Age and growth of European barbel *Barbus barbus* (Cyprinidae) in the small, mesotrophic River Lee and relative to other populations in England

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ABSTRACT

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Suspected of being in decline, the European barbel *Barbus barbus* population of the River Lee, a heavily-modified river in South East England, has been the subject of investigations to identify factors associated with perceived population decreases. Population surveys between 1995 and 1999 captured a total of 912 individuals, and standard length (SL) frequency analyses between years suggested that the population decline was not related to juvenile recruitment but rather to a recruitment bottleneck in fish 300–340 mm SL. This bottleneck probably results from insufficient available habitat suitable to this size class. Of the sampled fish, scales were removed from 764 and were used in a scale ageing exercise among three researchers. Analyses of their independent age estimates revealed variable interpretations, which arose from uncertainties relating to the difficulty of analysing scale patterns from relatively large, slow-growing fish. Nevertheless, error was within published acceptable margins, and age estimates revealed *B. barbus* in the river to age 10 years, lower than in many UK rivers. The SL-at-age growth curve was characterised by very fast growth in the initial years of life. Thus, the causal factors in the decline of this *B. barbus* population appear to have been in the adult life-stage habitat and were likely related to the loss of longitudinal connectivity, mainly due to the presence of water retention structures. River and aquatic ecosystem remediation strategies should therefore focus on enhancing longitudinal connectivity in conjunction with the ongoing improvement of water quality and ecosystem integrity.

RÉSUMÉ

L'âge et la croissance du barbeau européen *Barbus barbus* (Cyprinidés) dans la petite mésotrophique rivière Lee et comparaison à d'autres populations en Angleterre

Mots-clés :
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recrutement

Soupçonnée d'être en déclin, la population de barbeau européen *Barbus barbus* de la rivière Lee, une rivière fortement modifiée dans le Sud Est de l'Angleterre, a fait l'objet d'investigations pour identifier les facteurs associés à la diminution ressentie de la population. Le suivi de population entre 1995 et 1999 a permis la capture de 912 poissons, et l'analyse des fréquences de longueur standard (SL) entre années suggère que le déclin de la population n'était pas lié au recrutement des juvéniles, mais plutôt à un goulot d'étranglement du recrutement chez les poissons de 300–340 mm SL. Ce goulot d'étranglement résulte probablement d'une insuffisance de l'habitat disponible approprié pour cette classe de taille.

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Des poissons échantillonnés, les écailles ont été prélevées sur 764 individus et utilisées pour un exercice de détermination de l'âge par trois chercheurs. Les analyses de leurs estimations de l'âge ont révélé des interprétations variables, provenant des incertitudes liées à la difficulté d'analyser les écailles de relativement gros poissons à croissance lente. Néanmoins, l'erreur était à l'intérieur des marges acceptables publiées, et les estimations d'âge ont révélé des *B. barbus* dans la rivière jusqu'à 10 ans d'âge, inférieur à celui observé dans de nombreux cours d'eau du Royaume-Uni. La courbe de croissance SL selon l'âge a été caractérisée par une croissance très rapide au cours des premières années de la vie. Ainsi, les facteurs de causalité dans le déclin de cette population de *B. barbus* paraissent avoir été liés à l'habitat des stades adultes et sont probablement liés à la perte de connectivité longitudinale, principalement en raison de la présence de structures de rétention d'eau. Les stratégies de restauration des rivières et des écosystèmes aquatiques devraient donc se concentrer sur l'amélioration de la connectivité longitudinale en collaboration avec l'amélioration permanente de la qualité de l'eau et de l'intégrité de l'écosystème.

INTRODUCTION

The European barbel *Barbus barbus* (L.) has considerable socio-economic importance as a sport fish (Britton and Pegg, 2011) and although is classed on the IUCN Red List as being of 'Least Concern', it is increasingly seen as 'flag' species for river conservation. Increasingly threatened within its native range (Peñáz *et al.*, 2003), the IUCN status of *B. barbus* therefore carries the caveat of being "locally threatened by water pollution and river regulation". In the UK, where *B. barbus* is native to eastern rivers between Yorkshire and the Thames (Wheeler and Jordan, 1990), declining population densities have been reported for some of the more urbanised rivers, including the River Lee, Hertfordshire (Pilcher and Copp, 1997; Watkins *et al.*, 1997). River regulation has been identified as a major threat to barbel populations (Pilcher *et al.*, 2004), with compounding adverse effects of elevated nutrient levels on the species' morphology (Tyler and Everett, 1993), physiology (Peñáz *et al.*, 2005) and migratory behaviour (Lucas and Frear, 1997; Vilizzi *et al.*, 2006). This contrasts with earlier, more optimistic assessments that suggested that *B. barbus* numbers were on the increase (Wheeler and Jordan, 1990). Thus, information on population size structure and growth is needed for rivers where *B. barbus* stocks are thought to be in decline so as to inform environmental managers in the formulation of habitat enhancement/rehabilitation and re-stocking strategies that aim to conserve the populations and increase the related angling amenity (Britton and Pegg, 2011; Pegg and Britton, 2011).

