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Growth and reproduction of threatened native crucian carp Carassius carassius *in small ponds of Epping Forest, south-east England*

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ABSTRACT

1. The crucian carp *Carassius carassius* is a species of cyprinid fish native to south-east England, but few studies exist on its growth and reproduction in England, and the species is threatened by introductions of its Asiatic congener, goldfish *Carassius auratus*. To increase knowledge of the crucian carp as a means of aiding its conservation, the present study assesses the growth (back-calculated length at age, body condition) and reproduction (fecundity, egg size, length and age at maturity) of crucian carp in small ponds of Epping Forest (north-east London, England).

2. Evaluation of growth and reproduction data with published data for populations from northern Europe (i.e. latitude $\geqslant 50°$) suggest that growth is very variable, even within the same area, and that data on reproductive indices, in particular length and age at maturity, are scarce. In England, the length at age trajectory of crucian carp living in sympatry with feral goldfish *Carassius auratus* did not differ significantly from allopatric crucian carp populations, but crucian carp body condition and relative fecundity (eggs per body weight) were highest, and mean age and standard length at maturity were lowest in sympatry with goldfish.

3. These data suggest that somatic growth and reproductive output may be maximized in crucian carp when confronted by coexistence with feral goldfish. However, the potential impact of goldfish introductions on crucian carp growth and reproduction requires further study, involving a much larger number of crucian carp populations, both in allopatry and sympatry with feral goldfish populations.

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KEY WORDS: endangered species conservation; sympatric compensatory growth; feral goldfish; illegal releases; acclimatization

INTRODUCTION

One of the less-well studied of the fish species native to parts of the British Isles is the crucian carp *Carassius carassius*. Indeed, until the recent papers by Copp *et al.* (2008a,b), the only known study of crucian carp biology in England was that of Marlborough (1967). The crucian carp was previously classed as non-native to the British Isles (Maitland, 1972), believed to have been introduced along with the common carp *Cyprinus carpio* in the late 15th century. However, the crucian carp was re-classified by Wheeler (1977) as native to south-east England for two reasons: (1) crucian carp pharyngeal bones were found in an archaeological site from the Roman period, which predates the known introduction of common carp in the 14th

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century (Currie, 1991); and (2) the crucian carp's pre-1960s distribution was similar to that of other, less cryptic, native freshwater fish that were known to have natural ranges limited to south-east England (Wheeler, 2000). In subsequent studies, Wheeler (1998, 2000) highlighted the threat to crucian carp posed by introductions of its Asian congener, goldfish *Carassius auratus*, which hybridizes with, and can subsequently replace, the native crucian carp (Hänfling *et al.*, 2005; Smartt, 2007). A similar threat to crucian carp, through reproductive interference, has also been reported elsewhere in Europe from introductions of congener gibel carp *C. gibelio* (Tóth *et al.*, 2005). This threat has been accentuated by the mis-identification of feral (brown) goldfish as crucian carp (Wheeler, 2000; Hickley and Chare, 2004), which raises questions about the validity of crucian carp distribution maps (Davies *et al.*, 2004; Maitland, 2004).

Despite its native status in the UK, the natural history of crucian carp in England has received little study, and this has been limited to growth (Marlborough, 1967; Copp *et al.*, 2008a,b), with age at maturity the only mention of the species' reproduction (Copp *et al.*, 2008a). Recently recognized as a threatened species (Smith and Moss, 1994; Environment Agency, 2003), the crucian carp is also of particular biological interest because populations in England represent the most western extent of the species native range. To aid in the species' conservation, the present study examines growth (back-calculated length at age, body condition) and reproduction (fecundity, egg size, length and age at maturity) of crucian carp in small ponds of Epping Forest (north-east London, England), with the latter compared with data from other native populations from comparable (northern) parts of Europe (i.e. latitude $\geqslant 50°$).

STUDY SITES

Crucian carp were collected in spring over two years (30 April and 1 May 2007; 7–8 April 2008) from four ponds in Epping Forest (Figure 1), a nature reserve area of north-east London (England) in which crucian carp is a species afforded protection by a concerted environmental management plan (Conservators of Epping Forest, 2002). Detailed descriptions of the four ponds (Hawcock Pond, Pizzole Pit Pond, Fairmeads Pond, Earl's Path Pond) are given elsewhere (Wheeler, 1998; Copp *et al.*, 2005). The ponds varied in area from 450 to 1760 m^2 (mean = 910 m^2) and water depth from 0.6 to 2.5 m (mean = 1.1 m), with some differences in aquatic and marginal vegetation. Fairmeads Pond (Lat. 51°39′02″, Long. 00°02′07″) is located in an open field, with some bushes and trees along one side of the pond. Invertebrate relative abundance (i.e. number of individuals per 3 min of pond net sampling) and species richness (i.e. number of species), measured in the week before fish sampling (using methods described in Williams *et al.*, 2003) were 871 and 30, respectively, with aquatic vegetation consisting of (in decreasing relative importance) reed mace *Typha latifolia*, yellow water lily *Nuphar lutea*, blatterwort *Utricularia* sp., Eurasian water milfoil *Myriophyllum spicatum* and 22 minor species, i.e. those < 5% (G.H. Copp, P. Williams, J. Biggs, A.S. Tarkan, M.J. Godard and K.J. Wesley, unpublished data).

