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Recovery of the crucian carp *Carassius carassius* (L.): Approach and early results of an English conservation project

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Abstract

1. The crucian carp *Carassius carassius*, a cyprinid fish characteristic of small ponds, is in decline throughout most of its European range, including in England where it is currently thought to be non-native.
2. The present study, undertaken by the Norfolk Crucian Project, reports on reductions in pond populations of crucian carp in Norfolk, eastern England as well as the success of recent introduction/re-introduction efforts in terms of crucian survival, recruitment and growth over the last 10 years.
3. A 72% decline in crucian carp distribution was observed between the 1950s–1980s and the 2010s. Of 18 crucian carp introductions/re-introductions to restored and suitable existing ponds, 17 were successful in terms of survival, increasing the number of current crucian sites in Norfolk by 37%. Recruitment of young crucian carp was demonstrated for 12 of the 18 stocked ponds, with apparent elevated juvenile growth relative to other English and European populations.
4. Delays in, or a lack of, crucian recruitment in some ponds appeared to result from the presence of other fish species (especially threespine stickleback *Gasterosteus aculeatus*) with predation and interspecific competition possible contributory factors.
5. This study shows that, through combinations of pond rehabilitation and stocking, it has been possible to achieve a substantial recovery of crucian carp populations in the study region. Although the crucian carp is currently presumed to be non-native within England, given other scientific studies that show a lack of adverse impacts of this species on native biota, and because it is greatly threatened in its native range, the call is sounded for more crucian carp conservation projects in other parts of England as well as in Europe more generally.

KEYWORDS

agriculture, fish growth, fish recruitment, fish re-introduction, *Gasterosteus aculeatus*, pond restoration, rare species

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1 | INTRODUCTION

The crucian carp *Carassius carassius* (L.) is a small, benthic-feeding cyprinid fish generally associated with still-water ecosystems, especially small ponds and river backwaters (Copp, 1989; Hohausová & Jurajda, 2005; Wheeler, 1998). It is widely distributed in northern and central Europe (Holopainen, Tonn, & Paszkowski, 1997; Lelek, 1980), including Great Britain (GB). However, the native range of the crucian carp in GB has been the subject of debate. Based on its predominant easterly distribution in England (Marlborough, 1966), which closely matches that of other British freshwater fish species thought to be native, such as silver bream *Blicca bjoerka* (L.), burbot *Lota lota* (L.) and spined loach *Corbitis taenia* (L.), combined with the discovery of crucian pharyngeal bones in deposits dating to the Roman era at an archaeological site in London (Jones, 1978; Lever, 1977), Wheeler (1977, 2000) concluded that the crucian carp was probably a native British species. However, owing to its absence in early British natural history literature, both Maitland (1972) and Rolfe (2010) considered the species to be non-native. Recent genetic research (Jeffries et al., 2017) for south-east England suggests that the crucian carp is likely non-native and supports the idea of a mediaeval introduction, although it is recognized that native status cannot be ruled out, with one scenario being an early crucian carp extinction in eastern England, followed by a more recent fifteenth-century introduction (Jeffries et al., 2017). To be definitive on this later scenario, older fossil evidence is required, but is currently lacking.

Throughout much of its native European range the crucian carp is believed to be threatened, with reference to decreasing populations in various areas, including the Danube Delta (Navodaru, Buijse, & Staras, 2002; Schiemer & Spindler, 2006), Poland (Witkowski & Grabowska, 2012), Finland (Holopainen & Oikari, 1992) and the Czech Republic (Lusk, Lusková, & Hanel, 2010). Research in GB has also revealed a substantial reduction of crucian carp distribution in its traditional, albeit introduced, stronghold in south-east England (Sayer et al., 2011). Although the crucian carp is classified on the IUCN Red List of Threatened Species as a species of 'Least Concern', this is accompanied by the caveat of a 'Declining' current population trend because of distribution contractions in its native range (IUCN, 2008). Hence, a clear need has been identified for European-wide conservation efforts to help protect the crucian carp from further decline.

Known causes of crucian carp decline across its range are many and include habitat loss linked to river regulation and the consequent disappearance of floodplain lakes and backwaters (Schwevers, Adam, & Gumpinger, 1999), pond infilling as a result of agricultural land-grabbing and urbanization (Wheeler, 2000) and pond terrestrialization (Sayer et al., 2011, 2013). In addition, genetic contamination and enhanced competition from non-native gibel carp *Carassius gibelio*, goldfish *Carassius auratus* and common carp *Cyprinus carpio* (Hänfling, Bolton, Harley, & Carvalho, 2005; Smartt, 2007; Wouters, Janson, Lusková, & Olsén, 2012) are thought to be of key importance, with gibel carp a particular threat to crucians in mainland Europe but not in England where it is currently absent. In the eastern English county of Norfolk (the focus for this study), woody vegetation

encroachment and consequent pond terrestrialization has been identified as the key factor in the decline of crucian carp populations in farmland ponds, with additional factors being pond desiccation caused by drought, hybridization with goldfish and common carp and predation by native introduced northern pike *Esox lucius* (Sayer et al., 2011).

Despite its recent reclassification as most likely to be non-native in GB, this region has initiated some of Europe's earliest crucian carp conservation projects. For example, a programme of pond rehabilitation, goldfish eradication and crucian carp stocking began in the 1990s in the conservation area of Epping Forest (Greater London area, south-east England) to protect the species (Conservators of Epping Forest, 2002; Copp, Wesley, & Vilizzi, 2005; Tarkan, Copp, Zięba, Godard, & Cucherousset, 2009). Similarly, in eastern England the Norfolk Crucian Project (NCP) was initiated in 2008 after which the crucian carp was designated as a local Biodiversity Action Plan (BAP) species in Norfolk (Copp & Sayer, 2010). Significantly influenced by these initiatives, a GB-wide National Crucian Conservation Project was established in 2014 (Copp & Sayer, in press), with a strong focus on the promotion of crucian carp angling, as well as conservation.

Given the infancy of crucian carp conservation, it is important that early research findings are highlighted so that future European projects might benefit from the knowledge gained, including successes and failures. The present study covers the first 10 years of NCP initiatives in relation to the Norfolk crucian carp BAP, especially the key aim of 'increasing the number of viable populations' (Copp & Sayer, 2010). A major focus of the NCP has been to estimate the degree of crucian carp decline, including the causes of its disappearance. In a survey of 40 ponds known to have supported crucians in the 1970s–1980s, a decline of $\approx 72\%$ in crucian distribution was reported (Sayer et al., 2011). Subsequently, the NCP applied a two-step conservation approach: (i) a search for surviving crucian populations to encourage their protection; and (ii) rehabilitation of currently highly terrestrialized, former crucian carp ponds by scrub and sediment removal (Sayer et al., 2013), combined with the re-introduction of crucians to these or other suitable ponds using genetically pure local source populations.

The aim of this article is to report on the NCP's initial progress, including updated information on the extent and causes of the recent crucian carp decline in Norfolk since the 1950s–1980s, and on the outcome of crucian conservation efforts over the last 10 years with particular regard to fish growth and recruitment following introductions/re-introductions. The importance and potential ramifications of the NCP's progress with respect to crucian conservation in GB and more widely in Europe are also discussed.

