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Movement and abundance of barbel, *Barbus barbus*, in a mesotrophic chalk stream in England

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Abstract. We studied movement and abundance of barbel, *Barbus barbus*, over three years (October 1995 to September 1998) in two stretches (Woolmer's Park, Holwell Bridge) of a section of the River Lee (Hertfordshire, England) delimitated by water retention structures. Of 349 tagged individuals (168 at Woolmer's Park; 181 at Holwell Bridge), 51.8 % and 13.3 % respectively were recaptured at least once, with a much higher rate of multiple recaptures at Woolmer's Park, where monitoring of movements was over a longer period, than at Holwell Bridge, where too few recaptures were made for further movement analysis. At Woolmer's Park, 77.1 % of the barbel showed limited (i.e. resident component) and the rest greater between-capture movements (i.e. mobile component). There was no preferential directional movement across size classes. Based on the available recapture data, population size (estimated through a Bayesian method) first increased moderately (1995–96) and then sharply (1996–97) at Woolmer's Park, and even further later at Holwell Bridge (1998–99). This may reflect a recovery phase in the local population, or possibly a rising part of a cyclic recruitment pattern, such as reported for barbel elsewhere and for other cyprinids in the UK. Habitat enhancement is recommended over stocking, given the adequate abundance of barbel in areas with suitable habitat. However, it remains unclear whether fencing-off of the banks from livestock will enhance 0+ barbel numbers, which appear to be low relative to some European rivers of similar width and depth.

Key words: tagging, weirs, habitat fragmentation, log-linear analysis, Bayesian analysis, diel density variations, mobile, resident

Introduction

The barbel *Barbus barbus* (L.) is an important sport fish in Continental Europe and on the British Isles, where it has been widely introduced to rivers outside its historical native range of south-eastern England (Wheeler & Jordan 1990). Here the barbel is increasingly threatened (Peňáz et al. 2002), and this is especially true in rivers of urbanised areas, which are often subjected to discharge regulation (Faulkner & Copp 2001), channelisation (including culverting), elevated levels of nutrients (e.g. Pilcher & Copp 1997), and endocrine disruptors from treated sewage effluent (Price et al. 1997, Jobling et al. 1998). The impact of these various factors is apparent in the reproductive biology of the species (Routledge et al. 1998), which may result in reduced recruitment (Peňáz et al. 2005). To compensate (or mitigate) population decline, environmental managers have two main options, namely (i) remove or alleviate the environmental stressors, and/or (ii) undertake compensatory stocking of fish. As the former may be difficult or expensive to achieve, stocking remains an often-used, though not necessarily sustainable, practice to address concerns of the angling community (e.g. Taylor et al. 2004).

One such impacted barbel population exists in the River Lee (Hertfordshire), a mesotrophic chalk stream (tributary of the River Thames) in south-eastern England, that drains an increasingly urbanised area north and east of London (currently containing over two million human inhabitants). In addition to channel regulation, the river's water quality is compromised by treated domestic effluents that contain oestrogenic compounds — these have been reported to affect barbel morphology (Tyler & Everett 1993) and reproductive status (Jobling et al. 1998), though the pathological implications remain equivocal (Barnes et al. 1993). The possible implications of these stressors to barbel recruitment success were highlighted in the early 1990s, when small numbers of > 1+ and no young-of-year (0+) barbel were observed during field studies on the River Lee (Pilcher & Copp 1997). Indeed, follow-up research, which focussed specifically on barbel (Copp & Bennetts 1996, Watkins et al. 1997), found the species to occur (during the day) in low numbers at age 0+, though older age classes can represent a considerable portion (in biomass) of the fish assemblage (Copp & Bennetts 1996). Further work on 0+ age class recruitment revealed that the species is under-represented in day-time samples (Copp et al. 2002, Copp 2005), possibly due to dispersal behaviour under conditions of reduced light (Vilizzi & Copp 2001), with the highest numbers found at dusk and night (Copp et al. 2005).

As a target species in the River Lee Fisheries Action Plan, the barbel is of particular interest because of its value as an angling amenity and as a characteristic species of the river. Indeed, the barbel has been recognised in the River Thames Strategy as a Category 5 species, i.e. species not on the UK biodiversity priority list (UK BAP 2001) but that "are considered by the Environment Agency and its partners to be of local biodiversity importance and for which the Agency should play a key role" (ATKINS 2004, p. 32). As part of a broader study of potential recruitment problems in the Lee's barbel population, the aim of the present investigation was to assess the movements and abundance of barbel in two stretches of the River Lee so as to inform management policies on habitat enhancement/restoration and re-stocking for conservation and angling amenity. To this end, our specific objectives were to: 1) determine the level of home stretch fidelity, especially whether the movement patterns of the barbel population consist of two portions (i.e. resident/mobile) as observed elsewhere (Peňáz et al. 2002); 2) estimate between-stretch and among-season variation in the abundance of adult barbel from mark-recapture data; 3) estimate the density of 0+ barbel in the study stretches to assess the potential effect of fencing-off; and 4) interpret the results in light of similar investigations of barbel such as in the River Jihlava, Czech Republic (Peňáz et al. 2002), and elsewhere in the UK (e.g. Hunt & Jones 1974a,b, Lucas & Batley 1996).

