Aquat. Living Resour., 1990, **3**, 283-294

Seasonal activities of female barbel *Barbus barbus* (L.) in the River Ourthe (Southern Belgium), as revealed by radio tracking

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Received January 22, 1990; accepted May 21, 1990.

Baras E., B. Cherry. *Aquat. Living Resour.*, 1990, **3**, 283-294.

Abstract

Two female barbel *Barbus barbus* (L.) were tagged with implantable radio transmitters and tracked in the Ourthe River (Southern Belgium) from April 12th to July 7th, 1989 to study their movements and activity rhythms during the spring-summer period. Both barbels defined a 1.6 km home range and occupied four residence areas. Greatest average daily movements within the home range limits occurred during the prespawning and spawning periods and were associated with variations of mean daily water temperature and level. Barbel 2 made a 9.6 km excursion from its spring home range and homed a week later in its residence area. Barbels displayed dusk and dawn activity patterns, characterized by the occupation of riffle areas. The activity timing was found to be dependent on water temperature while the size of daily activity area was more influenced by river flow conditions.

Keywords : *Barbus*, Cyprinidae, radio tracking, activity rhythms, spawning period, homing.

Activités saisonnières de barbeaux Barbus barbus *(L.) femelles étudiés par radio-pistage dans l'Ourthe (Belgique).*

Résumé

Deux barbeaux femelles, équipés d'émetteurs radio par implantation intrapéritonéale, ont été suivis par radio-pistage dans l'Ourthe (sud de la Belgique) du 15 avril au 9 juillet 1989 afin d'étudier leurs déplacements et rythmes d'activités printaniers et estivaux. Les deux individus pistés ont défini un domaine vital s'étendant sur 1,6 km de rivière et ont occupé chacun quatre gîtes. La fréquence et l'amplitude des déplacements effectués à l'intérieur du domaine vital étaient maximales au cours des périodes de préfrai et de frai, et étaient liées aux variations journalières de la température moyenne et du niveau du cours d'eau. Un des deux barbeaux pistés remonta le cours de l'Ourthe sur 9,6 km en mi-juin et fit preuve de homing en regagnant, après une semaine, le point de départ de son excursion (au mètre près). L'étude des activités circadiennes a révélé que les barbeaux présentaient des rythmes d'activités de type bimodal, caractérisés par une augmentation de la fréquence et de l'amplitude des déplacements au crépuscule et à l'aube. Le timing des activités dépendait principalement de la température moyenne du cours d'eau tandis que la surface de l'aire d'activité journalière était davantage influencée par le débit du cours d'eau.

Mots-clés : *Barbus*, Cyprinidae, radio-pistage, rythmes d'activités, période de frai, homing.

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(1) Fellow of the Belgian "Fonds National de la Recherche Scientifique".

Aquat. Living Resour. 90/03 283 12 $ 3.20/© IFREMER - Gauthier-Villars

INTRODUCTION

Since its introduction in the late 1950's, biotelemetry has been used extensively to monitor the activities and movements of migratory and resident fishes throughout North America and other parts of the world. The early studies dealt almost exclusively with cold water and commercially important species (salmons, shads, basses) and aimed at the development of more effective management techniques to meet public or private demands on the fishery. The results of these studies, proving biotelemetry to be an excellent and reliable means of studying fish movement, as well as the considerable advances in transmitting and decoding technology, led to the development of numerous tracking studies on various topics: fish migration, orientation mechanisms, movement patterns at obstructions, ecology and behaviour of native or introduced species, physiology of animals,... More recently, underwater telemetry has been applied to rare or endangered species or populations to allow the development of new management techniques based on a better knowledge and comprehension of fish behavourial ecology. Bibliographies on underwater telemetry research are provided in numerous review papers (Stasko and Pincock, 1977; Solomon, 1982; Winter, 1983).

Barbus barbus is an aggregative, lithophilous and rheophilous species, and displays, during the spawning period, a migratory or at least erratic behabiour towards well defined spawning grounds (Hancockl *et al.*, 1976; Philippart, 1977). It has been classified as threatened or endangered in most of the studies conducted in the early eighties in Western Europe (Banister, 1982; Lelek, 1980) and specially in Wallonie: Philippart and Vrancken (1983) revealed that the species was extinct or on the decline in several rivers affected by chemical and organic pollution, overfishing and principally habitat destruction due to dredging, canalization and bank modification.

Following this report on the decline in the River Meuse Basin of this ecologically valuable species, highly representative of the "Barbel zone", according to Huet's classification of rivers (1949), our laboratory has been developing several research programs on barbel ecology and physiology (Philippart, 1987). Objectives of the radio tracking programme were 1) to characterize the activity rhythms and movement patterns of barbels throughout the annual cycle; 2) to determine habitat requirements of barbels; 3) to investigate the influence of environmental and biological variables on time and space utilisation. This paper presents the results of a tracking study conducted in the River Ourthe during the spring-summer period. Data on autumn-winter activities and habitat studies will be published elsewhere.

STUDY AREA

This study was conducted on the Ourthe River, the main tributary (133 km) of the Meuse River in Southern Belgium (*fig.* 1). The study area, centred on the village of Hamoir (altitude: 113 m; 50°25'36" N, 5°32'25" E), is typical of the "Barbel zone", according to Huet's classification (1949) and contains large barbel populations studied since the early seventies (Philippart, 1977). The mean river width in the study area ranged from 20 to 30 m, depending on water level fluctuations throughout the study period.

