Environmental determinants of residence area selection by *Barbus barbus* in the River Ourthe

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Abstract

A biotelemetry experiment was designed to determine whether the selection of a residence area by adult barbel *Barbus barbus* (Cyprinidae) was dependent on the availability of physical habitat features, on the presence of fish shoals and/or on the presence of specific partners. The experiment took place in 3.0 km stretch of the River Ourthe (Belgium), where the latter features had been characterised by habitat and electric fishing surveys (1 190 fish ≥ 15 cm, at 265 locations). Six barbel (34.8-49.5 cm) belonging to a single shoal of 34 fish were tagged with 40 MHz radio transmitters, transplanted in pairs at different distances (–1 km, –30 m, + 1 km) from the capture site and tracked from 3 September to 7 October 1990.

Fish showed variable mobility patterns and home range sizes (200-2 400 m). They selected 17 residence areas of which the cumulative frequency of occupation ranged from 0.1 to 79.5 day × fish. The comparison between the residence areas selected, habitat suitability and the location of fish shoals in the study area indicate that the presence of a shoal of at least 10 resident fish within a suitable habitat (normalised suitability index ≥ 1.0) is necessary but not sufficient to guarantee its long term selection and occupation. Homing movements of transplanted fish were directed towards the activity area rather than to the residence area itself. The fish that did not home, selected residence areas in a part of the river with a higher availability of potential feeding areas. These elements are discussed within the context of habitat utilisation and foraging strategies by a gregarious species. It is suggested that resident fish of the same species may ease the exploitation of a non familiar environment by a naive fish, and that this may positively trade off the benefit provided by home site fidelity, depending on the availability of food resources.

Keywords: telemetry, habitat selection, homing behaviour, shoaling, fish.

Critères de sélection du gîte chez le barbeau fluviatile Barbus barbus *dans l'Ourthe (Belgique).*

Résumé

Une étude par biotélémétrie a été réalisée pour déterminer si la sélection de l'aire de résidence chez les barbeaux adultes *Barbus barbus* (Cyprinidae) était dépendante de la disponibilité des caractéristiques physiques de l'habitat, de la présence d'agrégats de poissons et/ou de partenaires spécifiques. L'expérience s'est déroulée dans un secteur de 3 km de l'Ourthe où ces caractéristiques ont été déterminées par études d'habitats et par pêche à l'électricité (1 190 barbeaux ≥ 15 cm capturés sur 265 localisations). Six barbeaux (34,8-49,5 cm), appartenant à un agrégat de 34 poissons, ont été marqués à l'aide d'émetteurs radio 40 MHz, transplantés par paires à différentes distances (– 1 km, – 30 m, + 1 km) du site de capture et suivis par pistage du 3 septembre au 7 octobre 1990.

Les barbeaux ont occupé de manière différente des domaines vitaux de 200 à 2 400 m. Ils ont sélectionné 17 aires de résidence dont la fréquence d'occupation cumulée variait de 0,1 à 79,5 jour × poisson. La comparaison des résidences sélectionnées par les poissons, la qualité de l'habitat et la localisation des agrégats de poissons dans le cours d'eau, indique que la présence d'un agrégat d'au moins 10 barbeaux au sein d'un habitat de qualité maximale (indice normalisé ≥ 1,0) est une condition nécessaire (mais non suffisante) à sa sélection et à son occupation à long terme. Les mouvements de retour des poissons transplantés ont été observés mais étaient davantage orientés vers l'aire d'activités que vers l'aire de résidence. Les poissons n'effectuant pas de retour au gîte ont sélectionné des aires de résidence dans un secteur du cours d'eau offrant une plus grande disponibilité en zones d'alimentation potentielles. Dans le contexte de l'utilisation de l'habitat et des stratégies d'exploitation des ressources par une espèce grégaire, il est suggéré que la présence de résidents de même espèce puisse faciliter l'exploitation d'un environnement non familier, cet avantage pouvant supplanter le bénéfice conféré par la fidélité au gîte, en fonction de la disponibilité des ressources alimentaires.

Mots-clés: télémétrie, habitat, comportement, espèce grégaire, poisson.

INTRODUCTION

Over the past decade, there has been a growing interest in the way freshwater fish use and select their habitat, both to evaluate the preferences and tolerance limits of the species or life stage and to model the impact of habitat modifications on the carrying capacity of the environment (*e.g.* Souchon *et al.*, 1995; Leclerc *et al.*, 1996). Developments of the Instream Flow Incremental Methodology (IFIM; Waters, 1976; Bovee and Cochnauer, 1977; Stalnaker, 1979; Bovee, 1986, 1996) and Physical Habitat Simulation (PHABSIM; 1-d, 2-d and 3-d modeling, Leclerc *et al.*, 1995; Heggenes *et al.*, 1996; Tarbet and Hardy, 1996) permitted the production, refinement and evaluation of dozens of habitat suitability curves for different fish species (*e.g.* Bovee, 1978; Lambert and Hanson, 1989). Most curves and models can account with a reasonable success for the overall pattern of fish distribution in a river, and represent valuable tools for the conservation of biodiversity or for stock management.

These models, however, fail to account for why an individual fish occupies a precise location in the river and not a similar habitat a few metres, hundred metres or kilometres away. The homing behaviour demonstrated by some fish clearly indicates that spatially distinct locations with seamingly equivalent habitat features are apparently very different. Apart from the most spectacular reproductive homing by anadromous salmonids, numerous studies have documented similar homing behaviours by resident fish species: consistent fidelity to spawning grounds year after year (L'Abé-Lund and Vøllestad, 1985; Crossman, 1990), return movement of transplanted fish (Malinin, 1970; Green, 1975; Hert, 1992; Yoshiyama *et al.*, 1992), or of fish displaced by high floods (Langford, 1979; Baras, 1992). Understanding why and how fish select a precise location will probably represent a further step in improving our way of understanding fish habitat models and of conceiving more powerful tools for their management.

