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Growth and reproduction of introduced goldfish *Carassius auratus* in small ponds of southeast England with and without native crucian carp *Carassius carassius*

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Summary

The ornamental Asiatic species, goldfish *Carassius auratus*, was introduced to open waters of the UK in the late 17th century. The species reproduces readily in small ponds and threatens native species, in particular crucian carp *Carassius carassius*, but surprisingly there are no known published studies on the growth and reproduction of feral pond populations of this species in the UK and relatively few elsewhere. The aim of the present study was to assess the growth (back-calculated length at age), body condition and reproduction (fecundity, egg size, length and age at maturity) of goldfish living in small ponds of Epping Forest (northeast London, England), either alone (allopatry) or with (sympatry) native crucian carp, in order to provide the necessary background information to inform the risk assessment of this non-native fish species. Growth increments in the allopatric goldfish populations were similar, with progressively declining growth increments with increasing age. This contrasts with goldfish living in sympatry with crucian carp *Carassius carassius*, where growth increments remained high for ages 1–2, 2–3 and 3–4. Body condition values varied little, but goldfish living in allopatry had significantly greater condition than those living in sympatry with crucian carp. Sexual maturity was achieved by at least some age 1+ fish in all populations, with young mean ages (1.0–1.7 years) and short mean standard lengths (50.0–63.4 mm SL) at maturity in females relative to an introduced population in Italy (2.1 years and 139.2 mm SL, respectively). The results are discussed within the context of life-history theory.

Introduction

The introduction of non-native ornamental fishes has a long history in the United Kingdom (UK) (Copp et al., 2007), with the introduction of the Asian cyprinid, goldfish *Carassius auratus* L., having occurred in 1694 (Lever, 2009). Goldfish were initially held in aquaria and later introduced to ornamental 'estate' ponds, but releases (or escapes) to the wild (Copp et al., 2005b) do not appear to be a new phenomenon (West, 1910). The species now occurs throughout the UK (Davies et al., 2004; Maitland, 2004; Copp et al., 2007), largely due to the release of unwanted pet fish (Andrews, 1990; Wheeler, 1998; Copp et al., 2005b). A major contributor to this wide distribution has been misidentification of *Carassius* species. The natural brown variety of goldfish has been accidentally stocked into many waters because is has been mistaken for its congener crucian carp *Carassius carassius* L., which is native to southeast England (Wheeler, 1977, 2000; Hickley and Chare, 2004). Goldfish have subsequently become a commonly encountered species in public ponds in both urban and rural settings (Wheeler, 1998; Copp et al., 2005b) and the species is also found in water courses (Hickley and Chare, 2004), with the highest proportion of records (for water courses) during the 1990s (Copp et al., 2006). There are a number of goldfish varieties available for sale in the UK, with at least five varieties identified in Copp et al. (2005b) as being associated with ponds close to roads, footpaths and habitations. Therefore, the genetic composition of feral goldfish progeny found in ponds is likely to represent a mixture of at least two or more varieties, with hybrids with congener crucian carp and with common carp *Cyprinus carpio* also being a common occurrence (Wheeler, 1998; Copp et al., 2005b; Hänfling et al., 2005).

Characteristic of many invasive fish species, the goldfish is an omnivorous forager, with a diet that includes planktonic crustaceans, phytoplankton, insect larvae, fish eggs and larvae, benthic vegetation, and detritus (Scott and Crossman, 1973; Maitland, 2004). As in other cyprinids, goldfish growth is influenced by temperature, food availability and genetic variability (Mitchell, 1979; Wootton, 1990), and like other *Carassius* species, feeding activity is expected to decrease with decreasing water temperature (Penttinen and Holopainen, 1992). The goldfish is reported to be a very robust species, able to withstand environmental stressors, including fluctuations in water temperature (e.g. Spotila et al., 1979) and declines in water transparency and oxygen levels (e.g. Rowe, 2007). It has also been reported to benefit from environmental disturbances to the receiving water bodies (Morgan and Beatty, 2007).