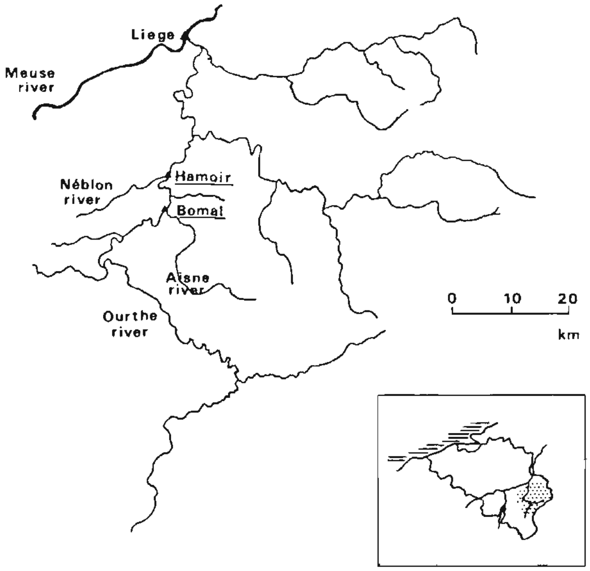

Figure 1.— *Study area: the Ourthe River in Southern Belgium* (Wallonie).

Water temperature was recorded continuously during the tracking period on a thermograph (Richard Instruments) installed in the study area. Mean water temperatures ranged from 7.8 to 23°C (*fig.* 2 C). River discharge was measured indirectly by checking daily the fluctuations of the water level on a limnimetric scale installed in Hamoir. Daily water temperature and level were significantly correlated with photoperiod (respective correlation coefficients $r=0.716$ and 0.500; 85 degrees of freedom (df)).

METHODS

Two female barbels (barbel 1: 408 mm, 833 g; barbel 2: 530 mm, 2,000 g) were captured by electrofishing (EPMC generator, DC, 400 V) in the study area on April 12th. The fishes were anaesthetized for 5 to 10 minutes with a 100 mg/l solution of MS 222 (Tricaïne Methanosulfonate). The activity-transmitters, produced by Advanced Telemetry Systems, had a weight in air of 8.5 g (lenght: 40 mm; diameter:

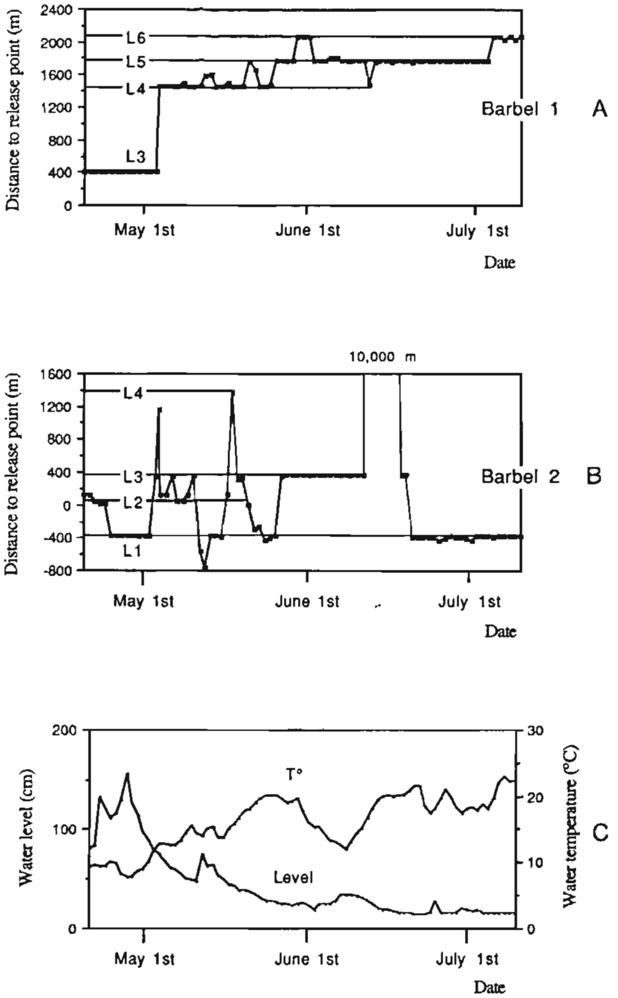

Figure 2. – Development of barbel movements (A and B) during successive days. Each dot represents the average daily position in residence area (L). Changes of mean water temperature and level are presented in graph C.

12 mm) or 16.0 g (lenght: 80 mm; diameter: 12 mm) and an average lifespan of 4 months. A frequency of 40 MHz was used. The surgical implantation procedure, adapted from Hart and Summerfelt (1975) and Vallière *et al.* (1986), was described in previous papers (Kalpers *et al.*, 1989; Baras and Philippart, 1989): the transmitter, sterilized with alcohol, was implanted in the abdominal cavity through a 20 mm incision made in the midventral line, between the pelvic girdle and the anus. The incision was closed with catgut material using atraumatic needles. The barbels were kept for 2 days in a PVC cage close to the release area in order to allow complete recovery from anaesthetization and tagging procedures, and to evaluate the success of surgical implantation. Their anal fins were clipped to allow subsequent identification by anglers.

Barbels were located at least daily, from the day of release (April 15th) till July 9th 1989. Daily monitoring began between 10 h 00 and 14 h 00. For each location, two fixes were taken from wooden marks of known position lining the banks of the river, using a portable receiver (Falcon Five, Wildlife Materials, Inc. or Fieldmaster, ATS, Inc) and a hand-held diamond antenna (ATS, Inc) equipped with a compass. Tests on transmitter location accuracy conducted both in the air and underwater revealed an astonishing overall angular accuracy of about ±2°, enabling the fish to be located within an approximately 2.5 m^2 area. The results of these tests were confirmed during the tracking period by electrofishing data.

