sector by observing spawner gatherings while walking along the study sector during the spawning period. Some of these spawning grounds had already been identified during earlier studies by PHILIPPART (1987) and BARAS (1992).

Barbel mobility was characterized by indicators at different spatial scales, defined below (BARAS, 1992):

– Net longitudinal movements: an indicator of spatial mobility corresponding to the distance separating two locations;

– Longitudinal home range: the area occupied by an individual where it developed all its activities. It is expressed by its longitudinal extension determined by the distance between the most upstream location and the most downstream location. For a single individual, it can be calculated at different time scales (daily, monthly, seasonal, annual) and can therefore contain (depending on the time scale chosen) the spawning area.

– Residence area: a reduced-surface zone in which the barbel is localized most frequently, outside of the spawning zone. It can develop one activity (feeding) in this zone or rest.

RESULTS

Six barbels out of nine marked in 1998 were also tracked in 1999 (Fig. 2). Barbels B3 and B5 were caught by line fishermen in July–August 1998 and the transmitters were returned. Fish B4 was found dead, much thinner, in the Ourthe on 4 May 1999, 10200m downstream from its last localization (6 July 1998).

Spawning migrations

In view of the divergence between the initial capture site and the localization after the post-spawning downstream migration, six of the nine barbels were marked, in 1998, probably during their migration towards the spawning sites. Consequently, it was impossible to date the start of migration, except for B4 and B8: 16 May and 11 May 1998, respectively. In 1999, the start of migration took place between 4 and 6 May, except for fish B2, which participated in no spawning migration after its transmitter was started up, and for B6, which was found on 28 April 1999 downstream of the Barvaux dam, near its spawning site, and which had therefore done its spawning migration before the transmitters were started up.

For 2 years, the migrations were unidirectional, from down- to upstream for all fish except B2 and B7, which in 1998 spawned 2500m downstream from the capture site (Fig. 2). The distance separating the upstream limit of the spawning migration from the resting place after downstream migration was between 250 and 22700m in 1998 and between 200 and 6780m in 1999 (Table 2). In view of the occupation of the same resting place by fish before (1999) and after (1998–99) the spawning period, these

values correspond to the total migration distances covered during the 2 years of tracking. The absence of migrations greater than 10000m in 1999 stems from the fact that the two fish that covered these long migration distances in 1998 (B3 and B4) could not be tracked or did not migrate at all in 1999 (B2). Movements were always fast, because the fish were localized near the spawning grounds less than 48h after the start of migration.
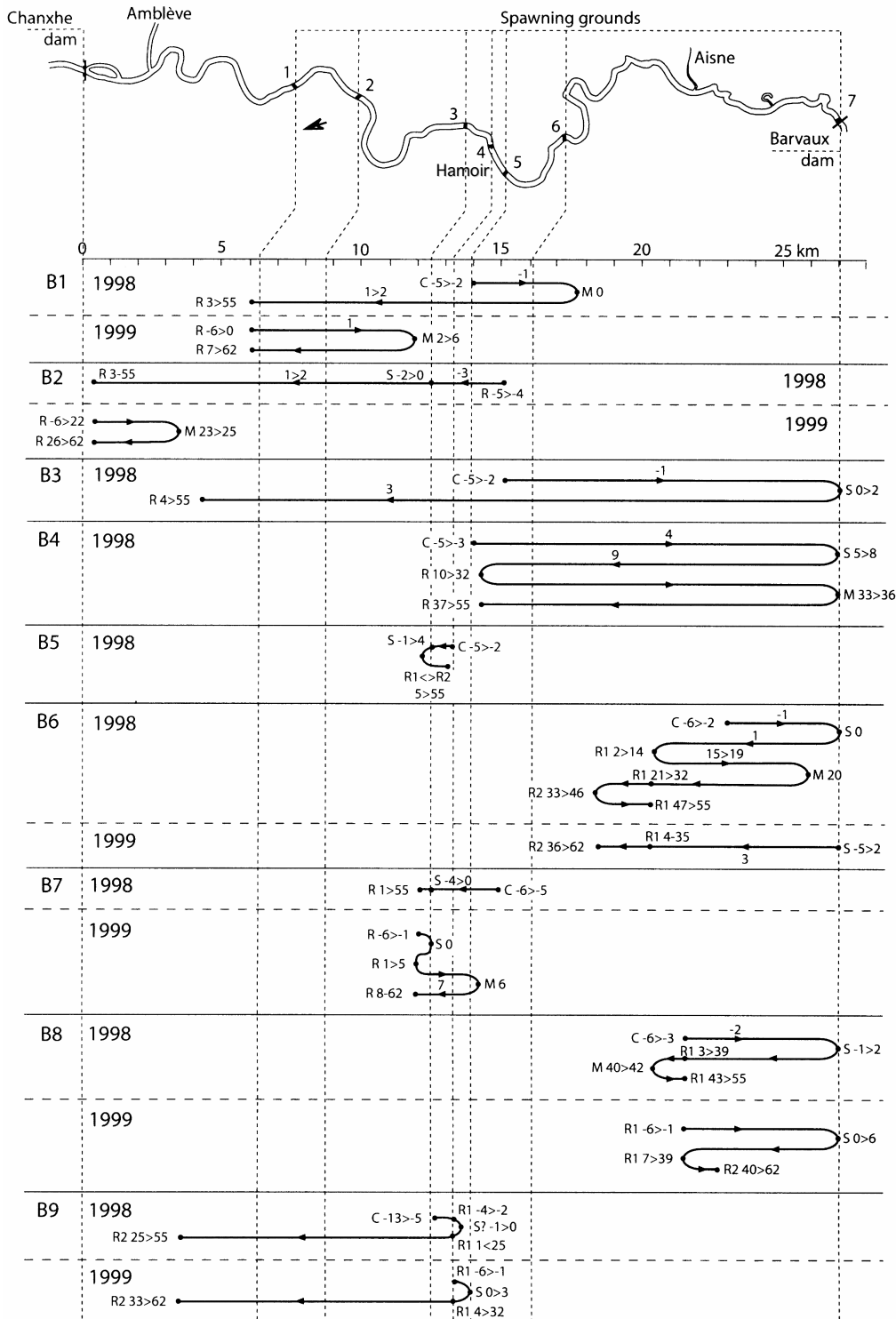