To investigate a perceived decline in the *B. barbus* population of the River Lee, a small mesotrophic water course in South East England, collaborative research focused on the possible casual factors (Copp and Bennetts, 1996; Pilcher and Copp, 1997) through studies of the species' environmental biology (e.g. Watkins *et al.*, 1997; Vilizzi and Copp, 2001, 2013a,b; Copp *et al.*, 2002, 2005; Vilizzi *et al.*, 2006). As a component part of this research programme, the aim of the present study was to assess the age and growth rates of River Lee *B. barbus*. Specific objectives were to: 1) determine inter-annual variation in population size structure; 2) assess seasonal and inter-annual variation in growth; and 3) compare the growth of *B. barbus* in the River Lee with other stocks throughout England.

MATERIAL AND METHODS

> STUDY AREA

The River Lee (catchment area = 1420 km²; human population ≈ 2 million) is one of the most heavily human-impacted river systems in the UK, with treated sewage effluent (11 000 m³·d⁻¹) representing up to 80% of the river's discharge during periods of low flow (NRA 1994a; Faulkner and Copp, 2001), which has consequences for the character of the river substratum (clogging with silt and biofilms, resulting in reduced sediment mobility; Vilizzi *et al.*, 2006).

A major left-bank tributary of the River Thames, the R. Lee is of chalk stream origin, with a mean annual discharge of $1.09 \text{ m}^3 \cdot \text{s}^{-1}$ (Faulkner and Copp, 2001). The study stretch comprised three reaches in the upper course of the river, where the river bed slope is $\approx 2.93 \text{ m} \cdot \text{km}^{-1}$: 1) from Lemsford Reserve (51.793946N, 0.22895873W) to Stanborough Park (51.787283N; 0.22236586W); 2) from Holwell Bridge (51.772461N; 0.15165210W) to Letty Green Bridge (51.773503N; 0.14358401W); and 3) from Letty Green Bridge to the eastern extent of Woolmers Park (51.771418N; 0.12814522W) (Figure 1).

Reach 1 (Lemsford-Stanborough) was about 1800 m in length and was characterised by a substratum of mainly sand and gravel, with occasional silt and large rocks. From upstream to downstream, riparian vegetation went from thick and abundant (in the nature reserve) to patchy and relatively thin as the river flows through the park. Channel width varied 6–10 m, with water depths mostly $< 0.5 \text{ m}$ except in one occasional pool (maximum depth = 2 m). Management of the stream course was virtually nil upstream, but manicured downstream in the park.

Reach 2 (Holwell-Letty Green) had a length of $\approx 1000 \text{ m}$ and is situated ≈ 9 river km downstream of Reach 1, flows through unfenced, private (sheep) pasture land, where the river substratum varied considerably (*i.e.* silt and fine sand in back-eddy areas adjacent to pool, with gravel and cobbles in the riffle sections). From upstream to downstream, riparian vegetation went from a thin strip of trees and bushes to open field with only a few overhanging trees and occasional reed beds. Water depth varied from shallows of $< 20 \text{ cm}$ to deep ($> 1.5 \text{ m}$) bends. Management of the stream edges was not apparent, with sheep trampling of the shallower stream banks.

Reach 3 (Letty Green-Woolmers) was about 700 m long and flows through a private estate, beginning upstream with a sinuous section that passes through a small, thick wood, leading into a more open section bordered by a few trees, passing under a driveway bridge, which has a deep ($> 2 \text{ m}$) downstream of it. The river then passes into a sequence of runs, pools and riffles that begins within a fenced pasture area (cows) followed by thick woodland in which the river is joined by a small, short stream. The riparian border varied from virtually nothing (mostly fencing and tall wild grasses) to $> 40 \text{ m}$ width. Stream width was 3–12 m, with depths up to 2 m or 3 m. In-stream management had been limited to the removal of fallen trees and bushes (see Copp and Bennetts, 1996).