We studied activity rhythm patterns over eight 24 h cycles: the barbels were tracked continuously and the numbers of fixes were proportional to the frequency and amplitude of movements. This tracking strategy might be qualified as "opportunistic", but, in our opinion, is more representative of fish activity than a regular-interval sampling (e. g. 10 minutes): indeed, many "out and home" movements could occur during the interval between fixes. Fix displacement, the linear distance between two consecutive fixes, was used as a measure of movement.

Angular coordinates were converted into X-Y coordinates using a programme developped on a Macintosh computer, plotting fish positions on a topographical map of the river and calculating the length and speed of movements ("X-Y PGM Track", Baras and Cherry, 1989).

Seasonal home range was expressed as distances between upstream and downstream limits of fish locations, excluding locations representing obvious wandering from home range calculations. Since home range size generally increases with the amount of observations, and as these observations are supposed to be independent, we used daily positions of fishes in their resting place to estimate home range size. We defined the "resting place" as the spot characterized by a clumping of radio locations and by minimum activity of the animal (absence of variation of transmitter pulsation rhythm). Close resting places, a few metres apart within the same habitat, were described as belonging to the same "residence area". We refer to "activity centre" as the area where the animal develops its activities (e. g. feeding, spawning) and to "daily activity area" as the surface containing all daily animal locations in residence areas and activity centres.

RESULTS

Seasonal movement patterns and distances travelled

We divided the 86 day tracking study in 6 periods (*table* 1) based on the observation of barbel spawning on four spawning sites in the study area.

Table 1. – Summary of tracking data and river characteristics during the six periods defined in the study. Movements refer to distances travelled daily between residence areas.

		Movements of barbel 1 (m)			Movements of barbel 2 (m)			Period characteristics	
Period	N (days)	Mean (m)	S.D. (m)	Range (m)	Mean (m)	S.D. (m)	Range (m)	Mean water Temperature (°C)	Mean water level(cm)
pre-prespawning	15	67.73	254.91	0-989	98.67	208.25	0-730	9.8	105.5
prespawning	14	25.71	32.00	0-100	370.00	414.00	0-1,240	14.5	54.0
spawning	7	128.57	129.03	0-300	230.00	253.90	20-730	19.3	31.0
postspawning	14	48.57	98.52	0-280	2.14	5.79	0-20	15.7	26.0
post-postspawning	14	47.14	103.36	0-300	1,425.00	3,469.00	0-9,600	19.04	20.0
summer	17	24.71	66.53	0-280	11.77	15.51	0-50	19.5	17.0

fish acclimation	April 12-19	
pre-prespawning	April 20-May 4	spawning-3 weeks
prespawning	May 5-18	spawning-1 week
spawning	May 19-25	spawning
postspawning	May 26-June 8	spawning + 1 week
post-postspawning	June 9-22	spawning + 3 weeks
summer period	June 23-July 9	spawning + 5 weeks

As results of the feasibility study (Kalpers *et al.*, 1989) showed that the postsurgery stress could extend to 8 days, observations from the acclimation period were not taken into account, except the return of the two barbels to their point of capture, 2 days after their release in the river.

Movements of barbel 1 (*fig.* 2 A).

From April 20th to May 3rd, the barbel was detected in the residence area where it was captured (L3, 375 m upstream of the release point). No consistent movement was detected during this 14 day period characterized by high discharge and low temperature. During a 24 h cycle monitored on May 3rd and 4th, we recorded a major upstream movement (1,079 m) associated with a change of residence area (L3-L4). The fish enlarged its activity area during the 18 following days, increasing progressively the amplitude and frequency of movements. On May 20th, it developed its activities over a 300 m long area and explored different microhabitats, including its main residence area (L5) and spawning area (S, 120 m downstream of L4), where it was observed spawning the following day, between 8 h 00 and 10 h 00.

The fish returned to L4 soon after spawning and, 3 days later (May 24th), moved 300 m upstream to its main postspawning residence area (L5). From May 29th to June 2nd, the fish was detected in its fourth residence area (L6) before returning to L5. During the 32 following days, the barbel was found to confine its activities around this area, if we except the L5-L4 movement recorded on June 10th, during an exceptional temperature increase (8.1°C in 8 days). The last change of residence area (L5-L6) was monitored on July 4th, between 6 h 20 and 7 h 30.

Movements of barbel 2 (*fig.* 2 B).

On April 15th, the fish was located on the spot where it had been captured by electrofishing 3 days earlier (L2, 75 m upstream of the release point). Its activities were confined to a 100 m zone centred on this residence area till April 26th, when it moved 450 m downstream to L1, after the river flow increased in a spectacular way following heavy rainfalls. From May 3rd to May 26th, the fish travelled daily over long distances within a 1.6 km home range. It changed its residence area almost every day and explored all types of habitat, including small tributaries, such as the Néblon River (mean width 3.5 m), where it migrated 250 m upstream on May 12th. The amplitude and frequency of these movements reached their climax at the beginning of the spawning period, on May 20th.

At the end of the spawning week, the barbel moved 765 m upstream to residence area L3, that had been visited on several occasions during the prespawning period. The postspawning period (May 26th to June 8th) was characterized by a consistent stability of barbel 2, confining its activities to a 30 m long area around L3. On June 10th, despite intensive tracking research, we couldn't detect the fish within the limits of the study area. The extension of the research zone to 6 km during the following days was also unsuccessful. At this stage of the study, specially when considering the spring home range and the stability during the postspawning period, the most likely explanation was precocious transmitter failure.