Earl's Path Pond (Lat. 51°39′05″, Long. 00°02′38″) is situated within a forested area, and as such is encircled by trees; invertebrate relative abundance and species richness were 251 and 28, respectively, with aquatic vegetation consisting of the non-native New Zealand pygmyweed *Crassula helmsii*, yellow flag *Iris pseudacorus* and 15 minor species.

Hawcock Pond (Lat. 51°41′11″, Long. 00°05′10″) is located in a secluded wood about 35 m from a major road. Invertebrate relative abundance and species richness were 358 and 27, respectively, with aquatic vegetation consisting of (in decreasing relative importance) peat moss *Sphagnum* sp., sedge hop *Carex pseudocyperus*, soft rush *Juncus effuses*, reed mace *Typha latifolia*, yellow flag *Iris pseudacorus*, water mint *Mentha aquatica*, pennywort *Hydrocotyle vulgaris* and 14 minor species.

Pizzole Pit Pond (Lat. 51°40′08″, Long. 00°04′59″) is situated in the same secluded wood as Hawcock Pond, but is about 50 m from a main road. Invertebrate relative abundance and species richness were 480 and 28, respectively, with aquatic vegetation consisting of (in decreasing relative importance) common duckweed *Lemna minor*, Eurasian water milfoil *Myriophyllum spicatum*, floating pondweed *Potamogeton natans*, greater spearwort *Ranunculus lingua*, branched bur-reed *Sparganium erectum*, water mint *Mentha aquatica* and 14 minor species. In two of these ponds (Hawcock and Pizzole Pit), crucian carp was the only fish species present (i.e. allopatry), whereas in the other two ponds (Fairmeads, Earl's Path), crucian carp live in sympatry with goldfish but no other fish species were present.

METHODS

Crucian carp specimens were collected by electrofishing using a generator-powered DC electrofishing unit from a fibreglass boat powered by an electric motor, using the same protocol (equipment, speed of movement, etc.) as described in Copp *et al.* (2005). Owing to low fish numbers in Earl's Path Pond, the fish from this pond were combined with those from Fairmeads Pond, and henceforth are referred to as Earls/Fairmeads ponds. Crucian carp densities were estimated on a catch per unit effort (CPUE) basis (number of fish per 10 min) as described by Copp *et al.* (2005) from two to three 'timed' electrofishing passes. CPUEs were calculated for 2007 only, as sampling in 2008 was selective for the smaller individuals. Immediately after capture, the crucian carp were killed with an overdose of 2-phenoxyethanol, immersed in a slurry of iced water and chilled to freezing. The number of fish killed was kept to a statistical minimum in respect of the species' threatened status.

In the laboratory, the specimens were defrosted and each was measured for standard length (SL, measured from the tip of the snout to the posterior extremity of the hypurals), fork length (FL) and total length (TL) to the nearest mm and wet weight to the nearest 0.1 g. For ageing, a sample of scales was taken from the shoulder of each specimen. The fish were dissected, with gonads (if any) weighed and examined to determine sex. Females were classified as immature and mature, according to whether their ovaries contained non-yolked/indistinguishable eggs or yolked eggs, respectively. Mature ovaries were sub-sampled (0.01 g) from anterior, middle, and posterior portions of each ovarian lobe and fixed in 3.6% buffered formaldehyde. A PC-based image analysis (Aphelion, ADCIS France) with commercially available software GFA (Pilkington Image Analysis Systems London, UK) was performed for follicle counts and measurements (of yolked eggs). The fecundity of females was

