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Growth of barbel, *Barbus barbus*, in the River Jihlava following major habitat alteration and estimated by two methods

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Abstract. Growth in length and weight, based on a combination of scale annulus interpretation and back-calculation using the Fraser-Lee model, was studied in male and female barbel, *Barbus barbus*, from a section of the River Jihlava sampled in 1999–2001. Results were compared with growth data obtained with similar methods in 1976, prior to construction and functioning of a hydropower scheme complex, and during the period of the scheme's partial operation (1980–1984). Recent growth rate, under seemingly fully-stabilised environmental conditions and complete adaptation of the barbel population, showed the highest values, especially in males. A distinct sexual dimorphism in growth rate was also confirmed, with females growing faster than males, though to a lower extent than recorded both during previous periods and from several other localities. Further, upon comparison of back-calculated lengths for previous years of recently tagged-and-recaptured fish (1999–2001) with observed lengths directly measured at corresponding ages, no significant differences were overall found between the results obtained by either method in most age groups. Finally, the linear Fraser-Lee model proved a sufficiently accurate and practical method for back-calculating lengths for previous years of life also in barbel.

Key words: hydropower scheme, back-calculation, tagging, recapture

Introduction

The stream habitats of the middle course of the River Jihlava, along with the fish communities inhabiting them, have been considerably altered in the course of the last three decades by the construction and filling of two mid-stream reservoirs at Dalešice and Mohelno operating in a pump storage regime, and by an upstream nuclear power plant at Dukovany, which is part of the same hydropower scheme.

This typically sub-mountainous and fast-flowing stream section (typical 'barbel zone') has always represented a suitable habitat for the barbel, *Barbus barbus* (Linnaeus, 1758). Indeed, in recent years barbel's dominance (25.5 % of total abundance; 42.9 % of total biomass) and yields (7.2 % of total fishermen's catch) has significantly exceeded current levels recorded in most other streams of the Czech Republic and elsewhere in middle Europe, where it has overall become rather rare and is currently regarded as a 'near-threatened' species (Lusk 1996, Lusk & Hanel 2000, Peňáz et al. 1999, 2003).

For the above reasons, the section of the River Jihlava downstream of the power scheme has been the subject of extensive research on various aspects of the barbel's biology, including (i) movements and migration, (ii) population dynamics, with emphasis on gradual development and changes in abundance, size and sexual population structure, and (iii) reproductive biology, with special reference to hormonal disruption, hermaphroditism and sex reversal (Peňáz 1977, Peňáz & Štouračová 1991, Peňáz 1999, Peňáz et al. 2002, 2003, 2005). Notably, all of the above studies have relied on scale-based age estimates, despite problems in these calcified structures due to transparency and somewhat lower interpretability compared to the scales of most other cyprinids.

As an outcome of the aforementioned studies, the unique availability of a relatively high number of tagged barbel has allowed investigation of growth based on direct measurements of recaptured, individually-tagged fish, along with comparison with back-calculated lengths from standard scale-based growth analysis. The latter has also allowed verification of the method, which, because of its easier implementation, may have scope for wider applicability in ecological research on barbel.

In light of the above, the present study aims at 1) contributing knowledge on barbel's growth potential in both sexes following about twenty years of operation of the Dalešice-Mohelno Hydropower Plant, under the assumption that the fish community in the downstream section of the River Jihlava has eventually stabilised and become adapted to the markedly altered environmental conditions therein; 2) assessing how gradual habitat changes following construction and operation of the power scheme have eventually affected barbel growth rate; and 3) comparing barbel growth data based both on scale annulus interpretation and on back-calculation methods against empirical data from a long-term field experiment on tagged and recaptured individuals.

Study Area

The study section of the River Jihlava, located between river km 46.0 and 49.1, is strongly influenced by the release from a large upstream power scheme consisting of (i) the Pump Storage Hydropower Plant (PSHP) Dalešice, (ii) the Balance Reservoir (BR) Mohelno along with its two mid-stream impoundments (water area 480 and 118 ha, and commissioned in 1978 and 1977, respectively), and (iii) the integrated Nuclear Power Plant (NPP) Dukovany (4 × 440 MW; operation started gradually in 1985–1987). Mean annual discharge in the downstream river section, after the unreturnable intake of cooling water from NPP, amounts to 5.50 $m^3 s^{-1}$. This section is now mainly characterised by more balanced hydrological and temperature regimes, better water quality, and appearance of a secondary and predominantly salmonid fish community. Technical features, main environmental impacts, and consequences of this power scheme upon the ichthyocoenose are described in detail by Peňáz et al. (1999).