However, on June 15th, we detected a signal 500 m downstream of the confluence of Rivers Ourthe and Aisne (L7, village of Bomal), 9.6 km upstream of the fish's previous localization. The fish was tracked all day long and showed no significant movement. The following day, the signal was lost again, despite intensive tracking coverage on a 10 km sector centred on Bomal. On June 17th, the barbel was back in residence area L3, occupying exactly the same resting place as before the 10 km upstream excursion. On June 19th, the barbel was found to have moved 750 m downstream to residence area L1, already occupied during the first weeks of the study period; it remained here till the end of the study period.

Home range and residence area occupation (table 2)

If we except the excursion of barbel 2 to residence area L7, representing obvious wandering behaviour, both barbels defined a 1.6 km home range and occupied four residence areas each. They shared residence areas L3 and L4, although simultaneous presence within the same residence area was detected only once (L3, May 3rd). Despite these similarities, the patterns of space occupation by the two fishes were quite different. Barbel 1 tended to exploit its home range in a sequential way, since it occupied its residence areas almost successively. On the contrary, barbel 2 was more dependent on a main activity area and its residence area L1 (and to a lesser extent L3), that might be considered as an operating centre and a starting point of excursions to secondary activity areas. This "radiative" tendency was particularly obvious during the prespawning period, when the barbel progressively enlarged its home range during excursions starting from L1 or L3.

Comparison of movements

The average daily movement for each of the six periods was the total distance travelled by the fish divided by the length of the period (*table* 1). These movements should be considered as minimum values for the distances actually travelled by the fishes as out and home movements could take place between daily fixes. We used t-tests to compare the movements (Z-scores) of the two fishes within periods. Null hypotheses were rejected at $p \leqq 0.1$.

Statistical analysis of movements of barbel 1 showed a significant resemblance ($t = 0.052$; $p = 0.959$; 29 df) between the prespawning and summer periods, characterized by a consistent fidelity to well defined activity areas (respectively around residence areas L4 and L5-L6). On the contrary, it appeared that the distances travelled during the spawning week were significantly higher than those recorded during the pre-prespawning ($t = 2.881$; $p = 0.01$, 27 df), prespawning ($t = 2.881$; $p = 0.01$; 19 df) and summer ($t = 4.226$; $p \leqq 0.001$; 22 df) periods.

Spawning period movements of barbel 2 were also significantly different from those recorded during the

Table 2. – Characteristics and occupation of residence areas. Negative distances refer to locations downstream of the release point.

Home area	Characteristics	Distance to release point (m)	% of occupation barbel 1	% of occupation barbel 2
L1	pool ; rootwad and sunken trees	- 300	0.0	44.5
L2	counter current cove ; rocks	+ 150	0.0	9.8
L3	pool ; rootwad and sunken trees	+ 465	16.0	35.7
L4	rocks and crevices in schist banks	+ 1,504	25.9	2.5
L5	rocks and crevices in schist banks	+ 1,784	44.5	0.0
L6	lateral pool associated with rootwad	+ 2,084	12.3	0.0
L7	pool ; rootwad and sunken trees	+ 10,000	0.0	7.5
S	low gradient riffle	+ 1,664	1.2	0.0

postspawning ($t=3.324$; $p=0.003$; 19 df) and summer ($t=3.747$; $p=0.001$; 22 df) periods when we observed reduced amplitude or frequency of the movements. The summer period was also significantly different from pre-prespawning ($t=1.719$; $p=0.096$; 30 df) and prespawning ($t=3.577$; $p=0.001$; 29 df) periods, and was characterized by a consistent stability, since the average daily movement was close to zero (*table* 1).

Comparisons between fish movements within periods proved the absence of significant differences between the two barbels, except during the prespawning period ($t=2.36$; $p=0.026$; 26 df), when barbel 2 was hyperactive, changing its residence area almost everyday while barbel 1 was stabilized in residence area L4. On the contrary, summer movements were statistically similar ($t=0.055$; $p=0.952$; 32 df).

Distribution of movement in relation to environmental factors

All major movements occurred when mean water temperature ranged from 10 to 22°C, but there was no direct relationship between mean water temperature and the average daily distance moved by the fish: e. g., movement patterns of barbel 2 during the summer period were significantly different from those recorded during the spawning and post-postspawning period (respectively, $t=3.647$; $p=0.001$; 22 df and $t=2.194$; $p=0.10$; 29 df) while mean water temperatures were almost identical (respectively, 19.50, 19.30 and 19.04°C). Similar considerations could be stated as regards discharge influence on fish movement, since most major movements were recorded while the water level was low and steady.

However, we believe that fish could be more sensitive to the variations of a parameter than to its absolute values. Therefore, we tested, on a period basis, the influence of the percentages of variation of water temperature and level on fish average daily movement. The results tend to prove that average daily movements of the barbels increased in parallel with water temperature increase and water level decrease during the prespawning, spawning and postspawning periods. This influence was less obvious for periods furthest from spawning (pre-prespawning and summer periods).

Activity rhythms

Four 24 h tracking cycles were monitored for each fish in order to study the evolution of circadian activities during the spring-summer period. The interval between two consecutive cycles within the same period was reduced to 6 days to compare activities under similar temperature, discharge and photoperiodic conditions (*table* 3). The results are presented in *figure* 3.

Table 3. – Environmental characteristics during the 24 hours tracking cycles.