Fig. 2. – Mobility of the radiotracked barbels in the River Ourthe in 1998 and 1999. The study zone is situated between the Chanxhe and Barvaux dams. The different spawning beds identified were numbered 1–7, downstream to upstream. Individual movements are represented on continuous lines along a distance scale, with mention of the capture site localization (C), the residence area (R), the spawning bed (S) and the upstream limit of migration with no spawning bed observed (M). The time spent by the fish at the different sites and the duration of its migration are indicated on the graphs. Day 0 corresponds to the date of the first episodes of spawning observed in the population for the year considered.

TABLE 2

Mobility characteristics of the barbels radiotracked in the Ourthe in 1998 and 1999. The statistics include nine fish in 1998 and six in 1999 (see the text for details).

	1998	1999
Post spawning home range* (m)	Range: 340-12855	Range: 280-10100
Length of spawning migration (m)	Range: 250-22700	Range: 200-6780
Date of migration to the spawning ground*	9 to 16 May	< 28 April to 6 May
Date of post spawning homing	14 to 22 May	6 to 11 May

* after the tagging in 1998

Activity on spawning sites

In both 1998 and 1999, spawning began after a substantial rise in the temperature. In 1998, spawning was observed from 12 to 16 May, for a minimal daily water temperature between 16.6 and 18.0°C, and a flow rate ranging from 9.8 to 12.04 m^3s^{-1} cm. In 1999, spawning spread over the period from 4 to 6 May with a minimal daily water temperature between 13.1 and 13.2°C and a flow rate from 10.13 to 10.66 m^3s^{-1}, with activity starting up again on the spawning sites on 11 May. The radiotracked fish spent between 1 and 8 days in the spawning area (less than 100m upstream or downstream). Nevertheless, the time spent on the spawning site itself did not extend beyond 1 day, except for fish B5 (4 consecutive days).

TABLE 3

Localization of the spawning sites identified in the study zone and use by the radiotracked barbels.

