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Age and growth rates of a translocated chub *Squalius cephalus* chalk-stream population with comparison to indigenous riverine populations in England

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Abstract – Introduced fishes into lowland rivers can result in invasive populations establishing and then dispersing, where knowledge of their life history traits contributes to understandings of their invasion ecology. Here, the age and growth rates of a translocated chub *Squalius cephalus* population were assessed in the River Frome, a lowland chalk-stream in Southern England, where chub was introduced approximately 15 years ago. The results were assessed in relation to 35 riverine indigenous chub populations in England. Across these populations, individual chub were present to lengths over 550 mm and aged to at least 19 years old. In samples collected from the River Frome, however, no fish were present over 300 mm and age 4+ years. Growth rate analyses of both the annual length increment produced between age 1 and 2 years (juvenile growth rate) and length at the last annulus (adult growth rate) revealed that both of these were relatively high in the River Frome population, being among the fastest of all sampled populations. It is suggested these fast growth rates were the response of the fish to their new environment, facilitating their establishment and colonisation through, for example, enabling reproduction at relatively young ages.

Keywords: Alien fish / latitudinal position / longitudinal position / invasion

1 Introduction

Introductions of riverine alien fishes potentially result in sustainable populations establishing that naturally disperse and colonise much of the river basin (Dominguez Almela, 2020, 2021a). Those alien fish that develop invasive populations can then have major consequences for the native fish community due to, for example, increasing predation and/or competitive pressures (Gozlan *et al.*, 2010). In river basins, options for managing invasions can be limited, with optimal outcomes usually achieved by relatively early management interventions (Britton *et al.*, 2011; Dominguez Almela *et al.*, 2021b). Therefore, initial assessments on the colonisation rates and life history traits of newly introduced species can assist managers determine the extent of the invasion risk (Vilizzi *et al.*, 2019).

Assessments of age and growth rates of the colonising fish population can greatly assist the risk assessment process (Nolan *et al.*, 2019), especially as growth rates can be a strong proxy of other life history traits (Oyugi *et al.*, 2011). Understanding the spatial extent of fish invasions has been assisted through studies on how the invader's life history traits are being expressed (Vila-Gispert *et al.*, 2005; Olden *et al.*, 2006), especially where the environmental drivers of spatial differences in trait expression are identified (Benejam *et al.*, 2009; Nolan *et al.*, 2019). It is well established that within species, fish growth tends to differ over spatial gradients (Przybylski, 1996; Pegg and Pierce, 2001; Tedesco *et al.*, 2009). As these patterns are often related to climatic and temperature differences (Oyugi *et al.*, 2011) then these spatial patterns are often evident over a latitudinal and/or longitudinal range (Britton *et al.*, 2013; Nolan *et al.*, 2019).

Chub *Squalius cephalus* is encountered from the northern latitudes of Scandinavia to southern latitudes of the Mediterranean, where water temperatures are generally between 4 and 20 °C (Kottelat and Freyhof, 2007). Their range includes invasive populations in Italy (Haubrock *et al.*, 2021) and Ireland (Caffrey *et al.*, 2008), although the latter population has been eradicated following the initiation of management interventions (Caffrey *et al.*, 2018). Considered indigenous to Britain, the species has a relatively widespread distribution in lowland rivers, where their populations support recreational fisheries for catch and release angling (Bolland *et al.*, 2007). Their status in south-west England is, however, uncertain. While archaeological evidence suggests dace *Leuciscus leuciscus* was present in rivers such as the Dorset Stour in 500 BC, suggesting their colonisation of these rivers through connections with rivers of mainland Europe following