None of the reaches is open to angling activity except at the extreme downstream end of Reach 2. River discharge varied between 0.5 and $5.0 \text{ m}^3 \cdot \text{s}^{-1}$; discharge peaks usually occurred in winter and daily flow patterns were strongly influenced by discharges of treated domestic effluent (Faulkner and Copp, 2001). However, only the Lemsford Reserve stretch (the closest to the upstream treatment plant) has occasionally been found to fail non-statutory river quality objectives (NRA, 1994b; Copp *et al.*, 2007). Combined with surface run-off from agricultural land, the water quality of the river is typically mesotrophic. Generally consistent with the barbel zone (Huet, 1949), other fish species present (in relatively high abundance) were chub *Leuciscus cephalus*, European minnow *Phoxinus phoxinus*, gudgeon *Gobio gobio*, stone loach *Barbatula barbatula*, European bullhead *Cottus gobio* and dace *Leuciscus leuciscus*, with occasional occurrences of roach *Rutilus rutilus*, perch *Perca fluviatilis*, three-spine stickleback *Gasterosteus aculeatus* and (stocked) brown trout *Salmo trutta* (Copp and Bennetts, 1996; Pilcher and Copp, 1997; Copp *et al.*, 2005). In this part of the river, benthic invertebrates have been found to be dominated by *Baetis rhodani*, *Ephemerella ignita* and Chironomidae larvae (Copp *et al.*, 2005), and drifting invertebrates by *Caenis robusta*, *B. rhodani*, *E. ignita*, *Asellus aquaticus* and Chironomidae (Edmonds-Brown *et al.*, 2004).

> FISH COLLECTION AND MEASUREMENT

Barbus barbus were collected during 58 scheduled and incidental sampling excursions (Vilizzi *et al.*, 2006) between August 1995 and April 1999. Fish were captured using a back-pack electrofishing unit (Deka 3000: Deka-Geratebau, Rudolf Muhlenbein, VincentiusstraBe 13, 3538 Marsberg, Germany) whilst fishing in an upstream direction. Previous depletion sampling

revealed the maximum standard length (SL) size of *B. barbus* in Reach 3 to be of 450 mm (Copp and Bennetts, 1996), and more widely in the River Lee rarely exceed 500 mm (G.H. Copp, unpublished data). Upon capture, fish were measured (nearest mm) for SL, fork (FL) and total length (TL), weighed (nearest g) and examined for sex (using external features and running sexual products during the reproductive season only, typically May to July). Up to five un-regenerated scales were removed from the antero-medial region of the body immediately below the lateral line (Peňáz and Štouračová, 1991), cleaned of mucus and stored in paper envelopes for subsequent examination. In the laboratory, scales were mounted between glass slides after soaking briefly in 20% sodium hypochlorite and rinsing in distilled water. The criteria of Chugunova (1963) were followed for annulus identification, with the scales inspected with a dissecting microscope (10–20×) under transmitted light. An annulus was taken as a transition between two uninterrupted zones of closely- and widely-spaced circuli, with anastomosis as an essential criterion for identification. To ensure the consistency of age interpretation, three interpreters (A, B and C) counted annuli on the scales under study. Whenever the pattern of closely- and widely-spaced circuli could not be consistently identified the preparation was scored as ‘uninterpretable’. The interpreters were given no indication of the date of capture, length or weight of the fish.

> DATA ANALYSIS

Inter-annual variation in size structure was examined by plotting of length-frequency distributions from 1995 to 1998, with each year taken to represent the ‘growth season’ of the three ‘biological seasons’ (*i.e.* reproduction, growth, over-winter) as described by Cattaneo (2005). For *B. barbus*, the growth season (*i.e.* when fish are feeding actively) was nominally taken as starting on June 1. Annual size structures were summarised using proportional stock density (PSD), which was calculated as the ratio of quality-sized fish to stock-sized fish (cumulative sums) multiplied by 100. The following size classes (TL) were defined (Abernethy, 2006): (i) “Zero” fish (<280 mm) have little recreational value being smaller than stock size, but ecologically represent an indicator of successful recruitment (*i.e.* young-of-year and immatures, noting that male barbel generally mature at a smaller size than females); (ii) ‘Stock’ fish (280–410 mm) have a minimum size of 20–26% of the world-record length; (iii) ‘Quality’ fish (410–530 mm) fall into the 36–41% range and are generally of appeal to anglers; (iv) ‘Preferred’ (530–660 mm; 45–55%) are of even higher appeal; (v) ‘Memorable’ (660–840 mm; 59–64%) is the size most anglers remember catching; and (vi) ‘Trophy’ (>840 mm; 74–80%) is a size considered worthy of acknowledgement. Notably, the percentage ranges for each size class correspond to appropriately defined portions of the Weithman’s sigmoid curve (Gabelhouse, 1984). For each year of sampling, PSD was computed in the R language and software environment v2.14.2 (R Development Core Team, 2010) using libraries FSA and NCStats (Ogle, 2011a). Given the similarity in maximum reported size for *B. barbus* and common carp *Cyprinus carpio carpio* (www.fishbase.org), the size classes for the latter species as provided in Ogle (2011a) were extrapolated to *B. barbus*.