This stage of understanding can be difficult to reach as the potential criteria and environmental cues responsible for the selection of a residence area by fish are manifold since they operate at a community level. They include the availability and suitability of habitat, the profitability and benefit resulting from the familiarity of the environment (optimal foraging strategies; Hart, 1986), the avoidance of predators and the relationships with competitors and conspecifics. For territorial species, the latter parameter essentially refers to selective or interactive segregation (*e.g.* Kalleberg, 1958; Ebersole, 1985; Kennedy and Strange, 1986). For gregarious species like most European cyprinid fishes, the latter parameter rather refers to indifference, search for conspecifics to form large shoals (*see* Baras and Cherry, 1990) or for specific partners (*i.e.* schooling).

The discrimination between the roles of habitat suitability, home site fidelity, shoal fidelity and the search for specific partners in the selection of a residence area necessarily requires an experimental design based on the transplantation of fish originating from the same shoal. It includes a) capturing a representative shoal; b) tagging of individual fish with radio transmitters; c) dividing the shoal into (at least) three groups to be released at the capture site, transplanted upstream and downstream of this site at distances less than the home range, and d) radio tracking to identify the habitats selected by fish and any possible regathering of partners. It further requires a) preparation of habitat suitability curves for the life stage of the species, both for resting and feeding activity, b) assessing habitat availability in the river section and c) determining the position of fish shoals in this section at the time of the experiment. As a corollary, these conditions imply that the study should be conducted at a time of the year when fish show a consistent fidelity towards their residence area and when there is a low probability that meteorological events might interfere with habitat variables.

For these reasons, the experiment was conducted on a pattern of cyprinid fish behaviour which has been documented during the past decade. The common barbel *Barbus barbus* is a large cyprinid fish highly representative of rivers and streams of the barbel zone in Central and Western Europe (Huet, 1949). Adult *B. barbus* live in shoals, occupy precise residence areas and can show precise homing behaviour, after free migration or displacement (Baras and Cherry, 1990; Baras, 1992). Tagging studies indicated that members of a single shoal could be captured at the same location after several months or years (Philippart, 1977). Habitat suitability curves, home range, seasonal and daily mobility patterns were recently produced for this species (Baras, 1992, 1993*a*, *b*, 1995) and facilitated the design of this experiment, which took place in late summer 1990, in the River Ourthe (Belgium).

MATERIAL AND METHODS

Study area

The study was conducted in the River Ourthe which is the main tributary of the River Meuse in Belgium. The study area (3.0 km in length) is centred on Hamoir-sur-Ourthe (50°25'36'' N, 5° 32'25'' E) and is typical of the barbel zone (mean width: 20-30 m; slope: 1.5 ‰). *B. barbus* averages 50 % of the fish biomass (Philippart, 1987). Other dominant species of the fish fauna are brown trout (*Salmo trutta fario*), grayling (*Thymallus thymallus*) and rheophilous cyprinids (*Leuciscus cephalus*, *Leuciscus leuciscus* and *Chondrostoma nasus*). The study area is devoid of any major obstacle that could interfere with the free passage of fish.

Definitions

In order to avoid any confusion or misunderstanding, it is necessary to define the terminology used in the rest of the manuscript. The overall surface of river occupied by a single fish during a 24-h cycle is defined as the *daily activity area*. It encompasses a resting place, an activity centre, where the fish demonstrates feeding activity, and routes in between. A *residence area* encompasses either a single resting place or several neighbouring resting places within the same habitat type (*e.g.* places a few metres away in a large shelter such as an assemblage of boulders). The *net daily journey* is defined as the distance between the residence areas occupied at 24-h intervals. In this manuscript, I will refer to *homing* according to the definition proposed by Gerking (1959), *i.e.* as the return movement to a place formerly occupied instead of going to an equally probable place, regardless of its reproductive or trophic context. Movements and journeys take place within a single or between morphodynamic areas (*i.e.* natural riffle-pool sequence encompassed by two changes in the slope of the river). Depending on geomorphological features, the length of morphodynamic areas in the study area on the River Ourthe ranges from 30 to 550 m. In accordance with the Oxford dictionary, the wording shoal (instead of school) will be used to define an aggregation of fish which are presumed not to behave synchronously.

Distribution of habitats and of fish shoals

Habitat availability in the study area was assessed from measured locations spaced 1 m apart on transects at 5 m (rapid, riffle, run) or 10 m intervals (pool, glide). Depth was measured to the nearest cm and water velocity, 10 cm above the substratum, was measured using a magnetic current meter (Marsh Mc Birney, model 201). Potential shelters such as rootwads, clumps of *Ranunculus* or *Potamot* sp., rocks or boulder assemblages were systematically searched and located. The measurements were taken in July 1990, at a water level similar to that in the first week of the tracking experiment (checked daily on a limnimetric scale in Hamoir-sur-Ourthe). Depth and water velocity above the substratum ranged from 0 to 186 cm and from 0 to 99 cm s^{-1}, respectively.

Each habitat cell (*i.e.* area encompassed by four adjacent measures) was allocated two normalised suitability indexes (NSI), respectively as a feeding area and as a residence (resting) area for large (30-60 cm fork length) *B. barbus*. NSI were obtained as follows:

a) Each habitat feature (depth, velocity and shelter) was compared to curves of habitat utilisation that were produced in the course of previous electric fishing and radio tracking surveys in the same river (Baras, 1992), referring to resting and feeding fish.

b) For each variable at a measured location, a NSI was allocated, using the equation proposed by Gosse (1982, modified by Bovee, 1986): NSI = 2 (1-p), where p is the minimum proportion of the utilisation curve of the variable that encompasses the observation (approach using non parametric tolerance limits); *e.g.* 50, 75, 90, > 90 % grant NSI of 1.0, 0.5, 0.2 and < 0.2.

c) The score assigned to the cell was the minimum NSI in the set of determinant variables (depth, velocity, and shelter for rest).