Perhaps as a consequence of its long history in the UK (Lever, 2009), the goldfish is not mentioned in UK legislation that deals with non-native species (e.g. the 'Wildlife and Countryside Act 1981') and as such the species is 'exempt' from controls under the 'Import of Live Fish Act 1980' and subsequent orders (see Copp et al., 2005a). Despite this long history, feral goldfish have received no study in the UK other than as experimental model species (e.g. Smartt, 2007) and indeed relatively little attention elsewhere in its introduced ranges in southern Europe (Lorenzoni et al., 2007), Asia Minor

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(İzci, 2004; Patimar, 2009), Canada (Munkittrick and Leatherland, 1984) and Australia (Mitchell, 1979; Morgan and Beatty, 2007; Rowe, 2007; Baumgartner et al., 2008).

A particular problem with the genus *Carassius* is species determination (Wheeler, 2000; Hickley and Chare, 2004). For example, specimens of gibel carp *Carassius gibelio* (see Kottelat, 1997) are sometimes mistakenly referred to as goldfish. Indeed, there is much confusion in the literature on the *Carassius* species, with the common name 'goldfish' attributed incorrectly to *C. gibelio*. Similarly both 'golden carp' (e.g. Mitchell, 1979) and more commonly 'crucian carp' (mainly in translated papers) have been used inappropriately for *C. auratus*. However, the goldfish is not known to possess the gynogenetic reproductive capabilities of the gibel carp (e.g. Vetemaa et al., 2005), and there are now morphological means of distinguishing the species.

Published research on feral goldfish is restricted to southern Europe (Lorenzoni et al., 2007), Asia Minor (İzci, 2004; Patimar, 2009), Canada (Munkittrick and Leatherland, 1984) and an increasing number from Australia (Mitchell, 1979; Morgan and Beatty, 2007; Rowe, 2007; Baumgartner et al., 2008), with there being no previous papers on the growth and reproduction of feral goldfish from the more northern latitudes of Europe. The aim of the present study was to examine the environmental biology of feral goldfish in the more northerly ponds of eastern England, which lie at latitude 51°N. The specific objectives were to: (i) assess the age-specific growth and body condition of pond-dwelling populations of feral goldfish; (ii) evaluate the species' reproductive traits (fecundity, egg diameter, length and age at maturity) in UK ponds; and (iii) compare the results, where possible, with data from native and introduced locations using literature sources that have been verified as dealing with goldfish *Carassius auratus*. The present study constitutes one of three related papers on the environmental biology of *Carassius* species in six 'natural' ponds of Epping Forest, Essex (England). The first paper examined the age and growth of native crucian carp *Carassius carassius* in four ponds, two containing feral goldfish and two ponds without (Tarkan et al., 2009), and the present study is the natural complement, examining the environmental biology of goldfish in two ponds containing crucian carp and two ponds without. The third paper endeavours to assess the impact of feral goldfish on the growth and reproduction of crucian carp and on the recipient pond ecosystems through detailed assessment of the aquatic plants and invertebrates of the six ponds (Copp *et al*., 2010).

Material and methods

Goldfish were collected on 30 April and 1 May 2007 from four ponds in Epping Forest (Fig. 1), an area of northeast London (England) that is subject to a common environmental management plan (Conservators of Epping Forest, 2002). Detailed descriptions of the four ponds (Fairmead, Earl's Path, Carrolls, and Johnsons ponds) are given in Wheeler (1998), with some additional detail in Copp et al. (2005b) and Tarkan et al. (2009). The ponds varied in surface area from 450 to 1760 m^2 (mean = 910 m^2) and in water depth from 0.6 to 2.5 m (mean = 1.1 m), with some differences in aquatic and margin vegetation.

Fairmead Pond (51′39″02°N; 00′02″07°E) is located in an open field, with some bushes and trees along one side of the pond. Invertebrate relative abundance and species richness (i.e. no. of species), measured in the week prior to fish sampling (using methods described in Williams et al., 2003) were 871 and 30, respectively. Aquatic vegetation consisted 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 (Copp *et al*., 2010).

Earl's Path Pond (51′39″05°N; 00′02″38°E) is situated within a forested area, and as such is encircled by trees; invertebrate relative abundance and species richness were 251 and 28, respectively. Aquatic vegetation consisted of the non-native New Zealand pygmyweed *Crassula helmsii*, yellow flag *Iris pseudacorus* and 15 minor species (Copp *et al*., 2010).