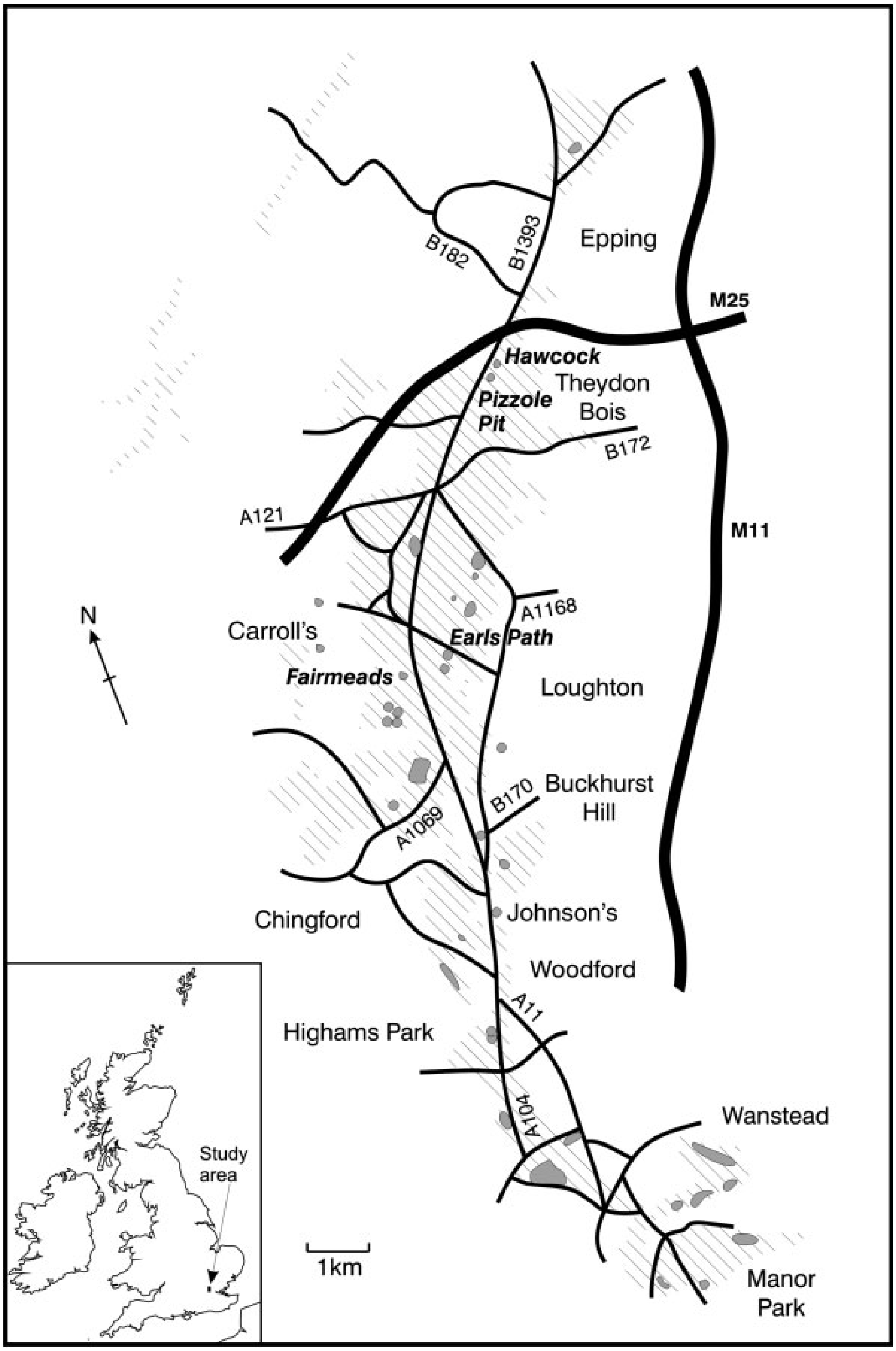

Figure 1. Map of Epping Forest (Essex, England) with the ponds studied (Hawcock, Earl's Path/Fairmeads, Pizzole Pit) labelled by name (in bold italics).

estimated gravimetrically (Bagenal, 1978): $F = GW \times D$ where F is the number of mature oocytes spawned by a female in a single spawning, GW is the weight of the ovary and D is the density of mature oocytes (number of oocytes g^{-1} of ovarian tissue).

Age determination was made by counting true annuli (after Steinmetz and Müller, 1991) using scale impressions on acetate strips, read on a micro-projector (magnification: 48× and 24×). Two independent age determinations were made by two different operators. When the results were different, an additional determination was made; if there was still disagreement, the sample was rejected. Age determinations were also validated by opercula examination for a sub-sample (10%) under a binocular microscope (20×). The annual increments of scales were measured from the focus to the posterior edge along the antero-posterior axis using 48× magnification. Linear ($R = a + b\mathrm{SL}$) and non-linear ($R = c\mathrm{SL}^d$) models, where R is scale radius, SL is fish standard length, and a, b, c, d, are constants obtained from regression analyses

(Bagenal and Tesch, 1978), were fitted to determine which equations best describe the relationship between body length and scale radius. SL at previous ages was back-calculated following three proportional methods: the scale-proportional hypothesis, the body-proportional hypothesis, and the Fraser–Lee hypothesis (Francis, 1990), but estimates from the third of these were closer to observed SLs for all pond crucian populations so it was used. Mean age and length at maturity of each population were estimated for females and males collected in April and May in 2007 and April in 2008. Age at maturity was calculated from the percentage of mature females in each age-class using the formula of DeMaster (1978), as adapted by Fox (1994):

$$\alpha = \sum_{x=0}^{w} (x)[f(x) - f(x-1)]$$

where α is the mean age of maturity, x is the age in years, $f(x)$ is the proportion of fish mature at age x, and w is the maximum age in the sample. A modified version of this formula (10 mm SL intervals in place of age-classes; Trippel and Harvey, 1987) was used to calculate mean SL at maturity. GSI (100× ovary weight/total body weight).

Non-linear (power) relationship for SL versus weight was determined using all fish data collected during the study (Ricker, 1975, 1979). Relative body condition (Le Cren, 1951) was calculated to account for variation in body condition due to size differences (Copp, 2003); $LK = w/w'$, where w is the observed body weight and w' is the expected weight as estimated from the SL-to-weight relationship ($W = a + \mathrm{SL}^b$, where in this case $a = 0.0268$ and $b = 3.1187$) using the entire data set. For relative body condition, values > 1.0 indicate that the individual is in better condition than an average individual of the same SL range, whereas LK values < 1.0 indicate that the individual is in worse condition than an average individual of the same length. Use of this index requires that populations are sampled at the same time of the year (Knaepkens *et al.*, 2002). Fish condition was also assessed by Fulton's condition (plumpness) factor ($K = w10^5 \times \mathrm{SL}^{-3}$) (Mills and Eloranta, 1985) to allow a standard comparison of crucian carp body condition between the present results and those previously published elsewhere.