The variations of habitat suitability in the river section are illustrated in Figure 1*a*, *b*.

The distribution of fish shoals was studied during an intensive survey of the river section by electric fishing (EPMC generator, 2.5 KVA, DC) in late August 1990, just before the beginning of this experiment. The assumption that electric fishing was adequate for this type of survey relied on the results of a preliminary investigation on the behaviour of radio-tagged *B. barbus* during electric fishing operations (Baras, 1992). This investigation indicated that radio-tagged fish captured by electric fishing had not been displaced by the fishing team. The fish that had not been captured on the first attempt and had moved to another habitat systematically escaped later on. This result suggests that the probability of capturing *B. barbus* in an habitat other than its original resting place presumably is very low. During the electric fishing survey, the river stretch was systematically explored: the distances between successive immersions of the anode were circa 2 m. All fish captured on a well defined site (single immersion of the anode; accuracy of 1 to 4 m^2 depending on habitat structure and complexity) were considered as belonging to the same shoal. Fish were counted, measured and released on the capture site. Each captured shoal was precisely located in order to assess the spa-

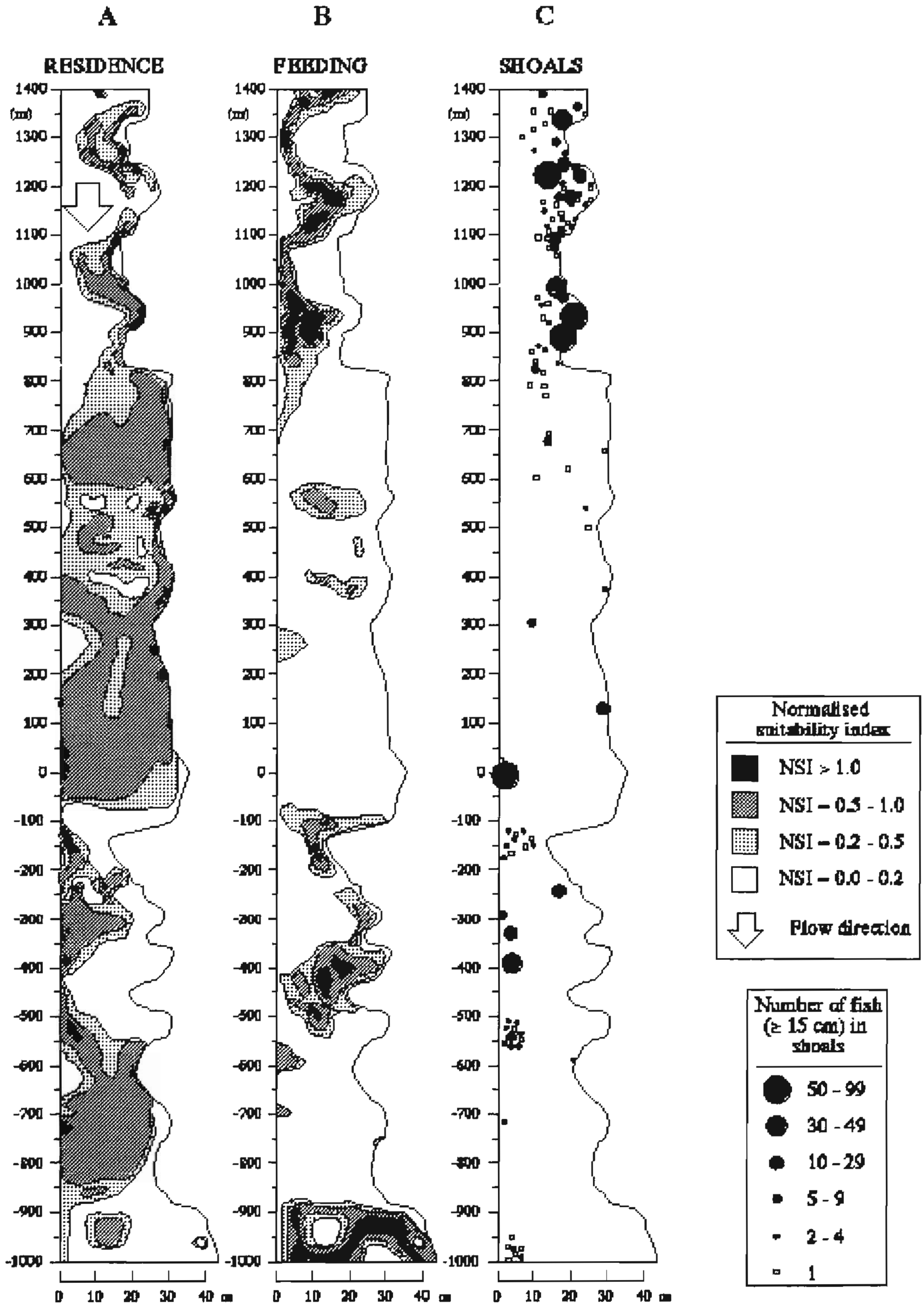

Figure 1. – Map of the study area in the River Ourthe. The right bank of the river is linearised and the river width is exaggerated by 7.5 fold for a more understandable display. Negative and positive values on the vertical axis refer respectively to sites downstream and upstream of the capture site (sited at 0, on the right bank of the river). A and B: suitability of river habitat (normalised suitability indexes, NSI) as residence (A) or feeding areas (B) for *B. barbus*, based on utilisation curves produced during previous studies (Baras, 1992). C: distribution of shoals of *Barbus barbus* (fish ≥ 15 cm) in the river in late August - early September 1990, as observed during an intensive survey using electric fishing.

tial availability of this resource at the time of the experiment.