Carrolls Pond (51′39″07°N; 00′00″23°E) is located between a forested area, a private residence and a road; invertebrate relative abundance and species richness were 522 and 23, respectively. Aquatic vegetation consisted of reed mace, non-native rush *Juncus inflexus*, yellow flag and 11 minor species (Copp *et al*., 2010).

Johnsons Pond (51′36″34°; 00′01″19°E) is situated in an open field area adjacent to a main road, opposite commercial shops; invertebrate relative abundance and species richness were 224 and 34, respectively, and due to over-grazing by Canada goose *Branta canadensis*, aquatic vegetation was sparse, consisting of *Juncus inflexus*, yellow flag, reed mace, creeping bentgrass *Agrostis stolonifera* and four minor species (Copp *et al*., 2010). In two of these ponds (Carrolls, Johnsons), goldfish is the only fish species (i.e. allopatry), whereas in the other two ponds (Fairmead, Earl's Path), goldfish live in sympatry with crucian carp. No other fish species were present in these ponds.

Fish were collected by electrofishing from a fiberglass, electric motor-powered boat using the catch per unit effort (CPUE) sampling strategy (i.e. fish per minute electrofishing; see Copp et al., 2005b). Immediately after capture, the goldfish were killed with an overdose of 2-phenoxyethanol, immersed in a slurry of iced water and chilled to freezing.

In the laboratory, the fish were defrosted and individually measured for standard length (SL) to the nearest mm and weighed (W) to the nearest 0.1 g. A sample of scales for aging was taken from a standard area between the lateral line and dorsal fin of the fish. Gonads were removed, weighed and examined to determine sex. Females with ovaries containing non-yolked or indistinguishable eggs were classified as immature, and those with ovaries containing yolked eggs (even if spent) were classified as mature. All ovaries were weighed to the nearest 0.1 g and three sub-samples were taken from each gonads (from anterior, middle and posterior region) and each sub-sample was about 106 mg (the actually size of the sampling tube of PCA image analysis system). Samples were fixed in 3.6% buffered formaldehyde. To test whether the ovaries were homogenous with respect to follicle diameter and density (number of follicles per gram of ovary), samples were taken from anterior, middle, and posterior pieces. The estimation of fecundity was based on the gravimetric method (Bagenal, 1978). Follicle counts of sub-samples and measurements were performed using the PC-based image analysis system Aphelion (ADCIS, France), with commercially available software GFA (Pilkington Image Analysis Systems).

Age was determined as described by Steinmetz and Müller (1991) using scale impressions on acetate strips, read on a micro-projector (magnification: 48× and 24×), with age determination cross-checked using independent readings by a second reader. Age readings were validated by examination of the opercula of 10% of the sample under a binocular microscope (20×). Linear and non-linear models were fitted to determine what equations best describe the relationship between body length and scale radius. The body-scale relationship was best described by a power function. Hence, the lengths were back-calculated with the equation $L_i = (S_i/S_c)^b \times L_c$, where L_i is the standard length of fish at age i, L_c the standard length of fish at capture, S_i the radius of scale at age i and S_c the radius of scale at capture (Bagenal and Tesch, 1978). SL at previous ages was back-calculated by the body-proportional hypothesis (Francis, 1990) as no significant differences were found between the estimates and the observed size (Students' *t*-test, P > 0.05). Mean age at maturity and gonadosomatic index (GSI = 100 × ovary weight / total body weight) of each population were estimated for only those females collected. Age at maturity was calculated from the percentage of mature females in each age-class using the formula of DeMaster (1978):

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

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 TL intervals in place of age-classes; Trippel and Harvey, 1987) was used to calculate mean TL at maturity.

As per Ricker (1975, 1979), the linear relationship for TL vs weight was determined using data from all fish collected. To account for variation in body condition due to size differences, relative body condition was calculated as in Copp (2003) using the formula of Le Cren (1951), which requires populations to be sampled at the same time of year: $K = w/w'$, where w is the observed weight of each individual and w' is the expected weight using the length-weight relationship ($W = a + L^b$, where in this case $a = 0.0425$ and $b = 2.962$). K values > 1 or < 1 indicate that the individual is in better or worse condition, respectively, than the average individual of the same SL range.