Variation in sex ratio (number of males divided by the number of females) was tested by χ^2 test while differences in condition values between each population, between back-calculated lengths and observed lengths and between mean relative fecundity values of the populations were tested using Students' *t*-tests. Mean back-calculated SL values were tested for differences between ponds using the Mann–Whitney 'U' test. Simple linear regressions were used to test the relationships between fecundity, egg diameter and female SL. The equations were calculated for each sampling year and age class separately, and the slopes were compared using analysis of covariance (ANCOVA; Zar, 1999). ANCOVA was also used to compare length–length relationships of fish among the ponds. Analysis of variance (ANOVA) was used to test the null hypothesis of significant differences in fecundity, egg diameter and age-specific relative condition among age classes.

RESULTS

In total, 134 crucian carp were collected from Hawcock Pond (CPUE = 50.0), 23 specimens from Earl's Path Pond (CPUE = 1.7), 62 specimens from Pizzole Pit Pond (CPUE = 18.9) and 69 specimens from Fairmeads Pond (CPUE = 4.1) (Table 1). Sex ratio did not deviate from unity in any of the ponds (Table 2: $P > 0.05$, χ^2 values for Hawcock, Pizzole Pit and Earls/Fairmeads ponds were 0.13, 0.83 and 1.36, respectively). Maximum age in all ponds was 6–7 years.

The slopes of the relationships between SL, FL and TL of crucian carp did not differ between ponds and sexes (ANCOVA, $P > 0.05$). The growth increments in the two allopatric crucian carp populations (Hawcock and Pizzole Pit ponds) were similar (Table 1), with progressively declining growth increments as age increases. The growth trajectory for the crucian population living in sympatry with goldfish was similar, although incremental growth in older age classes declined less quickly than in the allopatric populations. These differences were supported by mean SL at age, which was significantly greater (Mann–Whitney, $P < 0.01$) in crucian from Earls/Fairmeads ponds than in Hawcock and Pizzole Pit ponds (Figure 2, Table 2). This trend of increasing crucian carp growth was not significantly correlated with invertebrate relative abundance (i.e. food availability). Le Cren's factor (*LK*) was significantly lower (Students' *t*-test, $P < 0.001$) in crucian carp from Hawcock Pond (0.93) than those from Earls/Fairmeads ponds and Pizzole Pit Pond, with crucian carp from Earls/Fairmeads ponds being significantly plumper (1.11) than those from Pizzole Pit Pond (1.01). Age-specific *LK* was significantly different between age classes (ANOVA, $P < 0.001$), increasing with age, in Earls/Fairmeads ponds (from 0.93 at age 2 to 1.20 at age 6) and Hawcock Pond (from 1.00 at age 1 to 1.81 at age 5), whereas in Pizzole Pit relative condition was not significantly different (ANOVA, $P > 0.05$) between ages, and varied between 0.99 (2 years old) and 1.20 (6 years old).

Mean age at maturity of both male and female crucian carp was later in Pizzole Pit Pond than in Hawcock and Earls/Fairmeads ponds (Table 2). The youngest mature fish were age 1+ (Pizzole Pit and Hawcock ponds), and the oldest mature male and female were age 7+ and 6+, respectively. No fish <50 mm SL (i.e. 0+ and 1+) were captured in Earls/Fairmeads ponds, and therefore the mean lengths and ages at maturity given for Earls/Fairmeads ponds are approximations (Table 2). The shortest SL at maturity was in Pizzole Pit, being a 40 mm SL female.

Mean egg diameter was 1.12 ± 0.26 mm (ranging from 0.74 to 1.32) for Pizzole Pit, 0.98 ± 0.2 (ranging from 0.76 to 1.34) for Hawcock and 1.12 ± 0.5 (ranging from 0.90 to 1.29) for Earls/Fairmeads ponds. Egg diameter was not significantly correlated (Spearman's Rank correlation test, $P > 0.05$) to SL or W for any of the crucian carp populations (Pizzole Pit $n = 27$, Earls/Fairmeads $n = 8$ and Hawcock $n = 40$). Mean absolute fecundity in mature female crucian carp was 2970 eggs (SE = 394), ranging from 408 eggs (a female of age 2+) to 9391 eggs (a female of age 6+) in Pizzole Pit, 2118 eggs (SE = 348), ranging from 402 (a female of age 2+) to 11418 eggs (a female of age 6+) in Hawcock Pond and 6643 eggs (SE = 828), ranging from 2857 eggs (a female of 3+) to 11042 eggs (a female of age 5 +) in Earls/Fairmeads ponds. Absolute fecundity and egg diameter increased with age classes in all pond populations

Table 1. Year of hatching, number of specimens (n), mean standard length (SL) in mm at capture, mean back-calculated lengths-at-age, standard error (SE), and mean annual growth increments using the scale radius to SL regression equation (linear [$R = a + b\mathrm{SL}$] and non-linear [$R = c\mathrm{SL}^d$], where R is scale radius, SL is fish standard length, and $a = 17.242$, $b = 6.6184$, $c = 0.0835$, and $d = 1.0966$) for crucian carp (males, females and juveniles combined) from Epping Forest Ponds (Essex, England) collected in April 2007. The overall means by age class are given in Table 2.