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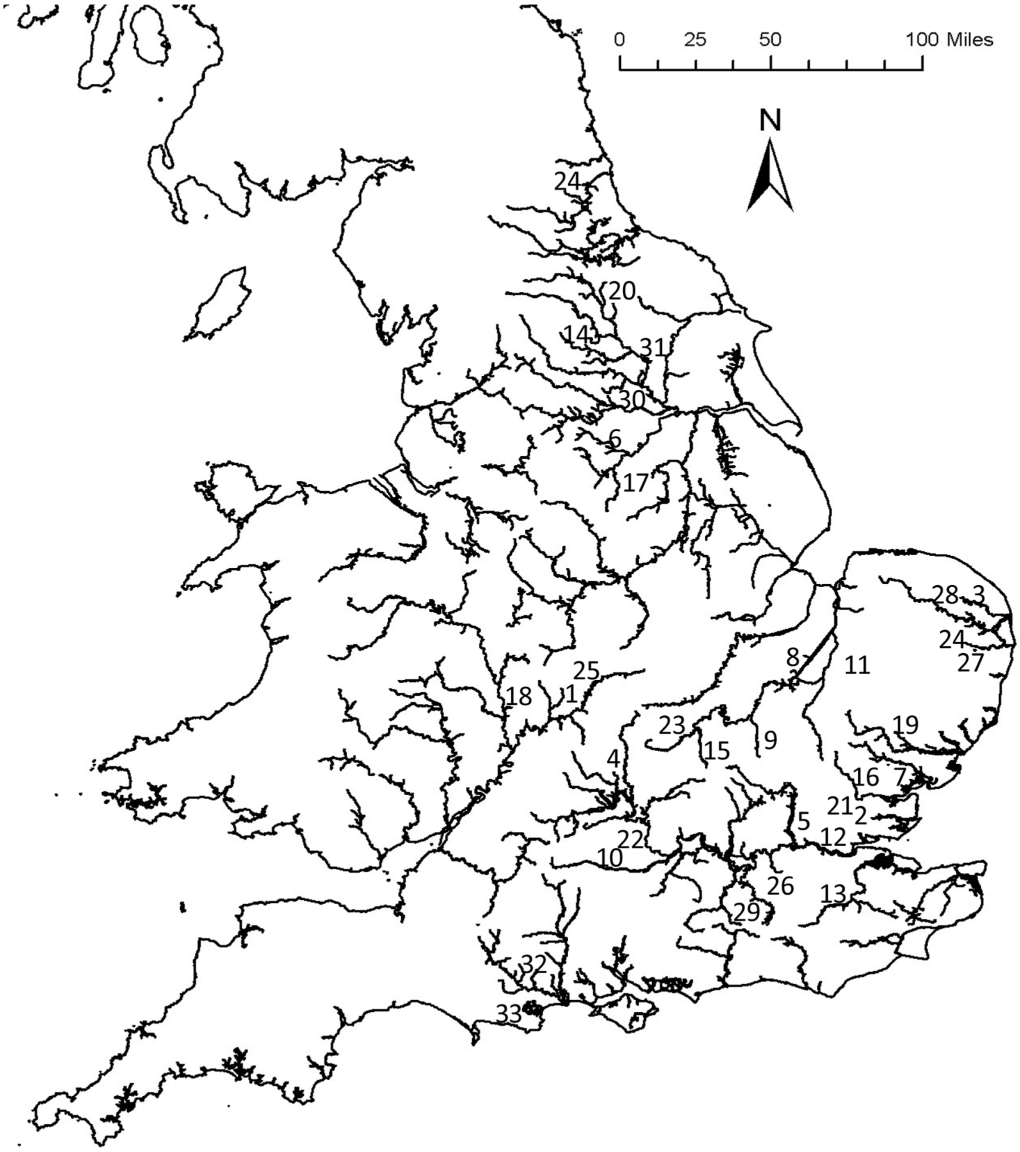

Fig. 1. Approximate locations of the rivers sampled for their chub *Squalius cephalus* populations that were used in analyses (1. Alne, 2. Blackwater, 3. Bure, 4. Cherwell, 5. Colne, 6. Dearne, 7. Gipping, 8. Great Ouse, 9. Ivel, 10. Kennet, 11. Lark, 12. Lee, 13. Medway, 14. Nidd, 15. Ouzel, 16. Pant, 17. Rother, 18. Salwarpe. 19. Essex Stour, 20. Swale, 21. Ter, 22. Thames Oxford, 23. Tas, 24. Tyne, 25. Warwickshire Avon, 26. Wandle, 27. Waveney, 28. Wensum, 29. Wey, 30. Wharfe, 31. Yorkshire Ouse, 32. Dorset Stour, 33. Frome.

the end of the last glacial maximum (Wheeler, 1976), this evidence is lacking for chub. Moreover, chub have been absent from a number of chalk-streams in this area of England, including the River Frome (Fig. 1), a highly productive chalk-stream whose dace population (considered as indigenous) has previously been the subject of considerable research attention (*e.g.* Mann, 1974; Mann and Mills, 1985; Mills *et al.*, 1985).