Materials and Methods

Fish were captured using a gasoline-powered electro-fishing unit (250 V, 1.5–2 A, 50 Hz). Specimens > 120 mm standard length (SL) captured (and/or recaptured) during the reproductive season were sexed based on external characters (mainly, release of milt or eggs) and included into the analyses. In order to identify growth, sexual characters, movement activity and home range fidelity of individual barbel, anchor tags (Floy Tag, type FD-94) were fixed to the dorsal musculature of the fish on the left side of the body near the insertion of the dorsal fin, with different coloured tags applied in consecutive years (i.e. yellow: 1999; white:

2000; red: 2001). Except for two records by anglers, all recaptures were by electro-fishing. Altogether 995 individuals were tagged, with scale samples taken from 135 recaptured fish (87 males, 40 females, and 8 undetermined). Some of the fish examined were recaptured twice or even more times. In total, 156 pairs of observed and back-calculated standard lengths were available for statistical analysis.

Growth analysis

Scales, mounted dry between glass slides, were interpreted for age estimation with a C. Zeiss apparatus for microfilm and microfiche reading (17×). This allowed measurement of the distances between scale foci and individual annuli on the lateral (dorso-ventral) diameter (1 mm on scale = 17 mm on projector screen; 1 scale bar = 0.0588 mm). All fish captured during late spring (May–June) were considered to have just completed the year mark (= annulus), whereas individuals from autumn excursions exhibited a '+' increment on the edge of the scale.

Upon examination of the type of relationship between SL and scale diameter, the Fraser-Lee model was used for back-calculating corresponding lengths attained at previous years of life. This method is believed to describe accurately the linear body–scale relationship, which is given by (e.g. Ricker 1975, Francis 1990, Holčík 1998, Klumbs et al. 1991):

$$SL_i = c + (SL - c) \times (S_i/S),$$

where SL_i is the standard length of the fish when annulus *i* was formed, SL is the standard length at time of capture, S_i is the distance from the scale focus to the annulus *i*, S is the total scale radius, and *c* is the intercept ('correction term') on the length axis of the linear regression between SL and S.

Growth curves were modelled both by polynomials and by the von Bertalanffy growth function (VBGF) (e.g. Ricker 1975, Francis 1988):

$$SL_t = SL_\infty (1 - e^{-K(t - t_0)}),$$

where SL_t is the standard length at age *t*, SL_∞ is the asymptotic (potential) length, *K* is a constant expressing the rate at which SL_∞ is approached, and t_0 represents the theoretical age at which the predicted mean standard length is zero. Growth in length (SL) and weight (W) was modelled separately for all fish (including unsexed individuals) as well as for males and females by the VBGF. For growth in weight, the exponential of the VBGF was from the corresponding W–SL relationship.

For the VBGF, starting values for SL_∞, W_∞, K and t_0 were obtained by the Ford-Walford method (Kimura 1980) implemented in Excel®, with final values of parameter estimates fitted by the NONLIN module of SYSTAT v.11 for Windows. Whenever convergence could not be achieved, the t_0 value was constrained to its initial Ford-Walford estimate. The package Unistat® 5.1 was used for all other statistical computations. Thus, following summary statistics, all data sets were checked for normality by the Kolmogorov-Smirnov 'goodness-of-fit' and by the Shapiro-Wilk tests. Accordingly, either the parametric paired *t*-test or the non-parametric Mann-Whitney *U*-test was used.

Results

The relationship of standard length (SL) vs lateral scale diameter (S) was proportional and described by a linear regression with intercept:

$$SL = 19.140 + 6.169\ S\ (R^2 = 0.9288),$$

showing that the length at which scales first appear in juveniles is about 19 mm. This justified the use of the Fraser-Lee method for back-calculation of lengths for previous years of life.

Actual growth, modelled both polynomially (Fig. 1) and by the VBGF (Fig. 2a) for SL and by the VBGF only for weight (W) (Fig. 2c), tended to slow down in both sexes after about 5–6 yrs. However, VBGF curves for males and females tended to diverge prominently beyond the latter ages, whereas polynomial curves were overall overlapping. The older age attained by males was 10+ yrs, with a maximum SL of 325 mm (TL = 393 mm, W = 520 g); whereas females exhibited a distinctly longer life span up to 17 yrs, with a maximum SL of 510 mm (TL = 590 mm, W = 2140 g) (Table 1). Finally, the W–SL relationship was very similar in males and females (Fig. 2b).