Spawning site		1	2	3	4	5	6	7
Localization* (m)		6375	8750	12500	13300	13975	16100	26625
Used by	*1998*	–	–	B2-5-7	–	B9(?)	–	B3-4-6-8
tagged barbels n°	*1999*	–	–	B7	–	B9	–	B6-8
Swam past by	*1998*	–	–	–	B2-7	B2-7	B1-3-4	–
tagged barbels n°	*1999*	B1	B1	–	–	–	B4	–

* distance from the downstream limit of the study area (barrage de Chanxhe)

Interannual fidelity to the spawning site

Seven spawning beds used by the barbels every year were observed from 1989 to 1999 in the sector studied (Table 3). These sites were made up of large central deposits of gravel (sites 1, 3, 5 and 7) or by lateral convex banks covering a smaller area (sites 2, 4 and 6), three of which (3, 5 and 7) were used by the radiotracked barbels. The fish did not spawn systematically at the site nearest to the resting place occupied before the migration start-up. Indeed, the spawning route of several barbels (five in 1998 and two in 1999) included at least one indexed spawning site.

Of the six barbels tracked in 1998 and 1999, three (B6, B7 and B8) were localized at the same spawning site both years (Fig. 2; Table 3). Fish B9 was localized at spawning bed no. 5 on 4 May 1999 and 400m downstream on 12 May 1998. However, it cannot be systematically excluded that it spawned at this site in 1998. Fish B2 visited spawning site no. 3 in 1998, but undertook no spawning migration in 1999. Finally, fish B1 could not be localized near any spawning bed in 1998, even though it migrated 12300m upstream. In 1999, it stayed 3 days (6–10 May) 500m downstream from spawning site no. 5. None of the barbels was localized in 1999 on a spawning site different from the one used in 1998.

Post-spawning homing, interannual fidelity to the summer resting place

The six barbels tracked for the 2 years all manifested precise post-spawning homing in 1999 and fidelity from one year to the next to the resting place occupied during the pre- and post-spawning period. In 1999 all fish, with the exception of B6, which had already done its spawning migration, were found in their respective resting places they had occupied after the downstream migration in 1998 (Fig. 2). They were localized again in the same places after the downstream migration in 1999. Returning to the resting place within 48h was observed for all fish between 14 and 22 May in 1998 and between 6 and 11 May in 1999.

Mobility outside the spawning period

Excluding spawning migrations, the home range of the fish tracked was between 340m and 12855m in 1998 and between 280m and 10100m in 1999 (Fig. 2). Six of the nine radiotracked barbels only occupied a single resting place regularly during the tracking period (B1, B2, B3, B4, B7 and B8). In 1998, two barbels left the resting place occupied after the downstream migration that followed spawning and migrated towards a secondary resting place, situated downstream from the first. This behaviour was repeated during the same period in 1999. Fish B6 left its resting place (between 13 June 1998 and 9 June 1999),

situated in a deep calm, and stabilized 2210m downstream in a similar habitat. Similarly, fish B9 moved from one resting place to another 10060m downstream (7 June 1998 and 7 June 1999). Fish B5 was localized alternately (1998) in a resting place near spawning site no. 3 and another situated 700m upstream of the first.

Other distant movements were observed outside of the spawning migrations. Amongst the most remarkable, let us cite the movements made by fish B4 (12675m upstream, from 14 to 17 June 1998, returning to the resting place on 18 June) and B6 (5650m upstream, from 27 May to 1 June 1999, returning to the resting place on 2 June 1999).

DISCUSSION

This study is original in that it provides individual daily tracking of six female barbel spawners over two consecutive spawning seasons. Radiotelemetry techniques, in particular duty cycle transmitters, allowed us to target a precise period in the annual life cycle of the species and to track the fish for more than 1 year. It cannot immediately be excluded that a behavioural disturbance was not induced by implanting the transmitter and the fish carrying it. However, the methodology implemented here was identical to that which had been used in previous studies on *Barbus barbus* (BARAS, 1992, 1995; LUCAS & FREAR, 1997), which showed that the fish was highly tolerant to the transmitter implantation operation. In addition, the low values of the transmitter weight to fish weight ratio (1.32–2.12%; Table 1) can reasonably exclude that there was significant alteration in its swimming capacity.