More than 1 400 barbel (6.1-52.6 cm) were captured, of which 1 190 corresponded to adult individuals (≥ 15 cm FL). The fish were captured in 265 capture locations: 112 locations corresponded to the capture of a single fish and 76 others to the capture of small shoals of less than five fish. Eleven shoals gathered more than 20 fish (28-71 individuals) and represented 49.0 % (N = 583) of the adult barbel population captured during the electric fishing survey (Fig. 1*c*). Obviously, the sites containing large and small shoals did not differ in size and space available.

Selection of the site for experiment

The site for this field experiment was selected on two-criteria: habitat suitability (NSI > 1.0 for resting) and effective occupation by barbel. It corresponded to a near shore pool (1.1 m deep, water velocity < 10 cm/s) sheltered by a sunken tree. These features are as close as possible to the preferences of large (≥ 30 cm) barbel for habitat variables (Baras, 1992). This residence area had been occupied several weeks in a row by barbel in previous tracking sessions (Baras and Cherry, 1990) and could therefore be considered as a suitable site for the experiment.

Fish tagging and tracking

On 28 August 1990, a shoal of 34 barbel (24.1-49.5 cm, FL) was captured by electric fishing (EPMC generator, DC, 2.5 KVA) at this site. Six individuals (F1-F6; 34.8-49.5 cm) were selected to be equipped with radio transmitters (Advanced Telemetry Systems-ATS, Inc.; 70 mm long x 12 mm in diameter; 15 g; activity, motion-sensitive, circuit; 40 MHz), following the surgical implantation procedure described in Baras and Philippart (1989). All 34 fish were stocked for six days in a 2 m^3 PVC cage nearby the capture site. According to previous feasibility studies (Baras, 1992), this delay is enough for a complete recovery from radio-tagging procedures and permits the observer to evaluate the success of surgical implantation. In order to minimise the possible effects of prolonged denutrition on fish behaviour and performance, larvae of chironomids were distributed twice a day, at dawn and dusk.

No mortality, infection, rupture of the incision zone or weight loss was observed in any of the six radio-tagged barbel. Just before release, the shoal was divided into three groups (with two radio-tagged individuals in each) to avoid any bias resulting from releasing alone fishes that are typically gregarious. The three groups were released in three distinct locations: close to (30 m downstream) the capture site (12 fish including F3 and F4), 920 m downstream (11 fish including F1 and F2), and 960 m upstream of this site (11 fish including F5 and F6). The distances between the capture and release sites (circa 1 km) were determined according to the conclusions of previous tagging (Philippart, 1977) and tracking (Baras, 1992, 1993*b*) studies which both indicated that the mean home range of barbel does not exceed 1.2 km. The weak discrepancy between the distances of release for the upstream and downstream groups originated from the necessity to release fish in habitats similar to the capture zone (pools 30-50 m upstream of rapids) to avoid a potential bias originating from habitat dissimilarities (Blair and Quinn, 1991). The three groups were released on 3 September 1990, between 12:00 and 13:00 (GMT +2).

Monitoring began immediately after release and was continuous during the first 48 hours, using Fieldmaster receivers and loop antennas (ATS Inc.). Fish were located to an accuracy of 1-2 m^2 by reference to labelled marks lining the banks of the river and biangulation using conventional methods (Baras and Cherry, 1990). During the rest of the experiment, fish were located at least daily, at times of the day (between 10:00 and 14:00) when they usually rest in residence areas in summer and early autumn (Baras and Cherry, 1990; Baras, 1995). Additional fixes (once per hour) were taken during the activity periods at twilight to detect any possible return to the original residence area. Fish activity was discriminated from rest by using the pulse rate variations of the motion-sensitive transmitters.

The end of the experiment was scheduled for early October (35 days after its beginning), before autumn rainfalls and floods modify the habitat features in the river. During the whole experiment, the variations of water level and water temperature were monitored by a limnigraph and a thermograph (Richard Instruments, s.a.) installed in Hamoir-sur-Ourthe.

RESULTS

Fish mobility and homing

On the day of release, the two barbel released downstream demonstrated a high mobility. They travelled 200 m upstream together within the 10 first minutes but selected separate residence areas, a few metres apart. In the first evening, F1 moved upstream and joined F2 in its residence area. Both fish moved further upstream, occupied the same activity centre and selected the same nocturnal residence area during the first night. F1 occupied this residence area during the next two weeks, feeding at dusk and dawn in and around the activity centre occupied the previous evening. On 19 September, F1 had homed to its capture site. It showed consistent fidelity to this resting place and associated activity area till the end of the experiment (7 October 1990). F2 resumed its upstream progression on 4 September and was detected in the early morning a few metres away from its capture site. The fish travelled further upstream and occupied a new residence area (340 m upstream of the capture site) till

5 September 1990, when it homed to its capture site. On September 25, the fish was detected 1.3 km upstream and settled in this part of the river till the end of the radio tracking survey.

Both fish (F3 and F4) that were released in the vicinity of the capture site homed within 5 min. F3 consistently occupied this residence area and associated activity centre 35 days in succession, whilst F4 behaved much more erratically. On the first evening, it moved 400 m upstream and was detected in five different residence areas during the next 35 days. All residence areas were located within a single, 550 m long, morphodynamic unit. Returns to previously occupied places were frequent.