Upon comparison of growth rates recorded both during the period prior to alteration of the stream habitat (1976) and in the initial phase after operation of the hydropower scheme (1980–1984), recent growth rate (1999–2001) in barbel was notably faster, and this was especially due to higher maximum lengths attained by males. However, more formal (e.g. VBGF-based) comparisons among the different periods could not be made because of overall linear (i.e. non-asymptotic) growth displayed by barbel in 1976 and 1980–1984 (cf. also Table 1).

Analysis of back-calculated and empirical lengths (i.e. directly observed on tagged and recaptured fish) revealed overall no differences (except for age group VI) at the $\alpha = 0.95$

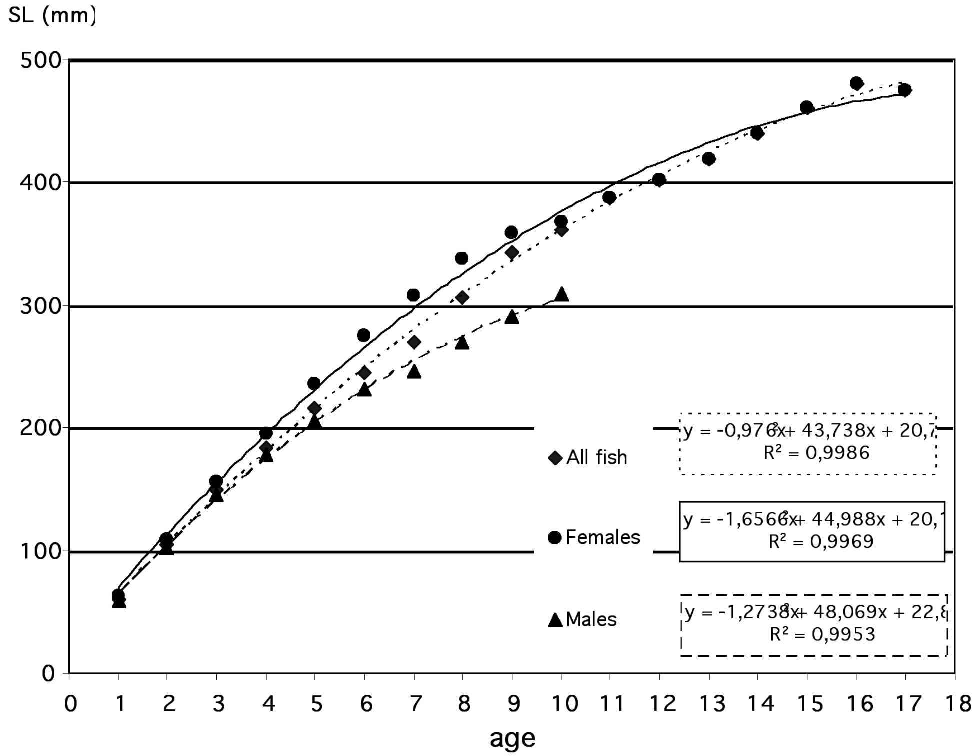
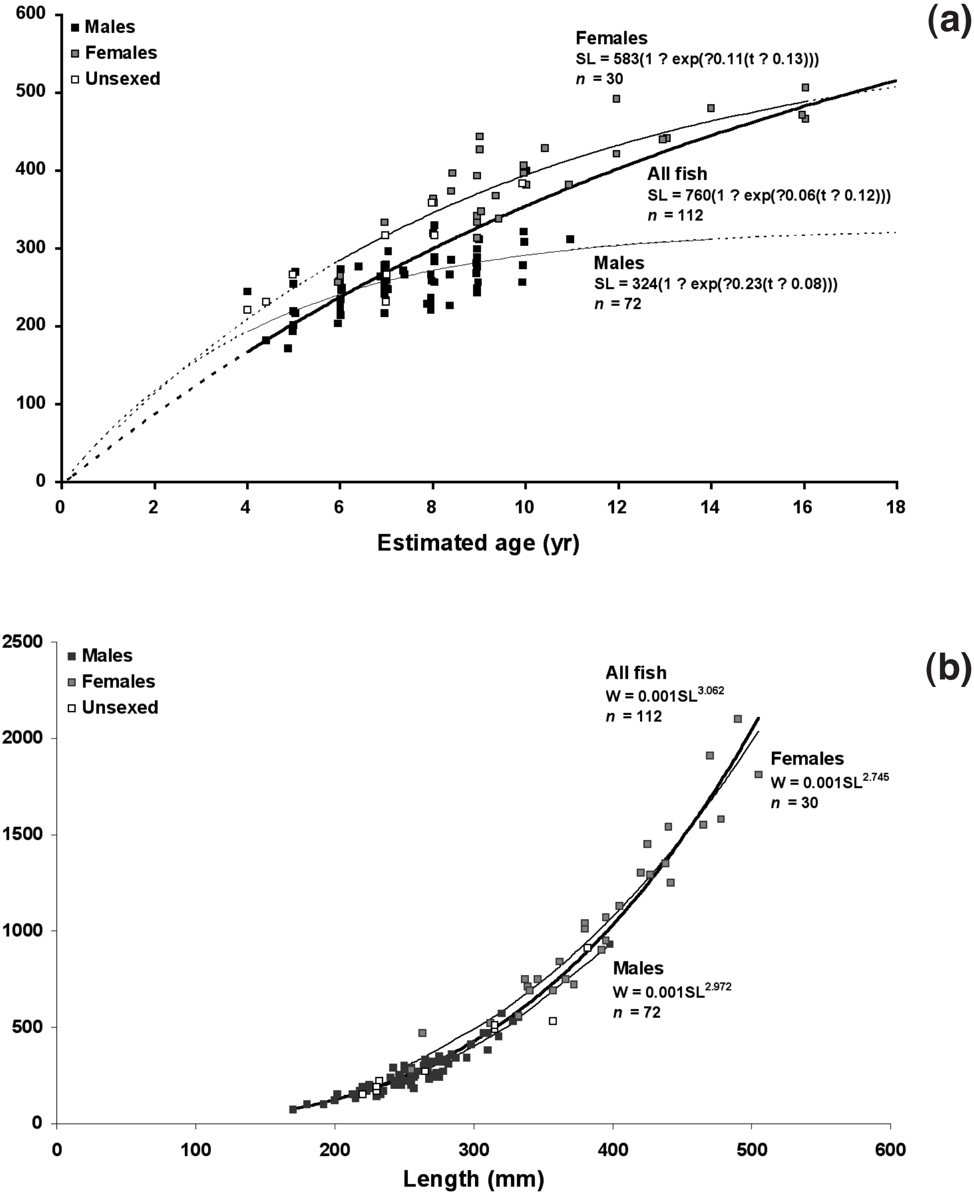