Bias and precision of annulus counts were analysed by statistical and graphical methods for each pair of replicate counts from the three interpreters. Accordingly, an age bias plot (Campana *et al.*, 1995) was generated and a test of symmetry (Hoenig *et al.*, 1995) computed from the corresponding age-agreement table. In this table, the main diagonal represents the frequency of fish for which the same estimated age is obtained by any combination of two interpreters, whereas each cell off the main diagonal represents a difference in estimated age between the interpreters. If there are no systematic differences between interpreters, then it is expected that the disagreements in estimated age would fall randomly on either side of the diagonal, producing an approximately symmetric age-agreement table. Precision, defined as the reproducibility of estimated ages between interpreters (Campana, 2001), was computed as percentage agreement, average percent error (APE), and by the coefficient of variation (CV). All computations were in R using libraries FSA and NCStats and following guidelines in Ogle (2011b).

Growth of *B. barbus* in the River Lee was described in terms of weight-SL (WL), SL-at-age (LAA), and weight-at-age (WAA) relationships both for the entire stock and for males and females separately. For computation of LAA and WAA relationships, the mean estimated age from the three interpreters was adjusted by taking June 1 as the nominal hatching date of each annual cohort in the sampled stock, with the final estimated age of each fish expressed as a decimal:

$$\text{age (as integer)} + (\text{days from June 1 to date of capture}) / 365.25.$$

Fitting of WL relationships and of the von Bertalanffy growth model (VBGM) to LAA and WAA data was in R using libraries FSA, NCStats and nlstools and following guidelines in Ogle (2011c,d). For the VBGM, which has been found to provide unrealistic estimates of ultimate size (Živkov *et al.*, 1999; Copp *et al.*, 2004), both the Beverton-Holt and Gallucci-Quinn parameterisations were used, the former providing estimates of SL_{inf} (or W_{inf}), k and t_0 for comparisons with other studies and the latter facilitating between-sex comparisons by means of parameter $\omega = FL_{\text{inf}} \cdot k$ (or $W_{\text{inf}} \cdot k$), which has been shown to capture the essential features of growth and to facilitate growth-rate comparisons (Charnov, 2010). For WAA growth computations, the Beverton-Holt adaptation of the VBGM was used (Ricker, 1975), but with the slope parameter fixed at $b = 3$ due to computational constraints. Following Ogle (2011d), between-sex growth comparisons were by hierarchical fitting of eight VBGMs in total under both parameterisations as follows: (i) a general model with separate parameter estimates for individuals of each sex; (ii) three models with one parameter in common between sexes; (iii) three models with two parameters in common between sexes; and (iv) one common model with the same parameter estimates for both sexes (also to account for uncertainty in sexing some individuals). After fitting of the individual models, the Akaike (AIC) and Bayesian Information Criterion (BIC) were computed to select the best-fitting model, with preference given to BIC in case of disparity of outcomes for reasons of model parsimony (Burnham and Anderson, 2003). Notably, SL was used as the reference measure for length in all growth models. This was to facilitate comparisons with other *B. barbus* stocks (see below) and because SL (or, equivalently, FL) measurements are not affected by possible damages or erosion of the lobes of the caudal fin.

Mean LAA values (combined sexes) for *B. barbus* stocks from rivers throughout England were collated from literature as well as unpublished data, with FL converted into SL whenever applicable (conversion factor as per www.fishbase.org). Both the VBGM and a log-log quadratic model (LLQM) were fitted to the LAA data for each stock (*cf.* Vilizzi and Walker, 1999; Britton *et al.*, 2012). Fitting of the VBGM was in FiSAT II v1.2.2 (www.fao.org) using a maximum SL value of 1000 mm (maximum reported length for *B. barbus*; anonymous reviewer, pers. comm.) and with a starting t_0 value ranging from -2 to 2 (or fixed at 0 in case of lack of fit). Whenever the VBGM could not be fitted because of less than seven LAA values in a stock, or due to linear (*i.e.* non-asymptotic) growth, the stock was excluded from analysis. Also, for consistency with the other stocks the VBGM was re-fitted to the River Lee *B. barbus* stock of the present study based on the mean LAA values. Fitting of the LLQM was in S-Plus 6 Professional for Windows®. The resulting VBGM and LLQM parameters for the different *B. barbus* stocks were then subjected separately to principal component analysis (PCA) following normalisation (PRIMER v6: Clarke and Gorley, 2006). Finally, for the VBGM the growth parameters φ' and ω were also computed for each stock (Živkov *et al.*, 1999; Charnov, 2010), and an overall VBGM curve was fitted to the LAA data from all available *B. barbus* stocks from England (*i.e.* including those for which a VBGM and/or a LLQM could not be fitted because of the above constraints) using the same fitting procedures as above for the R. Lee population.

RESULTS

In total, 912 *B. barbus* were captured between 1995 and 1998, of which 148 from Reach 1, 396 from Reach 2, and 368 from Reach 3. The largest size achieved was 500 mm SL, the largest weight 2000 g, and the oldest estimated age 10 years (sex unknown).

Figure 1

The three study reaches on the River Lee (Hertfordshire, England): Reach 1, extending downstream from Lemsford Reserve to Stanborough Park; Reach 2, extending from Holwell Bridge to Letty Green Bridge; and Reach 3, extending from Letty Green Bridge to the eastern extent of Woolmers Park.