A major introduction pathway for freshwater fish is recreational angling, where new species are introduced to inland waters to enhance the angling experience (Gozlan *et al.*, 2010). While these fishes include non-native species being introduced into novel habitats (Nolan *et al.*, 2019), they also include indigenous fishes being moved to areas within countries where they are non-indigenous (Winfield *et al.*, 2008; Britton *et al.*, 2011). The initial recording of chub in the River Frome, reported anecdotally in 2008 in its lower, tidal reaches, was considered to be the result of an unregulated release, most likely by an angler attempting to diversify the species available for exploitation. This is because there were no opportunities for natural dispersion from neighbouring river catchments where chub was already present (*e.g.* River Dorset Stour) due to no hydrological connection, and in the vicinity of the river where the species was initially recorded, there were fishery or aquaculture sites where chub were present (personal observation, the authors). The species has since been dispersing upstream, but with corresponding ecological data

Table. 1. Results of multiple linear regression testing the effects of the abiotic variables on the standardised growth residuals of chub according to (A) length at the last annulus (age 1 to 10 years) and (B) length increment produced between ages 1 and 2 years.

Effect	Regression coefficient	*t*	*P*
A			
Intercept	–2011 ± 600	–3.35	<0.01
Latitudinal position	44.3 ± 11.1	3.97	<0.01
Longitudinal position	9.27 ± 9.51	–0.98	0.34
Flow (Q_{50})	–4.35 ± 1.95	–2.22	0.04
Total N	0.87 ± 3.28	0.27	0.79
Phosphate	1.60 ± 3.78	0.42	0.68
Dissolved oxygen	–0.97 ± 1.34	–0.72	0.48
Altitude	0.61 ± 0.41	1.49	0.15
Distance from source	0.05 ± 0.30	0.17	0.87
Intercept	166.96 ± 78.91	2.12	0.04
B			
Latitudinal position	–1.71 ± 1.47	–1.17	0.25
Longitudinal position	–5.22 ± 1.25	–4.14	<0.01
Flow (Q_{50})	–0.22 ± 0.26	–0.85	0.41
Total N	–0.12 ± 0.43	–0.29	0.78
Phosphate	0.58 ± 0.50	1.18	0.25
Dissolved oxygen	–0.33 ± 0.18	–1.87	0.07
Altitude	–0.13 ± 0.05	–2.42	0.02
Distance from source	0.01 ± 0.04	0.11	0.91

on their population being highly limited. Given the importance of the river for Atlantic salmon *Salmo salar*, where the population has been monitored for over 50 years but is in decline (*e.g.* Simmons *et al.*, 2021), then the release of chub into the river is a potential concern given their potential sharing of habitat and spawning areas, and omnivorous diet that includes facultative piscivory (Caffrey *et al.*, 2008).

To overcome this initial local knowledge gap on invasive chub ecology, the aim of this study was to assess the age and growth rates of this invading population, and compare these results within an age and growth dataset comprising of 35 indigenous populations from across other rivers in England. This spatial comparison is important, given chub are known to exhibit considerable spatial variation in somatic growth rates (Mann, 1976; Bolland *et al.*, 2007), although most previous studies have been localised to single watersheds (Mann, 1987; Pryzbylski, 1996; Tedesco *et al.*, 2013), with the only spatial comparison in England limited to only 13 populations (Liu *et al.*, 2015). Consequently, expanding these spatial comparisons to a wider selection of riverine populations provides more comprehensive insights into the spatial variability of chub growth rates and the environmental factors that influence them (Beardsley and Britton, 2012; Liu *et al.*, 2015). The growth analyses focused on two aspects: adult growth (analysing back-calculated lengths at the last annulus) and juvenile growth (length increments produced between age 1 and 2 years) (Beardsley and Britton, 2012; Britton *et al.*, 2013).