Relationships between fecundity, egg diameter and female SL were tested using non-linear (power curve) regressions. The equations were calculated for each sampling location and age class separately, and the slopes were compared using analysis of covariance (ANCOVA; Zar, 1999). Analysis of variance (ANOVA) was used to test the null hypothesis of significant differences in fecundity and egg diameter among age classes (Zar, 1999). Note that the assessment of fecundity was limited to a few specimens from Earl's Path / Fairmead and Johnsons ponds because at the time of sampling most individuals of the populations were already spent. Therefore, all available fecundity values were combined for proper comparisons. ANCOVA was also used to compare length-length relationships of fish among the ponds. Differences in sex ratio (number of males divided by the number of females) and condition were tested using the chi-squared and Students' *t*-tests, respectively.

Results

A total of 222 goldfish specimens were collected from Carrolls Pond (CPUE = 10.09 individuals / min), 181 specimens from Earl's Path Pond (CPUE = 3.02), 34 specimens from Johnsons Pond (CPUE = 0.48) and four specimens from Fairmead Pond (CPUE = 0.06). Owing to low fish specimen numbers in Fairmead Pond, these fish were combined with those of Earl's Path Pond, and from now are referred to as Earl's Path / Fairmead ponds (Table 1). In Carrolls and Earl's Path / Fairmead ponds, sex ratios did not deviate from unity ($\chi^2 = 0.015$, P > 0.05), but in Johnsons Pond a significantly higher proportion of males was observed ($\chi^2 = 7.53$, P < 0.01, Table 2). Maximum age in all ponds was 5–6 years.

In longitudinal body growth, the slopes of the relationships between SL, FL and TL of goldfish did not differ between ponds and sexes (ANCOVA, P > 0.05). The growth increments of individuals in the allopatric goldfish ponds (Carrolls, Johnsons) were similar (Table 1), with progressively declining growth increments as age increase. This contrasts with the goldfish living in sympatry with crucian carp, where growth increments remained high for ages 1–2, 2–3 and 3–4. These differences are reflected in the shorter mean lengths at age (Mann–Whitney, P < 0.01) in Carrolls and Johnsons ponds relative to Earl's Path / Fairmead ponds (Fig. 2, Table 2). This trend of increasing crucian carp growth was not significantly correlated with invertebrate relative abundance (i.e. food availability) ($r^2 = 0.04$, P < 0.001). Condition values of individual fish varied between 4.02 and 4.46, with goldfish in Johnsons Pond being significantly larger than those in Earl's Path / Fairmead ponds (Students' *t*-test, P < 0.001).

Sexual maturity was achieved by at least some age 1+ fish in all populations, with the oldest mature females being age 5+ (Table 2). The youngest estimated mean age at maturity (in both males and females) was observed in Earl's Path / Fairmead ponds (Table 2). No fish of < 50 mm SL (i.e. 0+ and 1+) were captured in Johnsons Pond, and all individuals captured were mature.

Mean egg diameter was 1.00 ± 0.14 mm (ranging from 0.81 to 1.22) and no differences in mean egg diameter were observed between age classes (ANOVA, P > 0.05). Egg diameter was not significantly correlated (Spearman's Rank correlation test, P > 0.05) to SL or W for any of the goldfish populations (Carrolls n = 24, Earl's Path / Fairmead n = 7, Johnsons n = 6). Mean fecundity in mature female goldfish was 12 783 eggs (SE = 2 090), ranging from 1491 (a female of age 1+ from Carrolls Pond) to 52 033 eggs (a female of age 5+ from Johnsons Pond), and tended to increase with age classes in all pond populations but most remarkably in Carrolls Pond (ANOVA, P < 0.001). Mean relative fecundity was 270 eggs g^{-1} (SE = 23.5).