Year class	n	SL at capture		Back-calculated body lengths at age													
		SL	SE	Age 1		Age 2		Age 3		Age 4		Age 5		Age 6		Age 7	
				SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE
Hawcock Pond																	
2006	1	50.0		50.0													
2005	33	66.5	0.9	47.3	0.8	64.6	1.0										
2004	19	78.2	2.0	44.7	1.4	64.5	1.7	77.0	2.0								
2003	13	97.0	2.4	44.8	1.8	68.9	2.3	85.2	2.3	95.8	2.8						
2002	9	112.1	2.3	44.0	1.1	67.6	1.5	86.1	1.7	100.6	2.0	111.5	1.9				
2001	2	130.0	6.0	44.0	0.4	74.1	2.5	100.9	2.1	115.9	6.9	124.3	5.6	130.0	6.0		
Mean SL increment (mm)				22.3		19.4		16.8		13.8		12.1					
Earl's Path/Fairmeads ponds																	
2005	13	70.2	1.6	43.6	1.4	83.5	1.6										
2004	5	84.6	1.1	44.7	0.9	75.2	1.0	89.6	3.0								
2003	9	98.4	2.3	48.1	1.6	82.0	2.1	98.2	2.8	109.5	3.7						
2002	8	110.7	3.4	47.0	2.3	76.7	3.0	99.0	2.6	112.6	2.8	123.2	3.7				
2001	2	130.3	2.6	45.5	0.7	75.5	8.9	94.2	1.6	107.0	3.0	117.5	1.3	127.9	0.5		
2000	1	135.0		36.7	–	59.0	–	81.4	–	109.3	–	126.1	–	142.8	–	148.4	
Mean SL increment (mm)				31.0		17.2		17.1		12.6		13.1		13.0			
Pizzole Pit Pond																	
2005	4	58.5	6.0	36.9	2.0	56.8	4.6										
2004	31	73.1	1.1	34.0	0.7	55.4	0.9	71.1	1.1								
2003	8	91.1	5.0	34.4	1.8	57.5	2.9	77.6	3.6	89.4	4.3						
2002	8	104.1	3.7	38.2	2.0	61.1	2.4	75.2	2.8	90.0	3.7	103.2	3.5				
2001	1	120.0		29.4	–	59.6	–	89.8	–	103.2	–	113.3	–	120.0	–		
Mean SL increment (mm)				23.5		20.4		15.8		14.1		11.7					

(ANOVA, $P<0.001$). Mean relative fecundity was significantly higher in Earls/Fairmeads ponds (231.0 eggs $\mathrm{g}^{-1} \pm 31.0$) than in Hawcock Pond (107.8 eggs $\mathrm{g}^{-1} \pm 5.7$) and Pizzole Pit Pond (130.6 eggs $\mathrm{g}^{-1} \pm 7.8$) ($P<0.001$).

Relationships of absolute fecundity versus body size (both length and weight) differed statistically among crucian carp populations in all ponds studied (ANCOVA, $P<0.05$). In Pizzole Pit Pond, absolute fecundity (FEC) was significantly related to SL ($\mathrm{FEC} = 0.0306(\mathrm{SL})^{2.557}$, $r^2 = 0.74$, $P<0.001$, $F = 52.32$) and to weight ($\mathrm{FEC} = 176.78(\mathrm{Wt})^{0.8828}$, $r^2 = 0.78$, $P<0.05$, $F = 83.56$). These relationships were also significant for fish from Hawcock Pond ($\mathrm{FEC} = 0.0026(\mathrm{SL})^{3.0439}$, $r^2 = 0.76$, $P<0.001$, $F = 68.98$, $\mathrm{FEC} = 104.54(\mathrm{Wt})^{0.9904}$, $r^2 = 0.77$, $P<0.001$, $F = 123.04$) but not from Earls/Fairmeads ponds ($\mathrm{FEC} = 6.817(\mathrm{SL})^{1.4999}$, $r^2 = 0.49$, $P>0.05$, $F = 3.46$; $\mathrm{FEC} = 1169.7(\mathrm{Wt})^{0.4984}$, $r^2 = 0.54$, $P>0.05$, $F = 3.33$), where the range of sizes was narrow and numbers of specimens were low.

DISCUSSION

Elsewhere in Continental Europe, the growth of crucian carp has received considerable study, but in England information on reproduction remains limited (Table 2). Among-population variations in growth are quite common in fish, and this is true for crucian carp in northern latitudes (Table 2). This variability is apparent even within the same country (Table 2), such as Kuikkalampi versus Hammaslahti in Finland or Earls/Fairmeads versus Pizzole Pit and Hawcock ponds in England (Figure 2). First-year growth of crucian carp was characterized by two clusters of back-calculated values (Figure 2), with short SL values at age 1 from Finland and Poland populations. However, a few crucian carp populations in Poland (Lake Przerwanki, Sumówko) demonstrated exceptionally larger growth increments betweens ages 1 and 2 (Figure 2). However, only the Lake Przerwanki population demonstrated consistently fast growth after age 2, with the Sumówko population demonstrating a similar fast rate from age 5 onwards, whereas, in all other populations, incremental growth rates were generally similar. The growth trajectories of crucian carp populations in England were intermediate relative to populations elsewhere in Northern Europe (Figure 2), with the Earls Path/Fairmeads populations demonstrating the fastest growth recorded to date in England.