Table 1

Inter-annual variation in size structure (total number and relative percentage of fish) and proportional stock density (PSD, with 95% confidence intervals) of European barbel *Barbus barbus* in the River Lee. Z = Zero; S = Stock; Q = Quality; P = Preferred; M = Memorable; T = Trophy (see text for definition of size classes). See also Figure 2.

Year	n	Size class						PSD
		Z	S	Q	P	M	T	
1995	196	76 (39)	35 (18)	81 (41)	4 (2)	0 (0)	0 (0)	71 (62–78)
1996	70	46 (64)	6 (8)	18 (25)	2 (3)	0 (0)	0 (0)	75 (55–88)
1997	321	107 (33)	79 (24)	135 (41)	8 (2)	0 (0)	0 (0)	63 (56–69)
1998	304	110 (36)	66 (21)	128 (41)	5 (2)	0 (0)	0 (0)	66 (59–72)

Length-frequency distributions for the four years of study were distinctively bimodal due to a predominance of fish in the smaller (Zero) and larger (Quality) size classes and a gap in the middle-sized (Stock) class (Figure 2). This pattern was reflected by the relative proportion of size classes in the R. Lee population (Table 1), with Quality fish being more abundant and present in identical proportions in all years except 1996, when Zero fish were predominant. Preferred fish always represented a minor proportion of the catch, and neither Memorable nor Trophy fish were ever caught. Finally, PSD was similar in 1995 and 1996, and slightly higher in those years relative to 1997 and 1998 (Table 1).

Figure 2
Size structure of *B. barbus* in the River Lee over four years of study with indication of size classes and their annual progression (0+, 1+, 2+, 3+ = age classes). Z = Zero; S = Stock; Q = Quality; P = Preferred. See also Table I.

Table II

Bias (test of symmetry) and precision of age estimates for *B. barbus* in the River Lee based on scale annulus counts from three interpreters. APE = Average Percentage Error; CV = Coefficient of Variation. Significant *P* values in bold ($\alpha = 0.05$). See also Figure 3.

Interpreters	<i>n</i>	Bias			Precision		
		<i>df</i>	χ^2	<i>P</i>	Agreement	APE	CV
A vs. B	673	28	36.87	0.122	46.51	8.49	12.01
A vs. C	687	27	52.22	0.002	44.25	9.11	12.88
B vs. C	687	26	46.05	0.009	55.36	6.57	9.29

In total, 764 scales were examined for annulus counts. The proportion of scales discarded as uninterpretable was 8.2% ($n = 58$), 12.4% ($n = 84$) and 10.1% ($n = 70$) for interpreters A, B and C, respectively. Pair-wise bias comparisons showed a tendency for interpreters B and C to over-estimate annulus counts beyond seven annuli (Figure 3), even though these differences were statistically significant only relative to interpreter C, hence not between interpreters A and B (test of symmetry: Table II). Conversely, agreement was higher between interpreters B and C, whose corresponding APE and CV values were lower relative to interpreter A vs. B and C (Table II). For this reason, choice of assigning a mean estimated age to fish based on annulus counts from all three interpreters (rather than age estimates based on one interpreter only) was deemed appropriate.

The mean estimated value for the coefficient *b* in the WL relationship was <3 , and upon comparison between sexes there was no significant difference in slopes ($P > 0.05$), although the intercept for males was larger ($P < 0.001$) than for females (Table III, Figures 4a, 4b). Growth in SL for the entire stock was asymptotic and differed between males and females, with the latter attaining a larger asymptotic SL, which was reflected by a higher growth parameter ω (Table III, Figures 4c, 4d). Growth in weight for the entire stock also was asymptotic and differed between males and females, the latter attaining a higher asymptotic weight, which was faster in early years of life (as indicated by parameter *k*) compared to males (Table III; Figures 4e, 4f).

For inter-population comparisons, mean LAA data were available for 25 English *B. barbus* stocks in total, with a maximum estimated age (scale annulus counts) of 15 years (Table IV). A VBGM could be fitted to 19 of the stocks under study, whereas a LLQM to 23 of them (Table V). Compared to other stocks, growth of *B. barbus* in the R. Lee was very fast in the first two years of life compared to most of the other stocks and was similar to that in the Severn (1974 and 2012) (Figure 5), even though growth parameters φ' and ω fell within the range of the stocks under study (Table V). The largest SL_{inf} value was achieved by the Bristol Avon stock, and the largest *k* (and ω) by the 2012 Severn stock (Table V; Figure 5). The overall VBGM for the 25 English *B. barbus* stocks resulted in the growth parameters $SL_{inf} = 567.4$ (± 21.3 SE), $k = 0.156$ (± 0.014 SE) and $t_0 = 0.518$ (± 0.140 SE) (Figure 6).