2 Materials and methods

The River Frome is a lowland chalk-stream in southern England that flows for approximately 70 km from its source (50.50. 24° N; 02.36. 12° W) to its tidal limit (50.40. 38° N; 02.07. 30° W). The fish assemblage is dominated by European minnow *Phoxinus phoxinus* and is renowned for its population of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* (Simmons *et al.*, 2020). The lower river becomes increasingly wider and deeper (but rarely exceeds 20 m width and 2 m depth), with some indigenous species of the Cyprinidae family present, including dace and roach *Rutilus rutilus.* Scale samples of chub were collected using a combination of electric fishing in side channels and rod and line angling in the main river channel. Although sampling commenced in 2011, the majority of scales were collected in 2021. Following their ageing, their data were then added to a wider dataset comprising of 35 more populations from across England (Fig. 1). These populations were sampled between July and October of 2013 to 2018 by electric fishing by the Environment Agency, the inland fisheries regulatory authority of England. In all cases, following their capture, the fish were measured (fork length, nearest mm) and between 3 and 5 scales removed for ageing purposes and stored in paper envelopes (Stienmetz and Muller, 1991). They were subsequently aged on a projecting microscope at Bournemouth University, where age estimates were determined through the interpretation of annual marks. To maximise ageing accuracy, a quality control procedure was used where up to 25% of scales were aged independently by another individual (Musk *et al.*, 2006). Due to the sampling method, no age validation method could be used. Following the aging of scales, they were measured to enable estimation of their lengths at annulus 1 and 2, and at the last annulus, to be derived by back calculation using the scale proportional method (Francis, 1990).

To analyse adult growth rates, the back-calculated lengths at the last annulus (‘length at age’ hereafter) were used (Electronic material, Tab. E1). An issue with ageing of chub scales is that in larger, older individuals, their annual length increments are relatively small and result in the annuli on the scale margin overlaying each other. This can result in the accuracy of the scale ageing decreasing as fish age increases, especially in older individuals (Musk *et al.*, 2006). Consequently, to minimise the influence of ageing inaccuracies in the data analyses, the only length-at-age data that were included in the analyses were from fish that were still producing relatively large annual length increments at their captured age (age 10 years; *cf.* Results). Following this finalisation of the length-at-age data to be included in the analyses, the next step was to plot these data against fish age (Beardsley and Britton, 2012). Because the data used here only included fish that were still producing relatively large annual length increments then the relationship between fish age and length could not be described using growth models (Vilizzi and Walker, 1999). Instead, a linear regression model was used that best fitted these data (Akaike's information criterion; AIC) (Lappalainen *et al.*, 2008). This regression model was then used to determine the standardised residuals of the lengths at age of each individual fish. These standardised residuals were then tested between the different populations using ANOVA, with the mean standardised residual (±95% confidence limits) per population also plotted for comparative purposes (Beardsley and Britton, 2012). To analyse juvenile growth rates, the following steps were used: (i) calculate the length increment between age 1 and 2 for each individual fish; (ii) calculate the mean increment between age 1 and 2 for all the sampled fish; (iii) determine the standardised residual of each fish, where the residual is the observed increment minus the mean increment for all fish. The standardised residuals were then tested and compared between the rivers as already described for the length at the last annulus.