Relationships between fecundity and body size (both length and weight) differed statistically among goldfish populations for all ponds studied (ANCOVA, P < 0.05) with the exception of fecundity vs SL between Johnsons and Earl's Path / Fairmead ponds (ANCOVA, P > 0.05). In Carrolls Pond, linear regression analysis revealed a significant relationship between fecundity (FEC) and SL ($FEC = 0.0012(SL)^{3.4261}$, $r^2 = 0.74$, P < 0.0001, $F = 40.79$) and weight ($FEC = 137.49(W)^{1.1142}$, $r^2 = 0.77$ P < 0.05, $F = 76.28$). These relationships were also significant for Johnsons Pond ($FEC = 0.0182(SL)^{2.9275}$, $r^2 = 0.90$, P < 0.0001, $F = 16.27$; $FEC = 355.63(W)^{0.9446}$, $r^2 = 0.97$, P < 0.001, $F = 137.79$), whereas in Earl's Path / Fairmead ponds these relationships were not significant ($FEC = 8 \times 10^{-10}(SL)^{5.6818}$, $r^2 = 0.45$, P > 0.05, $F = 4.32$; $FEC = 251.13(W)^{0.1343}$, $r^2 = 0.27$, P > 0.05, $F = 2.11$).

Discussion

The paucity of information on the environmental biology of feral goldfish populations is apparent from our extensive review of the literature (Table 2). European populations show a relatively early maturity, and growth appears to be variable,

Table 1
For goldfish *Carassius auratus* (males, females and juveniles combined) from ponds in Epping Forest (Essex, England) collected on 30 April 2007 and 1 May, the 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 TL regression equation. The overall means by age class are given in Table 2

Year		SL at capture		Back-calculated lengths at age (in mm) Age 1		Age 2		Age 3		Age 4		Age 5		Age 6	
Class	n	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE
Earl's Path / Fairmead ponds															
2007	20	45.4	0.7												
2006	84	67.7	1.6	60.1	1.0										
2005	20	99.0	1.8	57.9	1.5	98.2	1.6								
2004	7	121.3	1.2	59.4	1.7	94.9	3.3	117.0	2.3						
2003	2	169.0	4.5	49.4	6.6	90.3	16.7	139.8	2.1	169.0					
2002	2	195.0	2.5	50.9	13.8	87.0	26.1	132.5	21.1	168.8	13.0	191.8			
Mean SL increment (mm)				37.0		37.2		39.2		22.9					
Carrolls pond															
2006	11	53.5	2.8	47.6	2.4										
2005	40	76.8	3.0	45.5	1.5	73.8	2.8								
2004	34	112.3	2.2	49.0	1.7	91.4	2.9	111.2	2.2						
2003	12	133.6	3.8	49.1	1.3	90.8	3.2	115.1	2.6	129.2	2.7				
2002	5	151.0	5.9	47.2	2.2	90.7	5.3	121.8	5.8	141.2	5.7	154.6	5.8		
2001	1	154.0		47.8		84.9		105.6		131.9		144.6		154.0	
Mean SL increment (mm)				38.6		27.1		20.7	15.5	4.4					
Johnsons pond															
2006	1	52.0		52.0C											
2005	4	79.8	5.0	46.8	2.7	81.5	5.1								
2004	7	97.1	3.3	46.6	3.9	80.8	4.0	98.5	3.5						
2003	18	122.5	3.0	41.7	1.9	79.3	2.9	103.9	3.1	120.7	3.0				
2002	3	141.7	1.7	44.4	2.7	86.2	3.2	110.3	4.6	126.6	3.9	139.9	3.0		
2001	1	155.0		50.7		78.9		108.9		129.3		146.5		155.0	
Mean SL increment (mm)				34.3		24.1		20.1		17.7		11.8			

Table 2
Latitude (Lat.), back-calculated total lengths (SL in mm) at age (A) for both sexes combined, Fulton's condition index (*K*) for which all SEs were < 0.20, mean SL at maturity (LaM) and mean age at maturity (AaM) and sex ratio (no. males ÷ no. females) of introduced goldfish *Carassius auratus* populations from various sources: 1) present study, small ponds; 2) Munkittrick and Leatherland (1984), a pond of 200 × 60 m; 3) Lorenzoni et al. (2007), with detailed information provided by M. Lorenzoni; 4) İzci (2004); 5) Patimar (2009); 6) Mitchell (1979), a backwater of the River Murray at Cobdogla, the Millbrook Reservoir and a small farm dam at Uraidla; 7) Morgan and Beatty (2007), with mean values for both sexes calculated from the reported data