DISCUSSION

The size-class distributions of *B. barbus* in the R. Lee during the four years of study revealed a chronological progression of young fish through the Zero class in 1995 to 1997, and beginning to enter the Stock class by 1998 (Fig. 2). The Quality class of larger fish remained relatively constant, albeit with a dip in numbers overall in 1996. The apparent gap around 300–340 mm TL at the lower end of the Stock class resembles a recruitment bottleneck similar to that described for nase *Chondrostoma nasus* in regulated stretches of the upper River Rhône (Persat and Chessel, 1989). Similar to *B. barbus*, *C. nasus* is a large-bodied benthic species, and a gap in recruitment between smaller and larger size classes (extending over a range of 600 mm) was attributed to insufficient suitable habitat in the by-passed, natural stretches of the river, where a minimum discharge regime is in place for hydroelectric production (Persat and Chessel, 1989). In the upper R. Lee, the main channel is not by-passed,

Figure 3
Age-bias plots with pair-wise comparisons of *B. barbus* scale annulus counts from three interpreters. See also Table II.

Table III
Parameter estimates (with 95% lower and upper confidence intervals: LCI and UCI, respectively) for weight-length (WL), length-at-age (LAA) (standard length: SL, mm), and WAA relationships for *B. barbus* in the River Lee. For the von Bertalanffy growth model (VBGM), the Beverton-Holt (B-H) and Gallucci-Quinn (G-H) parameterisations are given for males and females. See also Figure 4.

Parameter	WL			VBGM (LAA)			VBGM (WAA)		
	Estimate	SE	LCI	UCI	Parameter	Estimate	SE	LCI	UCI
Overall					Overall				
a	-9.81	0.07	-9.95	-9.68	SL_{inf}	591.0	36.7	528.3	695.3
b	2.79	0.01	2.76	2.81	k	0.139	0.016	0.106	0.172
					t₀	-0.081	0.129	-0.360	-0.133
Sex					Sex				
a_M	-9.17	0.38	-9.93	-8.41	B-H				
a_F	-9.09	0.38	-9.90	-8.28	SL_{infM}	404.3	20.7	375.5	459.8
b	2.67	0.06	2.56	2.66	k	0.325	0.070	0.195	0.458
					t₀	0.892	0.427	-0.221	1.543
					SL_{infF}	441.5	22.0	409.4	502.1
					G-Q				
					ω_M	131.3	22.0	86.9	177.7
					k	0.325	0.070	0.183	0.470
					t₀	0.892	0.427	-0.334	1.510
					ω_F	143.4	24.0	95.6	193.8
					ω	574.6	55.7	485.8	702.6
					k_M	0.739	0.093	0.565	0.959
					t₀	2.103	0.320	1.386	2.694
					k_F	0.461	0.077	0.325	0.637

Figure 4

Growth relationships for *B. barbus* in the River Lee with estimated ages from scale annulus counts. (a, b) Weight-standard length relationship for the entire stock and for males and females separately; (c, d) Standard length-at-age based on the von Bertalanffy growth model (VBGM) for the entire stock and for males and females separately; (e, f) Weight-at-age based on the VBGM for the entire stock and for males and females separately. See also Table III.

Table IV
Mean LAA values (SL, mm) for English B. barbus stocks. Estimated ages are based on scale annulus counts. References (Ref.) are: 1) Hunt and Jones (1975), 2) Taylor et al. (2004), 3) Britton et al. (2012), 4) unpublished, and 5) present study.

ID	River	Estimated age															Ref.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1	Severn (1971)	50	115	166	216	270	298	340	399	433	502	528					1
2	Severn (1972)	55	86	125	158	191	217	242	259	278	276	289	309				1
3	Arrow	40	91	133	216	291	330	328	380	370	398	398	408	502		2	
4	Derwent	50	85	167	222	203	351	407		482	488	491	505	412	419	444	2
5	Nidd	36	76			315	329	357	430	455	469	418	419				2
6	Teme		83		209		330		371	349	424	411	488	461	449	479	2
7	Thames	42	116	194	216			415	466	471	493	532		564			2
8	Bristol Avon	41	93	145	186	206	309				367	435	470				2
9	Dane	44	99	140	186	254	298	299	330								3
10	Don			146	214	251	283	359	414	407	504	439	461	503	497	503	3
11	Ivel	48	90	134	223	296		429	397	465	429	500	527	569	554	612	3
12	Kennet		90	153	182	236	310	405	366	387	428	461	480	525	526	516	3
13	Loddon		98	152				313	427	419	458	443	470	442	441	552	3
14	Medway	37	110	161	207			361	422	476		555		515			3
15	Mole	46	81	151	207	279	347	394	431	433	388						3
16	Rother	48		183	188	289	327	341	370	391	421	399	407				3
17	Soar	50	89	188	247	299	371		434	502	454	499	454	529		569	3
18	Wey	53	93	167	265	297	371	410	434	450	446	489	459	530	525	432	3
19	Wharfe	40		198	256	283	341	368		428							3
20	Alne			206	227				555		408						4
21	Calder		218	255	282	298	339	370									4
22	Dearne		209		364	372	402	420									4
23	Severn (2012)	155				356			454	490		432	442	432			4
24	W Avon			306													4
25	Lee	112	178	206	285	331	363	381	400	396	455						5

Table V
VBGM (SL, mm) and log-log quadratic model (LLQM) parameters (with standard errors: SE) for 23 English B. barbus stocks (ID from Table IV). See also Figure 5.