2 | MATERIALS AND METHODS

2.1 | Study area and site selection

Norfolk is a low-lying (<100 m a.s.l.), predominantly agricultural, region of eastern England. Climatically Norfolk is mild and dry with a mean annual rainfall of 600–700 mm and mean daily maximum temperatures in the ranges 6–8 and 20–23°C during the winter and

summer months, respectively. The region currently supports more than 22,000 ponds (Alderton, 2016) most of which are marl and clay pits and livestock watering ponds dating to the eighteenth and nineteenth centuries (Prince, 1964; Sayer et al., 2013). Ponds were selected for a site visit and further investigation if they were found to meet two criteria as follows: (i) known occurrence of crucian carp in the recent past, especially during the 1950s–1980s; and (ii) known occurrence of fish (even if unknown species) in the recent past. To evaluate these criteria, discussions were held with landowners, farmers and local anglers on the environmental and fish histories of Norfolk ponds, including on past pond drying and management events and on fish kills and fish introductions. In particular, efforts were made to acquire responses from local people who were actively angling for crucian carp in Norfolk ponds during the 1950s–1980s. All individuals encountered who provided information on the historical occurrence of crucian carp were able to demonstrate (to C. D. Sayer) the ability to make accurate distinctions between crucian carp, goldfish and common carp and associated hybrids. These determinations were made either from photographs or from live specimens captured in the field. As additional verification, fish in several ponds identified by local people as containing the species during the 1950s–1980s were found to be true crucian carp, suggesting accurate identification abilities.

Of the 154 ponds believed to have supported crucian carp in the 1950s–1980s, 26 ponds were not sampled either because the ponds were highly overgrown by trees and scrub (>90% canopy shading), making sampling impossible and crucian carp presence highly unlikely ($n = 4$), or because the pond was known to dry up regularly owing to local drainage changes or natural pond succession and terrestrialization ($n = 14$), or because the pond had been recently filled in as a result of agricultural land-grabbing or local development ($n = 8$).

The remaining 128 ponds included in this study were mostly small (generally <50 m maximum diameter), shallow (generally <1 m) and highly alkaline (typically >100 mg CaCO₃ L⁻¹). Local pond settings ranged from arable fields (including ponds in open field and hedge-side positions) to meadows and (in a few cases) coniferous and deciduous woodland.

2.2 | Fish and environmental sampling

Fish surveys of the 128 ponds deemed as possible sites for contemporary crucian carp occurrence were undertaken during 2008–2019, with some ponds surveyed in multiple years to facilitate studies of crucian population dynamics, growth and reproduction (Tarkan et al., 2016), genetic character (Jeffries et al., 2016, 2017) and comparisons with eDNA-based survey (Harper et al., 2018).

Fish were captured using double-ended fyke nets, fitted with otter guards, during spring (March–April) and on two occasions in autumn (October 2008 and 2009). These seasonal intervals tend to avoid both elevated water temperatures and in turn the typical period of crucian carp spawning (May–July; Aho & Holopainen, 2000), thus minimizing the stresses placed upon fish while in the fyke nets. Fyke nets were deployed overnight (≈16 h) and positioned so that they

bisected the maximum dimension of the pond. In this way the number of fyke net ends used was generally proportional to pond size. This approach provided catch-per-unit-effort (CPUE) estimates of relative fish densities (i.e. number of fishes captured per fyke net end per 16 h exposure). Captured fish were transferred to large plastic buckets (garden trugs) containing freshly collected pond water, with many buckets used for large catches to ensure fish welfare. All captured fish species were identified to species level and counted. For crucian carp, all individuals, or a random sample equivalent to 100–150 specimens in the case of large catches, were weighed to the nearest 0.1 g (wet mass) and measured as total length (TL) to the nearest 1 mm. Scale samples were collected from all weighed and measured fish from the area between the lateral line and dorsal fin and stored in paper envelopes in a cool, dry room for subsequent determination of age and growth.

2.3 | Crucian carp stocking

During 2010–2016, crucian carp were stocked into 18 ponds, 10, six and two of which were re-introductions to recently restored ponds, introductions to other suitable ponds and introductions to newly excavated ponds, respectively (Table 1). For introductions/re-introductions of crucian carp to ponds, fish were taken from two or three local (same river catchment) donor ponds known from previous surveys to contain harvestable populations of genetically pure crucian carp (Jeffries et al., 2017). A total of 30–60 crucian carp were selected for release into each recipient pond with an equal number of individuals taken from each donor population. Selected fish were all >89 mm TL and hence assessed to be sexually mature based on size at maturity data for the study region (Tarkan et al., 2016).

Re-surveys of stocked ponds were generally undertaken after two years allowing sufficient time for juvenile fish to attain a catchable size. In the case of the three initial introductions undertaken in 2010, however, fyke net surveys were undertaken after one year. For seven ponds (nos 2, 24, 27, 47, 71, 87, 95, 131) sampling was also undertaken in subsequent years to monitor the populations, and in the case of three ponds showing a lack of juvenile recruitment (nos 27, 95, 131), to check for subsequent reproductive success (Table 1). The occurrence of juvenile fish in the stocked ponds was assessed for each sampling occasion using fish TL data, with fish smaller than any introduced fish (<89 mm TL) assumed to have originated in that pond as a result of successful spawning and recruitment.

2.4 | Fish ageing

Assessments of crucian carp growth among newly recruited and stocked adult fish (termed 'original fish' hereafter) were made for five stocked pond populations (nos 24, 71, 87, 98 and 99). Fish scales were aged for a minimum of 100 fish in each pond using a compound microscope (Leica ICC50HD) and a dissecting microscope fitted with a Zeiss AxioCam ERC5s camera. Scales were flattened

TABLE 1 Crucian carp re-introductions/introductions as part of the Norfolk Crucian Project 2011–2019, with data given on crucian carp presence between 1950 and 1980 (indicated as: Y = Yes, N = No, N[†] = new pond, U = unknown) and pond character (M Cov = macrophyte cover %)