Water body	Lat.	Mean back-calculated SL at age A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	*K*	Females n	LaM	AaM	Males n	LaM	AaM	Sex ratio	Source
Carrolls pond	51°39′N	48	86	113	134	150	154					4.06	105	63.4	1.7	101	54.1	1.4	0.96	(1)
Earl's Path / Fairmead	51°39′N	56	93	130	169	192	–					4.02	65	54.2	1.2	66	56.1	1.1	1.01	(1)
Johnsons pond	51°36′N	47	81	105	126	143	155					4.46	9	*50.0*[1]	1.0	25	*65.0*[2]	*1.5*[3]	2.78	(1)
Cambridge (Canada)	43°21′N	–	68	127	148	186	–	–	–	–	–	–	42	–	–	16	–	–	0.38	(2)
Lake Trasimeno (Italy)	43°09′N	88	138	197	245	276	–	–	–	–	–	–	732	139.2	2.1	44	105.9	0.4	0.06	(3)
Lake Eğirdir (Turkey)	37°80′N	172	196	233	268	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(4)
Alma-Gol wetland (Iran)	37°23′N	–	–	–	–	–	–	–					561			56			0.10	(5)
Ala-Gol wetland (Iran)	37°21′N	–	–	–	–	–	–	–					545			43			0.08	(5)
Cobdogla (Australia)	30°14′S	89	129	183	238	253	260	269	275	280	291	–	–	–	–	–	–	–	–	(6)
River Vasse (Australia)	33°42′S	183	258	315	348	357	366	–	–	–	–	–	–	–	–	–	–	–	–	(7)
Uraidla (Australia)	34°48′S	55	76	93	101	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(6)
Millbrook (Australia)	34°49′S	117	147	232	250	266	277	301	324	335	344	–	–	–	–	–	–	–	–	(6)

[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 < 50 mm SL were captured, so LaM value assumes that 50% of fish were mature in each of the missing SL classes (40–49, 50–59, 60–69, 70–79 mm), which is effectively the mean of the estimates if fish in each size class were 0 and 100% mature, respectively.
[3]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 0 and at 100% mature, respectively).

even at similar latitudes (Table 2), such as Earl's Path / Fairmead vs Carrolls and Johnsons ponds in England, or Uraidla vs Millbrook in Australia (Fig. 2). Equally variable is sex ratio, with some populations dominated by females in most cases and in one case by males (Table 2). These variations may be due to either environmental conditions or to the length of time since introduction. In gibel carp (*C. gibelio*), Vetemaa et al. (2005) reported near unity sex ratios in mildly saline waters but