ID	River	VBGM					LLQM								
		SL _{inf}	SE	k	SE	t ₀	SE	φ'	ω	a	SE	b	SE	c	SE
1	Severn (1971)	—	—	—	—	—	—	—	—	0.433	0.118	1.446	0.156	−0.161	0.050
2	Severn (1972)	—	—	—	—	—	—	—	—	0.694	0.150	1.184	0.195	−0.151	0.062
3	Arrow	517	56	0.17	0.04	0.70	0.35	4.66	87.9	−0.434	0.276	2.517	0.355	−0.497	0.111
4	Derwent	506	52	0.22	0.07	0.93	0.48	4.75	111.2	−0.274	0.454	2.388	0.569	−0.468	0.172
5	Nidd	490	102	0.24	0.10	0.90	0.34	4.76	117.6	−0.939	0.472	3.124	0.636	−0.666	0.204
6	Teme	514	43	0.18	0.05	1.04	0.48	4.68	92.5	−1.441	0.403	3.630	0.467	−0.799	0.133
7	Thames	717	80	0.13	0.03	0.63	0.24	4.82	93.2	−0.403	0.199	2.526	0.261	−0.486	0.082
8	Bristol Avon	836	268	0.07	0.04	0.41	0.40	4.69	58.5	0.200	0.213	1.674	0.277	−0.213	0.087
9	Dane	494	140	0.15	0.07	0.50	0.34	4.56	74.1	0.159	0.262	1.759	0.369	−0.268	0.126
10	Don	557	63	0.19	0.05	1.49	0.54	4.77	105.8	−1.592	0.613	3.734	0.670	−0.808	0.181
11	Ivel	748	95	0.11	0.03	0.66	0.34	4.79	82.3	0.041	0.283	1.897	0.357	−0.291	0.108
12	Kennet	640	69	0.13	0.03	0.93	0.43	4.73	83.2	−0.696	0.405	2.717	0.464	−0.525	0.131
13	Loddon	540	67	0.18	0.07	1.07	0.59	4.72	97.2	−0.869	0.556	3.013	0.654	−0.631	0.187
14	Medway	728	185	0.12	0.05	0.71	0.41	4.80	87.3	−0.392	0.237	2.421	0.311	−0.442	0.098
15	Mole	543	145	0.19	0.10	0.85	0.49	4.75	103.1	0.057	0.466	1.837	0.629	−0.263	0.206
16	Rother	475	45	0.20	0.05	0.55	0.33	4.65	95.0	−0.239	0.247	2.428	0.324	−0.503	0.103
17	Soar	600	51	0.17	0.03	0.73	0.30	4.79	102.0	−0.301	0.297	2.436	0.375	−0.474	0.115
18	Wey	529	31	0.22	0.05	0.82	0.30	4.79	116.3	−0.400	0.303	2.614	0.379	−0.543	0.115
19	Wharfe	547	57	0.18	0.04	0.55	0.17	4.73	98.4	−0.844	0.160	3.180	0.225	−0.720	0.077
21	Calder	—	—	—	—	—	—	—	—	2.408	0.373	−0.369	0.479	0.246	0.152
22	Dearne	—	—	—	—	—	—	—	—	−0.405	0.588	3.196	0.764	−0.844	0.244
23	Severn (2012)	458	54	0.35	0.21	−0.16	0.83	4.87	160.5	0.995	0.284	1.563	0.394	−0.368	0.127
24	Lee	518	64	0.18	0.05	−0.27	0.40	4.68	93.2	1.199	0.212	0.965	0.286	−0.119	0.094

Figure 5

Principal component analysis (PCA) plot for *B. barbus* stocks in England based on the VBGM (top) and LLQM (bottom) parameters (cf. Table V).

but it is interrupted throughout its course by water retention structures (*i.e.* weirs and reservoir dams), which result in *B. barbus* movements during normal discharge conditions being restricted to the confines of consecutive weirs (Vilizzi *et al.*, 2006). Tagged *B. barbus* in a concurrent study (Vilizzi *et al.*, 2006), which encompassed Reaches 2 and 3, have been recaptured both upstream and downstream of the weirs that delimit this stretch of river; drifting *B. barbus* eggs and larvae have also been reported for this same stretch of river (Copp *et al.*, 2002). These studies suggest that likely exceptions to confined movement include the downstream displacement of small *B. barbus* (over the water retention structures) during virtually all discharge rates, and the upstream movement by some larger *B. barbus* during extreme high discharge events (evinced by angler captures of tagged barbel; Vilizzi *et al.*, 2006).