Pond information		Stocking		Year 1		Year 2		Year 3		Year 4		Year 5		Year 6		Year 7													
Pond No.	Present	Area (m ²)	Max. depth (cm)	M Cov (%)	Other species (%)	Date of stocking	No.	S	R	N	Y	N	Y	N	Y	N	Y	CPUE	No.	CPUE	No.	CPUE	No.	CPUE	No.	CPUE	No.	CPUE	No.
27	Y	1800	120	90	Ga	3/2011	30	Y	N	7	0.7	8	0.62	n.s.	-	6	0.60	4	0.33	n.s.	-	22	1.80 ^a						
24	Y	550	200	85	-	3/2011	30	Y	Y	2	0.5	68	11.30	n.s.	-	131	21.80	82	13.70	n.s.	-	108	13.50						
47	Y	2,400	240	5	Rr, Tt, Se	3/2011	30	Y	Y	0	0	2	0.33	n.s.	-	1	0.17	1	0.70	n.s.	-	106	17.70						
71	N	375	100	100	-	3/2011	30	Y	Y	n.s.	-	46	11.50	n.s.	-	487	121.80	n.s.	-	358	89.50	n.s.	-						
87	N [†]	700	150	100	Se, Pf	3/2011	30	Y	Y	n.s.	-	69	11.50	18	2.25	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-				
98	N	600	120	95	-	4/2013	50	Y	Y	n.s.	-	251	31.40	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-				
99	N	120	120	15	Tt	4/2013	50	Y	Y	n.s.	-	104	26.00	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-	n.s.	-				
95	N [†]	400	200	100	-	4/2013	50	Y	Y	n.s.	-	5	1.67	1	0.33	n.s.	-	n.s.	-	n.s.	-	102	12.80	-	-				
2	Y	820	160	80	-	7/2014	60	Y	Y	n.s.	-	37	6.20	100	17.00	n.s.	-	46	8.00	-	-	-	-	-	-				
68	N	525	120	85	-	4/2015	50	Y	Y	n.s.	-	5	0.83	n.s.	-	3	0.50	-	-	-	-	-	-	-	-				
122	U	4,000	100	100	-	4/2015	50	Y	Y	n.s.	-	205	15.70	n.s.	-	n.s.	-	-	-	-	-	-	-	-	-				
4	Y	2,655	120	70	Pf, El, Rr, Tt	4/2015	50	N	N	n.s.	-	0	n.s.	-	n.s.	-	-	-	-	-	-	-	-	-	-				
31	Y	2,400	120	85	Rr	3/2016	40	Y	Y	n.s.	-	78	6.50	n.s.	-	-	-	-	-	-	-	-	-	-	-				
44	Y	880	80	50	Ga	3/2016	40	Y	N	n.s.	-	3	0.75	n.s.	-	-	-	-	-	-	-	-	-	-	-				
85	Y	225	140	85	-	3/2016	40	Y	N	n.s.	-	1	0.30	n.s.	-	-	-	-	-	-	-	-	-	-	-				
16	Y	370	240	90	Ga, Se, Rr	3/2016	40	Y	N	n.s.	-	6	1.00	n.s.	-	-	-	-	-	-	-	-	-	-	-				
134	N	4,500	130	2	-	4/2016	60	Y	Y	n.s.	-	55	4.60	n.s.	-	-	-	-	-	-	-	-	-	-	-				
92	Y	200	100	100	-	4/2016	50	Y	N	n.s.	-	18	3.00	n.s.	-	-	-	-	-	-	-	-	-	-	-				

Note: Other sp. refers to the other fish species (fish codes: Ga, *Gasterosteus aculeatus*; Rr, *Rutilus rutilus*; Tt, *Tinca tinca*; Se, *Scardinius erythrophthalmus*; Pf, *Perca fluviatilis*; El, *Esox lucius*) present at the time of crucian carp stocking with stocking information given as: date of stocking (month/year) and number of fish stocked (no.). Whether crucian carp survived (S) and recruited (R) post-stocking is given as Y (Yes) and N (No). Numbers of crucian carp captured (No.) and crucian catch-per-unit-effort (CPUE) in post-stocking surveys are given with bold type highlighting the presence of juvenile fish indicative of successful recruitment.

Abbreviation: n.s. = not sampled.

^aCPUE increased owing to a 2017 stocking of juvenile fish undertaken by the Environment Agency.

between microscope slides and all scales (typically $n = 4-5$) from each fish were viewed (Britton, 2007). On occasions where a fish sample consisted entirely of replacement scales, that individual was removed from the dataset. The camera attached to the dissecting microscope was coupled with image analysis software (AxioVision Rel. 4.8lnk) and a calibrated measuring tool was used to determine the scale radius (R) and radius of annuli from the scale focus to either the dorsal or ventral edge along the dorso-ventral axis. These measurements were used for back-calculating TL at age. Both non-linear and linear equations were fitted to all TL and R data to determine the model that best described the relationship between TL and R (Bagenal & Tesch, 1978). The best fit body-scale relationship was linear and consequently the Fraser-Lee equation was used to back-calculate TL at age (Francis, 1990), as used successfully in previous studies of crucian carp growth (Tarkan et al., 2009, 2016). This equation takes the form:

$$Lt = c + (TLc - c)(St/R)$$

where Lt is the TL when annulus t was formed, TLc is TL at capture, St is the distance from scale focus to the annulus t and R is the scale radius. Finally, c (27.911) is the y-intercept on the TL axis in its linear regression with R ($TL = 3.347 \times R + 27.911$, $R^2 = 0.674$, $P < 0.001$, $n = 501$). Thus, the overall intercept c acts as a 'weighting factor' to reduce bias resulting from differences in the size distribution of the examined populations (for this procedure see Tarkan et al., 2016).

Second-year growth, calculated as the difference between first- and second-year fish TL, was chosen as a means of comparing crucian carp growth between ponds as it is considered to be a good overall estimator of juvenile growth (Tarkan et al., 2009; Tarkan, Gaygusuz, Godard, & Copp, 2011). To make an assessment of the general suitability of eastern England for crucian carp growth, crucian carp TL at age 2 for the present study was compared with available data for this measure from previous multi-pond studies undertaken in Norfolk ($n = 16$; Tarkan et al., 2016), Hertfordshire ($n = 3$; Tarkan et al., 2011, 2016) and Essex ($n = 4$; Tarkan et al., 2009) in south-east England and with the comparable (latitude $\geq 50^\circ$) European countries of Poland ($n = 11$; Białokoz, 1977; Ciepiewski, 1967; Skrzydło, 1977; Szczerbowski, Zakeś, Łuczyński, & Szkudlarek, 1997; Zawisza & Antosiak, 1961), Russia ($n = 2$; Dmitriyeva, 1957) and Finland ($n = 3$; Holopainen & Pitkänen, 1985).

Original stocked fish in all five studied stocked ponds were identified from the age of the fish and the known date of introduction. Point of stocking was identified in the life of the fish and the absolute growth rate (AGR) a year before and a year after stocking was calculated with the equation:

$$AGR = (Lt - Li)/t$$

where Lt is the final fish length, Li is the initial fish length and t is time in years. The AGR is a widely accepted method for comparing results in fish growth studies (Lugert, Thaller, Tetens, Schulz, & Krieter, 2016).

2.5 | Data analysis

Data for all original fish from the ponds were grouped together and \log_{10} -transformed for normality after a Kolmogorov-Smirnov test was run on the data. A paired Student's t -test was used to compare the growth of original fish one year before and one year after stocking. Only original fish with at least two years of growth (since hatching) prior to stocking and two years of growth after stocking were used to ensure sufficiently comparable data.

To aid in the interpretation of patterns in crucian carp second-year growth, a multiple linear-regression model was applied to measures of percentage macrophyte cover (for macrophyte survey methods see Sayer et al., 2012), pond size (m^2), year-class strength, calculated as the percentage frequency of each year class (Tarkan et al., 2011) and crucian carp CPUE. A forced-entry method was applied in which all parameters entered into the model were not given a hierarchy. All analyses were undertaken in SPSS version 24. The Durbin-Watson test was applied to examine the assumption of autocorrelation in model residuals. A value >2 indicates a negative correlation, whereas a value <2 indicates a positive correlation. Multi-collinearity was tested using the variance inflation factor, which indicates whether a predictor has a strong linear relationship with other predictors.