To test the effect of environmental parameters on adult and juvenile chub growth rates, environmental data were sourced from the same rivers as the growth data, with the data extracted from the sampling areas closest to the chub sampling locations, and covering the same time periods. River characteristics (distance of sampling location from source, stream width and flow data) were sourced from the National River Flow Archive (2021), and all data for water chemistry (dissolved oxygen, ammonia, phosphate and nitrate) and temperature (mean, minimum and maximum temperature) were sourced from the Water Quality Archive (2021) of the Environment Agency. These abiotic variables were used as these have been used to test factors influencing the growth rates of other cyprinid fishes across similar spatial scales, with different combinations of chemical and catchment characteristics having significant influences on these growth rates (*e.g.* Britton *et al.*, 2013; Liu *et al.*, 2015). To test the extracted environmental variables that explained most of the spatial variation in chub growth, multiple linear regression was used, where the mean standardised residuals per river was the dependent variable and the fixed factors were the extracted environmental data outlined above. Prior to model construction, the fixed factors were tested for their correlation (Pearson's) and where variables were significantly correlated, only one of the variables was retained. The decision over which correlated variables to retain was then made according to their use in other relevant fish growth and found to have significant effects (Britton *et al.*, 2013; Liu *et al.*, 2015). Accordingly, longitudinal position and phosphate (as orthophosphate) were retained due to their significant effect on barbel growth rates (populations in western areas in rivers of and of orthophosphate were faster growing; Britton *et al.*, 2013), and nitrate levels (as total N) and latitudinal position for their significant effects on chub growth in other studies (faster growing populations with decreasing latitude and altitude, and increasing nitrate; Liu *et al.*, 2015). The variables of Q_{50} (flow exceeded 50% of the time) was retained as it is a strong descriptor of hydrological conditions and dissolved oxygen was retained as it is a key indicator of stream health (Franklin, 2014). Distance of the sampling location from the source of the river was also included as per Tedesco *et al.* (2009). The variables were entered together so that the regression coefficient, t-value and significance of each fixed factor was estimated in the models.

3 Results

In summer 2021, 84 chub were sampled from the River Frome, where they were the main species present in both electric fishing and angling surveys (with the exception of *P. phoxinus*), with lengths ranging from 64 to 295 mm (mean (± 95% CI): 153 ± 178 mm) (Fig. 2a), and with a maximum age of only 4+ years. The long-term dataset comprised of a further 2162 chub sampled from 35 rivers in England, where fish were present between 40 and 554 mm and up to the age of at least 19 years old, and from years classes 1998 and 2014 (Fig. 2a). Due to concerns over the accuracy of ageing scales from the larger, older fish, the data-set used for subsequent analyses was cropped to using fish aged up to the age of 10 years old as, up to this age, relatively consistent annual length increments were still being produced, but these were reduced considerably at older ages (Fig. 2a).

The cropped dataset (including the River Frome) comprised of 1694 chub, with the relationship between age and back-calculated length at the last annulus being linear ($R^2 = 0.92$; $F_{1,1692} = 19365.2$, $P < 0.01$; Fig. 2b). Analysis of the standardised residuals revealed significant differences between the rivers (ANOVA: $F_{35,1658} = 7.81$; $P < 0.01$), where chub in the River Frome were among the fastest growing, along with the River Thames and Wandle (Fig. 3A). The multiple regression model was significant (Adjusted $R^2 = 0.48$; $F_{8,25} = 2.95$; $P = 0.02$), with the significant factors being latitude (faster growth at higher latitude) and flow (faster growth in lower values of Q_{50}) (Tab. 1A).

The length increments of chub between age 1 and 2 year varied between 20 and 100 mm, with mean increments differing significantly between the rivers (ANOVA: $F_{34,1658} = 14.56$; $P < 0.01$) (Fig. 3B). The largest mean standardised residuals of these increments were produced in the River Frome, with relatively large increments also evident in the Rivers Lark, Bure and Tud (Fig. 3B). The relationship between the standardised increments and the mean standardised residuals of the lengths at the last annulus was positive and significant (Fig. 3C). The multiple regression model was significant (Adjusted $R^2 = 0.33$; $F_{8,25} = 2.99$, $P = 0.02$), with the significant factors being longitudinal position (faster