Study Area

The River Lee, which has a catchment area of 1420 km^2, is a major tributary of the River Thames and is situated to the north and east of London. The Lee is of chalk stream origin and has a mean annual flow of 1.08 m^3 s^{-1}. In the upper half of its course it has a relatively natural stream bed and banks, except where water retention structures are present (mainly weirs); but it receives treated sewage effluent at a rate of 11,000 m^3 d^{-1} (about 0.13 m^3 s^{-1}), which during low flow periods can represent up to 80% of the river discharge during drier periods (NRA 1994, Faulkner & Copp 2001). The lower course of the river was highly regulated during the early 20th century, resulting in a series of man-made canals and connected side-loops (the former meander sections) to permit navigation between London, the city of Hertford and parts of the county of Essex.

The study area (National Grid Reference: TL 288 100) consisted of two river stretches comprised of riffle–run–pool sequences located within Woolmer's Park (1000 m) and Holwell Bridge (575 m) in the Cecil Gascogne Estates, Hertfordshire (Fig. 1). The Woolmer's Park stretch was bordered by woods for approximately half its length, with the remaining part being fenced off from cattle grazing land. In the Holwell Bridge stretch, riparian vegetation (trees, bushes) was either absent or relatively sparse, and the river was not fenced off from grazing sheep. The aggregate surface area of pools was approximately equal in the two stretches (G.H. Copp, unpublished), but those in the Holwell stretch were situated in sites unlikely to be disturbed by humans, whereas one of the pools at Woolmer's Park was under a bridge used daily by estate vehicles. These two stretches, which were sub-divided into 'sections' numbered in downstream order, lie within a sector of the river delineated by two weirs. The upstream (Essendon) weir lies about 250 m upstream of section 1, whereas the downstream (Water Hall) gauging weir lies about 700 m downstream of section 28. The two river stretches have a mean width of about 6 m, a maximum depth of about 2 m, and bottom substrata dominated by gravel, overlain in places by sand, silt and/or clay deposits (Copp & Bennetts 1996). Discharge varies from 0.5 to 5 $m^3 s^{-1}$, with peaks usually in winter and daily discharge patterns strongly influenced by releases of treated domestic effluent (Faulkner & Copp 2001). Thus, combined with surface run-off from agricultural land, water quality in most of this river is typically mesotrophic, with characteristic fish and macroinvertebrate species (for biota, see Copp & Bennetts 1996, Pilcher & Copp 1997, Copp et al. 2005, Edmonds-Brown et al. 2005). An areally-weighted mean cross-sectional site velocity has been calculated as 0.293 m s^{-1} for stream section 17 (Fig. 1).

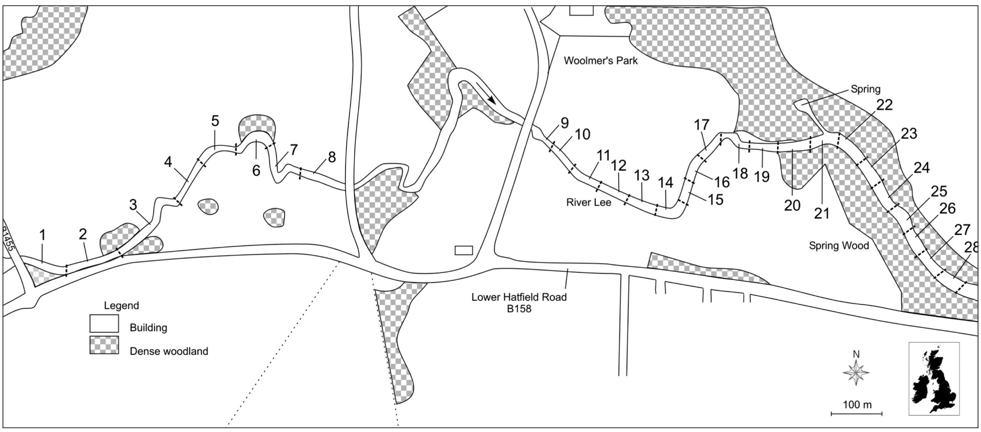

Fig. 1. The study site on the River Lee between Holwell Bridge (road B1455, left of map) and Woolmer's Park, Hertfordshire (England), with 28 labelled sections. Weirs are situated approximately 250 m upstream of section 1 (Holwell Bridge), and 1000 m downstream of section 28 (Woolmer's Park).