Comparisons of second-year crucian carp growth between Norfolk stocked ponds as well as TL at age two among Norfolk stocked pond crucians and pond populations from other parts of England and Europe were made by permutational univariate analysis of variance (PERANOVA), based on a one fixed-factor design in each case following normalization of the data and using a Euclidean dissimilarity measure. A distance matrix was subjected to 9,999 permutations of the raw data and tested for significance including *a posteriori* pair-wise comparisons (PERMANOVA+ version 1.0.1 for PRIMER version 6; Anderson, Gorley, & Clarke, 2008). The advantage of PERANOVA over traditional parametric analysis of variance is that the stringent assumptions of normality and homoscedasticity in the data, as typical of a fully parametric ANOVA, and which very often prove unrealistic when dealing with real-world ecological datasets, are significantly relaxed (Anderson & Robinson, 2001).

3 | RESULTS

3.1 | Crucian carp decline in Norfolk

Based on interviews and information provided by local stakeholders, 102 ponds in the study area are known to have contained crucian carp populations during the 1950-1980s (Figure 1). Our surveys showed that 27% of these ponds retained crucian carp into the present day with crucians also found in two ponds where the species was not recorded during the 1950s-1980s owing to more recent stocking events in the 1990s. This indicates a 72% decline in crucian carp distribution over the last 40-70 years. Of the 29 crucian-supporting ponds, five also contained goldfish, seven contained common carp (including wild carp, mirror carp and koi carp varieties) and six and five ponds, respectively,

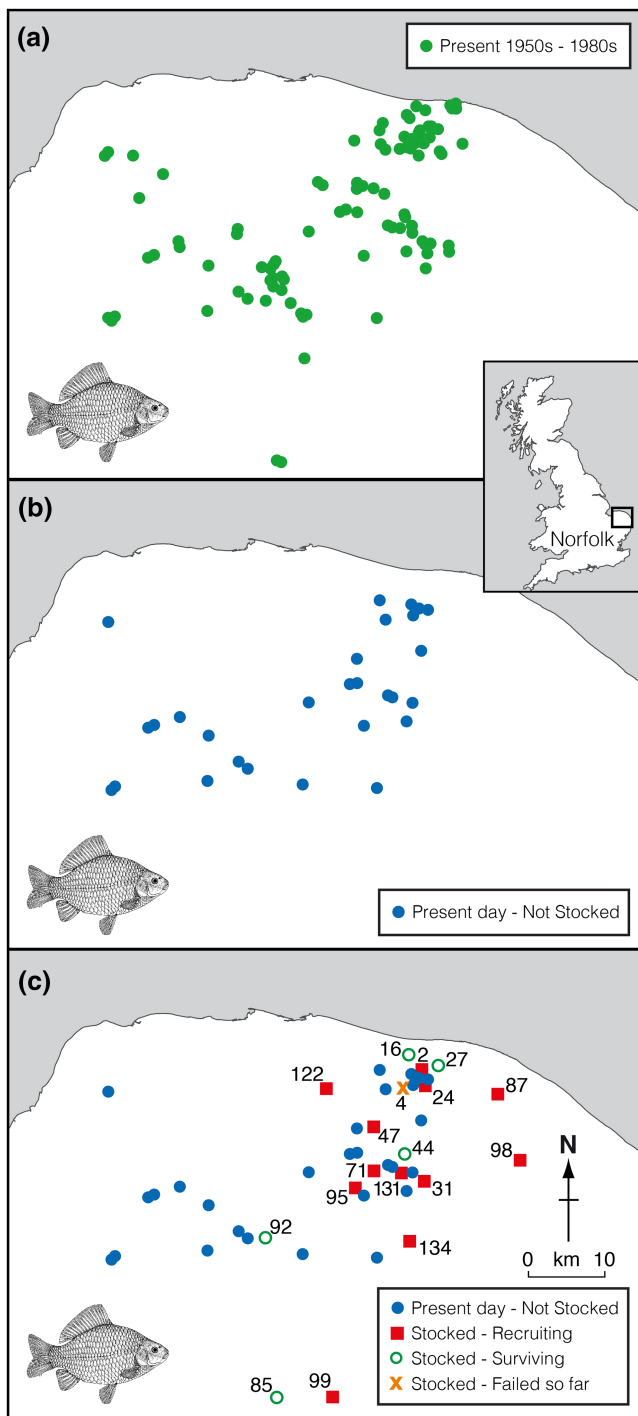


FIGURE 1 Distribution of crucian carp in the northern half of the county of Norfolk (a) in the 1950s–1980s; (b) in the present-day (2019) excluding ponds stocked with crucian carp by the Norfolk Crucian Project since 2011; and (c) in the present-day (2019) including ponds stocked with crucian carp by the Norfolk Crucian Project since 2011. In (c) ponds where fish failed to survive, ponds where fish survived but are not thus far recruiting and ponds where fish survived and are recruiting are highlighted. Ponds featured in the text are numbered (as in Table 1)

supported hybrids of crucian carp with goldfish and common carp. Other native fishes captured in the surveys included roach *Rutilus*

rutilus, Eurasian tench *Tinca tinca*, rudd *Scardinius erythrophthalmus*, Eurasian perch *Perca fluviatilis*, northern pike, European eel *Anguilla anguilla*, threespine stickleback *Gasterosteus aculeatus*, ninespine stickleback *Pungitius pungitius*, common bream *Abramis brama* and gudgeon *Gobio gobio*, with two hybrids of native species (*R. rutilus* × *S. erythrophthalmus* and *R. rutilus* × *A. brama*) also observed.

In total, 75 ponds supported crucian carp populations during the 1950s–1980s, but lost them subsequently. The combination of stakeholder interviews and field observations showed that pond terrestrialization (Figures 2a and 3) and resulting deteriorating habitat (loss of macrophytes and prolonged anoxia) were the likely dominant cause of crucian carp disappearance (31 ponds, 41%). Other inferred causes of loss were pond desiccation caused by drought (especially the droughts of 1976 and 1988–1992) or local changes in hydrology (11 ponds, 15%; Figures 2b and 3), pond in-filling resulting from agricultural land-grabbing (six ponds, 8%), pollution events (six ponds, 8%), introduction of northern pike (four ponds, 5%), mass coverage of ponds by Lemnaceae (four ponds, 5%; Figure 2c), competition with common carp and hybrids thereof (two ponds, 3%), deliberate fish removal (two ponds, 3%) and reedswamp encroachment (two ponds, 3%). In the case of seven (9%) ponds, however, it was not possible to determine an obvious cause of crucian carp disappearance. Among the ponds that contained crucian carp, 18 were found to have sizeable numbers (CPUE ≥ 10), with seven ponds containing low numbers (CPUE ≤ 4).

3.2 | Success of re-stocking and growth performance of stocked fish

Of the 18 surveyed introduction/re-introduction ponds survival was demonstrated for 17 ponds, with fyke net sampling only failing to capture crucian carp in pond 4 (Table 1). Recruitment of crucian carp was established for 12 ponds. In the case of five ponds (nos 16, 27, 44, 85, 92), no juvenile fish were recovered and for pond 27 (stocked in 2011), this was following four samplings after stocking following which (in 2017) thousands of individuals of juvenile crucian carp were stocked by the Environment Agency. Eight ponds (nos 24, 47, 71, 87, 95, 98, 99 and 122) attained sizeable populations of crucian carp (CPUE ≥ 10) comparable with existing strong pond populations in the study area. Six of these ponds (nos 24, 71, 87, 98, 99, 122) attained a CPUE ≥ 10 after 2–3 years, but ponds 47 and 95 took seven and six years, respectively, to attain this CPUE. For one pond (no. 68), crucian carp recruitment was limited to a single individual two years post-stocking.