Growth variations observed in the English populations of crucian carp may simply reflect environmental differences (food availability or quality) among the ponds. However, no relationship was observed between food availability and growth, which in both crucian carp (Table 2) and goldfish (Tarkan *et al.*, unpublished data) was observed to be faster, especially with respect to older age classes, when the two species live in sympatry (in low abundance) rather than in allopatry (in higher abundance). The slowest growth of crucian carp reported for England was in Lake Bayfordbury, which contains no goldfish and a relatively low density of crucian carp (Copp *et al.*, 2008a) but food resources did not appear to be limiting (Copp *et al.*, 2008b). Co-existence of these congeners may provoke a maximization of somatic growth potential (growth rate and plumpness), which in crucian carp is known to be adversely affected by intra-specific competition when the food shortage increases (Holopainen *et al.*, 1997).

Table 2. Latitude (Lat.) in °N of water bodies in northern Europe (i.e. latitude ⩾50°N), back-calculated standard lengths (SL) at age (A), Fulton's condition index (*K*), mean SL at maturity (LaM) and mean age at maturity (AaM) and the sex ratio (males ÷ females) of crucian carp populations (males and females combined).

Location	Lat.	Mean back-calculated SL at age (mm)											Female			Male			Sex ratio	Source
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	*K*	*n*	LaM	AaM	*n*	LaM	AaM		
Earl's Path/ Fairmeads (UK)	51°39	44	75	93	110	122	135	148		–	–	3.89	40	50.0[1]	1.5[2]	51	52.5[1]	1.5[2]	1.28	Present study
Pizzole Pit Pond (UK)	51°40	35	58	78	94	108	120	–	–	–	–	3.44	34	40.0	2.1	24	50.0	2.4	0.79	Present study
Hawcock Pond (UK)	51°41	46	68	87	104	118	130	–	–	–	–	3.40	66	50.0	2.0	62	60.0	2.0	0.94	Present study
Bayfordbury Lake (UK)	51°46	38	57	74	88	101	113	121	134	142	148	3.50	–	77.5[2]	3.5	–	81.3[2]	3.3	1.30[3]	Copp *et al.* (2008a)
Lake Sumówko (PL)	51°46	35	52	71	90	112	131	143	155	171	–	–	40	–	–	44	–	–	1.1	Szczerbowski *et al.* (1997)
Lake Skopy[4] (PL)	54°06	30	43	55	64	72	81	91	102	108	–	–	–	–	–	–	–	–	–	Białokoz (1977)
Lake Pogorzelisko[4] (PL)	50°23	37	61	86	108	122	169	197	212	–	–	–	–	–	–	–	–	–	–	Białokoz (1977)
Olsztyn pond-A[5] (PL)	53°47	24	41	55	66	77	89	109	135	–	–	–	–	–	–	–	–	–	–	Skrzydlo (1977)
Olsztyn pond-B[5] (PL)	53°47	20	36	51	65	76	87	101	–	–	–	–	–	50.0	2.0	–	51.0	2.0	0.30	Szczerbowski *et al.* (1997)
Lake Przerwanki (PL)[5]	54°08	36	77	118	151	176	198	216	230	224	–	–	–	–	–	–	–	–	–	Ciepielewski (1967)
Lake Bimbinek (PL)[5]	54°17	33	60	85	120	157	192	–	–	–	–	–	–	–	–	–	–	–	–	Zawisza and Antosiak (1961)
Lake Arklickie (PL)[5]	54°17	33	62	89	119	157	181	217	–	–	–	–	–	–	–	–	–	–	–	Zawisza and Antosiak (1961)
Lake Oswin (PL)[5]	54°17	32	62	90	117	143	182	–	–	–	–	–	–	–	–	–	–	–	–	Zawisza and Antosiak (1961)
Glubokoye/ Andreyevskiy (RU)[6]	55°45	18	45	71	100	128	152	174	194	212	–	–	–	*14.5*	*4–5*	–	14.5	4.5	–	Dmitriyeva (1957)
Kur'kovskiy Pond (RU)[6]	55°45	16	37	62	87	106	–	–	–	–	–	–	–	*14.5*	*4–5*	–	14.5	4.5	–	Dmitriyeva (1957)
Hermanninlampi (SF)	62°39	28	45	63	82	90	105	121	–	–	–	–	–	–	*3–4*	–	–	–	–	Holopainen and Pitkänen (1985)
Kuikkalampi (SF)	62°39	24	42	53	62	73	82	87	–	–	–	–	–	–	–	–	–	–	–	Holopainen and Pitkänen (1985)
Hammaslahti (SF)	62°39	41	77	88	–	–	–	–	–	–	–	–	–	–	*>3.0*	–	–	–	–	Holopainen and Pitkänen (1985)

[1] No fish <50 mm SL were captured, so LaM value assumes that 50% of fish of 40–49 mm SL were mature (i.e. the mean of the estimates if fish in this size class were 0% and 100% mature, respectively).