Cycle	Date	Sunset	Sunrise	T°min (°C)	T° max (°C)	Water level (cm)
1	April 25-26 April 26-27	20h56 20h56	06h25 06h25	7.6 7.2	10.0 8.9	110-146 140-156
2	May 3-4	21h05	06h12	11.6	13.0	75-68
3	May 31-June 1 June 5-6	21h46 21h51	05h35 05h32	13.7 17.1	18.0 20.0	25-26 28-34
4	June 27-28 July 3-4	22h00 21h58	05h32 05h36	17.1 17.3	20.0 21.0	16-17 17-18

Cycles studied during the pre-prespawning period (*fig*. 3 A and A') were characterized by the absence of movements beyond the limits of the residence areas. Activities of barbel 1 were distributed almost homogeneously throughout the cycle while barbel 2 was more active during the afternoon. On the contrary, during the prespawning period (*fig*. 3 B and B'), both fishes were found to be static during daytime. They started moving upstream almost simultaneously in the early evening, progressing in a "rest-and-go" manner, moving on short distances (± 100 m), resting or exploring the surroundings during 15 to 20 minutes and moving upstream again. They both stopped progressing upstream between 22 h 00 and 23 h 00, staying in their respective home area till the end of the cycle and showing little activity.

No 24 h cycle was completed during the spawning week, but fixes were taken at regular interval and several 3 hours cycles were conducted at different times of the daily cycle. These data, as well as observations on barbel behaviour on spawning grounds, tend to prove that they develop spawning activities only during daytime and show little or no activity at dusk and dawn during this period.

During the postspawning period (*fig*. 3 C and 3 C'), the two individuals exhibited quite different activity patterns: barbel 1 changed its residence area twice (L6-L4 and L4-L5) while barbel 2 confined its activities within the limits of its residence area. Summer activity patterns (*fig*. 3 D and 3 D') were characterized by dusk and dawn peaks corresponding to the occupation of riffle areas. No movements were recorded during daytime if we except two "out-and-home" movements (at 10 h 00 and 15 h 00) of barbel 1 between L6 and a new resting place where the fish showed no particular activities. These movements took place while large groups of kayaks were passing over the spot where the fish was resting.

Comparison between activity rhythm patterns

We divided each 24 h cycle in eight 3 hours periods (*fig*. 4), in each case summing the total distance travelled during the period, expressed as a percentage of the total distance travelled during the 24 h cycle. In

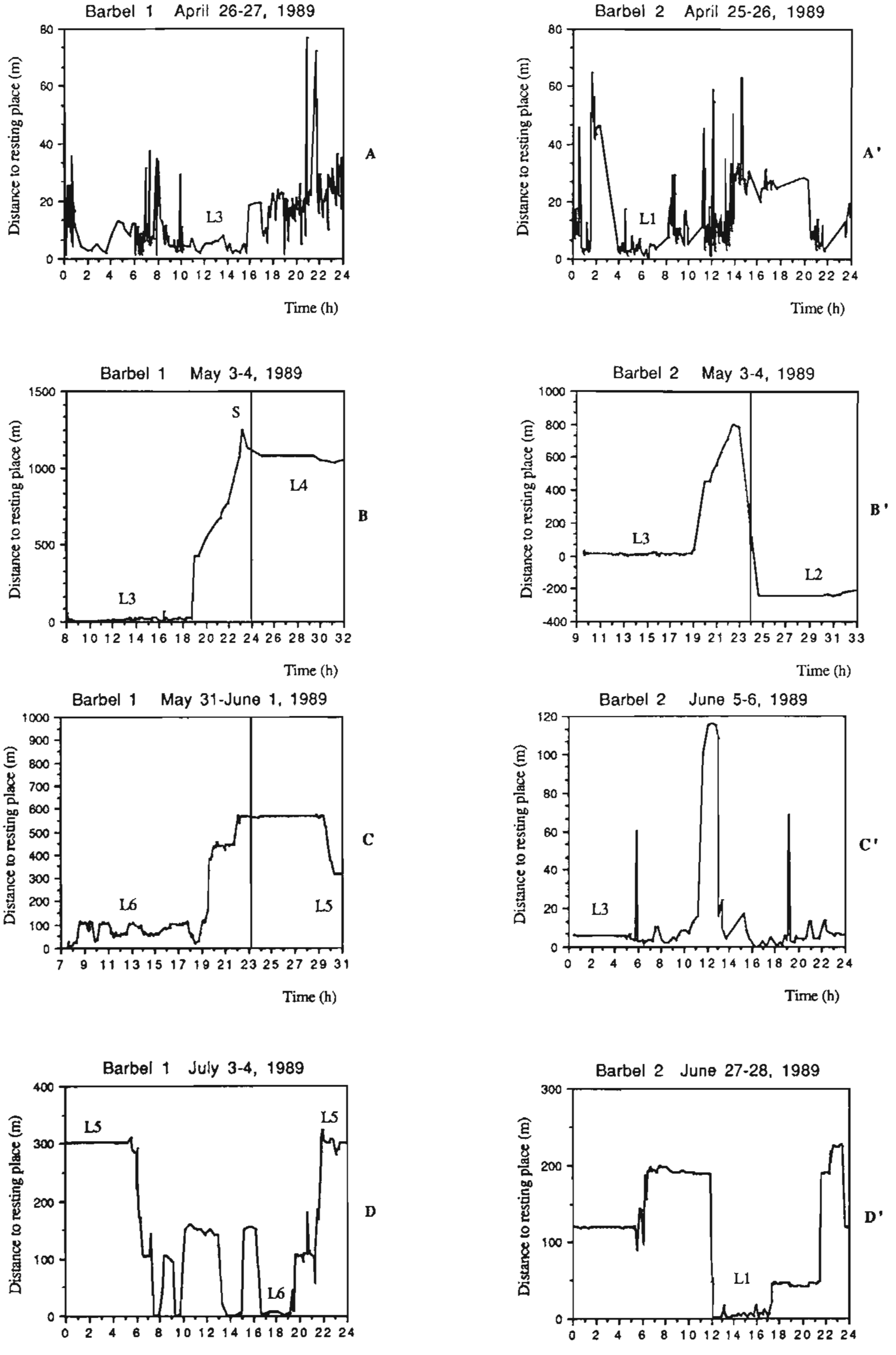

Figure 3.— Track diagrams recorded during 24 h cycles. Fish locations are expressed as distances to the residence area occupied at the beginning of the cycle. In order to facilitate visualization and intuitive perception of the activity rhythm patterns displayed by barbels, we present diagrams with a time scale ranging from 0 to 24 h, except when the residence area at the end of the 24 h cycle was different from the one identified at the beginning of the cycle (diagrams B, B' and C).

order to compare activity timings between cycles taking place under very different photoperiodic conditions, the limit between period 1 and 2 was fixed at sunset.