Mean second-year crucian carp growth was highest in pond 87 (64 ± 22 mm) and lowest in pond 99 (19 ± 4 mm) (Figure 4). Significant differences in second-year growth were detected among all newly recruited crucian carp populations in Norfolk ($F_{4,395} = 75.436$, $P = 0.0001$), with the exception of a non-significant difference ($t = 0.7452$, $P = 0.462$) between ponds 98 and 24.

There were significant differences ($F_{6,37} = 5.2417$, $P = 0.0006$) for crucian carp TL at age two years among three European

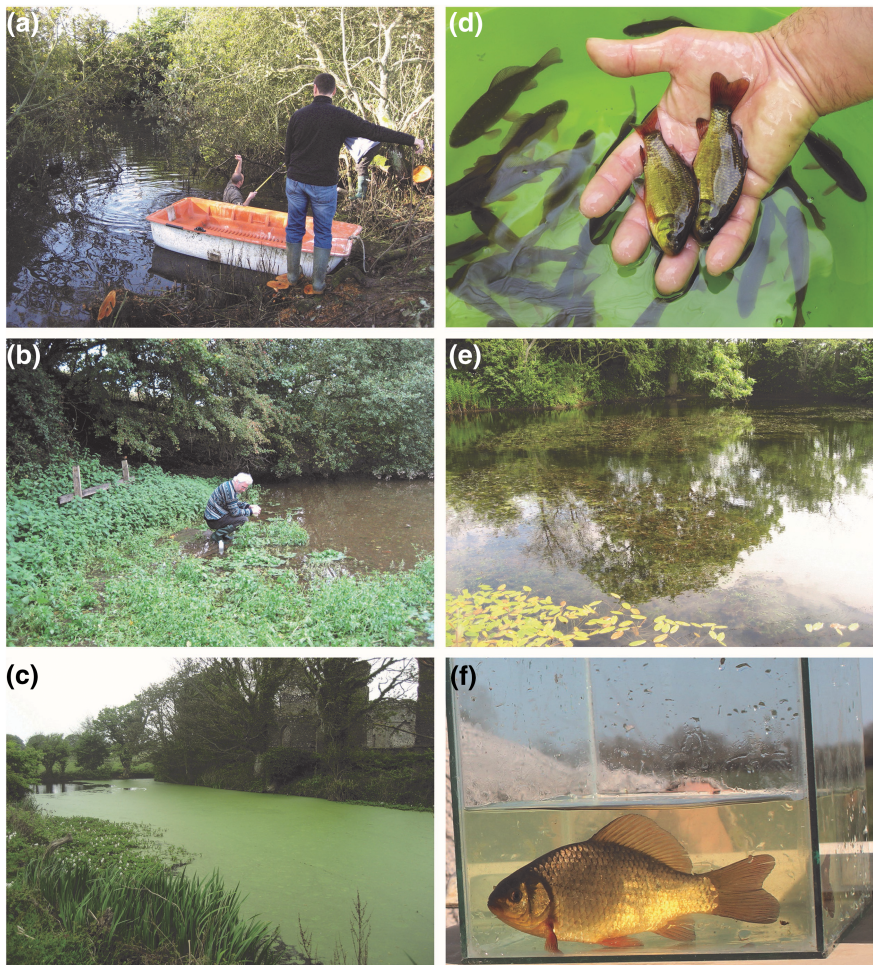


FIGURE 2 (a) A highly terrestrialized farmland pond; (b) a former crucian carp pond exhibiting a severe water-level reduction; (c) a farmland pond covered by common duckweed *Lemna minor*; (d) juvenile fish captured from a stocked pond; (e) a typical macrophyte-dominated farmland pond supporting crucian carp; and (f) a crucian carp captured from a small farmland pond: Photo Andy Hind. Note that (a) and (e) are the same pond (pond 2 in this study) before and after restoration by major scrub and sediment removal

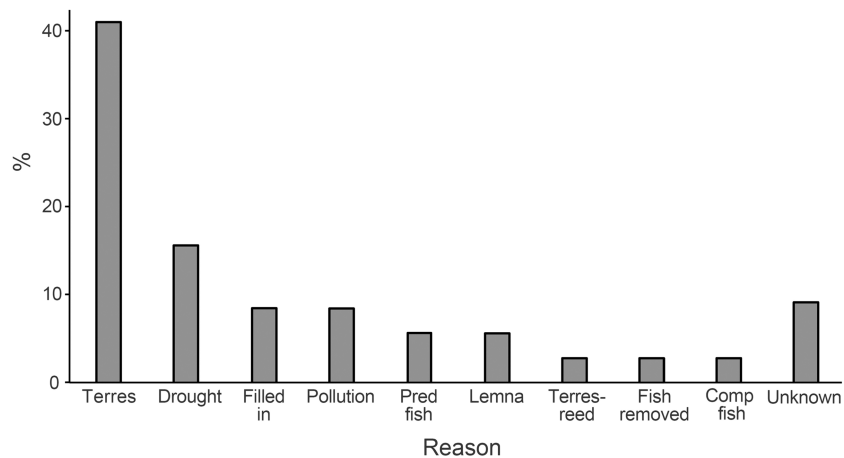


FIGURE 3 Inferred causes of crucian carp decline in Norfolk between the 1950s–1980s and the present day. Terres = pond affected by terrestrialization owing to encroachment of scrub around pond; Drought = pond dried up; Filled-in = pond lost to deliberate in-filling as part of agricultural land-grabbing or local development; Pollution = crucian carp lost owing to a known pollution event; Pred fish = crucian carp likely to have been preyed upon by northern pike; Lemna = pond covered by *Lemna minor* and/or *Lemna minuta*; Terres-reed = pond affected by terrestrialization owing to major emergent plant (especially *Phragmites australis*) encroachment and loss of open water habitat; Fish removed = crucian carp removed following a deliberate pond draining-down event; Comp fish = crucian carp adversely affected by competition with other fishes

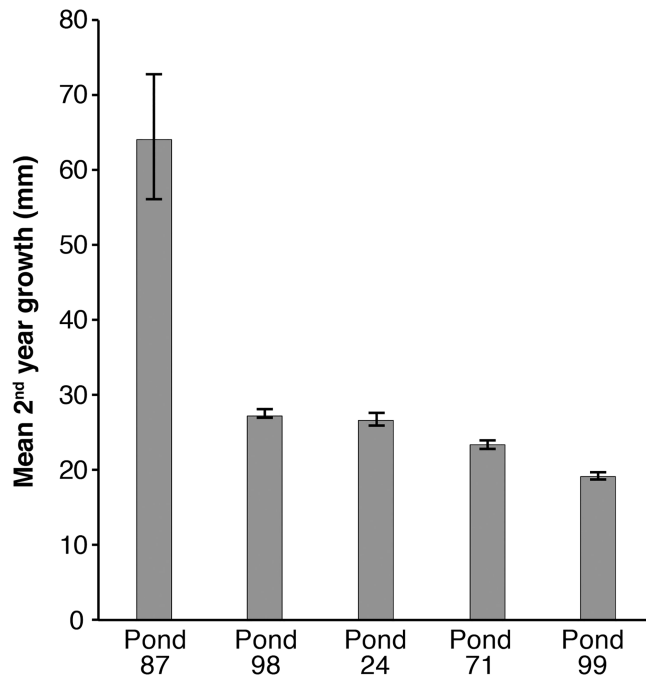


FIGURE 4 Comparison of mean second year growth (calculated as the difference between first- and second-year fish total length (TL) in mm) of recruited fish in all study ponds. Error bars give standard errors