Materials and Methods

Barbel were captured by electric fishing, tagged (if of sufficient size: i.e. > 140 mm) and released between October 1995 and September 1998. Tagging began during depletion samplings in Woolmer's Park (sections 9–28: Fig. 1) in October 1995 (Copp & Bennetts 1996), followed by: (i) regular sampling (monthly April to October, 2–3 monthly otherwise) by continuous electric fishing (for about 180 minutes) until October 1997; (ii) weekly daytime (G.H. Copp, unpublished) and 24-h point sampling (Copp 2005) during June and July 1997 within sectors 9–17 (same study site as Watkins et al. 1997); (iii) incidental 24-h sampling (sections 15–17) in late August and early September 1997 (see Copp et al. 2005). Owing to a change in land ownership at Woolmer's Park, the site for routine sampling (from April to September 1998) was displaced to the river stretch immediately upstream of Woolmer's Park, the so-called 'Holwell Bridge' stretch (sections 1–8: Fig. 1). In this new stretch, a complementary study of young and small fishes (using the methods described in Copp 2005) was undertaken, consisting of 160 PASE samples collected at midday (12:00–13:00), dusk (18:00–19:00), midnight (00:00–01:00) and dawn (05:00–06:00) on 26–27 August 1998 in sections 1–8 (Fig. 1). These data were contrasted with those collected in sections 9–28 (Fig. 1) at the same times of day on 7–8 August 1996 (re-analysed data from Copp 2005) and in 1997 on 28–29 July, 4–5 August and 7–8 August (re-analysed data from Copp et al. 2005).

After being measured for standard length (SL), barbel of SL > 140 mm (estimated age ≥ 1+: L. Vilizzi, unpublished) were marked by means of individually-numbered yellow plastic anchor ('spaghetti') tags, which were fixed on the left body side into the dorsal musculature, just below the anterior edge of the dorsal fin (Peňáz et al. 2002). Vaseline jelly was then applied to the tag anchor site to minimise the risk of infection. The effect of tags on fish behaviour, survival and growth was minimised by the type of tags used and their careful application, and there is evidence for these tags to be durable and easy to recognise in the field even after long periods (Peňáz et al. 2002). Tagged and recaptured fish were always released at the point of capture, with the distance between centres of sections (of successive recaptures) taken as the minimum distance moved by the fish between capture/recapture events.

Data analysis

All data on fish specimens included in this study derive from the sampling excursions described above and do not include three anecdotal anglers reports, received via K.J. Wesley (Bedwell Fisheries Services), of tagged barbel captured by rod and line (see Results). Relationships between size class (SL: at 50 mm intervals, from 150 mm), tagging (Tag Status: tagged or recaptured), and stream section (Stretch: Woolmer's Park, Holwell Bridge) were analysed by log-linear analysis in a three-way contingency table (Quinn & Keough 2002). Fitting was hierarchical, starting with a saturated model of complete dependence (i.e. one including the highest three-way interaction term) down to a no-interaction model of complete independence (i.e. without interaction terms). The 'best' model was then selected by an analysis of deviance, based on a combination of G^2 goodness-of-fit statistic and Akaike Information Criterion (AIC) followed by 'judicious choice' (made by the first author). Analyses were carried out under S-Plus 2000 Professional Release 3 for Windows®.

Frequency analysis of distances was used to determine whether fish movements were uni- or multi-modal. Based on the frequency distributions, fish were subsequently categorised according to the distance moved between capture points (unsigned: see below) as per Peňáz et al. (2002), i.e. 'resident' (fish found to inhabit the same stream section(s) during virtually every sampling event), or 'mobile' (fish found to inhabit a variety of non-contiguous stream sections). For barbel at Woolmer's Park, association between mobile and resident components, relative to individual size classes, was assessed by the Fisher's exact test (Everitt 1993). Individual- (i.e. averaged over multiple recaptures) and recapture-based distances (between the original mark and subsequent recaptures), moving upstream and downstream, were assigned negative and positive values, respectively, and plotted into frequency distributions. Estimates were thus obtained of mean signed (i.e. '−' for upstream vs '+' for downstream) movement distance. To detect preferential upstream or downstream movement, a *t*-test was used to determine whether mean signed movement differed significantly from zero. Normality was tested by the Anderson-Darling (A-D) statistic, kurtosis of movement distribution by the online applet at http://www.wessa.net/skewkurt.wasp. As shown by Skalski & Gilliam (2000), assessment of the degree of kurtosis of the frequency distribution of signed displacements provides for a good indicator of individual-level variation in movement behaviour.