We used linear regression tests to compare the distribution of movements between the cycles of each fish at different periods and between the cycles realized on the two fishes within the same period.

It appeared that activity rhythm patterns changed throughout the study period since we could not draw

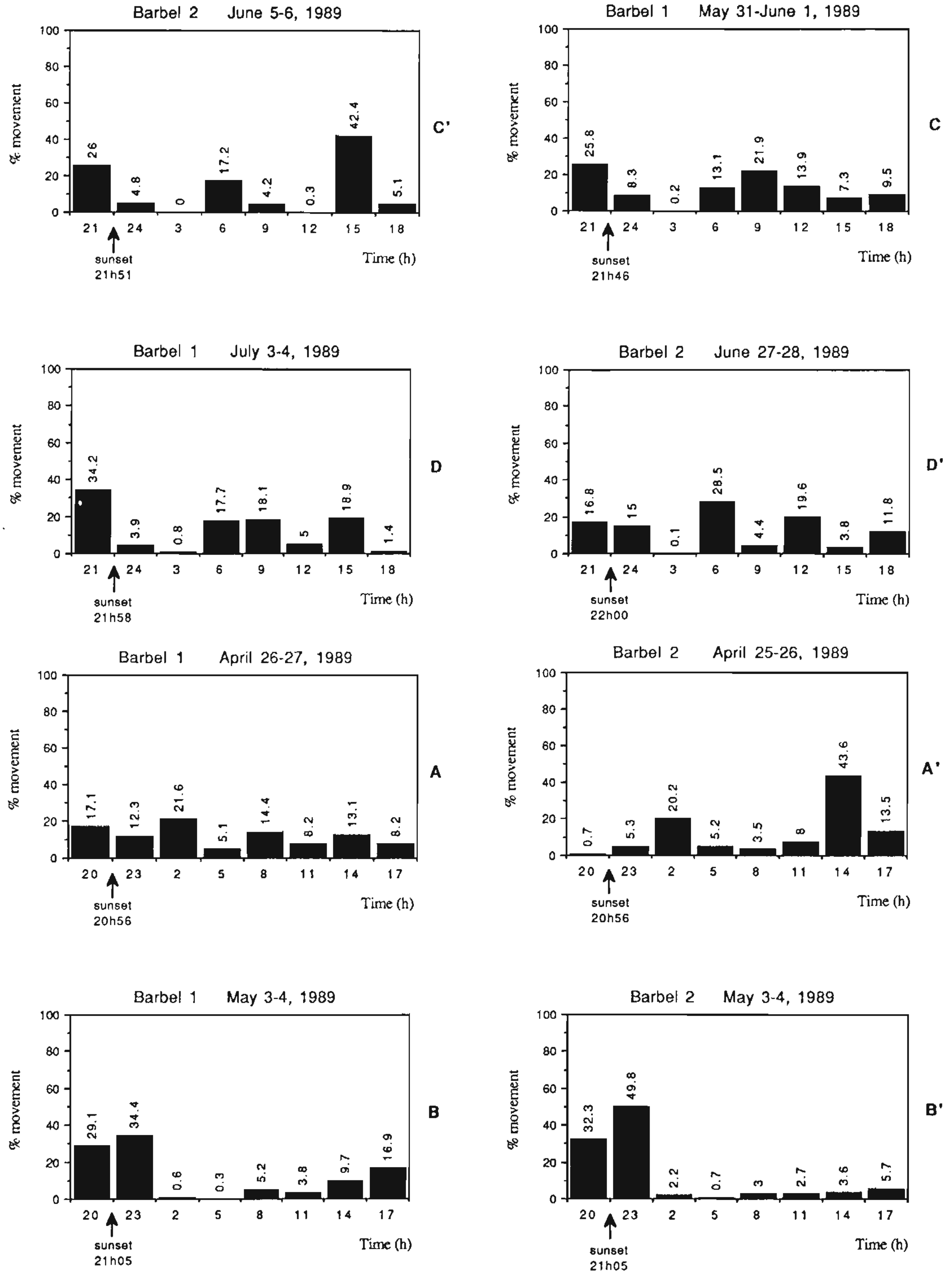

Figure 4.— Bar charts showing distribution of movements during 24 h cycles. Each cycle was divided into eight periods lasting 3 hours each. Limit between periods 1 and 2 was fixed at sunset. Each bar represents the total distance travelled during the period, expressed as a percentage of the total distance travelled during the 24 h cycle.

any significant parallel between cycles realized at different periods, except between postspawning and summer cycles of barbel 1 ($r=0.763$; $p=0.028$; 15 df). Moreover, pre-prespawning, prespawning and summer cycles of barbel 2 were significantly different ($p \geq 0.95$).