The two fish (F5 and F6) released 960 m upstream behaved quite differently from the moment of release. Just after release, F5 moved to a resting place 2-3 metres away from the release site while F6 moved 40 m downstream. During the first evening, F5 moved 150 m upstream to an activity centre and associated residence area that were occupied during the 6 following days. The fish resumed its upstream progression on 10 September and settled 380 m upstream of the release point (1340 m upstream of capture site) till 28 September. F6 also twice changed its residence area during this period, but on different days (19 and 20 September). On September 29, both fish moved during a sudden increase of water level following heavy rains. F6 reoccupied the residence area occupied on the release day while F5 migrated downstream on more than 1.2 km and settled 130 m upstream of its capture point till the end of the experiment. By contrast, F6 resumed its upstream progression when the water level decreased and settled precisely in the same residence area as that occupied by F5 before its downstream movement.

Mobility patterns

The three groups of fish displaced at different distances (F1-F2, F3-F4 and F5-F6) showed similar patterns of mobility : neither the frequency of net daily journeys (χ^2 = 2.1, p = 0.34, df = 2) nor the mean length of these journeys (ANOVA, F = 0.36, p = 0.70, df = 44) differed significantly. By contrast, the homing abilities and the time spent in the morphodynamic unit encompassing the capture site differed substantially. Of the two fish released 1 km upstream, only F5 homed to within its original morphodynamic unit and this movement took place on 29 September, *i.e.* the 27th day following the release. On the contrary, both fish released 1 km downstream homed precisely to the capture site (after 1 and 16 days out, for F2 and F1, respectively), although F2 only passed through its home site before moving further upstream. Consequently, the times spent by three groups within the morphodynamic unit where the shoal was captured differed significantly: 69, 44 and 8 days × fish (out of 70 possible day × fish: *i.e.* 35 day × two fish per group), respectively for the fish released at the capture site, downstream and upstream of this site (χ^2 = 110, p < 0.01, df = 2).

Selection of residence areas

During the 35 day experiment, the radio tagged fish used 17 residence areas. Four areas were not associated to a maximum NSI but these areas with lesser suitability were poorly frequented by barbel (only three of 210 day × fish; *i.e.* 35 day × six fish). Six residence areas with NSI > 1.0 had a cumulative frequency of occupation (CFO) ≥ 5 % (≥ 11 day × fish), with a maximum of 38% (79.5 day × fish) for the capture site. Habitat suitability stood as a necessary condition for the selection of a residence area by fish but was not enough to account for its long term selection (contingency table on residence areas with NSI < and > 1.0 vs CFO < and ≥ 5 %; χ^2 with correction of continuity = 1.19, p = 0.275; df = 1).

All six residence areas with CFO ≥ 5 % corresponded to places where shoals of 10 or more fish were captured during the electric fishing survey. The residence areas with lower CFO were associated to much smaller shoals (0-13 fish). The comparison between the size of shoals (< 10 fish vs ≥ 10 fish) and the CFO (< 5 % vs ≥ 5 %) was significant at the 0.05 level (χ^2 with continuity correction = 5.58, p = 0.019, df = 1). The degree of significance was improved when exclusively considering residence areas with NSI ≥ 1.0 (χ^2 with continuity correction = 8.14, p = 0.004, df = 1). These results indicate that barbel select a site occupied by a shoal (≥ 10 fish) among the distribution of potentially suitable residence areas.

Regathering of shoal members

During the 35 days of tracking, several radio-tagged barbel were detected simultaneously in the same residence area. If we exclude the first tracking hours when the simultaneous occupation of a single residence area by two radio tagged fishes can be regarded as a direct consequence of the experimental schedule, 11 situations were observed that corresponded to a regathering of two or three fish (Fig. 3). Six of these 11 situations took place in the residence area where the shoal was captured and two other ones within the same morphodynamic unit (for fish F2 and F4, F4 and F5, respectively). The three other situations all involved F2, that has been in contact with all other radio-tagged barbel during the experiment. It should be pointed out that most regatherings took place in the activity centres first, before the fish travelled together to the residence area (*e.g.* F2 joining F6 in its activity centre on 25 September; Fig. 2). The regatherings were most temporary and never resulted into stable associations, as illustrated by the situations involving F2 and F4 (Fig. 3). On the last day of the tracking study, the six fish were observed as three pairs (F1-F3, F4-F5 and F2-F6) that were different from those at the beginning of the experiment (F1-F2, F3-F4 and F5-F6).

