Received: 5 May 2020 | Revised: 9 January 2021 | Accepted: 12 January 2021

DOI: 10.1111/jai.14175

ORIGINAL ARTICLE

Journal of Applied Ichthyology DWK WILEY

Consistency in the life history traits of four invasive *pseudorasbora parva* populations in Southern England

Gareth D. Davies[1,2] | J. Robert Britton[2]

[1]National Fisheries Services, Environment Agency, Bromholme Lane, Brampton, Huntingdon, Cambridgeshire, United Kingdom

[2]Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, United Kingdom

Correspondence
Robert Britton, Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Fern Barrow, Poole, Dorset, BH12 5BB, UK.
Email: rbritton@bournemouth.ac.uk

Abstract

Life history plasticity can be a strong predictor of the establishment and invasion success of introduced fishes. Here, the life-history traits of four *P. parva* populations in adjacent ponds in Southern England were measured throughout 2013 to determine the timing and length of their reproductive season and the extent of trait plasticity. The relative abundance of the populations (as catch per unit effort) was similar, with low variability in their traits relating to reproductive effort and somatic growth. All the populations were male dominated. Both sexes matured at small body sizes, with fish as small as 30 mm being mature in both sexes, with the age at maturity for both sexes being age 1+ years. The peak spawning period, characterised by female fish investing heavily in reproduction when their gonado-somatic index (GSI) values were highest and declined thereafter, occurred in May and June, and after a mean of 212 ± 24 degree-days >12°C, and with water temperatures being 13.2–14.6°C. There were no further peaks in GSI, despite the species being considered to have prolonged spawning periods across spring and summer. These results also suggest that whilst the expression of life-history traits of invasive fishes often vary with density, they can be highly consistent between populations at similar abundances and locations.

KEYWORDS

gonado-somatic index, invasion; non-native, life history

1 | INTRODUCTION

Non-native fishes have the capacity to cause substantial ecological consequences in receiving ecosystems through the detrimental impacts of increased predation and inter-specific competition that can lead to food web alterations and shifts in ecosystem functioning (Cucherousset & Olden, 2011; Gozlan et al., 2010). The risk-based management of non-native fishes is reliant on understanding the ability of that species to establish, impact and disperse in the spatial area in question, i.e. its potential to be invasive (Britton & Orsi, 2012). Fundamental to this are analyses of the life-history traits of the species, as these tend to be strong predictors of establishment success (Olden et al., 2006; Vila-Gispert et al., 2005). High plasticity in the expression of these life history traits is particularly advantageous to introduced species as it enables greater adaptive responses to novel environments (Davies & Britton, 2015a), with this evident in successful invasive fish, including pumpkinseed *Lepomis gibbosus* (Záhorská et al., 2017) and round goby *Neogobius melanastomus* (Ľavrinčíková et al., 2005). Consequently, examining spatial and temporal patterns in the life-history traits of introduced fishes can improve understanding of why some species establish and become highly invasive whilst others are unsuccessful (Cucherousset et al., 2009; Gozlan, Britton, et al., 2010).

Studies on the life history traits of non-native and invasive fishes provide data suitable for analysing how aspects of their ecology vary across broad spatial scales, such as for comparisons of trait expression between their native and invasive areas (Gozlan et al., 2020). Some life history traits, such as fast growth and early maturation with a high reproductive effort (e.g. gonado-somatic index), can increase the probability of an introduced fish establishing invasive populations (Fox et al., 2007), although the expression of these traits in this manner might, however, only be apparent early in the establishment period. Traits of slower growth rates, delayed maturity and reduced reproductive effort might then be expressed as the population establishes at higher population abundances (Davies & Britton, 2015a). This progression from rapid to slower development might involve trade-offs between individual investments in reproduction (e.g. high investment, larger egg sizes) versus population densities that could result in elevated levels of competition for food resources (Bøhn et al., 2004; Fox et al., 2007; MacArthur & Wilson, 1967).

The topmouth gudgeon *Pseudorasbora parva* (Temmink & Schlegel) is a highly invasive cyprinid fish species from Asia that has achieved pan-European distribution since its introduction in the 1960s (Gozlan, