Movements of barbel, *Barbus barbus* (Pisces: Cyprinidae)

† *Dedicated to the late Professor Antonín L e l e k - our friend and colleague*

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A b s t r a c t . Altogether 701 adult barbel, *Barbus barbus* were captured by electrofishing and individually tagged to study their local displacement and movements in a stretch of the River Jihlava (Czech Republic). A total of 149 fish were recaptured and 105 of them (70.47 %) were considered as ”resident” because they were always recaptured in the same, relatively restricted (250 - 780 m) stream section, which always contained a pool and was demarcated naturally by riffles on both edges. The remaining 44 recaptured specimens (29.53 %) belonged to the “mobile” part of population, their movements encompassing two (or exceptionally more) adjacent stream sections and at maximum a distance of 1680 m downstream or 2020 m upstream. The proportion of mobile barbel, relatively low in smaller and middle size classes, increased in the largest size classes (451–550 mm of SL). A rather limited extent of movements also suggests a relatively small area of home range in the studied stretch, which nevertheless provides satisfactory resources and favourable conditions required by barbel over their entire life cycle. The extent of movements and corresponding proportion of mobile fish appear to be increasing with diminishing habitat patchiness. In the stretch of River Jihlava studied, with a rich patchy heterogenous habitat and well developed riffle-pool-raceway structure, each section (pool) can be considered as a more or less isolated spatial unit containing its own, and in a certain degree, isolated component of a metapopulation.

Key words: tagging, resident and mobile fish, territoriality, metapopulation, riffle-pool development

Introduction

The barbel *Barbus barbus* (Linnaeus, 1758) is a popular and much studied species whose biology is still insufficiently understood. Unfortunately it is also a species currently vanishing from many European rivers. Already four “International Round Tables” (Montpellier – France in 1989, Liége - Belgium in 1993, Liblice – Czech Republic in 1995 and Thessaloniki – Greece in 1997) have been devoted to this and other *Barbus* species, providing a good information tool of actual knowledge and a solid base stimulating their further research.

Within this context, the barbel is also the subject of an extensive research project on the River Jihlava, Czech Republic. The construction and operation of hydroelectric complex on this stream and its close vicinity created conditions that interfered with natural environmental stimuli (temperature, photoperiod) triggering gonad maturation and spawning of the barbel (P e ň á z et al. 1999). The population appeared to be suppressed for a period after the sudden change in habitat caused by the start of hydroelectric operation operating energy complex. Subsequently, the adaptation processes seems to have been completed and the barbel population was found again viable, prosperous and dominating the fish community (P e ň á z et al. 1999). The aim of present partial study was to analyse and quantify the movements of barbel as well as to assess the results relative to situation existing in some other rivers and barbel populations studied in a similar way (Steinmann et al. 1937, Hunt & Jones 1974, Pelz & Kästle 1989, Baras 1995, 1997, Lucas & Batley 1996).

Study Area

Our survey took place in a 3.0 km stretch of the River Jihlava (Czech Republic), a fifth-order stream (tributary to the River Svratka, Danube basin) near the village of Hrubšice between river kilometers (RK) 46.00 and 49.05 (49°07' N, 16°15' - 16°20' E) (Fig. 1). The study stretch is characteristic of submountain streams, running through an incised valley, morphologically heterogenous, corresponding to a barbel zone (Huet 1949) and actually influenced by an upstream located energy operating hydro- and nuclear complex. The main environmental impacts exerted on the river, described in particular by Peňáz et al. (1999), were a regulated discharge and reduced temperature variations. These, rather favourable habitat changes were followed by considerable changes in composition of fish assemblage. The former fish community dominated by barbel and other stream cyprinids was replaced by a salmonid community dominated by brown trout *Salmo trutta* m. *fario*, however, the barbel maintained a strong and in fact increased presence in present fish community, which consists of at least 25 species. Except of barbel, species recorded during experimental electrofishing were rainbow trout *Oncorhynchus mykiss,* brook trout *Salvelinus fontinalis,* grayling *Thymallus thymallus,* roach *Rutilus rutilus,* chub *Leuciscus cephalus,* dace *L. leuciscus,* rudd *Scardinius erythrophthalmus,* tench *Tinca tinca,* nase *Chondrostoma nasus,* gudgeon *Gobio*

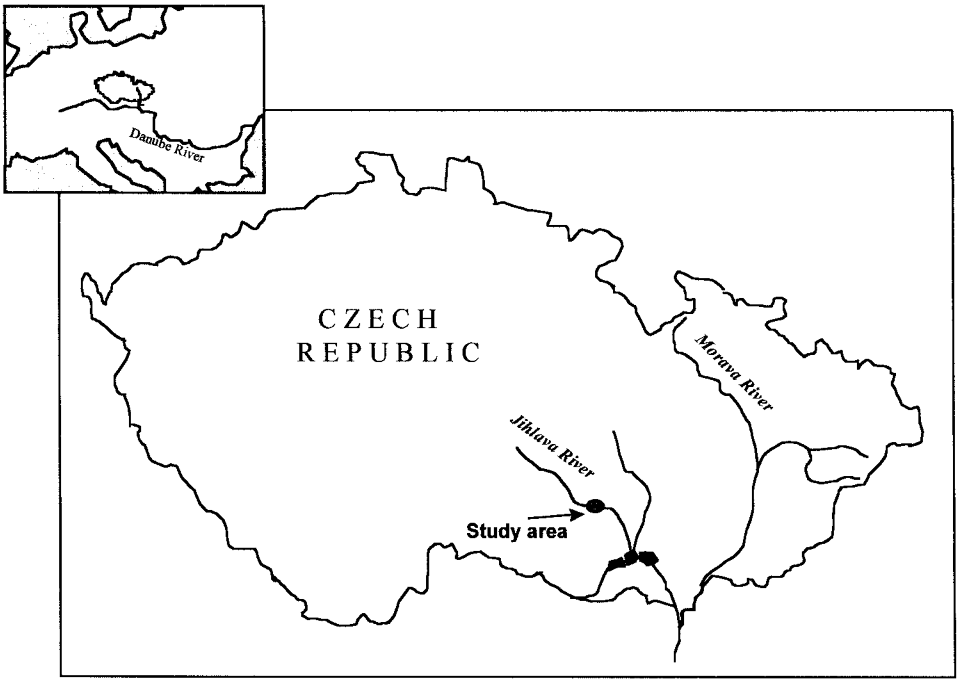

Fig. 1. Map of the study area.

gobio, bleak *Alburnus alburnus,* spirlin *Alburnoides bipunctatus,* crucian carp *Carassius carassius,* common carp *Cyprinus carpio,* eel *Anguilla anguilla* and, in addition, by sport fishing were recorded also common bream *Abramis brama,* Eurasian perch *Perca fluviatilis,* pike-perch *Stizostedion lucioperca,* asp *Aspius aspius,* ide *Leuciscus idus,* goldfish *Carassius auratus* and grass carp *Ctenopharyngodon idella* (P e ň á z et al. 1999).

The habitat of river under study was very heterogenous and had a typical patchy "riffle – pool – raceway" structure, with fully natural and stabilised river bed and banks, with abundant spawning grounds but with no tributaries habitable for barbel (Table 1). The study stretch was divided into seven sections (A–G), each containing a complete set of various microhabitats, mainly a deeper pool, long raceway and separated between adjacent sections by riffles as natural boundaries. These patches differ mainly by depth and flow velocity: riffles were characterised by a water velocity of 0.4–1.7 $m.s^{-1}$ and a depth of 20–50 cm, raceway by 0.2–0.5 $m.s^{-1}$ and 20–80 cm while the pools by 0–0.4 $m.s^{-1}$ and a depth of 50–180 cm. The shallow parts of raceways are often overgrown by dense macrophytes (*Batrachium fluitans, Callitriche* sp.) during spring and summer.

Table 1. Sections of the stretch of River Jihlava under study and their environmental characters (RK = river kilometers).

Section	RK	Area hectares	Length m	Proportion of patches, % riffle	pool	raceway
A	46.00–46.48	0.97	480	6	32	62
B	46.48–47.26	1.58	780	10	18	72
C	47.26–47.59	0.75	330	5	16	79
D	47.59–47.91	0.70	320	9	15	76
E	47.91–48.43	1.05	520	14	25	61
F	48.43–48.68	0.57	250	12	15	73
G	48.68–49.10	0.85	420	10	15	75
Total		**6.47**	**3100**	**9.54**	**20.02**	**70.44**

Methods and Material

A gasoline powered electroshocker (DC, 250 V, 1.5 – 2 A, 50 Hz) was used to collect the fish. Electrofishing excursions were carried out on 15 dates: 10.05.99, 24.05.99, 02.06.99, 21.06.99, 03.11.99, 10.11.99, 17.05.00, 31.05.00, 08.06.00, 22.06.00, 19.10.00, 23.10.00, 31.10.00, 24.04.01 and 26.04.01. All fish except of barbel ≥ 120 mm of SL were after capture immediately released.

After being measured, weighed and examined for sex according to external features (mainly running sexual products) recognisable only during reproduction season, 701 barbel were individually marked by means of the anchor full plastic tags (Floy Tag - type FD-94). Tags were fixed on the left body side into the dorsal musculature, just below the anterior edge of dorsal fin. Different colours of tags were applied in consecutive years (yellow 1999, white 2000, red 2001). The effect of tags on fish behaviour, survival and growth was minimised by the type of tags used and their careful application. The tags proved to be durable and easy to recognise in the field even after long periods (2 years).

The tagged and recaptured fish were always released in centres of the same particular sections (see Table 1). The distance between centres of sections where the fish were released and centres of sections where they were recaptured, was considered as distance that a recaptured fish had moved.

All recaptures were obtained by the experimental fishing exclusively. Barbel do not represent a favourite coarse fish in sport fishery conducted in the stretch of River Jihlava under study, where presently the brown trout and other salmonid fishes have been preferably appraised, nevertheless, 30 to 87 individuals were caught by anglers annually during 1998–2000 in the fishing ground Jihlava 5B located between RK 45.9 and 55.6 (19 hectares) and encompassing also the river stretch under study. Despite the fact that the fishermen were informed about the tagging project, none have so far reported capturing a tagged barbel. Occasionally, the fishing ground concerned is also stocked by artificially reared one-year-old barbel in a quantity amounting 1000–3700 individuals annually.

The fish were classed according to their recapture rate and location as:

1) specimens with restricted home range (i.e. inhabiting permanently only the same single stream section where they were captured, after tagging released and eventually recaptured); they are designated as *resident* (also home or stationary) fish; and

2) specimens with a larger home range (extending over the two or more neighbour stream sections, i.e. those recaptured at least once beyond the boundaries of the home section where they were originally released); these specimens are designated as *mobile* or stray fish.

The differences in frequencies of recaptures of individual size classes and stream sections were analysed by means of chi-square test (Sokal & Rohlf 1981). The unequal numbers of fish tagged in individual size categories and subsequent stream sections, as well as different length and area of these sections, were respected when computing the expected frequencies. The stream section G, where only one fish was tagged, was excluded from the statistical analyses.

Results

Recapture rate

In total 149 of 701 tagged barbel (21.26 %) were recaptured (Table 2). Of them, 117 were recaptured once, 24 twice, seven specimens three times and one fish was recaptured four times. The distribution of recaptures among subsequent stream sections fluctuated 10.7–32.9 % (Table 2). Recapture frequencies plotted against consecutive recapture categories showed a distinct exponential relation (Fig. 2), which may have resulted from a higher natural mortality, eventual loss of tags. However, most likely it is caused by the fact that always only a minor part of population has been caught and the probability of recapture was thus relatively low. The expected values of successive multiple recaptures, calculated by means of the recapture coefficient C_r were not significantly different from the observed values in total ($\chi^2 = 1.465$; $P<0.05$) nor in all subsequent recapture categories (Table 3). The C_r coefficient can be thus considered, under these environmental conditions and using the fishing methods described, valid for calculating the quantities of the single or multiple recaptures of marked fish.

Resident and mobile fish and their home range

Of the 149 barbel recaptured and analysed for their movements, 105 specimens (70.47 %) could be classed as resident, i.e. steadily living in a single stream section - a fairly confined

Table 2. Tagging and recapture results with barbel in the River Jihlava; proportion of resident and mobile fish.

Section	Number of tagged fish	Recaptured fish, N/% resident[1]		mobile[2]		all	
A	159	9	5.66	8	5.03	17	10.69
B	286	77	26.92	17	5.95	94	32.87
C	96	6	6.25	7	7.29	13	13.54
D	44	8	18.18	1	2.27	9	20.45
E	71	3	4.22	8	11.27	11	15.49
F	44	2	4.54	3	6.82	5	11.36
G	1	0	-	0	-	0	-
Total/Mean	**701**	**105**	**14.98**	**44**	**6.28**	**149**	**21.26**[3]

[1] fish recaptured in the same of successive stream section as they were released after tagging
[2] fish recaptured at least once outside of the home section where they were captured and released when tagged
[3] S.D. = ±7.26

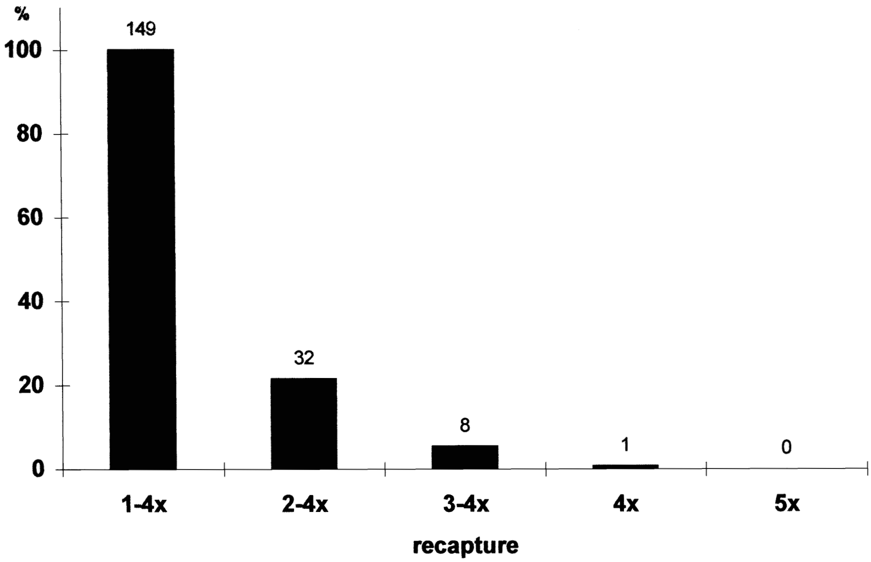

Fig. 2. Recapture rate of the barbel from the River Jihlava, Czech Republic, in successive multiple recaptures. Recapture category 1-4 explained in the legenda to Table 3.

(250–780 m) area demarcated by the two riffles (Table 2). This group of fish did not move beyond stream riffles and respected them as boundaries of their home range. The remaining 44 (29.53 %) of recaptured barbels moved in various, however rather restricted, extent from their home section where they were first caught and after tagging again released. According to our arbitrary and perhaps rather rigorous criteria, these fish were categorised as mobile part of barbel population under study. The home range of mobile barbel is thus formed by the two or even more of stream sections. Mobile barbel crossed the riffles, however, 93.2 % of them have been recaptured within a distance (1000 m from the place of their release after tagging. No difference was found between the numbers of mobile fish wandering upstream and those wandering downstream (Table 4).

Table 3. Recapture frequencies of the barbel in the River Jihlava and the difference between actual and expected values in consecutive recapture categories (1 – number of fishes recaptured 1–4 times; 2 = fish recaptured 2–4x; 3 – fish recaptured 3–4x; 4 – fish recaptured 4 times; 5 – fish recaptured 5 times); number of tagged fish = 701.

Recapture category	Number of recaptured fish actual N_a	theoretical N_t	expected[1] N_e	Recapture coefficient[2] C_r	χ^2	P	df
1	149	701	150.72	4.65	0.020	>0.05	1
2	32	613	28.34	21.63	0.473	>0.05	1
3	8	569	5.66	100.61	0.972	>0.05	1
4	1	537	1.15	467.93			
5	0	480	0.22	2176.36			
Sum	**190**		**186.08**		**1.465**	**>0.05**	**2**

[1] Expected frequency $N_e = N_t/C_r^n$, where n = recapture category (1–4).
[2] Recapture coefficient was computed as weighted mean of shares N_t/N_o of successive recapture categories (1–4)

Table 4. The distribution of mobile barbel according to the distance of movement realised in the River Jihlava, Czech Republic.

Distance from Home section (m)	Fish recaptured downstream		Fish recaptured upstream	
	number	%	number	%
0–500	2	4.55	6	13.64
501–1000	19	43.18	14	31.82
1001–1500	0		0	
1501–2000	1	2.27	1	2.27
2001–2500	0		1	2.27
All	**22**	**50.00**	**22**	**50.00**

An above-average number of barbel were recaptured in that stream section exhibiting a lower proportion of pools (D), whereas the lower recapture rate was found in a section with a higher pool proportion and low area of riffles (A). Resident fish were more frequently recaptured, compared to the mobile ones, in the section with low proportion of pools (D) whereas the mobile fish dominated the resident ones in the section with the above-average proportion of pools and riffles and low proportion of raceways (Table 5).

Table 5. Chi-squared test for significant difference (P < 0.05; denoted by a < or > symbol) between prevailing habitat patches and the numbers of tagged and recaptured fish in subsequent stream sections (< = observed values less than expected; > = observed value greater than expected; R = resident > mobile; M = mobile > resident; NS = nonsignificant difference, P > 0.05).

Stream section	Riffle	Pool	Raceway	No of fish tagged	recaptured	Resid/mobile fish
A	<	>	NS	>	<	NS
B	NS	NS	NS	>	NS	NS
C	<	<	<	>	NS	NS
D	NS	<	NS	<	>	R
E	>	>	<	<	NS	M
F	NS	NS	NS	<	NS	NS

Influence of fish size

All tagged fish as well as all recaptured fish were divided into 50 mm size (SL) classes and the recaptured fish additionally subdivided into the resident and mobile parts (Table 6). Only one tagged fish was recaptured within the smallest size class (100 – 150 mm), however, the proportion of recaptured fish increased in consecutive size classes within the size range 151 – 550 mm of SL (Fig. 3) and this relation showed to be significant (Pearson correlation coefficient, r = 0.915; P<0.001; N = 10). The probability of recapture thus increases with the size of fish, which may also result from higher susceptibility of larger fish towards the D.C. electricity. With an apparent fluctuation in individual size classes, the proportion of resident barbels predominated in the size range until SL of 450 mm, whereas the proportion of mobile fish exceeded that of resident ones in the two largest, less frequented size classes (451 – 550 mm SL) (Table 6).

A further analysis, which followed after the size classes were collected by a 100 mm interval into four size categories only, resulted in following conclusions:

1) The number of recaptured individuals belonging to subsequent size categories was not equal in the total sample of fish ($\chi^2 = 10.49$; $P < 0.025$; d.f. = 3) whereby an above-average number of mobile individuals was captured in the smallest size category ($p < 0.005$).

2) Neither it was equal in the subsample of resident individuals ($\chi^2 = 10.399$; $P < 0.025$; d.f. = 3) in which the above-average number was found in the size category 301– 400 mm ($p < 0.025$).

3) The unequal number of recaptures existed also in mobile fish ($\chi^2 = 18.943$; $P < 0.005$; d.f. = 3) and they were higher than the expected one in the highest size category 401 - 500 mm ($P < 0.005$).

The comparison of frequencies of recaptured mobile and resident fish (contingency table 2x4) showed that they were not equal ($\chi^2 = 15.51$; $P < 0.05$; df = 3). Against expectations, more resident fish were caught than mobile ones in the size category 301–400 mm ($P < 0.025$), whereas more mobile than resident individuals were recaptured in the largest size category 401–500 mm ($p < 0.005$).

Table 6. Recapture data of *Barbus barbus* analysed according t the size (SL) and residentiality; (size related with the date of tagging).

Size class mm, SL	No of tagged fish	No of recaptured fish						Proportion* of	
		all fish		repeatedly recaptured				resident fish	mobile fish
		n	%	1x	2x	3x	4x	n	n
51–100	1	-	0						
101–150	14	1	7.14	1				1	
151–200	99	17	17.17	13	4			10	7
201–250	310	67	21.61	51	10	5	1	48	19
251–300	139	28	20.14	23	4	1		20	8
301–350	81	21	25.93	18	2	1		18	3
351–400	20	5	25.00	4	1			4	1
401–450	15	4	26.67	2	2			2	2
451–500	19	5	26.32	4	1			2	3
501–550	3	1	33.33	1					1
Total	**701**	**149**	**21.26**	**117**	**24**	**7**	**1**	**105**	**44**

* Proportion expressed in per cent of total number of all recaptured fish

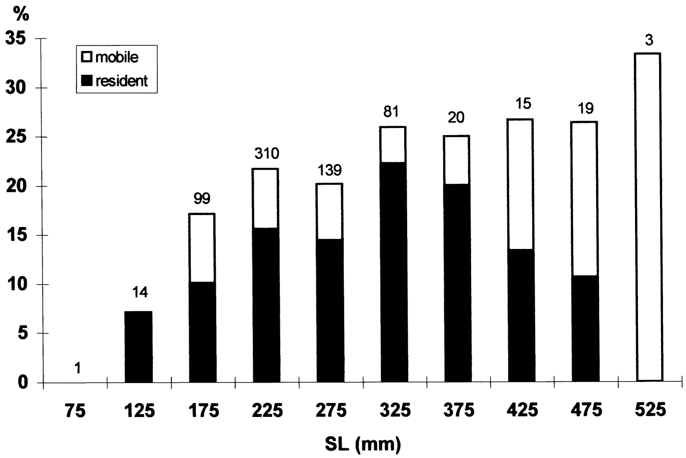

Fig. 3. Dependence of recapture rate and mobility of barbel upon their size in the River Jihlava, Czech Republic. (Expressed as percentages of the fish recaptured against fish tagged in consecutive size classes).

Discussion

General nature of barbel's movements

According to Gerking (1953), many stream fishes live in very restricted areas during most, if not all, of their life. The problem of their local movements has to be recognised from the two viewpoints. Firstly, home range (sensu Gerking 1953) is understood as the area over which the fish normally travels, searching for the optimum element of habitat (patch, microhabitat) required at given time and phase of its life cycle (foraging, spawning, nursery, resting, hiding, wintering etc.). In the gregarious barbel, home range selection and occupation is conditioned not only by the availability of suitable physical habitat, mainly feeding areas, but also by the actual status and abundance of the population and by the presence of sufficiently numerous shoals (Baras 1997). In our study, home range and its area were considered only indirectly, based on the location where tagged fish have been released and repeatedly recaptured and on the extent of movements exerted.

Secondly, territory is any area that is defended, mostly with elements of aggressive behaviour. Generally, territorial behaviour concerns mainly reproductive territories and is markedly pronounced in monogamic species spawning in couples, in nest-building and in the egg and offspring protecting or guarding species and as such the territoriality could rather be a seasonal phenomenon. Nothing of this seems to be the case in barbel, which spawn collectively in numerous aggregates, and are neither hiding nor guarding their eggs and not exhibiting any kind of parental care for young. However, some features of territorial behaviour could be recognised in barbels' spawning behaviour. The chase-away interactions between males, mainly between the courting ones, have a character of spatial competition and defence (Hancock et al. 1976, Baras 1994, Poncin et al. 1996). Furthermore, the territoriality may be a true behaviour pattern of the barbel population under study because of its sound structure, characterised by a high reproduction potential and recruitment whilst simultaneously subjected to a low predation and fishing pressure. This situation is expected to increase competition for territories and food resources, eventually creating aggressive behaviours and the subsequent emigration into underpopulated areas of submissive (smaller, younger) individuals, which may appear as "strays" (mobile fish) in our observations. A similar pattern has been reported for by-passed sections of the upper River Rhône, where reductions in deep-water habitat due to flow to a hydroelectric plant resulted in smaller and younger nase to emigrate because the available deep-water habitat was occupied by older and larger nase (Persat & Chessel 1989). Such aspects of territorial behaviour, however, still were not satisfactorily understood in the barbel.

Strong recruitment of young fish, together with behavioural dominance of old fish would substantiate the expectation that rather young fish would become mobile and search for new territories. However, rather the opposite situation seems to be true in the River Jihlava, where the mobility rate increased with increasing size (and age) of fish. Similar fact was generally stated also by Gerking (1953) and specially for the barbel found by Hancock et al. (1976). This pattern may be associated with a higher reproduction activity in larger barbel as well as their greater susceptibility to being caught by electrofishing. However, Baras (1995) found no relation between fish size and patterns of locomotory activity.

The barbel's locomotory activity and extent of movements exhibit clear diel and seasonal patterns and are mainly related to the temperature and length of day. Foraging was found the main stimulus determining the localised activity in the diel scale, whereas spawning is the main motivation for movements of the seasonal scale (Lucas & Batley 1996).

Baras (1995) found the diel and seasonal locomotory activity patterns in the barbel thermal-dependent and a temperature of 4.0 °C, when barbel entered a dormancy period, as a thermal lower limit for its activity. However, water temperatures below 4 °C are less common in our study area during winter months due to the influence of energy operating complex (see Peňáz et al. 1999).

Spatial dimension of movements in different rivers

Bibliographic sources report much variation in the barbel's movements in various riverine habitats and often this species is considered as a "wandering" fish. Some of barbels tagged by Steinmann et al. (1937) were re-captured in a distance more than 300 km from their release site. Regardless of ability of some individuals to move over long distances, most barbel populations have been characterised as resident, of course often with different criteria used for the distance fixed as the boundary between the residential and mobile movement patterns. For example Steinmann et al. (1937) considered as resident all fish recaptured within a ± 5 km distance from the site where they were released. These authors found that resident were 48 % of 216 recaptured individuals in the German stretch of the Danube, 54 % of 130 recaptures in the Austrian Danube, whereas 73.7 % of 38 recaptured fish in the River Main.