Great variability was found to characterize the respective mobility of the different barbels tracked during the spawning period. The distance separating the residence area occupied before spawning migration from the spawning site varied from 250 to 22700m. These observations are in agreement with observations of barbels on the River Severn (England) by HUNT & JONES (1974), and the River Jihlava (Czech Republic) by PENÁZ et al. (2002), who distinguished two fractions, mobile and static, within a single population. At the end of migration, the spawners grouped on spawning sites, relatively few in number considering the dispersion of individuals before spawning. Spawning activity was concentrated on only a few days (4 days in 1998; 3 days in 1999). Several hundred individuals can be observed simultaneously on the same spawning bed. This synchronization of spawners can be explained by considering the factors setting off spawning and the demands of the species in terms of spawning habitat, which are now well known. BARAS & PHILIPPART (1999) have clearly shown that the arrival of barbels on the spawning grounds of the River Ourthe and spawning start-up respond to an increase in water temperature (minimum daily T>13.5°C). Grouping of a large number of spawners at the spawning sites may result from their precise requirements in terms of spawning microhabitat (BARAS, 1994). This precise environmental control of the spawning activity tends to maximize the spawning success of the species by ensuring the embryos have a thermal environment favourable to their survival and their rapid development (BARAS & PHILIPPART, 1999).

The individual's attachment behaviour to a particular habitat was manifested in three ways in the barbels tracked during this study: (i) fidelity to the spawning site, (ii) post-spawning homing, which was observed by OVIDIO (1999) in the brown trout (*Salmo trutta*), and (iii) fidelity to a precise residence area, from one year to another. These observations, conducted on a small number of female individuals over a 2-year period, should, however, be interpreted cautiously, as a preliminary approach to the issue of *Barbus barbus* homing.

It is difficult to conclude that the use of the same spawning ground over 2 consecutive years, as was observed in three fish out of six resulted from a limited availability of favourable habitat that brought these fish together on the same site every year. Indeed, the spawning route of several barbels included active spawning grounds that were not visited. The expression of this homing behaviour as it was observed in the barbels tracked implies the existence of a mechanism by which this fidelity is acquired, as well as the development of precise sensory recognition of the site involved (BRAITHWAITE & BURT DE PERERA, 2006). The hypothesis of an early olfactive impregnation mechanism (between the emergence from gravel and smolt downstream migration) enjoys general agreement in terms of birth river fidelity on the part of the different anadromous salmonid species (GROVES et al., 1968; STABELL, 1984; QUINN & DITTMAN, 1990). This mechanism can explain the spawner's migratory orientation towards the birth river, through recognition and discrimination of olfactive landmarks that it has been exposed to and is sensitive to at the beginning of its life cycle. Transposing this theory to species such as the barbel whose movements are limited to a single stream implies the presence of olfactive markers specific to a precise site, and no longer to a river or a river reach. The attraction of spawners by other individuals already present at the spawning ground or the upwelling of ground water recognized by the fish (AUDET et al., 1985) have been suggested in this context. In addition, if the movements take place in a familiar and spatially restricted environment, the fish probably use visual landmarks for orientation (BRAITHWAITE & BURT DE PERERA, 2006). In this case, acquisition of fidelity to a precise site and learning the migratory routes suggests a social transmission of the information, with young individuals following the older ones during migrations (DODSON, 1988). This learning mode has clearly been demonstrated in certain ocean reef fish (Haemulidae; HELFMAN & SCHULTZ, 1984) and has been proposed by OLSON et al. (1978) to explain the spawning migrations as well as how the spawning sites were selected in walleye (*Sander vitreus*). This mode of acquisition and manifestation of fidelity to the spawning site (and to resting place(s)) is highly plausible in the barbel given its shoaling behaviour and the great spatial precision of post-spawning homing.

The adaptive value of spawner homing in *Barbus barbus* can undoubtedly be explained by the same arguments: spawner grouping and matching of the spawning microhabitat selected with the ecological demands of the embryos during the subgravel stage of life. This philopatric behaviour should also influence the mixing of genes within the population. If this were confirmed by other studies, it would also indicate a certain genetic isolation

of spawning zones despite their geographic proximity. However, this isolation cannot be expected to be strict and definitive, since the river dynamics of a stream can make spawning sites disappear or appear over the years. This type of phenomenon would inevitably cause an individual behavioural adaptation of the spawners that would be interesting to study.

In terms of river management, several recommendations can be made for these populations. Spawning beds (often targeted by riverbed cleaning works) should be maintained and protected, even if replacement sites seem available nearby or are constructed artificially. Given the great distances certain individuals travel, access to these spawning beds can only be guaranteed if fish can circulate freely on extended river stretches (several dozen kilometres). Dams whose construction cannot be avoided should be equipped with fish ladders that are effective and that can be used by different families of fish whose swimming and leaping capacities are sometimes quite different (OVIDIO & PHILIPPART, 2002; OVIDIO et al., 2007).

ACKNOWLEDGEMENTS

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