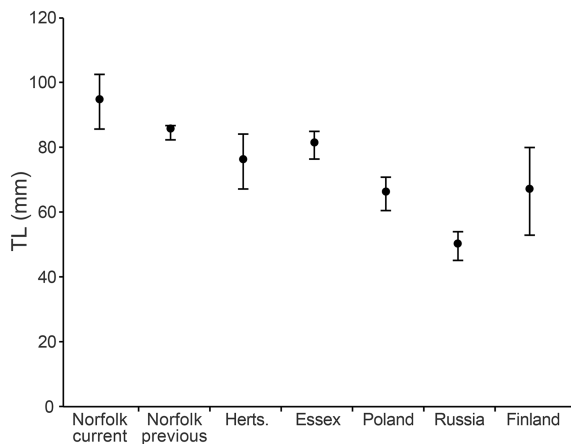


FIGURE 5 Comparison of crucian carp total length (TL in mm) at age two between Norfolk-introduced crucian carp (this study; $n = 5$) and previous data for pond populations of crucian carp for Norfolk ($n = 16$; Tarkan et al., 2016), Hertfordshire ($n = 3$; Tarkan et al., 2011, 2016) and Essex ($n = 4$; Tarkan et al., 2009) in south-east England, and for Poland ($n = 11$; Białokoz, 1977; Ciepielewski, 1967; Skrzydło, 1977; Szczerbowski et al., 1997; Zawisza & Antosiak, 1961), Russia ($n = 2$; Dmitriyeva, 1957) and Finland ($n = 3$; Holopainen & Pitkänen, 1985)

countries (Figure 5). Mean values for TL at age two years in Norfolk crucian carp populations, as reported previously (84.43 ± 44 mm), or as determined for the present study (93.85 ± 8.57 mm) were significantly higher than measured for populations in Finland (66 ± 13 mm), Poland (65 ± 5 mm) and Russia (50 ± 5 mm) ($P \leq 0.05$) (Figure 5).

Year class strength, crucian carp CPUE, pond size and macrophyte cover were used in the MLR model as predictor variables. All predictors were positively correlated with one another, especially crucian CPUE and pond size ($R = 0.511$, $P < 0.001$), but no correlations exceeded R values of 0.8, tolerance values were all above 0.2 and variance inflation factors were all < 10 , indicating a lack of multicollinearity. Assumptions of normality were met after the data were \log_{10} transformed. The Durbin-Watson value fell between 1 and 3 (1.831), indicating that residuals were uncorrelated. A forced entry multiple regression model was found to be a significant predictor of second-year growth ($F_{4, 414} = 40.518$, $P < 0.01$) with the predictors accounting for 28.1% of the variance. Regression coefficients for each predictor variable were also calculated (Table 2), with pond size found to have a positive relationship with second-year growth and year-class strength, crucian carp CPUE and macrophyte cover all having negative relationships. Crucian carp CPUE ($t(414) = -7.413$, $P < 0.01$), pond size ($t(414) = 10.669$, $P < 0.01$) and macrophyte cover ($t(414) = -6.726$, $P < 0.01$) were all significant predictors of second-year growth, but year class strength ($t(414) = -1.605$, $P > 0.05$) was not a significant predictor.

Some 43 original-stocked fish were captured from ponds 99 ($n = 27$), 71 ($n = 1$), 87 ($n = 2$) and 98 ($n = 13$), but no original fish were captured from pond 24. The oldest of these fish, from ponds 71 ($n = 1$) and 99 ($n = 2$), were aged eight years. The \log_{10} -transformed data generated a normal distribution and therefore met the assumptions of a paired t -test. Mean growth in the original fish differed significantly (t -test $P < 0.01$) before and after stocking, but exhibited a general decline in subsequent years (Figure 6). The mean growth rate a year before stocking was 18 mm TL year $^{-1}$ (± 10 mm), which was lower than the mean growth rate a year after (24 mm TL year $^{-1}$, -11 mm). Out of the 43 fish, only 10 had growth rates that decreased after stocking. Maximum and minimum growth rates one year after stocking were 58 and 13 mm TL year $^{-1}$, respectively.

4 | DISCUSSION

4.1 | Extent and causes of crucian carp decline

The crucian carp has undergone a substantial decline in Norfolk since the 1950s–1980s with the estimated 72% reduction of its distribution in the present study similar to the levels of decline reported by Sayer et al. (2011) since the 1970s–80s for a smaller study area. This extent

TABLE 2 Multiple regression model results for crucian carp second year growth

	<i>B</i>	<i>SE B</i>	β
Year class strength	−0.041	0.026	−0.072
CPUE estimate of density	−0.154	0.021	−0.363*
Pond size	0.461	0.043	0.529*
Macrophyte cover	−0.239	0.035	−0.305*

Note: $R^2 = 0.281$. Regression coefficients (*B*), standard error (*SE B*) and standardized coefficients (β) for each of the predictor variables are given. * $P < 0.01$.

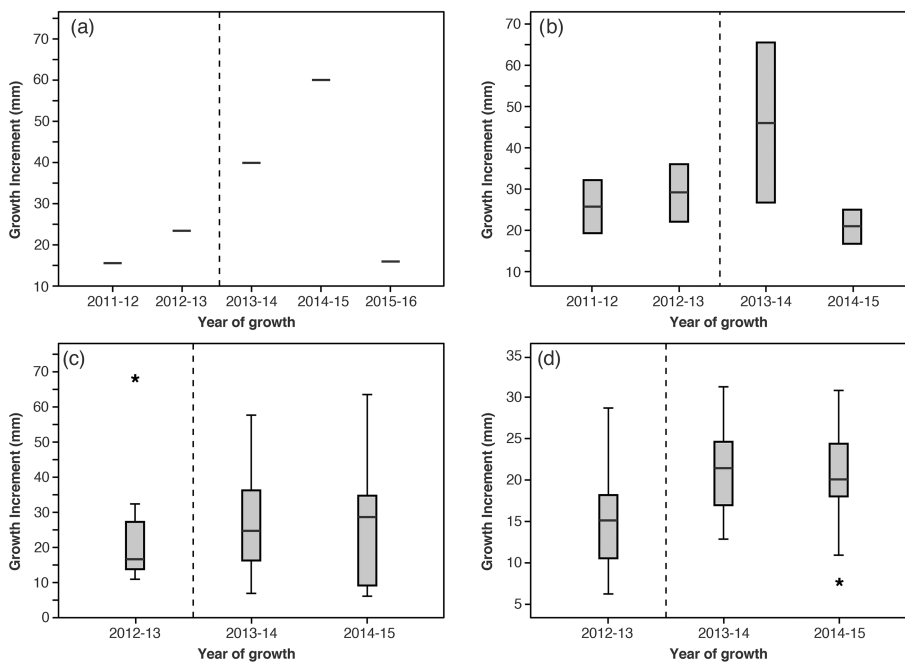


FIGURE 6 Comparisons of yearly growth increments (millimetres) for original-stocked crucian carp in ponds 71 (a), 87 (b), 98 (c) and 99 (d) in the present study. The dotted vertical line indicates the point of stocking in each pond. * Outlier fish