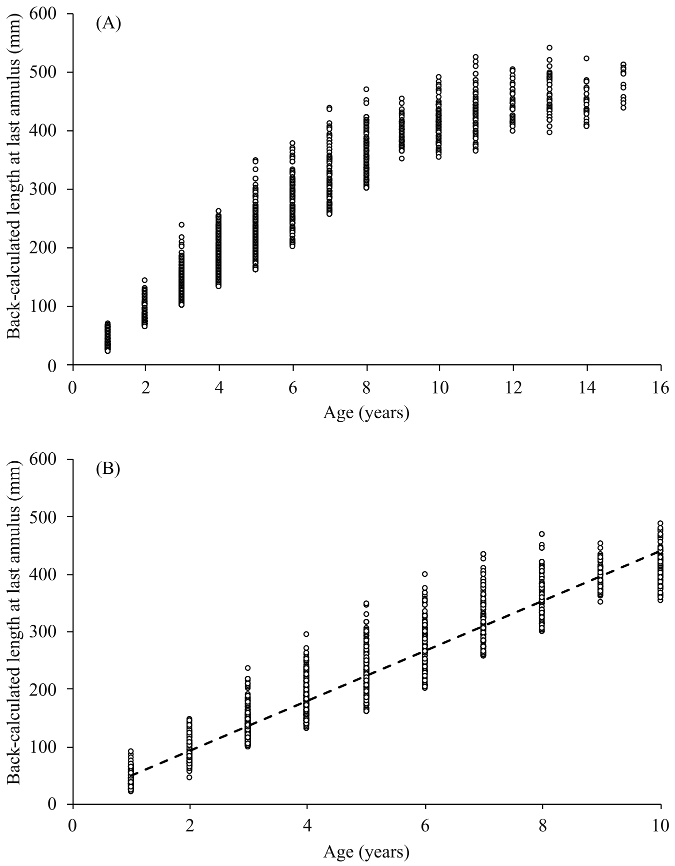

Fig. 2. Back-calculated lengths at the last annulus of chub *Squalius cephalus* across lowland rivers in England, where (A) all data up to age 15 years ($n = 2096$); and (B) the data used in analyses, where fish were only included to age 10 years due to ageing accuracy concerns above this age (n = 1694), and where the dashed line is the significant relationship between the variables according to linear regression.

growth in eastern areas) and altitude (faster growth at lower altitude; Tab. 1B).

4 Discussion

Across rivers in England, chub can grow to relatively large sizes and live for at least 19 years. In contrast, samples from the invasive population in the River Frome comprised of fish below 300 mm that were no older than four years old and, compared to the other analysed populations, were very fast growing. It is acknowledged that some larger, older chub are likely to be present in the river, with some anecdotal angler reports of fish captured to approximately 2.2 kg. However, given their absence in our samples, it is assumed these larger, older fish remain in very low abundance. In the River Frome samples, chub were the dominant species captured by rod-and-line angling (approximately 65% of all fish captured), and were the main species by biomass in electric fishing samples (European minnow were dominant by number). Thus, in the 15 years since their introduction, chub has established a population in the lower river, although the extent of their dispersal upstream remains uncertain.

As an introduced species establishes a sustainable population and starts to colonise their new environment, their abundance at the range front tends to be relatively low versus those in their core area (Masson *et al.*, 2016; Paton *et al.*, 2019). These spatial differences in populations abundances are then reflected in trait differences, such as in body size and fecundity, across the invasion gradient, with evident in a wide range of invasive freshwater taxa (*e.g.* fish, decapods and amphibians; Hudina *et al.*, 2012; Perkins *et al.*, 2013; Masson *et al.*, 2016). These spatial differences in trait expression are driven by a combination of phenotypic plasticity, natural selection and spatial sorting (Messager and Olden, 2019), with phenotypic plasticity a key feature of many highly invasive species as it enables rapid adaptation to the novel habitat (Chevin *et al.*, 2010). In alien fish, this trait plasticity is expressed through differences in their somatic growth and reproductive traits, with fish at the range front tending to be faster growing, reproducing earlier and then investing more in reproduction (Bøhn *et al.*, 2004; Fox *et al.*, 2007), with this expression facilitated by relatively low levels of intra-specific competition (Brownscombe and Fox, 2012; Grabowska *et al.*, 2021). Correspondingly, the fast growth rates observed in the translocated chub of the River Frome might be a response to their relatively low abundances in the river (although due to the river characteristics, estimates of population abundance could not be completed). However, the River Frome is also a lowland