Fig. 1. Growth in standard length (SL) of barbel, *Barbus barbus*, in the River Jihlava modelled by polynomial curves.

significance level (Table 2). Also, based on percentage difference between means of back-calculated and observed lengths for individual ages (summary statistics in Table 3), mean differences proved negligible, reaching up to 5 % in most cases. Only for age group III did such difference amount to 13.3 %, although this was based on only one individual. Whereas upon closer inspection of individual age groups, significant differences were only found for age groups VI ($P < 0.01$) and XIV ($0.01 < P < 0.05$), the latter however based on limited sample size ($n = 3$).



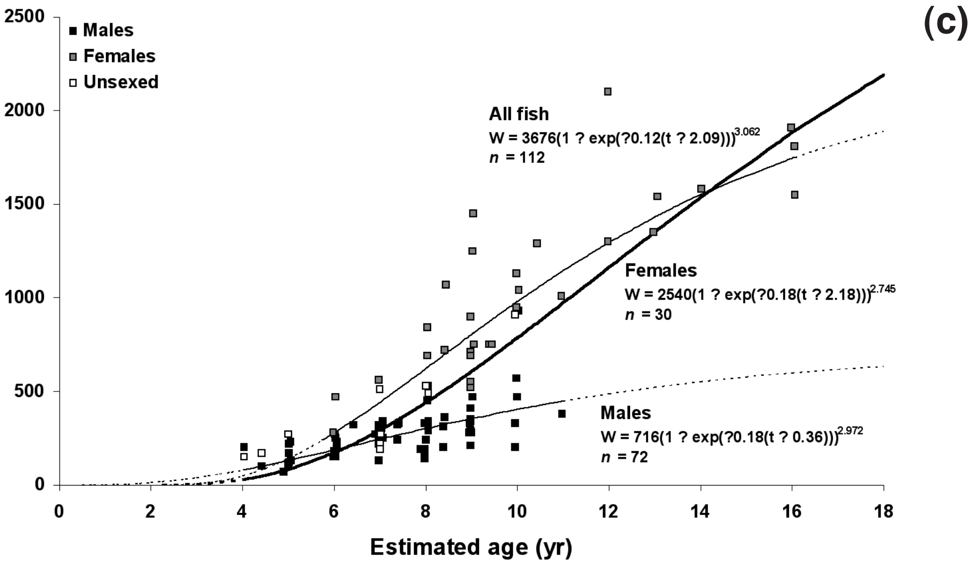


Fig. 2. Growth of barbel, *Barbus barbus*, in the River Jihlava. (a) Growth in standard length (SL) modelled by the von Bertalanffy growth function (VBGF); (b) relationships between weight (W) and SL; (c) growth in W modelled by the VBGF.

Table 1. Growth of male (M) and female (F) barbel, *Barbus barbus*, in the middle course of the River Jihlava as related to human-induced habitat alteration. Back-calculated standard lengths (SL, in mm) in consecutive periods: 1976, original state of intact river (P e ň á z 1977); 1980–1984, both impoundments of PSHP Dalešice filled and hydropower plants operational (P e ň á z & Š t o u r a č o v á 1991); 1999–2001, PSHP Dalešice and NPP Dukovany fully operational (*hoc opus*).

	Period					
	1976		1980–1984		1999–2001	
Age group	M	F	M	F	M	F
I	58	60	61	63	59	63
II	92	95	95	102	102	109
III	125	131	125	136	146	155
IV	152	166	151	165	178	196
V	178	198	175	192	206	235
VI	200	226	197	220	231	275
VII	217	254	214	243	246	308
VIII	237	275	228	265	269	337
IX	250	303	241	281	291	359
X		330	278	303	310	368
XI		379		322		388
XII		417		365		402
XIII		457		(410)		419
XIV		498				439
XV						461
XVI						480
XVII						(475)
n	213	137	145	85	87	40

Table 2. Comparison of mean standard lengths observed at the last and previous capture (c) and recapture (r), and corresponding back-calculated lengths using the Fraser-Lee model (c) in individually tagged and recaptured barbel, *Barbus barbus*, from the River Jihlava (1999–2001).

				Observed and back-calculated SL					
				Current year[3]		1 yr before		2 yrs before	
Age group	No fish[1]	No obs	SL[2]	r	c	r	c	r	c
IV	3	3	197.7	186.5	195.0	145.0	128.0	—	—
V	6	6	220.0	205.5	203.5	183.5	181.5	—	—
VI	28	34	254.7	240.9	241.3	227.9	225.8	190.6	206.0
VII	22	30	259.6	247.3	250.1	227.8	236.0	206.7	229.0
VIII	34	41	301.9	279.1	277.4	270.7	271.0	273.9	299.3
IX	16	20	355.0	377.0	360.0	326.8	326.0	289.2	293.9
X	6	7	370.0	390.0	390.0	354.3	364.5	274.0	298.5
XI	3	5	409.3	375.0	368.0	404.5	403.5	380.5	389.0
XII	2	2	429.0	—	—	419.5	428.5	—	—
XIII	1	1	440.0	—	—	—	—	394.0	423.0
XIV	1	1	478.0	457.0	475.0	—	—	—	—
XV	1	1	470.0	—	—	445.0	466.0	—	—
XVI	3	4	493.3	—	—	472.0	484.7	473.0	502.0
XVII	1	1	475.0	450.0	470.0	—	—	—	—
Mean	127		301.96	272.13	272.03	276.12	278.17	265.58	283.00
SD			76.19	67.98	69.01	82.19	82.22	76.68	76.76
n	127	156	127	40		78		38	

[1] Recaptured tagged fish only.
[2] Mean value at last recapture.
[3] Fish caught in autumn exhibiting recent seasonal growth ('+' increment on scales).

Table 3. Summary statistics for back-calculated (back) and observed (obs) standard lengths at corresponding age for barbel, *Barbus barbus*, from the River Jihlava.