In the River Severn, the barbel population is also divisible into the mobile and resident components (Hunt & Jones 1974b), however, in a much larger scale than found in the River Jihlava: 86 % of 531 recaptured barbels, considered as resident, moved within a 5 km distance from the point of release in the Severn (of them 54 % did not move at all and permanently occupied the same place). The remaining 14 % wandered more widely, both upstream and downstream, up to a maximum of 34 km from the site of tagging (the mobile fish). Total range over which the barbel were recaptured was 54 km. Similarly, in the River Nidd (a rather deep stream, sectioned by weirs, NE England, tributary to Ouse) some individuals moved nearly 20 km upstream. The radiotracking carried out in this river brought also the evidence that some tracked barbels moved regularly between the Rivers Nidd and Ouse and it was demonstrated that each of these rivers is used by them at different times of the year (Lucas & Batley 1996, Lucas & Frear 1997).

A short-term (12 days) radiotracking survey conducted on eight barbel in the River Nidda (tributary to the Main, Germany) showed that the fish behaved as significantly resident moving within a distance of 60–120 m only (Pelz & Kästle 1989).

In large rivers, the habitats required by stream fishes are often separated by very large distances relative to a species' dispersal abilities and considerable movements must be thus exhibited by the fish. Migration behaviour of the barbel could be also inferred from their seasonal occurence in fish ladders. For instance in a fish ladder built adjacent to the Střekov weir on the River Labe, the barbel was the most frequently (19–49 %) entering fish species during a survey conducted in 1993–1994 and a successful passage has been confirmed (Novotný & Punčochář 1996).

When compared to most of published data, the extent of movements and consequently the home range of barbel in the River Jihlava seem to be very limited and the resident character of behaviour is probably the most profoundly expressed of all studied populations despite the fact that we have fixed the maximum limit distance for movements of resident specimens to a relatively very low value of 250–780 m. The very heterogenous and patchy character of the study stretch (and in each of the stream sections as defined in our survey) may contribute to the observed patterns by ensuring very favourable conditions for all phases of the life cycle (gonad maturation, spawning, larval and juvenile nursery, foraging, hiding, wintering etc.) within a relatively very small area compared to other locations. Especially, the richness of available spawning sites reduces the need for extended spawning migrations and this is reflected in home range fidelity as well as their behaviour patterns.

Patchy habitat structure is followed by patchy population dispersion

According to Gerking (1953), in streams with a well developed riffle – pool structure, such as the River Jihlava, each pool (or better each stream section separated by riffles) can be considered as a more or less isolated unit containing a natural population of its own. The fish population of a small stream may thus be thought as a series of discrete, natural units rather than as a single, homogenous and freely missing group. This approach is, of course, near to the theory of metapopulation dynamics (Hanski 1996, Hanski & Simberloff 1997). Consequently, the set of local, more or less isolated, barbel population of the River Jihlava, exhibiting a dynamic turnover (extinction and colonisation; Harrison 1998) could thus be considered a case of metapopulation.

However, all this does not mean a fragmentation either of the physical habitat, or of the gene pool of the given population. Despite restricted extent of home range and well expressed residential behaviour, a sufficient gene exchange undoubtedly exists there as only a small genetic differentiation exists among the barbel populations of the Czech Republic (Šlechtová et al. 1998).

Importance of aquatic system connectivity

Riffles, despite not being crossed by majority of barbel population, i.e. by resident specimens, do not fragment the stream physically, in fact they easily could be crossed by the fish. This connectivity plays an important role in the formation and functioning of metapopulation (S c h m u t z & J u n g w i r t h 1999).

Barbel movements are notably restricted or impeded by the construction of dams, weirs and other water retention structures. This problem seems to be especially serious in those streams where natural habitat physical heterogeneity and riffle-pool development are in decline and the spawning migrations to remote sites are necessary. Longitudinal and/or lateral connectivity is thus crucial, as is instream and riparian cover (C o p p & B e n n e t s 1996), to the continued existence of barbel populations (B a r a s et al. 1994, L u c a s & B a t l e y 1996, L u s k 1996, L u c a s & F r e a r 1997, S c h m u t z & J u n g w i r t h 1999).

A c k n o w l e d g e m e n t s

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