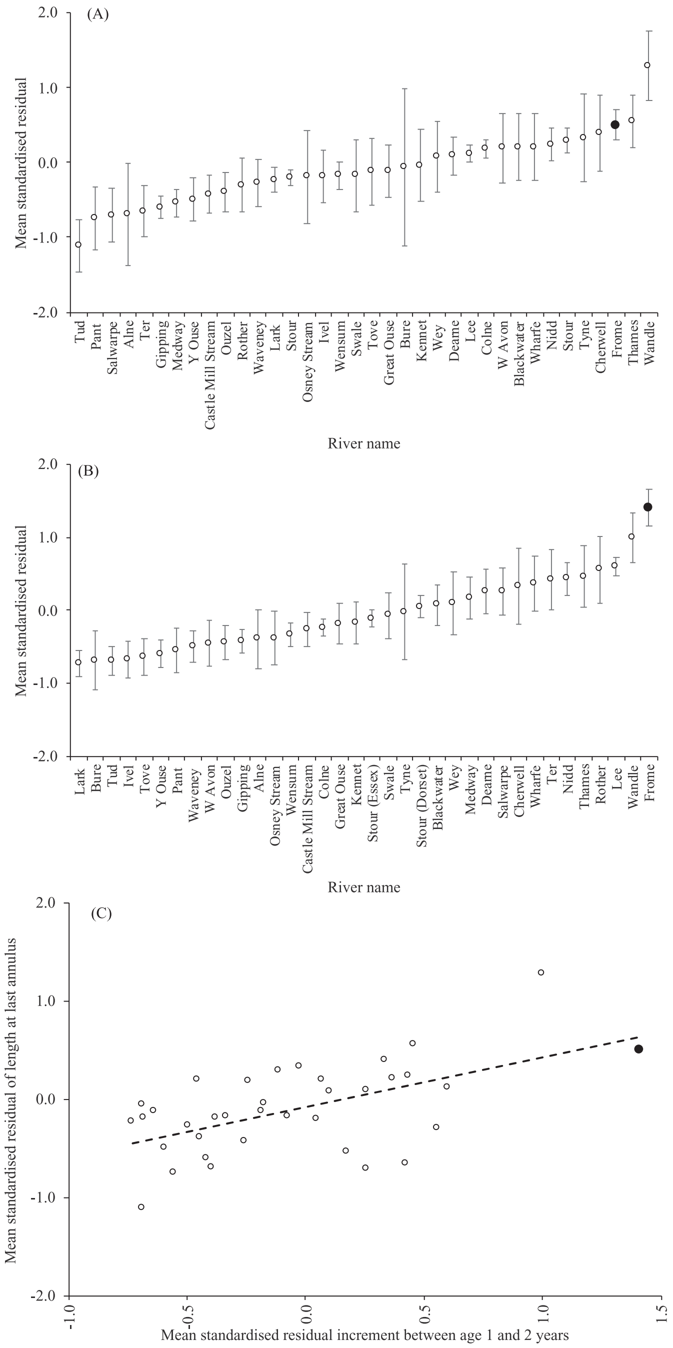

Fig. 3. Mean standardised residual (± 95% CI) by river of length at the last annulus (A) and length increment between age 1 and 2 years (B), and their significant relationship (dashed line) according to linear regression (C) ($R^2 = 0.32$; $F_{1,34} = 15.8$, $P < 0.01$). River Frome data are represented by the filled circles.

chalk-stream that produces very fast growing juvenile Atlantic salmon (*e.g.* migrating to sea as smolts at age 1+; Simmons *et al.*, 2020) and so its environment might also be highly conducive to producing fast growth rates of chub. However, a historical study on the growth of the trophically analogous dace in the river did not reveal such relatively fast growth rates in their population in the river (Mann, 1974).