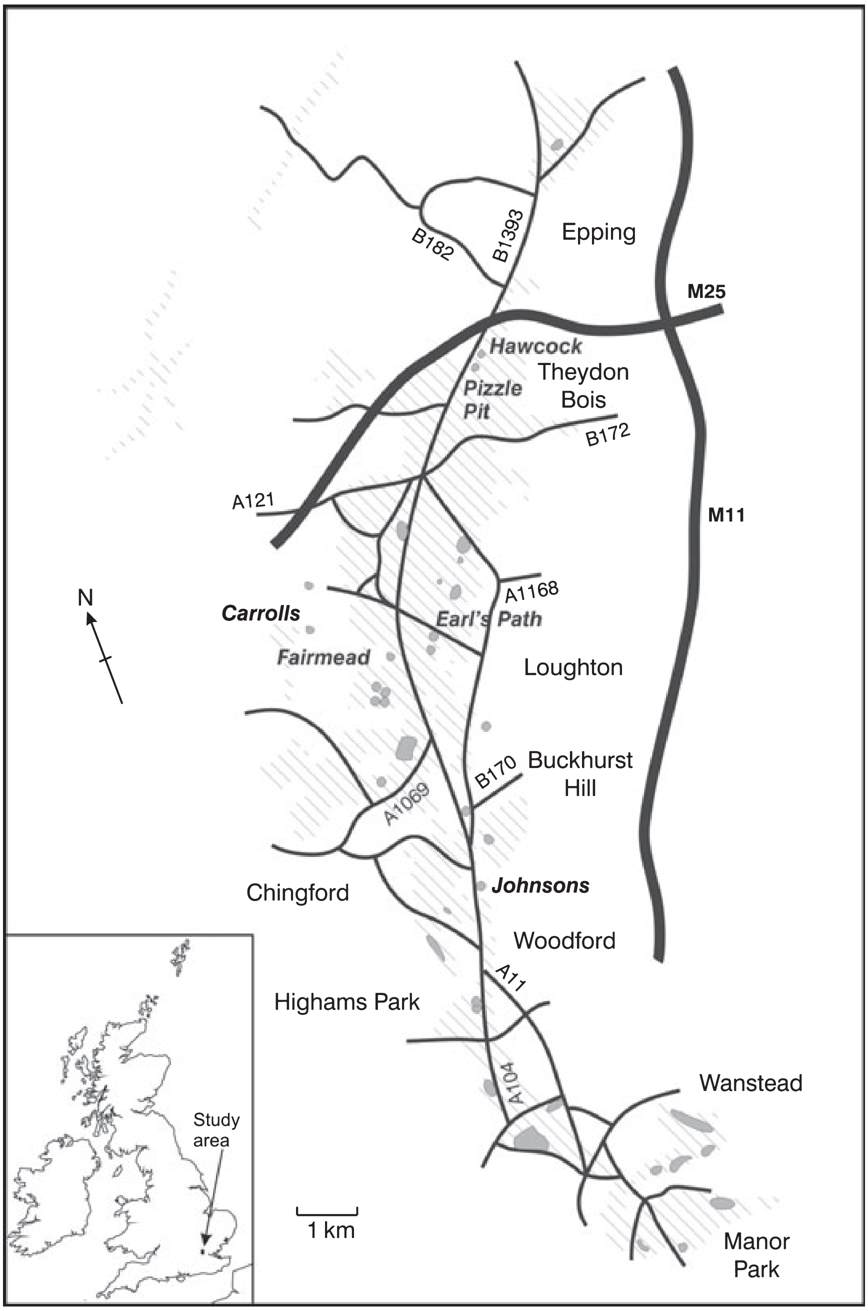

Fig. 1. Map of Epping Forest (Essex, England) with the studied ponds (Carrolls, Earl's Path, Fairmead, Johnsons) labeled by name (in bold italics)

a predominance of females (and gynogenetic reproduction) in freshwater populations. Whereas, the gibel carp population invading the middle River Danube was initially dominated by females (i.e. gynogenetic; Černý and Sommer, 1994) but shifted to sexual reproduction within a decade of their appearance (J. Černý, pers. comm.). The variations in goldfish sex ratio however cannot be due to gynogenetic reproduction, which is not known in this species, whereas the populations predominated by females (Table 2) are restricted to countries where goldfish were introduced within the last 100–150 years, e.g. the late 19th century for both Canada (Scott and Crossman, 1973) and Australia (Mitchell, 1979). This contrasts the goldfish populations in England, which derive from multiple introductions over many years, beginning at least as early as the 1690s (Lever, 2009).

Among-population variations in growth are common in fishes, and this is apparent in the available data for feral goldfish populations both in England and elsewhere (Table 2). The slowest growing goldfish population was at Uraidla (Australia), followed by those in England and Canada, with the fastest growth observed in Turkey and River Vase (Australia) (Fig. 2). The length at age of goldfish growth in the English ponds that also contained crucian carp (Earl's Path ⁄ Fairmead) were faster, and the condition factor lower, especially in ages 3+ and older. This may reflect a phenotypic response, (e.g. growth potential maximization) in goldfish when faced with a competing congener (crucian carp), or simply among-pond differences in food availability. There were non-significant trends of increasing goldfish growth with increasing invertebrate relative abundance in the Epping Forest ponds, however the number of goldfish populations was too low and other factors (e.g. surrounding environment, pond ecological succession status, presence or absence of crucian carp), to draw conclusions at this time.