	Age group																			
	IV		V		VI		VII		VIII		IX		X		XI		XIV		XV	
Statistic	back	obs	back	obs	back	obs	back	obs	back	obs	back	obs	back	obs	back	obs	back	obs	back	obs
n	13	13	25	25	33	33	42	42	20	20	8	8	3	3	4	4	3	3	3	3
Mean	187.8	196.8	221.0	224.8	245.7	256.8	268.5	270.4	298.4	301.4	366.5	369.5	399.7	399.0	402.0	412.0	458.3	481.0	472.0	484.7
Median	191.0	208.0	222.0	225.0	244.0	245.0	256.0	261.5	285.0	297.0	356.5	369.0	395.0	390.0	403.5	425.0	457.0	475.0	482.0	489.0
Variance	353.7	776.4	724.2	830.6	953.0	1643.9	1659.1	1510.6	2703.1	2880.0	2847.4	2208.0	160.3	613.0	496.7	868.7	197.3	351.0	604.0	770.3
SD	18.8	27.9	26.9	28.8	30.9	40.5	40.7	38.9	52.0	53.7	53.4	47.0	12.7	24.8	22.3	29.5	14.0	18.7	24.6	27.7
SE	5.2	7.7	5.4	5.8	5.4	7.1	6.3	6.0	11.6	12.0	18.9	16.6	7.3	14.3	11.1	14.7	8.1	10.8	14.2	16.0
CV	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.2	0.2	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.0	0.1	0.1
Min	162.0	140.0	165.0	140.0	207.0	200.0	210.0	225.0	235.0	225.0	296.0	295.0	390.0	380.0	375.0	368.0	445.0	466.0	444.0	455.0
Max	216.0	232.0	294.0	290.0	342.0	353.0	363.0	355.0	419.0	390.0	458.0	425.0	414.0	427.0	426.0	430.0	473.0	502.0	490.0	510.0
Range	54.0	92.0	129.0	150.0	135.0	153.0	153.0	130.0	184.0	165.0	162.0	130.0	24.0	47.0	51.0	62.0	28.0	36.0	46.0	55.0
Lower Quartile	172.0	183.0	205.0	215.0	228.0	233.0	238.0	236.0	261.5	259.5	328.0	339.0	390.0	380.0	384.5	395.5	445.0	466.0	444.0	455.0
Upper Quartile	195.0	215.0	232.0	240.0	256.0	277.0	286.0	297.0	328.5	335.5	404.5	410.0	414.0	427.0	419.5	428.5	473.0	502.0	490.0	510.0
Interquartile Range	23.0	32.0	27.0	25.0	28.0	44.0	48.0	61.0	67.0	76.0	76.5	71.0	24.0	47.0	35.0	33.0	28.0	36.0	46.0	55.0
Skewness	0.1	– 0.8	0.7	– 1.0	1.5	0.9	1.1	0.7	0.9	0.3	0.4	– 0.6	1.4	1.4	– 0.3	– 1.9	0.4	1.3	– 1.5	– 0.7
SE Skewness	0.6	0.6	0.5	0.5	0.4	0.4	0.4	0.4	0.5	0.5	0.8	0.8	0.0	0.0	1.0	1.0	0.0	0.0	0.0	0.0
Kurtosis	– 1.0	– 0.3	1.6	3.3	2.6	0.6	0.3	– 0.6	0.1	– 1.0	– 0.3	– 0.8	0.0	0.0	– 1.6	3.8	0.0	0.0	0.0	0.0
SE Kurtosis	1.2	1.2	0.9	0.9	0.8	0.8	0.7	0.7	1.0	1.0	1.5	1.5	0.0	0.0	2.6	2.6	0.0	0.0	0.0	0.0
Kolmogorov-Smirnov	—		—		0.1155		0.0308		—		—		—		—		—		—	
Shapiro-Wilk	0.3126		0.0959		—		—		0.0252		0.5032		0.4084		0.0851		0.7733		0.5711	
Paired *t*-test	0.1611		0.3755		0.0011**		—		—		0.6350		0.9418		0.2822		0.0203*		0.0811	
Mann-Whitney *U*-test	—		—		—		0.8580		0.8604		—		—		—		—		—	

* $P < 0.05$; ** $P < 0.01$

Discussion

In a comparative review of barbel's growth from different watercourses of the Czech Republic and other European countries, Š o v č í k et al. (2004) showed that growth rate of male barbel in the River Jihlava was the fastest within the entire Czech Republic, whereas females from the same population grew more rapidly than in the other Czech barbel populations only up to the age of 8 yrs, beyond which those from the Moravice and Svratka rivers exhibited faster growth. Also, the fastest growth ever recorded amongst the barbel populations so far studied was in the Romanian rivers Tisza and Muresh, albeit with an apparently shorter life span (D o v g a n 1962, G y u r k ó et al. 1964).