As such, the present study demonstrates that recruitment problems in the R. Lee may not be due to a shortage of juvenile habitat, as originally perceived (Pilcher and Copp, 1997; Watkins *et al.*, 1997; Copp *et al.*, 2002), but rather to some other factors that affect the intermediate-sized fish, the most likely being the impediment to free movement imposed by water retention structures. Similar to *C. nasus* in the Upper Rhône (Persat and Chessel, 1989), the recruitment gap in *B. barbus* of the R. Lee could be due to larger fish occupying the entire 'suitable' habitat, leaving none for up-coming recruits, which are forced to move elsewhere in the system.

Figure 6

Overall VBGM for 25 stocks of *B. barbus* in England (cf. Table IV).

Indeed, the sensitivity of larger barbel (*i.e.* >100 mm SL) to reduced habitat was demonstrated in Reach 3, where in an earlier study a significant decrease in mean SL (from 330 to 202 mm) was observed following removal of in-stream and over-hanging branches from that reach (Copp and Bennetts, 1996). Alternatively, this gap could be an artefact of inter-annual variations in recruitment or that of the discontinuous nature of this river system, which inhibits free movement of *B. barbus*, and thus biasing perception of the overall population structure.

The present study has evaluated bias and precision of age estimates in *B. barbus*, even though Britton *et al.* (2012) utilised a quality control procedure to minimise errors in age estimation based on the evaluation of a set of scales from each individual fish. Evaluation of bias and precision in fish age-growth studies is a valuable means, *inter alia*, of comparing the skill level of one interpreter relative to that of others (Campana, 2001), and the present study indicated a tendency for two (*i.e.* B and C) of the three interpreters to count more annuli relative to those counted by the other interpreter (A). A reason for this discrepancy could be attributable to the greater experience in ageing fish by Interpreter A (LV) relative to B and C. On the other hand, it can be argued that for the same reason Interpreter A may have been inclined to take a more conservative approach due to concerns with the limitations of scales relative to other structures in ageing older fish (*e.g.* Vilizzi *et al.*, 1998; Vilizzi and Walker, 1999). This assumption for *B. barbus* remains conditional on future comparative studies that are based on different ageing structures. Clearly, validation studies of the ages of *B. barbus* in the R. Lee will help resolve these interpretability issues, even though always within the constraints of age estimates based on non-destructive techniques (*e.g.* removal of scales), as opposed to methods involving the sacrifice of fish (*e.g.* otolith extraction), due to the conservation value of *B. barbus* populations in England (Britton and Pegg, 2011; Pegg and Britton,

2011). Finally, the APE and CV values achieved in the present study, albeit higher than those reported as 'desirable' in the age-growth literature (*i.e.* APE < 5.5% and CV < 7.6%), were still in accordance with those reported for scales (Campana, 2001).

The importance of precision in the scale age estimates relates to their role in assessing the age and growth rates of the R. Lee *B. barbus* in relation to other populations. Individuals were aged to age 10 and although this suggests that *B. barbus* were capable of a relatively long life span in the river, individual barbel in other English rivers have been recorded to be at least 20 years old (Britton *et al.*, 2012). Given the number of individual fish sampled in the R. Lee, it was assumed that no age classes were missed and so 10 years is close to their maximum attainable age under those river conditions. The SL-at-age data and growth models from the R. Lee were in accordance with other UK riverine populations and also those in Europe (*e.g.* Przybylski *et al.*, 2004; Prokeš *et al.*, 2006). Nevertheless, the SL-at-age data suggested a large growth increment in the first year of life compared with other rivers, with slowing thereafter and producing a maximum theoretical length (518 mm) that whilst in the range of other populations, may still be considered relatively low. Similar to the factors affecting *B. barbus* recruitment outlined above, these growth characteristics were acquired from three reaches within a much larger river basin but may be considered symptomatic of the environmental conditions of the habitats and their disconnection, *i.e.* favourable in the initial years of life for *B. barbus* but potentially limiting thereafter.

In summary, the present study reveals that the declining *B. barbus* stocks in the R. Lee was probably related to a recruitment bottleneck surrounding the progression of the 300–340 mm SL class into larger size classes, most probably linked to insufficient available habitat for fish of that size range and in the absence of known stocking (M. Carter, pers. comm.). Juvenile growth and recruitment does not appear to be problematic and thus options for improved management of the aquatic ecosystem from a *B. barbus* perspective should consider aspects of improved longitudinal connectivity and adult habitat enhancement, rather than focusing on spawning and nursery areas.

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