[2] No fish of age 0+ or 1+ were captured, so AaM value assumes 50% of age 1 fish were mature (i.e. the mean of the estimates when age 1 fish are at 100% mature, respectively).

[3] Sex ratio (calculated from original data) deviated significantly ($\chi^2 = 11.31$; $P<0.001$) from unity.

[4] Data for female fish only, latitude given for nearest known town.

[5] Mean for male and female values reported by Szczerbowski *et al.* (1997), with Lake Bimbinek assumed to be near other two lakes, hence same latitude.

[6] Data for ages 1–3 from Andreyevskiy Pond are combined with those of Glubokoye Lake due to low sample under and similar SLs at age, values for SL and LaM were estimated from 'body length' using the conversion factor 0.965 (N. Bogutskaya, pers. comm.), with the same value given for males and females, as the original text does not specify the sex.

However, there would be many factors likely to affect fish population growth rates, such as population density, food availability, pond ecosystem succession status, and local water temperatures. Temperature has been demonstrated as particularly important in the early growth of crucian carp (Laurila *et al.*, 1987), although in some populations it has been found to correlate with body condition (plumpness) but not juvenile growth (Copp *et al.*, 2008b). Therefore, the observed patterns require further investigation, with particular attention to temperature effects.

From the limited information on crucian carp reproduction, the onset of maturation in English populations appears to resemble that reported elsewhere in Northern Europe, occurring in the second year of life for both sexes. This is consistent with results of Szczerbowski *et al.* (1997) for water bodies (Lake Sumówko and Forest ponds) in Poland (Szczerbowski *et al.*, 1997) as well as for crucian carp in Bayfordbury Lake, which is <30 km north of the Epping Forest ponds. In Bayfordbury Lake, mature females were reported at age 2+ and virtually all females mature by age 3+ (Copp *et al.*, 2008a), although the specimens were sampled too late in the year to assess length and age at maturity. In Turkey, which is the southernmost extent of the species' introduced range, age 2+ has also been the reported age at maturity for the species (Becer *et al.*, 1998; Çetinkaya *et al.*, 1999). This consistent age at maturity across a wide latitudinal range contrasts with the much wider range of ages at maturity observed in both native (Mann *et al.*, 1984) and non-native species (Copp and Fox, 2007) of fish in Europe. Of particular note is the fact that age at maturity appears to be later than in goldfish of Epping Forest ponds, which consistently had ages at maturity <2.0 (Tarkan *et al.*, unpublished data).