The remarkable quality and suitability of the stream section sampled in the present study, not only for barbel but also for salmonids, is thought to be mainly the result of an advantageous synergistic effect of more stable temperature and discharge conditions, higher food resources and improved water quality, which were established during the period of full operation of the power scheme. The water temperature regime, in particular, has been modified, so that the annual peak in the temperature cycle is now delayed by 2–3 months, with lower temperatures occurring mainly during the barbel's reproductive season. These are most likely the reasons why the local population of barbel was strongly stressed after a sudden habitat change, as evidenced by a rapid decrease in abundance, fishery yields and growth rate (P e ň á z et al. 1999, 2003). Further aspects of important alterations in abiotic habitat conditions and fish community structure in the downstream section are discussed in detail by P e ň á z et al. (1999). The recently-observed slight decrease in growth of females, with consequent decreased difference between growth rates in both sexes, may also be due to more pronounced signs of senescence processes, along with recurrent masculinisation in older females (P e ň á z 1999, P e ň á z et al. 2005).

Studies assessing the accuracy of age and growth determination based on scale interpretation with fish of known age (e.g. H o f s t e d e 1970, M a n n & S t e i n m e t z 1985) or, as in the present study, on examination of scales from individually-tagged fish recaptured after one or more years (e.g. M a n n 1980), are still rather scarce despite their importance in light of their wider applicability. Although the exact age of the tagged barbel in our surveys was unknown, we were still able to estimate ages (by scale annulus counts), sizes and weights observed up to a certain time (i.e. dates of capture and subsequent recaptures), as well as growth increments in individuals over one or more years before their last recapture, which were also based on scale interpretation followed by back-calculation of corresponding lengths for previous years of life. Also, the problem of absence of the first annulus, which was reported by M a n n & S t e i n m e t z (1985) in rudd, was not encountered in our investigation. In the present study, therefore, we did not attempt to validate the accuracy of age determinations but rather that of back-calculated length increments for the past 1–3 years of life. However, correct identification of the first annulus does remain a crucial assumption for age and growth studies also in barbel, thus calling for validation by future related studies on young-of-year fish.

In an analysis of the validity of different methods for back-calculation of length in roach, H o r p p i l a & N y b e r g (1998) found the Body Proportional Hypothesis (BPH) to be the most accurate, followed in order by the Fraser-Lee method and by the Scale Proportional Hypothesis (SPH). However, the same authors found a moderately lower strength in the linear relationship for the Fraser-Lee model (R^2 = 0.80) compared to that of barbel in the present study; whereas upon application of the BPH and SPH methods, the resulting strength of the power function was slightly higher (R^2 = 0.83). For this reason, H o r p p i l a & N y b e r g (1998) concluded that the Fraser-Lee method tends to overestimate SL values in younger age groups and to underestimate those at older ages. This frequently observed effect is known as the 'Rosa-Lee Phenomenon', which also was clearly pronounced for barbel in the present study (Table 1). This means that the Fraser-Lee model of back-calculating lengths for foregoing years of life is sufficiently accurate and is thus validated for routine growth analyses even in the barbel.

According to B r y u z g i n (1968), J o h a l et al. (2001) and many other authors, differences between back-calculated and observed lengths are minimized when: (i) back-calculated lengths are based on a large number of random samples; (ii) measurements of the scale radius (cleithrum or urohyal length) are enough precise; (iii) determination of scale foci is precise; and (iv) scales are always sampled from the same area. We believe that all of these requirements were fulfilled in the present study.

Based on the findings of the present study, where observed and back-calculated lengths proved to be quite close (individual variation notwithstanding), it may be argued that methods based on scale intepretation may represent a convenient methodological tool for surveys in ecology and population dynamics of barbel, especially when calculation of average growth values in subsequent year-classes on large samples is required. This is especially true in light of the fact that growth estimation methods based on direct observation of tagged fish usually represent a rather costly and time-consuming procedure, hence not always applicable in standard routine management.

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