Barbel population size was estimated in the two stretches from mark-recapture data. Using spawning events observed at Woolmer's Park in consecutive years (G.H. Copp and L. Vilizzi, unpublished), an annual birth date was set to early June; and population size estimates were calculated separately for the years 1995–96, 1996–97, and 1997, as well as for the entire dataset 1995–97; whereas at Holwell Bridge, this was for the years 1998–99 (Table 1). Because of the low sample sizes, the Bayesian approach of Gazey & Staley (1986) was preferred over traditional methods for estimating population abundance (e.g. Sutherland 1996), which in such cases may yield estimates with substantial negative bias and large confidence intervals. Using Bayes' theorem (posterior probability ∝ likelihood × prior probability), the likelihood function is what modifies prior knowledge into posterior expectations (Ellison 1996). Therefore, the posterior probability of a given population size for barbel, based on the observed number of recaptures in the consecutive samples, was calculated by a binomial sampling distribution (i.e. likelihood) for the number of recaptures, given the population size and a discrete uniform distribution (i.e. prior probability) for population size, which was heuristically found and non-informative. Implementation of Gazey & Staley's (1986) sequential Bayes algorithm for estimation of population size used the Matlab® code written by T. Eguchi in his brief summary of Seber (1982; available at http://www.esg.montana.edu/eguchi/pdfFiles/markRecapSummary.pdf). This allows the posterior distribution at each iteration (equivalent to the number of sampling occasions) to be plotted and used as a visual diagnostic of the assumption of population closure, i.e. that population size does not change over the period of study. Thus, with a closed population, the posterior distribution should cluster about a single value; whereas a continuous trend towards a larger or smaller value would suggest that population size has changed over the period of study (i.e. violation of the closure assumption). The change in population abundance between Woolmer's Park in 1997 and Holwell Bridge in 1998–99 also was assessed after Gazey & Staley (1986) by computing the compound posterior distribution of the difference between the two seasons, which provides the probability of difference given the data. Implementation of the appropriate algorithm was also in Matlab® code written by the first author. Finally, diel variations in the relative density (numbers of fish per area sampled, as per Copp et al. 2005) of 0+ barbel in the Lee at Woolmer's Park and Holwell Bridge in 1996 and 1998, respectively, were tested using the Kruskal-Wallis test (corrected for ties).

Table 1. Summary data for tagged and recaptured barbel in two stretches of the River Lee (Hertfordshire, England). For each sampling date, the numbers of captured, marked and recaptured individuals is given, followed by the number of subsequent recaptures of fish tagged on that date (overall total recaptures, 1x—6x, by site are: Woolmer's Park = 49, Howell Bridge = 23). For estimation of population sizes, sampling dates at both locations are grouped into seasons, based on a major spawning event in June.

		Numbers			Recaptures					
Season	Date	Captured	Marked	Recaptured	1x	2x	3x	4x	5x	6x
	Woolmer's Park									
	05/10/1995	5	5	—	1					
	06/10/1995	15	9	0	2	3	1	1		
	27/10/1995	18	8	2	1			2		
	03/11/1995	10	10	1	3		1	1		1
	10/11/1995	6	6	0	1		1			
	27/02/1996	1	1	1	1					
	04/03/1996	2	0	2						
	22/03/1996	2	2	0	2					
	11/04/1996	14	13	5	4	3		1		
	23/04/1996	22	22	5	7				1	
	03/05/1996	5	5	11	3					
1995–1996	15/05/1996	3	1	5						
	30/05/1996	12	11	4	2	1				
	07/06/1996	1	0	1						
	04/07/1996	1	1	2						
	14/07/1996	12	9	2	1					
	23/07/1996	10	4	8						
	02/08/1996	10	5	4						
	07/08/1996	4	1	2	1					
	23/08/1996	2	2	7						
	04/09/1996	15	3	1						
	29/09/1996	5	0	5						
	11/10/1996	2	0	2						
	25/10/1996	1	0	1						
	27/10/1996	1	0	1						
	07/11/1996	1	0	1						
	29/01/1997	3	3	0		1				
	05/03/1997	3	3	2	1					
1996–1997	04/04/1997	1	0	1						
	09/05/1997	1	1	0						
	18/06/1997	20	20	5						
	15/07/1997	20	7	0						
	07/08/1997	1	0	1						
	16/09/1997	19	5	0	1					
1997	15/10/1997	21	11	5						
	Total	269	168	87	31	8	3	5	1	1
				Cumulative	31	47	56	76	81	87

Table 1. continued

Season	Date	Numbers: Captured	Marked	Recaptured	Recaptures: 1x	2x	3x	4x	5x	6x
1998–1999	Holwell Bridge									
	29/04/1998	51	30	—						
	26/05/1998	21	12	0		1				
	29/05/1998	28	10	0	1					
	03/06/1998	41	27	0	5					
	08/06/1998	3	3	0						
	10/06/1998	3	2	0						
	12/06/1998	14	9	0	1					
	16/06/1998	1	0	1						
	22/06/1998	10	6	0						
	26/06/1998	13	8	0	2					
	09/07/1998	36	22	0	2					
	31/07/1998	29	18	0	2					
	20/08/1998	16	8	0	1					
	27/08/1998	2	0	2						
	08/09/1998	23	12	7	4					
	17/09/1998	48	14	0	4					
	08/04/1999	13	0	13						
	20/04/1999	1	0	1						
	Total	353	181	24	22	1				
				Cumulative	22	24				
	Grand total	622	349	111						