of decline would place the crucian carp in the 'Endangered' category based on IUCN criteria for population size reduction (Bland, Keith, Miller, Murray, & Rodríguez, 2016). Comparable reductions in crucian carp distribution have been identified across several European countries, in some cases resulting in its inclusion on national 'red lists': Czech Republic (Vulnerable – Lusk, Hanel, & Luskova, 2004), Austria (Endangered – Wolfram & Mikschi, 2007) and Croatia (Mrakovčić, Buj, & Mustafić, 2007). Thus, despite the overall IUCN classification of 'Least Concern' with the caveat of a 'Declining' current population, the basis for establishing conservation projects focused on the crucian carp, and for IUCN re-classification, is strong.

Consistent with Sayer et al. (2011), pond terrestrialization appears to be the major cause of crucian carp loss (Figure 3), probably owing to combinations of poor habitat and food quality (reduced invertebrate abundance) and in particular prolonged periods of anoxia in overgrown ponds (Sayer et al., 2013). Crucian carp populations in more heavily overgrown ponds within the study area were generally small and dominated by a few large individuals. This pattern, combined with the absence of crucian carp in several highly overgrown ponds (Figure 2a) that used to support the species, strongly suggests that poor survival of eggs and/or juvenile fish may be a key bottleneck hampering crucian carp recruitment in ponds at advanced stages of pond terrestrialization, resulting in multiple local crucian carp extinctions in recent decades.

A further linked cause of crucian carp decline in Norfolk is a parallel reduced interest in angling in farmland ponds since the 1980s and as a result a reduction in informal fish movements and stocking events since this time. In the eighteenth century, there is evidence that inter-pond transfers of crucian carp were undertaken in Norfolk, as elsewhere in Europe, to provide fish for food (Janson, Wouters, Bonow, Svanberg, & Olsén, 2015). As such, a 'fish pond' culture clearly existed for crucian carp in England (Woodforde, Winstanley, & Jameson, 2008). By the turn of the twentieth century, however,

pleasure angling probably became the major motive for inter-pond transfers of crucian carp.

Discussions with local anglers revealed many crucian carp movements in Norfolk before the 1980s, with a few 'mother ponds' often used as donor sites for many surrounding ponds (Sayer et al., 2011). Thus, for at least two or three centuries, crucian carp persistence in farmland pond landscapes, which presented mosaics of largely hydrologically-isolated ponds, was promoted to a large extent by human actions. Such human movements of fish undoubtedly replicate the natural dispersal of crucian carp between backwater, oxbow and main channel habitats within natural floodplain hydrosystems (Copp, 1991; Hohašová & Jurajda, 2005). With a diminished cultural practice for moving crucian carp between ponds in recent decades, the distribution of the crucian carp has clearly been rendered more static. As farmland landscapes are highly dynamic, with ponds prone to terrestrialization, drought-induced desiccation and in some cases pollution, crucian carp populations are always vulnerable to extinction. Thus, without angler-mediated movements of fish or management of ponds to prevent them from getting overgrown by woody vegetation, conservation projects such as the NCP are urgently needed to save the crucian carp from further decline.

4.2 | Growth performance of stocked crucian carp

The greatest influences on the growth of juvenile fish were found to be pond size, followed by crucian carp CPUE (Table 2). A significant positive effect of pond size might be expected given that, especially during the early stages of crucian carp establishment, invertebrate food resources are more likely to be depleted where ponds are smaller and support higher fish densities. This finding is supported by other studies that have shown crucian carp density and resulting strong

intra-specific competition to be a key factor affecting second-year growth (Holopainen et al., 1997; Tarkan et al., 2011; Wootton, 1998). Intraspecific competition in crucian carp is also thought to be particularly intense, as clear ontogenetic shifts in diet are not thought to occur between size classes (Tonn, Paszkowski, & Holopainen, 1992).

A significant negative relationship between macrophyte cover and crucian carp second-year growth is hard to explain, given that plant-associated invertebrates are likely to be of high importance to crucian carp diet, although this may result from macrophytes promoting increases in fish density and hence again higher intraspecific competition (Holopainen et al., 1997). Caution needs to be exercised in the weight placed on the multiple regression model because of the small number of sites and poorly understood relationships between crucian carp and other fish species that may also affect growth. For example, in pond 87 a small population of larger perch (CPUE = 0.5) may have been preying on juvenile crucian carp, thus explaining high mean TL at age 2 in this site. In support of this idea, Brönmark, Paszkowski, Tonn, and Hargeby (1995) found that, when crucian carp co-existed with perch in Swedish lakes, they were of low density and individuals were larger. Further, coupled with pond 99 being the smallest pond, intraspecific competition with tench in this pond may have been a key factor explaining its lowest second-year growth, as tench have a similar feeding habit and diet to crucian carp (Copp & Mann, 1993; Giles, Street, & Wright, 1990). Clearly, more research is needed for a larger number of re-introduced crucian carp populations which considers growth in relation to pond size, habitat structure as well as the occurrence of other fish populations.

Growth of newly recruited fish, assessed by measurements of TL at age 2, was high relative to established populations in Norfolk (Tarkan et al., 2016), Essex (Tarkan et al., 2009) and Hertfordshire (Tarkan et al., 2016) and more generally in Europe (Figure 5). Nonetheless, crucian carp growth was highly variable, even within the relatively small geographical area of Norfolk studied. High growth rate variability is a common feature of many widely distributed fish species (Mann, 1991) and in this case may be attributed to variations in many biotic and abiotic factors, especially inter/intra-specific competition, temperature, hydrological regime and food abundance. Earlier studies on crucian carp growth in south-east England (ponds in Epping Forest, Essex and Bayfordbury Lake, Hertfordshire) suggest that temperature is unlikely to be the primary reason for observed growth variations with density-dependent and independent factors likely to be of greater importance (Tarkan et al., 2011, 2016).

The present study suggests that the growth rates of original-stocked fish increased after stocking. Crucian carp are thought to achieve sexual maturity by age 2 (Quince, Abrams, Shuter, & Lester, 2008) after which growth rates typically decline following the von Bertalanffy curve (Beverton & Holt, 1957). However, the results presented here (Figure 6) support the existence of growth plasticity throughout the crucian carp's life span (Tarkan et al., 2016). It is likely that, once stocked into ponds where fish are absent or low in abundance, as for the study ponds, food resources are poorly exploited, thus permitting brief increases in growth rates. This situation may contrast with the fish-filled environments characteristic of the ponds

from which crucian carp were stocked where higher fish densities may have depleted available food resources (Holopainen et al., 1997), resulting in the more typically observed pattern of declining growth rates with age (Tarkan & Vilizzi, 2015; Top, Tarkan, Akbaş, & Karakuş, 2016).