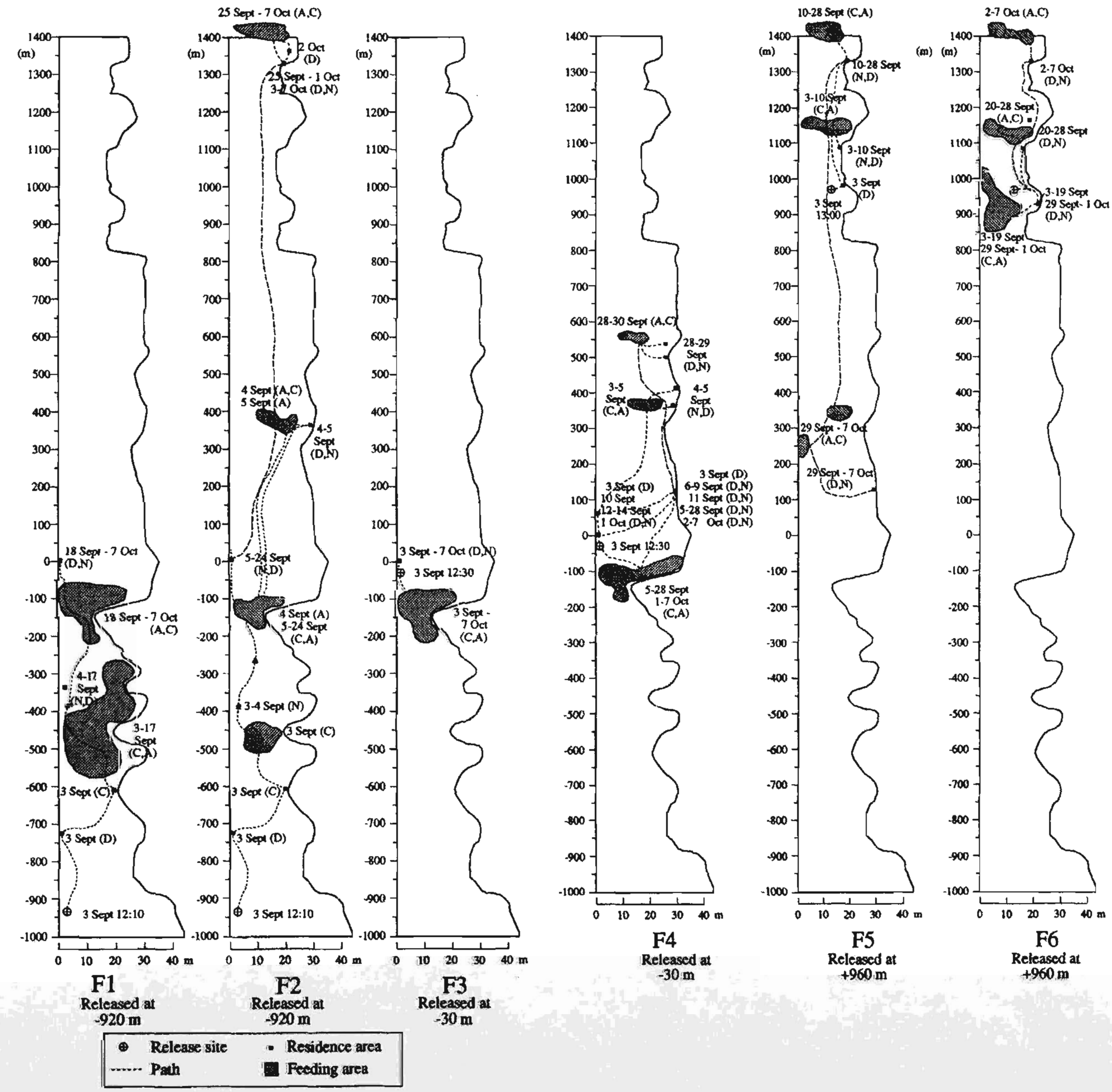

Figure 2. – Tracking maps for the six radio-tagged fish illustrating the mobility, residence and feeding areas occupied from 3 September to 7 October 1990. Study area as in figure 1. Labels nearby the residence and feeding areas correspond to the dates of occupation by fish and to the period of the daily cycle when it was detected in this part of the river: auroral (A), diurnal (D), crepuscular (C) and nocturnal (N). A label (C,A) indicates that the area was occupied by fish both at dusk and dawn but that the first time of occupation was at dusk.

DISCUSSION

Although the experiment started only six days after surgery, several elements indicate that the implantation procedure of the radio tags did not strongly affect the behaviour of the six fish. Indeed, there was no surgical complication and no infection observed before release. Similarly, the absence of weight loss between tagging and release indicates that the fish fed during the period when they were stocked in the cage, either on the larvae of chironomids that were introduced, or on natural prey passing through the cage. From the moment of all

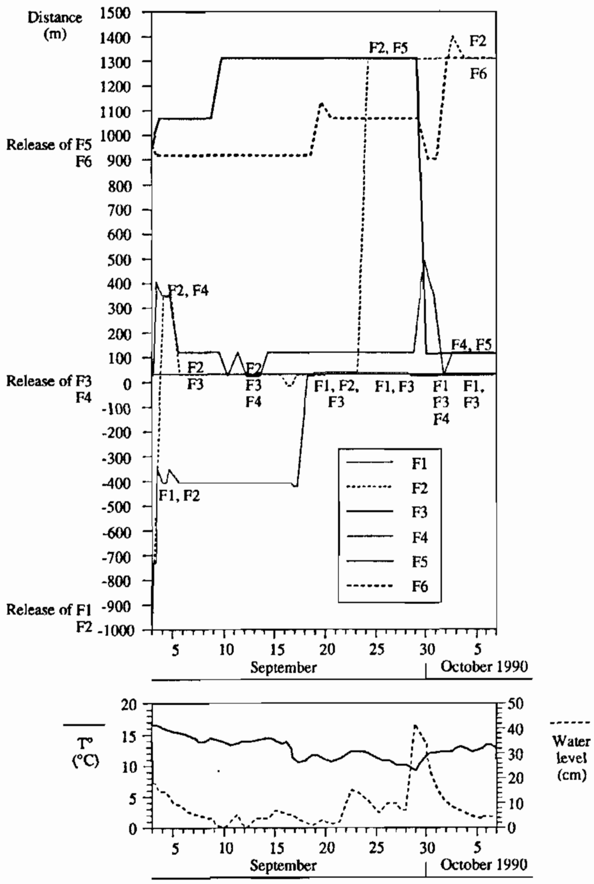

Figure 3. – Regatherings of radio-tagged fish (F1-F6) during the experiment. Negative and positive values on the vertical axis refer respectively to sites downstream and upstream of the capture site, sited at 0. Fish F3-F4 released 30 m downstream of the capture site on 3 September 1990. Fish F1-F2 and F5-F6 were transplanted on the same day 920 m downstream and 960 m upstream of the capture site, respectively. Labels on the graph correspond to fish located at the same place (*i.e.* overlap of error polygons of radio locations) during the experiment. Variations of mean daily water temperature and of water level are illustrated on the lower graph.

six fish showed a typical dusk and dawn activity rhythm pattern that was consistent with these observed during previous tracking studies on *Barbus barbus* (Baras and Philippart, 1989; Pelz and Kästle, 1989; Baras and Cherry, 1990; Baras, 1993*a*, 1995). With respect to performance and swimming capacity, all fish occupied riffles and shallow rapids as soon as the first evening. Three of them (F1, F2 and F5) even migrated through heavy rapids to gain access to upstream residence areas or activity centres. These different elements suggest that the behaviour of barbel throughout the experiment can be regarded as normal.