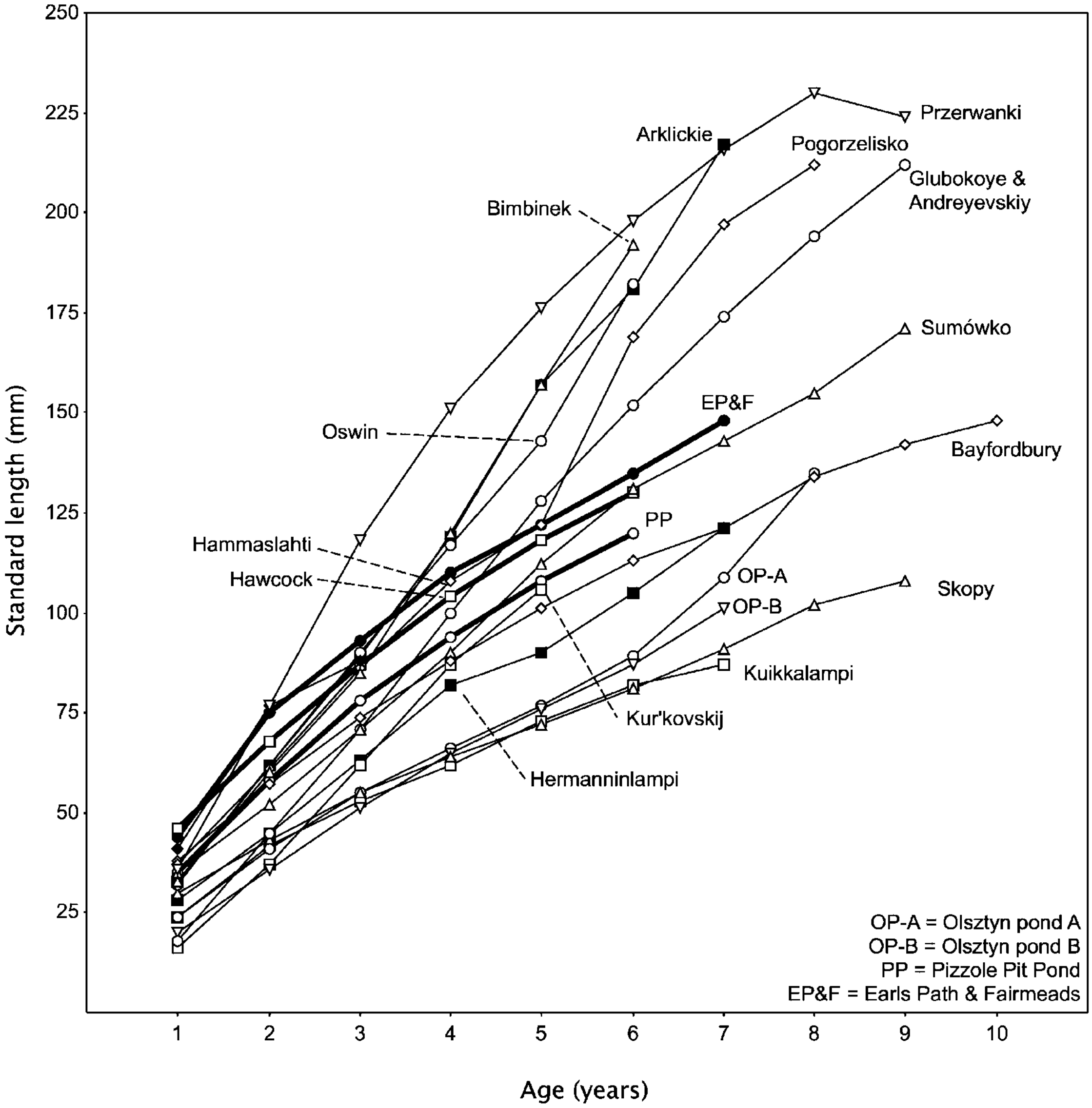

Figure 2. Mean back-calculated standard length at age of crucian carp *Carassius carassius* populations from the study ponds in England (Hawcock, Earl's Path/Fairmeads, Pizzole Pit) and from elsewhere in the introduced range (see Table 2 for site details).

The relative fecundity estimates for crucian carp populations in Hawcock and Pizzole Pit ponds are similar to those reported in Finland (Moisander, 1991), but the value from Earls/Fairmeads ponds was twice as high as the Finnish and that in the other English ponds. Moisander (1991) reported a higher relative fecundity value in a lake population (129.2 eggs g^{-1}) with piscivorous fish than a pond population (83.2 eggs g^{-1}) without. This suggests that presence of piscivorous fish, by foraging on small-bodied crucian carp, may lead the dominance of higher number of large-bodied crucian carp in the lake. Because fecundity and body size are positively correlated (see also Pihu, 1961), this could result in higher fecundities in the population. Piscivorous fish were absent in the Epping Forest ponds, but herons *Ardea cinerea* are known to prey on the fish in these ponds (Copp *et al*., 2005). In the present study, the higher fecundity of crucian carp in Earls/Fairmeads ponds may be the result of low fish densities and large fish body size (Table 2). Egg diameter was not significantly correlated with body size and the present values were similar to those reported elsewhere (Moisander, 1991; Holopainen *et al*., 1997).

To conclude, these data suggest that crucian carp is well suited to the relatively benign climate of England, despite being at the westernmost extent of the species' native range. Crucian carp populations have been known to be eliminated when common carp, goldfish and gibel carp are introduced, either through reproductive interference or habitat degradation and alterations to aquatic ecosystem food web and function (Wheeler, 2000; Navodaru *et al*., 2002; Hänfling *et al*., 2005; Tóth *et al*., 2005; Vetemaa *et al*., 2005; Gaygusuz *et al*., 2007; Smartt, 2007). The crucian carp populations in the present study were characterized by early maturation, intermediate growth, with some possible evidence for growth maximization in populations living in sympatry with the feral goldfish populations. The data suggest that crucian carp growth may not be easily affected by the presence of goldfish, but crucian carp reproduction may be more precocious (shorter length and younger age at maturity, Table 2). The principal threat to crucian carp of goldfish introductions therefore appears to be genetic contamination (Wheeler, 2000; Hänfling *et al*., 2005; Smartt, 2007). However, these provisional conclusions require a caveat for small sample size, given the preliminary nature of the present study. The potential impact of goldfish introductions on crucian carp growth and reproduction requires further study, involving a much larger number of crucian carp populations both in allopatry and sympatry with goldfish populations.

Taking the precautionary approach, crucian carp should be the subject of conservation measures as part of pond management plans and floodplain rehabilitation strategies for enhancing and maintaining aquatic biodiversity (Copp *et al*., 2008b). An example of this can be seen in the management plan for the 150+ ponds of Epping Forest in the north-east part of the city of London (Conservators of Epping Forest, 2002). Most of Epping Forest is registered as a Site of Special Scientific Interest (SSSI), and ponds within the Forest are rehabilitated on a rotation basis, including the removal of accumulated sediments to abate eutrophication and terrestrialization processes (Conservators of Epping Forest, 2002). As recommended by Copp *et al.* (2005) and consistent with the present study, crucian carp populations established in ponds situated at greater distances from public access routes (roads, pathways, car parks, fairground sites) are subject to regular monitoring and maintenance (removal of any non-native species observed) so as to enhance the chances of maintaining genetically pure self-sustaining populations. Similarly, the protection of local crucian carp genetic integrity is being enhanced through the stocking of rehabilitated ponds, selected for their greater distance from public access routes, using genetically-confirmed source populations. One such pond was stocked with crucian carp from Hawcock during 2007, and the results of a recent survey indicate successful reproduction in 2008 (K.J. Wesley, M.J. Godard and G.H. Copp, unpublished data).

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