4.3 | Recovery of the crucian carp

The present study shows that crucian carp populations can recover through concerted actions of pond rehabilitation and the use of genetically pure fish for stocking. Excluding an unknown number of fishery populations, by stocking crucian carp into restored and other suitable existing farmland ponds, the NCP has increased the number of known Norfolk crucian carp sites by 37%, representing a substantial increase in its distribution (Figure 1c). The majority of ponds stocked with crucian carp as part of the NCP quickly (after just 2–3 years) established sizeable populations (CPUE \geq 10). In addition, both stocked and juvenile fish were shown to grow exceptionally quickly after stocking. Hence, these initial results suggest that, if introduced into appropriate pond environments, both adult and juvenile crucian carp can thrive and rapidly establish new and substantial populations (Figure 2d). It is also notable that, in all cases, owners of the stocked ponds are supportive of the project and aware of the need to avoid introductions of common carp, goldfish and predatory fishes, as well as a periodic requirement (every 5–10 years) for pond management to arrest terrestrialization (compare the pond in Figures 2a and e). Thus, the NCP has created a number of successful 'ark sites' for the crucian carp and is rapidly reversing its decline as well as highlighting it as a fish species worthy of conservation.

Given the small number of pond populations involved, unsuccessful crucian carp survival (no. 4) or recruitment (nos 16, 27, 44, 85, 92) in some of the stocked ponds is difficult to explain with confidence. However, the presence of other fish species may be a factor. Four of the poorly performing ponds (nos 4, 16, 27, 44) contained other fish species at the time of crucian stocking, potentially that interspecific competition or predation may have been a factor in the crucian's poor post-stocking persistence or recruitment. For example, the apparent disappearance of crucian carp from pond 4 may have resulted from predation by a small population of pike, which were not known to be present in this pond before crucian carp stocking. Pike is known to exert an adverse impact on the performance of crucian carp (Brönmark & Miner, 1992; Nilsson, Brönmark, & Pettersson, 1995), and even eradicate congener goldfish from ponds (Copp et al., 2005). Ponds 16, 27 and 44 all had populations of threespine stickleback and for this species predation of crucian carp eggs or larvae is a probable (although unobserved) mechanism hampering crucian recruitment. In contrast, in ponds 31 and 99, despite supporting small populations of roach (no. 31) and tench (no. 99), crucian carp showed rapid post-stocking recruitment, indicating that the presence of some fish species may not always be inhibitory. An extended period of post-release monitoring may be necessary to observe such recruitment successes. For example, pond

47 contained a fish assemblage composed of roach, rudd and tench prior to crucian stocking, and only produced one juvenile crucian carp individual in three surveys (2013, 2015, 2016) after stocking in 2011. However, in 2018, seven years post-stocking, the survey sample comprised large numbers of juvenile crucians, as part of a sizeable overall population (CPUE = 18).

Crucian stocking into fishless ponds appears to enhance the likelihood of crucian carp stocking success, although crucians fared poorly in some fishless ponds with excellent macrophyte habitat (nos 85 and 92). Therefore, further studies of a greater number of pond introductions are needed to determine potential habitat structure and other influences on crucian carp reproduction success and juvenile survival.

4.4 | The case for GB crucian carp conservation

Despite recent genetic evidence indicating that the crucian carp was most likely introduced into England in the fifteenth century, there are strong reasons to conserve it in GB. First, this and other studies show south-east England to be climatically highly suited to crucian carp reproduction and growth (Tarkan et al., 2009, 2011, 2016) and this, combined with an absence of gibel carp in virtually all GB waters and hence a prevalent pathway for hybridization, make south-east England an important potential centre for crucian conservation. Indeed, gibel carp has been expanding its distribution towards the Baltic Sea (Vetemaa, Eschbaum, Albert, & Saat, 2005; Wouters et al., 2012) and is consequently a growing threat to the remaining continental crucian carp populations in the wild.

There are other good reasons for initiatives in GB to conserve the crucian carp, however. In particular, owing to its long history of occurrence, the crucian carp is a culturally important species, held in high affection by anglers and local people (Rolfe, 2010). Further, in contrast to the common carp (Zambrano & Hinojosa, 1999), there is no evidence for crucian carp causing damage to stands of aquatic plants or populations of invertebrates and amphibians in ponds (Chan, 2010; Harper, 2019). On the contrary, emerging evidence suggests that the presence of crucian carp, in some ponds, enhances landscape-scale diversity of aquatic plants and invertebrates (Harper, 2019; Harper et al., unpublished data; Stefanoudis et al., 2017). There are also habitat-related benefits associated with crucian carp conservation: for example, several species-poor highly terrestrialized, ponds restored as part of the NCP, showed substantial increases in macrophyte, invertebrate and amphibian species richness following restoration (compare Figures 2a and 2e; Sayer et al., 2013).

Development of conservation plans for non-native species should not be the norm, and decisions in this respect need to be precautionary and based on sound criteria and science. Nevertheless, the present study adds weight to suggestions (Copp et al., 2005; Davis et al., 2011) for taking a less purist biogeographically-based approach to long-established non-natives that embraces their conservation in some scenarios, especially when threatened in their native range and when adverse impacts on native biota have not been demonstrated,

as for the crucian carp in GB. As suggested by Jeffries et al. (2017), it would seem counter-productive to abandon continuing conservation crucian carp efforts in England when this species is in major decline elsewhere. Further, studies of Europe-wide genetic structure (Jeffries et al., 2016) show that English crucian populations comprise a distinct part of the species' overall diversity, which renders these populations of wider importance.

The case for crucian carp conservation in GB bears similarities to the white-clawed crayfish *Austropotamobius pallipes* Lereboullet more widely in the UK, which, despite a very high level of conservation protection (UK BAP species and listing on Schedule 5 of the Wildlife & Countryside Act, 1981), is also questionably native, with no records of its occurrence in the UK before the mid-1600s (Holdich & Rogers, 1997). Nevertheless, for the white-clawed crayfish, the importance of conservation efforts in the UK appears to be widely accepted, especially given the species' European-scale scarcity. In addition, the huchen (or Danubian salmon) *Hucho hucho* (L.) provides a relevant example of a successful fish translocation outside of a species' native range for conservation purposes (Witkowski, 1996). This species became extinct in its natal River Danube tributary rivers (Rivers Czarna Orave, Czadeczek) in the 1950s as a result of water pollution and over-exploitation. In reaction to this problem, self-sustaining huchen populations were established through intensive stocking of two tributaries (the rivers Dunajec and Poprad) of the Polish River Vistula in its upper course, which were outside of its natural distribution range. Thus, the huchen was saved (*ex-situ*) by taking a less biogeographically-strict approach to translocation. These two species examples show the importance of being more open-minded with regard to the conservation of globally-threatened non-native species where scientific study supports it.

In conclusion, this study shows that 10 years of determined conservation work by the NCP has reversed the decline of wild populations of crucian carp in Norfolk, England. This reversal has been made possible by establishing good stakeholder-scientist relationships and through combinations of pond rehabilitation and introductions or re-introductions of crucian carp to suitable ponds. More research is needed to understand why crucian carp failed to reproduce in some ponds, and in particular the influence of habitat structure and interactions with other fish species on both crucian recruitment and growth. Following the blueprint established here, it is recommended that more local crucian carp conservation projects be established in other parts of south-east England and more generally in the species' native European range.

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