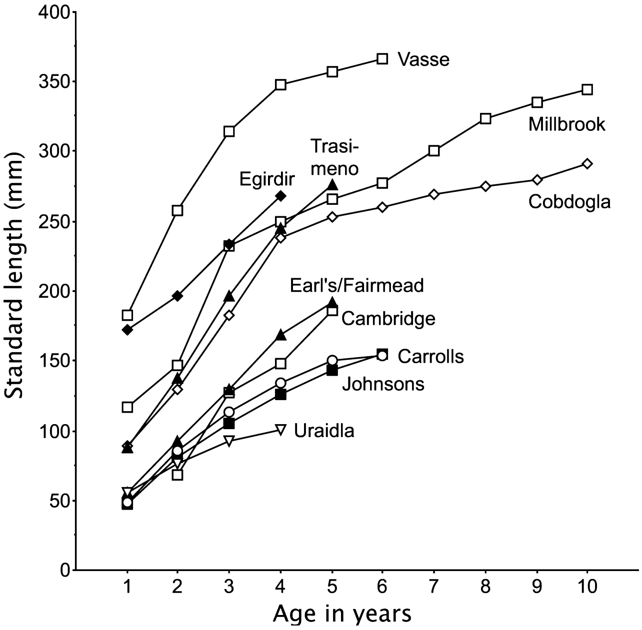

Fig. 2. Mean back-calculated standard length at age of feral goldfish *Carassius auratus* populations from the study ponds in England (Carrolls, Earl's Path ⁄ Fairmead, Johnsons) and from elsewhere in the introduced range (details in Table 2)

Piscivorous fishes were absent in the Epping Forest ponds, but herons *Ardea cinerea* are known to prey on goldfish in these ponds (Copp et al., 2005b), and predation pressure has been demonstrated to have a strong influence on body size in the goldfish congener species, crucian carp (e.g. Holopainen et al., 1991). Predation may also be a contributing factor (İzci, 2004) in the fast growth of goldfish in the warm waters of Egirdir Lake (Turkey), which contains the obligate piscivore, pikeperch *Sander lucioperca*. However, predators are absent in the fast growing Australian goldfish populations (Mitchell, 1979; Morgan and Beatty, 2007) as well as in Lake Trasimeno, Italy (Lorenzoni et al., 2007), which suggests that predation is not a primary factor in determining goldfish growth rates.

Life-history theory (Atkinson, 1994) predicts that ectotherm organisms will experience faster juvenile growth, precocious maturity, and shorter life-span, in response to elevated water temperatures. Therefore, the slow-growing goldfish populations in England should demonstrate delayed maturity, but the contrary was observed (Table 2). The mean age at maturity was below that observed in Lake Trasimeno (Italy), which experiences summer water temperatures ≥ 30°C (Lorenzoni et al., 2007). Mean egg diameter in the English populations was smaller and less variable (mean = 1.00, SE = 0.14 mm) than reported by Lorenzoni et al. (2007) for goldfish in Lake Trasimeno (mean = 1.27, SE = 0.1 mm; minimum = 0.74, maximum = 1.71). However, mean relative fecundity was higher and more variable in English goldfish populations (mean = 270, SE = 23.5 eggs g^{-1}) than that reported by Lorenzoni et al. (2007) (mean = 103, SE = 5 eggs g^{-1}). Higher egg production and smaller egg size in the pond populations of goldfish may be attributed to trade off between these two traits.

In conclusion, feral goldfish populations in England demonstrated early maturity and slow growth, with some possible evidence for growth maximization in populations living in sympatry with the native crucian carp. In light of reported declines in native cyprinid fish species, in particular crucian carp, following the introduction of non-native *Carassisus* species (Navodaru et al., 2002; Hänfling et al., 2005; Gaygusuz et al., 2007), future research on feral goldfish should endeavour to expand the database on growth and reproduction in native and introduced populations as well as to assess the potential impacts of these introductions to aquatic ecosystem food webs and ecosystem function (e.g. Navodaru et al., 2002; Copp *et al.*, 2010).

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