Results of tests between fishes within the same period revealed that the barbels exhibited quite different activity rhythm patterns, except during the prespawning period ($r=0.932$; $p=0.001$; 15 df). Differences between summer cycles ($r=0.199$; $p=0.637$; 15 df) were quite unexpected since we described both barbels developing their activities at dusk and dawn. We believe that the absence of significant correlation could be accounted for by the out and home movements of barbel 1 occurring when large groups of kayaks were passing over its residence area. Therefore, we suppressed these questionable movements and did another test. The result of this test proved that the two barbels displayed statistically similar activity rhythm patterns during the summer period ($r=0.908$; $p=0.001$; 15 df).

DISCUSSION

Amplitude and determinism of movements

The two female barbels displayed similar movement tendencies during the study period. Both fishes returned to their site of capture within the first 48 hours and showed little movement during the pre-prespawning period. The frequency and amplitude of movements increased significantly during the prespawning and spawning periods, reaching a climax on May 20th. The following periods were characterized by fish stability, except for a 10 km excursion of barbel 2. Similar movement patterns, characterized by peak movements during the spawning period and consistent stability in summer, were described in several tracking studies: Mesing and Wicker (1986) observed that movements of largemouth bass (*Micropterus salmoides*) increased progressively from March to June, but decreased sharply during the summer months and remained low during autumn and winter. Hubert and Lackey (1980) showed that distances covered by smallmouth bass (*Micropterus dolomieui*) between successive daily fixes were significantly higher in spring and autumn than during the summer and winter periods. First barbel tracking experiments, conducted in summer 1988, also showed consistent stability of the fish during this period (Philippart and Baras, 1989; Baras and Philippart, 1989).

As observed, temperature and discharge variations tended to influence fish activities during the periods which preceded and followed spawning activities, but were less likely to explain the variations of movements observed during periods furthest from spawning (early spring and summer).

All major residence area changes occurred when water temperature ranged from 10 to 22 °C, while cold (pre-prespawning) and hot (summer) periods were characterized by barbel stability. Langford (1981) also observed significant differences between daily journeys of bream (*Abramis brama*) tracked below and over 10 °C. Hubert (1979) showed that temperature could reduce smallmouth bass movements when exceeding the optimum. In addition to absolute temperature values, an increase of temperature might act as a stimulus tending to increase fish movement (as was demonstrated for barbels). Similar behaviour was observed by Mesing and Wicker (1986), reporting that several largemouth bass migrated a distance of 3 km after mean daily water temperature increased from 11.4 to 14.5 °C.

Residence area changes were less dependent on river flow fluctuations since most movements occurred while the water level was low and steady or slightly decreasing. Langford also found there was no consistent correlation between water discharge and bream net daily journeys. Similar conclusions were stated by Baras and Philippart (1989) and Pelz and Kästle (1989) on barbel summer movements. However, we observed a few downstream movements under high discharge conditions. Yeager (1982), tracking bass hybrids in Florida, also detected major habitat changes during periods of rising water. Langford (1981) observed similar behaviour of bream flushed downstream during sudden flow increase following heavy rainfalls. We believe that barbels moved downstream because they could not maintain their position in residence areas close to rapid zones under high discharge conditions or that the foraging energetic cost was too high, specially when considering the low water temperature during this period (<10 °C).

Activity rhythms

Like *Micropterus salmoides* (Mesing and Wicker, 1986) and *Micropterus dolomieui* (Emery, 1973), *Barbus barbus* may be classified as a crepuscular species according th Helfman's classification (1986): indeed, both barbels were most active during periods of rapidly changing light intensities throughout the study period, except during the spawning week, when movements were only observed during daytime. Dusk and dawn activities were almost always characterized by the exploration of riffles and corresponded to the feeding timings described by Karangwa (1974). These results on wild individuals confirm the study conducted on restocked individuals in the Méhaigne River (Baras and Philippart, 1989) and are substantiated by the results of Pelz and Kästle, tracking barbels in the Nidda River (Germany, July 1989). Moreover, the summer activity rhythms observed in the Ourthe River fit the model proposed by Baras and Philippart, emphasizing the role of light intensity and mean water temperature as synchronizers of barbel activity and the modulation of activity duration by water temperature.

However, we noticed some differences between the cycles studied at different periods. In early spring, activities began early in the afternoon and extended over longer periods. On the other hand, the size of daily activity areas was much more reduced and restricted to the limits of the residence areas.

The activity timing shift could be explained by dramatically low water temperatures (< 10 °C) in early spring, probably beyond the limits of barbel preferenda. In such thermal conditions, the fish would be active when water temperature reaches its daily maximum. This hypothesis, confirmed by more recent experiments on the influence of water temperature on activity timing (Baras, 1990), could also account for the differences between the activities recorded during the postspawning period: barbel 1 had a bimodal dusk and dawn pattern, while barbel 2 developed its activities during the afternoon. However, the mean water temperatures were significantly different, respectively 15.7 and 12.8 °C. So, from a thermal point of view, the postspawning cycle for barbel 2 was closer to early spring conditions and the activity timing was somewhat similar to the one observed during the pre-prespawning cycles.

If the activity timing is principally determined by water temperature, the size of daily activity areas is probably more influenced by river flow conditions. This hypothesis tends to be supported by observations realized during the postspawning period: indeed, despite low temperature conditions, barbels exploited their riffle activity areas during this low discharge period, while in early spring, riffles were transformed into heavy rapids and we recorded no consistent movements beyond the limits of the residence areas. In these conditions, barbels probably would have spent much more energy in maintaining their position in rapids than they would have derived from feeding activities.

Home range and homing

Barbels defined a home range extending over 1.6 km, which they exploited in a sequential or "radiative" way. These results are similar to those from electrofishing studies conducted on the Ourthe River by Philippart (1977), who estimated mean home range size at 1,173 m. The summer home range, however, was much more limited and almost restricted to the limits of the activity areas surrounding the summer residence area (maximum 300 m). Pelz and Kästle (1989) obtained similar results on the Nidda River, their barbels occupying single residence areas with distances between day and night locations ranging from 60 to 200 m.