Selection of the residence area: habitat suitability, shoaling and social context

Obviously, habitat suitability is a necessary condition behind the selection of a residence area by *B. barbus*, as indicated by the majority of residences with maximum NSI selected by the fish, as well as by the most temporary occupation of residences with lower suitability. Basically, this observation is not surprising and validates the habitat suitability curves determined in the course of previous surveys (Baras, 1992). The analysis of the movements of the radio tagged fish immediately after their release in the river further indicates that *B. barbus* positively trades off habitat suitability against versus proximity. Whilst potential residence areas with NSI $\leq$ 1.0 were available close to the site of release, all fish moved throughout this mosaic of habitats until they found a residence with a maximum NSI. This was particularly obvious for fish F1 and F2, that moved upstream over hundreds of metres before selecting a residence.

If the habitat suitability of a residence area emerges as a necessary condition for its selection by *B. barbus*, it is not enough to account for its frequent occupation or utilisation in the long run as some places with high NSI obviously were prefered to others. The comparison between the spatial distribution of fish shoals and the precise locations of the 17 residence areas occupied by the radio-tagged fish indicated that the presence of a shoal of resident conspecifics (N $\geq$ 10) within a suitable residence area was a favourable condition to guarantee its long term selection by others.

These results, however, do not totally account for the mobility patterns of the radio-tagged fish during the experiment. Indeed, except for F3, which consistently occupied a single residence area for 35 consecutive days, all fish left suitable places (*i.e.* suitable habitat occupied by a shoal of 10 or more fish). Since no major variation of water level was observed during the first part of the experiment (until 28 September), these movements can not be accounted for by a modification of the habitat features in the residences. Similarly, almost all fish travelled between distant residences and disregarded apparently suitable residences en route, suggesting that proximity was not a major factor in the selection of a residence area. This observation supports the analysis of the movements of the radio tagged fish just after post-release, as well previous results on the utilisation of the daily activity area by *B. barbus* (Baras, 1993*a*), in the sense that fish positively trade off other variables (habitat suitability, presence of shoals and other factors) against proximity.

In the list of hypotheses presented in the introduction of this paper, the search for specific individuals (social behaviour rather than shoaling behaviour) was considered as a possible determinant factor in the selection of a residence area by *B. barbus*. The results presented here seriously question the relevance of this hypothesis. Considering the experimental design, it could have been expected, within a social context, that fish released on the same site would have stayed or travelled together. Except for the first 5-10 minutes after release, when this behaviour was indeed observed, all radio-tagged fish behaved as "individu-

Table 1. – Utilisation of residence areas by radio-tagged barbel (F1-F6) originating from a single shoal and released nearby the capture site (F3-F4), 920 m downstream (F1-F2) and 960 m upstream (F5-F6). Negative and positive values for spatial locations refer to distances downstream and upstream of the capture site, respectively. The normalised suitability indexes are derived from habitat utilisation curves by barbel > 30 cm (Baras, 1992) and refer to residence areas exclusively. D and N stand for diurnal and nocturnal occupation, respectively. The numbers of fishes captured in the 17 residence areas refer to the distribution of fish shoals as observed during the survey by electric fishing at the beginning of the experiment (late August 1990; *see* also Fig. 1).

Residence N°	Location (m, versus capture site)	Normalised suitability index	Occupation by radio-tagged barbel (F#)	Cumulative occupation (day × fish)	Number of fish captured on the site
1	–720	> 1.0	F1, F2	0.4 D	3
2	–610	> 1.0	F2	0.1 D	2
3	–380	> 1.0	F1, F2	13.0 D, N	28
4	–340	> 1.0	F1	1.0 D	10
5	0	> 1.0	F1, F2, F3, F4	79.5 D, N	34
6	60	> 1.0	F4	5.3 D, N	0
7	125	> 1.0	F4, F5	38.2 D, N	10
8	370	> 1.0	F2, F4	3.5 D, N	3
9	420	0.5 - 1.0	F4	0.5 N	0
10	495	0.5 - 1.0	F4	1.0 D, N	1
11	540	> 1.0	F4	1.0 D, N	4
12	925	> 1.0	F6	19.5 D, N	61
13	975	> 1.0	F5	0.5 D	5
14	1080	> 1.0	F5, F6	17.0 D, N	12
15	1175	0.5 - 1.0	F6	1.0 D, N	13
16	1340	> 1.0	F2, F5, F6	38.0 D, N	36
17	1370	0.2 - 0.5	F2	0.5 D	10

als" rather than as "partners". Similarly, the eventual encounters of shoal members displaced to different sites did not lead to durable associations, as illustrated by barbel F2 that encountered all other five radio-tagged fish but did not stay for more than five consecutive days with the same individual. The only durable associations observed during the experiment took place within the morphodynamic unit where the shoal was captured in late August. Consequently, it is suggested that social factors have no or little importance in the selection of summer residence areas in the River Ourthe, in comparison to spatial, habitat or shoaling factors and that apparently durable associations observed in past mark-recapture studies are an epiphenomenon of habitat preferences, shoaling tendencies or of home-site fidelity.