The spatial variability in chub growth rates detected across the 36 populations here is consistent with studies on both the species (*e.g.* Mann, 1976; Bolland *et al.*, 2007) and cyprinid fishes more generally (Liu *et al.*, 2015). For example, European barbel, roach and dace have all demonstrated considerable spatial variability in their riverine growth that at least partially relates to differences in their environmental conditions, with biotic influences on riverine growth tending to be weaker (Britton *et al.*, 2013; Liu *et al.*, 2015). The environmental variables that significantly influence the growth of these species varies, with barbel being faster growing in conditions of higher biological and chemical water quality but the converse for chub and roach (Britton *et al.*, 2013; Liu *et al.*, 2015). In England, a study analysing 13 chub populations indicated latitude was important for growth (Liu *et al*., 2015). In our wider dataset, a significant effect of latitude and flow was detected in length at the last annulus although, counter-intuitively, the effect of latitude was positive (faster growth with increasing latitude). For flow, faster growth was detected at lower flow rates. Longitudinal and latitudinal positions of the sampling site had significant effects on increments produced between age 1 and 2 years. While both Przybylski (1995) and Tedesco *et al.* (2009) noted a significant effect of a longitude on chub growth, it is important to note these studies used a longitudinal gradient rather than actual position. These effects of latitudinal and longitudinal positions are likely to manifest through abiotic differences in the rivers, such as the effects of the interactions of climate, river geomorphology and the characteristics of the resident fish community (Oyugi *et al.*, 2011; Britton *et al.*, 2013; Liu *et al*., 2015).

The ageing of chub from scales is known to have the potential for inaccuracy through annuli misinterpretation (Mann and Steinmetz 1985; Britton *et al.*, 2004). While age validation studies can reduce these aging inaccuracies, such as mark-recapture studies using fish of known ages (Campana, 2001), this was unable to be completed here. Inaccuracy in the ageing of chub can be through two main sources. Firstly, the difficulty of ageing large, old fish has already been outlined due to multiple annuli on the scale margin and was the driver of using a dataset cropped at age 10 years (Musk *et al.*, 2006). However, this meant that the application of growth models, such as the von Bertalanffy growth model, could not be completed, preventing testing of relationships between the annual growth rate (K) and the maximum theoretical body size ($L_{\text{-infinity}}$) (Britton, 2007; Britton *et al.*, 2013). A second potential source of ageing inaccuracy of chub from scales is the position of their first annulus. Chub spawning can occur over extended periods that involves batch spawning, with larval production occurring in within populations in English rivers between as early as May and as late as August (Nunn *et al.*, 2007; Gutmann Roberts and Britton, 2020). Thus, chub from the same year-class might experience a relatively long or short first growth season, where individuals with the latter might only achieve a length of 20–25 mm in their first growth season (Gutmann Roberts and Britton, 2020), although these individuals can survive over-wintering and recruit (Nunn *et al.*, 2007). Given chub scales form when the fish is approximately 15 mm then this first annulus is likely to be very close to the scale focus and difficult to identify. Ageing errors were reduced here through careful examination of the scale focus and discussion between agers of what constitutes a first annulus on chub scales, although these errors are considered very difficult to eliminate completely.

In summary, the results here indicated that this translocated chub population in the River Frome is very fast growing in comparison to other populations in England. Although decoupling the drivers of this fast growth is difficult (*e.g.* their response to a productive chalk-stream environment versus a population that is early stage of invasion), these data nevertheless suggest that the species should continue to colonise the river, with this facilitated by rapid growth and, most likely, reproduction at relatively young ages. Thus, studies on the river that assess their integration into the fish assemblage and interactions with other species, such as Atlantic salmon, will be increasingly important. The relatively fast growth of this alien population was deduced through analysis of a larger data of 36 riverine chub populations across England that demonstrated high spatial variability that was at least partially driven by environmental variables and highlighted that this species can provide a strong model for testing the spatial and temporal influences on fish growth rates in temperate European rivers.

Supplementary Material

Table E1. Mean back-calculated length at the last annulus by age of chub Squalius cephalus from the 36 rivers in England that were used in analyses. Where there are missing mean lengths at age for a river, no fish were present in samples at that age.

The Supplementary Material is available at https://www.kmae.org/10.1051/kmae/2022013/olm.

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