Results

In total, 622 individual barbel (SL ≥ 100 mm) were caught during the study period of which 269 at Woolmer's Park and 353 at Holwell Bridge (Table 1). Of these, 349 were tagged, 168 at Woolmer's Park and 181 at Holwell Bridge. Overall, there were 111 (31.8 %) recaptures of tagged fish, 87 (24.9 %) at Woolmer's Park and 24 (6.9 %) at Holwell Bridge, representing 51.8 % and 13.3 % of the barbel monitored in the corresponding stretches, respectively. No additional fish were recaptured by us during the study period when sampling other stretches of the River Lee (unpublished data). However, three tagged individuals were subsequently (i.e. after September 1998) caught by anglers both upstream (two specimens) and downstream (one specimen) of the weirs that delineate the study area (K.J. Wesley, personal communication), but details on either tag number or fish size could not be obtained. Further, amongst the 49 individual barbel recaptured at Woolmer's Park, the proportions of single and multiple recaptures were relatively high; whereas at Holwell Bridge, a high proportion of single recaptures was contrasted by a small proportion of multiple recaptures.

The proportion of recaptured barbel (in 50 mm SL classes) in both stretches increased with increasing SL, reaching its maximum in the 350 mm size class (Table 2). Log-linear analysis resulted in two competing models, of which the model consisting of SL × Tag Status and SL × Stretch interactions was selected for its biological meaning. Comparing standardised residuals and raw frequencies, two contrasting patterns emerged: more barbel

Table 2. Log-linear analysis of the frequencies of recapture of barbel by size class (in mm SL) in two stretches of the River Lee (Hertfordshire, England). Both residuals and raw numbers of tagged and recaptured fish are given (for Woolmer's Park the latter differ slightly from those in Table 1 as some individuals were not measured for size), with the two size classes with the highest scores in bold.

	Residuals		Number			Number	
Size class	Tagged	Recaptured	Tagged	Recaptured	Proportion recaptured	Resident[1]	Mobile[1]
Woolmer's Park							
150	0.000	0.000	1	1	100.0	1	0
200	0.000	0.000	7	2	28.6	2	0
250	– 0.351	0.641	6	3	50.0	1	2
300	0.267	– 0.378	15	6	40.0	5	1
350	**– 0.845**	**1.336**	**40**	**24**	**60.0**	13	10
400	**– 0.544**	**1.983**	**67**	**10**	**14.9**	8	2
450	– 0.011	0.056	25	1	4.0	1	0
500	– 0.267	0.707	3	1	33.3	0	1
Total			164	48		31	16
Holwell Bridge							
150	0.000	0.000	0	0	0	—	—
200	0.000	0.000	0	0	0	—	—
250	0.526	0.000	4	0	0.0	—	—
300	– 0.289	0.408	11	7	63.6	—	—
350	**0.814**	**– 1.287**	**55**	**14**	**25.5**	—	—
400	**0.534**	**– 1.945**	**79**	**1**	**1.3**	—	—
450	0.010	– 0.053	28	1	3.6	—	—
500	0.267	0.000	4	0	0.0	—	—
Total			181	23			

[1] No record for one individual in the 350 mm class.

(than expected) in the 350 and 400 mm size classes were recaptured at Woolmer's Park, whereas the opposite was true at Holwell Bridge (Table 2).

In total, 48 of the 49 barbel recaptured at Woolmer's Park on one or more occasions were included in the analyses for movements (for one specimen, no information on tagging location was available). Mean unsigned distance moved was 202.0 ± 20.9 SE m (n = 48), mean individual-based signed − 30.3 ± 222.4 SD m (n = 48), and mean recapture-based signed − 37.5 ± 277.0 SD m (n = 86) (use of confidence intervals follows Skalki & Gilliam 2000). However, there was no relationship (Fisher's exact test: P = 0.365, n = 47) between size class and the proportion of resident vs mobile fish (Table 2). And despite a clear downstream movement (Fig. 2), no significant preference (upstream/ downstream) was apparent in either the individual- (t-test: P = 0.349) or recapture-