In addition to home range behaviour, we observed that barbels were attached to well-defined resting sites: both fishes occupied four residence areas and shared two of them. Recent results from further tracking and electrofishing studies revealed that one of these residence areas had been visited at least once by all the barbels we tracked and corresponded to a major gathering centre for female individuals within the sector of Hamoir-Lassus. The attachment of barbels to residence areas was also demonstrated at the beginning of this tracking study, when we displaced the fishes for transmitter attachment and acclimation. Both returned to their respective site of capture within 48 hours. Similar observations were made on male barbels in early spring and late summer 1989 (unpublished data). Moreover, barbel 2 was observed several times making excursions inside or outside its home range and returning exactly to its starting point, even after travelling over long distances (10 km), showing consistent homing behaviour.

Homing has been extensively studied and demonstrated in migratory anadromous salmonids, where there is convincing evidence that as many as 95% of spawners return to the stream in which they spent their early life-history stages (Harden Jones, 1968; Hasler and Scholz, 1983). Homing abilities of some resident fish species towards spawning grounds were also demonstrated in mark-recapture and tracking studies. Olson *et al.* (1978) obtained evidence of homing among spawning walleyes (*Stizostedion vitreum*) by marking and releasing adult individuals at spawning sites and comparing the distribution of recaptured fish among these sites during subsequent spawning seasons. Mesing and Wicker (1986), tracked largemouth bass in Central Florida lakes and observed repeated migrations of five bass to the same spawning areas. As regards cyprinids, Otis and Weber (1982) observed homing tendencies in carp (*Cyprinus carpio*) radio-tagged in the Lake Winnebago system; Tyus (1986) proved the fidelity of Colorado squawfish (*Ptychocheilus lucius*) to Yampa River spawning grounds, even after migrations of more than 150 km. Roach (*Rutilus rutilus*) were found to exhibit repeat homing with high precision in tributaries of Lake Arungen (L'Abée-Lund and Vøllestad, 1985).

Homing to non-spawning areas is also exhibited by resident fish species. Displacement experiments conducted on various species showed the return of fishes to their site of capture: white bass, *Morone chrysops* (Hasler and Wisby, 1958), smallmouth bass, *Micropterus dolomieui* (Hubert, 1979), largemouth bass, *Micropterus salmoides* (Mesing and Wicker, 1986), carp, *Cyprinus carpio* (Clifford, 1973) and bream, *Abramis brama* (Langford, 1981). Similar behaviours were observed in barbel populations in the Ourthe River: indeed, some barbels were captured more than 40 km upstream of their site of marking and returned to their previous home range a few weeks later (Philippart, 1977).

The reasons of this non-spawning homing are still to be determined. Homing in spawning migrations brings the fish back to a suitable environment for reproduction, at a period when other spawners will be present. We can draw a bioenergetic parallel, arguing that homing brings the barbel back to an environment it has already experienced and which it recognizes as suitable, such as residence and feeding areas with stable characteristics whatever the discharge fluctuations. Homing behaviour would then reduce the energetic expenditure needed to explore a new home range and would help in optimizing the efficiency of space exploitation. Another likely hypothesis, as barbels exhibit aggregative behaviour and as we showed that the residence areas identified for the tracked barbels were regions of high barbel density (unpublished data), would be that homing could be related to "group-fidelity" rather than to attachment to a well-defined place.

Mechanisms underlying homing behaviour and fish orientation were recently reviewed in McCleave *et al.* (1984), McKeown (1984) and Smith (1985). Adult salmonids recognize their home streams by olfaction, the "bouquet" of each stream being unique and generated by a combination of abiotic and biotic factors, such as pheromones released by juveniles (Nordeng, 1977; Smith, 1985). Similar considerations may apply to resident fish species exhibiting aggregative behaviour, such as cyprinids: wandering individuals might be attracted by the odour of conspecifics present in their residence area. In streams, these fishes would be able to home both downstream and upstream, as demonstrated in *Gobio gobio* (Stott *et al.*, 1963) and *Phoxinus phoxinus* (Kennedy and Pichter, 1975). However, they would tend to home faster if they had been moving downstream of their residence area, as observed on breams tracked with ultrasonic transmitters by Malinin (1970, 1971).

Another likely hypothesis would be that olfaction and vision could both act as complementary mechanisms in homing and that fishes would use visual cues and could recognize visually at close range their preferred residence area, as demonstrated on trout by Cunjac and Power (1987). These hypotheses should be confirmed or negated by our next tracking experiments on displaced groups and blind or anosmic fishes.

CONCLUSION

This tracking study helped us to collect more complete and precise data on barbel ecology, to describe the general scheme of time and space occupation during the spring-summer period and to demonstrate attachment of barbels to well defined resting places and residence areas which should be taken into account in any river management perspective. However, due to small sample size, the results presented and hypotheses stated should be confirmed by further tracking experiments on larger samples and during periods covering the annual cycle (Baras, 1990).

Acknowledgements

The authors wish to express their thanks to Dr. J. C. Philippart for constructive comments and fruitful discussions on barbel ecology. We are also highly indebted to our "tracking teachers", Dr. J. D. Winter and V. B. Kuechle, who shared with us their invaluable experience of telemetry and radio tracking. A special thanks to J.-M. Lambert, P. Absil and G. Rimbaud who assisted in data collection. This research was supported by the Belgian "Fonds National de la Recherche Scientifique" and by the Ministry of Nature Conservation and Fisheries of the "Région Wallonne" (Projects "Restoration of Barbel Populations" and "Habitat Requirement of Fish").

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