Selection of a residence area versus selection of an activity centre

In the first part of this discussion, I exclusively considered the selection of habitat by *B. barbus* with respect to residence areas. However, the results presented here strongly suggest that these notions apply more accurately to the activity centre or to the daily activity area (which can be roughly estimated as the morphodynamic unit encompassing the residence area; Baras, 1992). Indeed, each residence area occupied by a radio-tagged fish was connected to a single activity centre but an activity centre could be functionally connected to more than one residence. For instance, on days when fish F1, F2, F3 or F4 rested in the place where they were captured, they always exploited a single activity centre, located in a riffle area 100 m downstream. As attested by the mobility pattern of fish F4, it is most obvious that at least two other residences were functionally connected to this activity centre. Whilst this fish consistently occupied the same activity centre from 5 to 28 September, it changed its residence areas on four occasions during this period. Other situations on the tracking maps support the idea of multiple connections between a single activity centre and several residences (*see* Fig. 2). Conversely, each change of activity centre always resulted into the selection of a new residence area whilst the same activity centre could be exploited from different residences. In other terms, it is strongly suggested that, for adult *B. barbus*, the selection of the activity centre overrides the selection of the residence area itself.

Selection of the residence area: home site fidelity and homing

Home site fidelity can be reasonably evoked for two of the displaced fish (F1 and F2): both fish homed to the residence area where they were captured and, contrary to F3 and F4, there was no possible confusion between actual homing behaviour and the selection of the nearest suitable site. Since fish were transplanted at relatively short distances (less than the size of the annual home range; Philippart, 1977; Baras, 1992), these return movements to a formerly occupied place could be considered as routine home range movements (*see* also Yoshiyama *et al.*, 1992). However, the relatively low mobility of non transplanted *B. barbus* during summer (Baras, 1993*a*, *b*; fish F3-F4 in this study) makes the routine movement hypothesis rather unlikely. In addition, as alternative potentially suitable places were available between the release site and the capture site, these movement towards the original residence area can be regarded as actual homing behaviour rather than chance from random wandering due to the absence of valuable resources. To a lesser extent, the downstream movement of fish F5 in the morphodynamic unit encompassing the capture site can also be regarded as homing behaviour.

A key point in the understanding of homing and selection of residence area by fish is to answer to the question: when placed in apparently similar conditions, why do some individuals home and why do others not ?

The variability of homing rapidity, precision and of straying rates following displacement experiments has been documented by several authors who invoked different hypotheses: seasonal differences (Hasler and Wisby, 1958; Langford, 1979), fish size or condition (Moody, 1960), transplant distance exceeding home range (*e.g.* Mesing and Wicker, 1986) or reluctance to travel in non familiar or hazardous environment (Carlson and Haight, 1972; Green, 1975; Hert, 1992). The role of temperature is unlikely to be relevant within the thermal range experienced by the barbel. Similarly, the low condition of fish may indeed affect homing ability in *B. barbus* (*see* Baras, 1992) but its influence is probably limited to high water levels. The two latter hypotheses are also most unlikely since large barbel (≥ 35 cm) no longer have predators (except for anglers) in the River Ourthe and occupy annual home ranges larger than the transplant distance (Baras, 1992).

Another possible way to investigate the variability of home site fidelity and homing from a functional point of view is to evaluate the trade-off constraints between homing and non-homing and to determine whether homing may or may not provide a substantial advantage to transplanted fishes. The answer to this question basically depends on the social context of the species and on the overall suitability of the environment. In a suitable environment, there is a low probability of finding an unoccupied territory. In this context, most territorial species would probably find much harder to establish a new territory in an unfamiliar site than to home to their original place (Hert, 1990, 1992). By contrast, for gregarious species like *B. barbus*, there is no need to find an empty place to settle. On the contrary, this study suggested that the presence of a shoal of resident fish was a favourable condition to guarantee the long-term occupation of a residence area. Independently, the familiarity of the environment can represent a substantial advantage in time and space utilisation strategies (Hart, 1986). Previous telemetry studies on *B. barbus* showed that the consistent fidelity to a single activity area permitted a reduction of the duration of travels within the activity area as well as the wandering behaviour between feeding centres (Baras, 1992, 1993*a*).

When a fish is transplanted to a new environment, the loss of this advantage could be attenuated by the search for conspecifics and by shoaling behaviour, considering the possible associative learning through passive information transfer within shoals (Pitcher and Magurran, 1983). Thus, considering the possibilities of being introduced or trained to an unfamiliar environment by conspecifics, both home site fidelity and the selection of a new activity centre (and associated residence areas) can be regarded as valuable strategies in a shoaling species like *B. barbus*. The adequacy of the strategy will be intimately dependent on the overall suitability of the environment and especially on the availability of food resources. In the study area described in this paper, fish shoals, residence and feeding habitats were regularly distributed although the availability of feeding habitats apparently was substantially higher in the upstream part of the river than in the downstream part. This repartition could account for the homing movement of fish transplanted downstream in a less favourable environment than the capture site whilst fish transplanted upstream would have found better conditions.

CONCLUSION

These results illustrated the complexity of habitat selection by adult *Barbus barbus*, as the intersection between the suitability of residence areas, the search for conspecifics (apparently regardless of who is who) and home site fidelity, the latter criterion being tempered by the overall suitability of the morphodynamic unit as an activity area. The study further indicated that, for adult fish, proximity was always secondary with respect to other variables. These different elements suggest that adult *Barbus barbus* could compensate relatively narrow preferences or tolerance limits for habitat features by a flexible mobility pattern of which the strategic disadvantage of facing non familiar environment could be tempered by social facilitation. The actual efficiency of this strategy and the actual importance and role of social facilitation still remain to be investigated, by coupling transplantation experiments with long term tracking and growth studies, ideally in environments with different habitat availability.

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