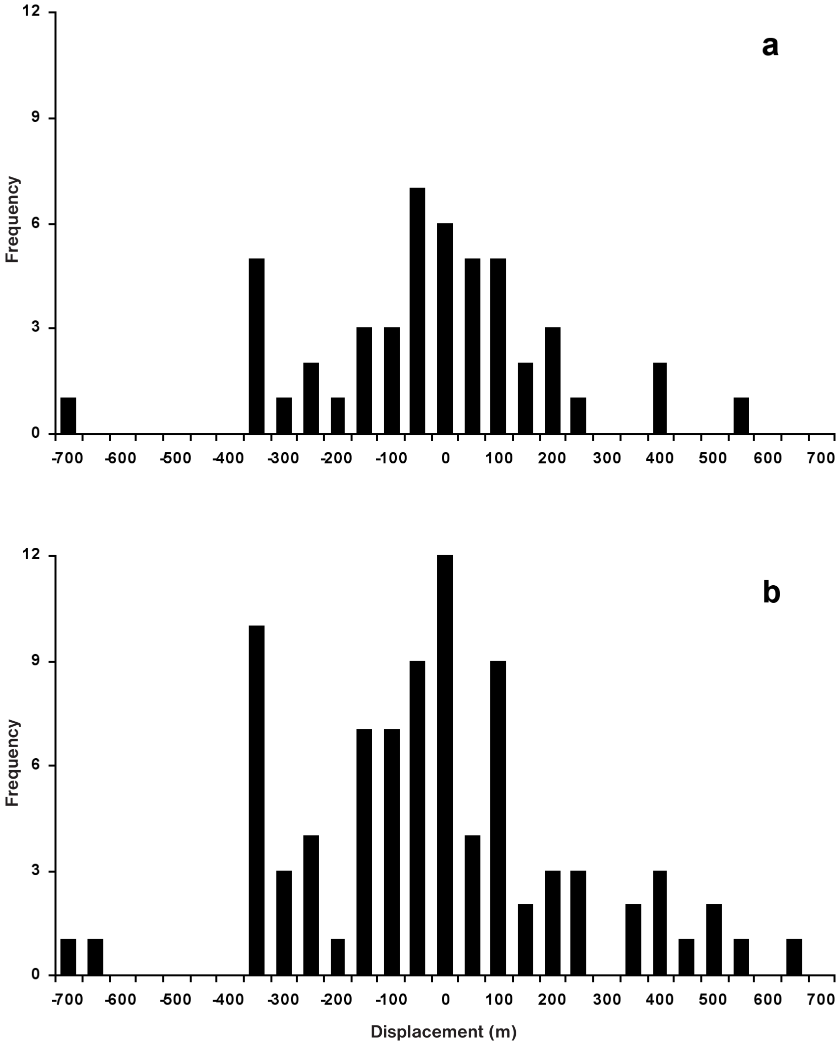

Fig. 2. Movement distribution for barbel in the River Lee at Woolmer's Park (Hertfordshire, England). Displacement is calculated as mean signed (i.e. upstream vs downstream) movement distance on (a) an individual and (b) a recapture basis.

based signed distances (t-test: P = 0.436). The frequency distribution of individual-based movement was normal (A-D statistic: $P > 0.05$) but slightly leptokurtic (γ_2 = 1.37, P = 0.04). The frequency distribution of recapture-based movements also was normal (A-D statistic: $P > 0.05$) but with no significant kurtosis (γ_2 = 0.45, P = 0.51). Overall, maximum, individual- and recapture-based unsigned distances moved were predominantly 100 to 400 m. However, a secondary peak was evident in both distributions (i.e. individual- and recapture-based) at 350 m signed distance moved, and this was related to the upstream mobile component (Fig. 2a,b). Therefore, a mean unsigned distance of |300| m was taken as the threshold value to distinguish 'resident' and 'mobile' barbel, with 37 barbel (77.1 %) being classed as resident and 11 (22.9 %) as mobile. Eight of the mobile individuals were re-captured in the spring–summer season, which suggests reproductive migratory behaviour. This contention was supported in part by the monthly length (SL) frequency distributions for 907 tagged and untagged barbel (Fig. 3), which reveal peaks around the 300–500 mm size classes.

Of the 17 barbel recaptured at Woolmer's Park more than once (Table 3), nine individuals were classed consistently as 'resident', one was classed consistently as 'mobile', and the remainder were classed as 'resident' on at least 50% of the recapture occasions. Of the individuals recaptured at least four times, i.e. those providing the greatest scope for interpretation of temporal (seasonal) variation, half were consistently 'resident', and half were classed on at least 50% of the recapture occasions as 'resident'. The direction of mobility was never consistently upstream or downstream in any specimen. With a caveat for small sample sizes in some size classes (Table 2), the intermediate size classes had the highest proportion of mobile barbel, with the lone large barbel being mobile during the study.

Based on the entire data set (1995–97), mean population size of barbel at Woolmer's Park was estimated at 317 individuals (2.5% and 97.5% quantiles: 271 and 376), with a 95 % probability that abundance was at least 278. However, when analysed by season, a clear trend

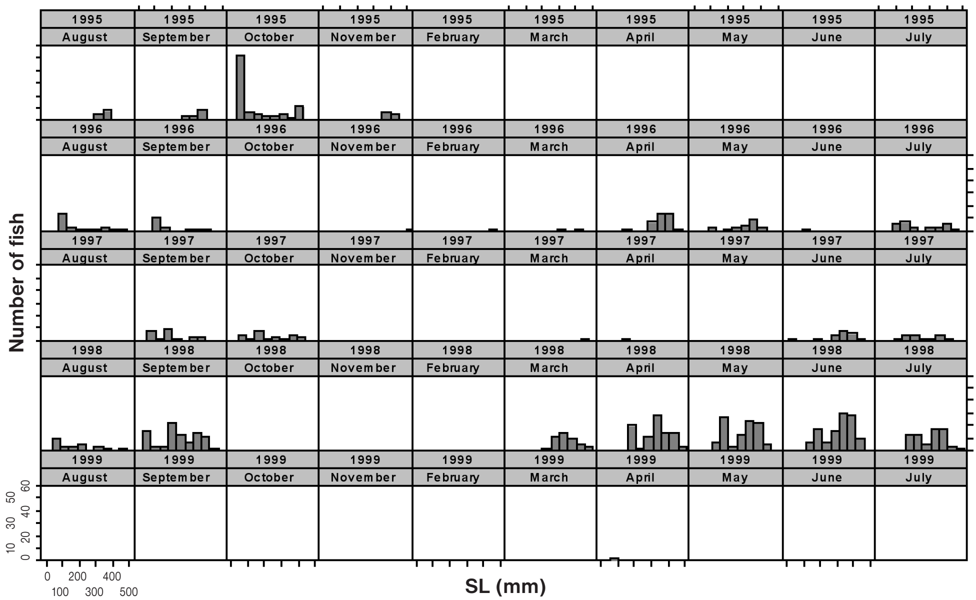

Fig. 3. Monthly standard length (SL) frequency distributions for 907 barbel sampled in the River Lee (Hertfordshire, England) at Woolmer's Park and Holwell Bridge during 1995–1999.

of increasing population size was evident, rising from 114 (*ibid*.: 93 and 146) in 1995–96 to 206 (*ibid*.: 169 and 260) in 1996–97, and then to 1237 (*ibid*.: 712 and 1996) estimated individuals in 1997, with a 95 % probability that abundance was at least 96, 174 and 768 individuals in those years, respectively. At Holwell Bridge, estimated mean population size was even higher at 1406 (*ibid*.: 948 and 2072) individuals, with a 95 % probability that abundance was at least 1008. Finally, upon comparison over time of the population sizes at Woolmer's Park in 1997 and at Holwell Bridge (1998–99), there was a 35 % probability that abundance increased in the latter.

Over the diel cycle in August, observed 0+ barbel densities were consistently higher at night (Table 4), but the differences with other times of day were not statistically significant (Kruskal-Wallis test) in any of the three sampling years (in 1996: $H = 3.762$, $P = 0.29$; in 1997: $H = 3.641$, $P = 0.30$; in 1998: $H = 0.355$, $P = 0.95$). It was not possible to compare directly between the un-fenced and fenced stretches, because sampling was in different years, but night-time densities in the un-fenced stretch at Holwell Bridge in 1998 were lower than in the fenced-off stretch at Woolmer's Park, where day-time and night-time densities for 1996 and 1997 were very similar.

Table 3. Breakdown of movement components for barbel at Woolmer's Park in the River Lee (Hertfordshire, England) recaptured more than once (cf. Table 1). For each individual, the status (R = resident; U = upstream moving; D = downstream moving) is reported for each recapture event.

Recaptured fish	1	2	3	4	5	6
1	R	R				
2	R	R				
3	R	R				
4	U	D				
5	R	R				
6	U	R				
7	R	U				
8	D	R				
9	R	R	R			
10	U	R	D			
11	R	R	R			
12	R	R	R	R		
13	U	D	R	R		
14	R	R	R	R		
15	R	D	U	R		
16	R	R	R	R	R	
17	D	U	R	R	R	R

Table 4. Mean density (individuals·m^2), with standard error (SE) and 95% confidence limits (CL) in parentheses, for 0+ barbel during different periods of the daily cycle (Dawn = 05:00–06:00; Day = 12:00–13:00; Dusk = 18:00–19:00; Night = 00:00–01:00) in a fenced-off stretch (Woolmer's Park: sections 9–28 in Fig. 1) in August 1996 (n = 20 per time interval) and August 1997 (n = 75 per time interval) as well as in an un-fenced stretch (Holwell Bridge: sections 1–8 in Fig. 1) in August 1998 of this study (n = 40 per time interval). Data for 1996 and 1997 re-analysed from C o p p (2005) and C o p p et al. (2005), respectively.

Location	Dawn	Day	Dusk	Night
Woolmer's 1996 (fenced)	—	0.70 (0.71/0.04)	—	1.41 (0.97/0.06)
Woolmer's 1997 (fenced)	—	0.56 (0.32/0.02)	—	1.88 (1.56/0.10)
Holwell 1998 (un-fenced)	0.70 (0.49/0.03)	0.70 (0.49/0.03)	1.06 (0.78/0.049)	1.06 (0.59/0.04)

Discussion

The River Lee was described in the 17th century as supporting amongst the best and most diverse coarse fisheries in the UK (Walton 1987). This is still true, despite regulation and deteriorated water quality, which have rendered the River Lee one of the most heavily impacted water courses in the UK (Pilcher & Copp 1997). Barbel in the Lee are highly valued amongst anglers for their size, form and vigour, and the densities of older (> 1+) fish appear to be comparable with those of other rivers where barbel are considered abundant, such as Bristol Avon, the River Severn and the River Trent (e.g. Hunt & Jones 1974a, Environment Agency 1998, 2004a,b). The distribution of barbel is characteristically dictated by available habitat, which is most abundant in the upper section of the River Lee (Pilcher & Copp 1997), but with localised concentrations in the more natural side loops of the lower section (Pilcher et al. 2004). This fragmented distribution suggests a metapopulation structure, with components separated (except during periods of elevated discharge) by water retention structures such as locks and weirs. The latter are known to impede barbel movements during crucial (i.e. spawning) migrations in some river systems (Baras et al. 1994), but in the River Lee some upstream movement past weirs appears to occur, as evinced by angler captures of tagged individuals upstream of Essendon weir (Fig. 1). Indeed, Lucas (2000) demonstrated that upstream migrations in barbel are mainly linked with elevated discharge events, including passage over weirs (Lucas & Frear 1997). Confinement may explain in part the high recapture rates recorded in the present study. However, the observed pattern of site fidelity, with resident and mobile components, has been observed for the species elsewhere (Peňáz et al. 2002). Thus, a relatively high proportion of tagged fish were recaptured at least once in both stretches under study (similar to reports by Peňáz et al. 2002), with the number of repeated captures highest in the stretch (Woolmer's Park) monitored over the longest period. Further, the observed spring–summer peaks in abundance of the larger size classes (SL) may be indicative of spawning movements of mature individuals (e.g. Baras 1994, Baras et al. 1994), although the possibility of sampling artefact cannot be ruled out.

The rising trend in barbel numbers in both stretches of the River Lee over the study period suggests that the population is in a recovery phase, possibly in the rising part of a cyclic recruitment pattern such as that reported for roach (e.g. Perrow et al. 1990) or as a result of immigration processes. For example, regular fluctuations in barbel numbers have been recently reported in the River Jihlava, where considerable increases in population size have previously been attributed to environmental changes associated with water retention measures (Peňáz et al. 2003). These increases were followed by a dramatic decline, which is thought to be linked to a recent invasion of migrating over-wintering cormorants (M. Peňáz, unpublished). Therefore, efforts to favour the apparent recovery of barbel in the River Lee should concentrate on habitat enhancement, including improvement of water quality, which appears to be a major physiological constraint (Jobling et al. 1998). Stocking seems unnecessary given the adequate abundance of barbel in areas with suitable habitat (Fig. 3; also Pilcher et al. 2004), which consists of deep pools, gravel and pebble bottoms along with in-stream cover for larger age classes (see Copp & Bennetts 1996) and shallow marginal areas with overhanging/floating vegetation for 0+ barbel (see Copp 2005, Copp et al. 2005). Suitable habitat appears to be adequate for most barbel life intervals, though spawning grounds may be reduced by the high levels of suspended matter (Faulkner & Copp 2001), which clogs the interstices of the alluvial sediments.

The low numbers of barbel larvae and 0+ juveniles relative to other, similar European rivers (e.g. Bischoff & Scholten 1996, Baras & Nindaba 2000) suggest that suitable habitat is a limiting factor. Although 0+ barbel did not regularly appear in daytime samples (e.g. Copp & Bennetts 1996, Pilcher & Copp 1997, Watkins et al. 1997), diel sampling revealed 0+ barbel densities to be consistently higher at night (Table 4). This supports Copp's (2005) suggestion that during daylight hours 0+ barbel inhabit marginal vegetation (i.e. *Menta aquatica*, *Veronica beccabunga*), which overhangs the shallow shoreline, and at night they move out into lentic areas adjacent to this marginal vegetation. Such marginal vegetation is more abundant in the section of the fenced-off stretch of the River Lee (Woolmer's Park, sections 9–28 in Fig. 1) than in the un-fenced stretch (Holwell Bridge, sections 1–8), where 0+ barbel were captured throughout the diel cycle (Table 4). Fence protection of river banks from cattle/sheep trampling is known elsewhere in England to favour some stream fishes, such as brown trout (Summers & Giles 1994). Comparisons of densities of 0+ barbel in the fenced and unfenced stretches of the River Lee (Table 4) may suggest that carrying capacity could be altered in the unfenced section, with night-time habitat therein not as suitable as in the fenced section. In light of the importance of nursery habitat to year-class strength (Mann 1997), the role of fencing and other factors in the recruitment success of barbel in the River Lee requires further investigation.

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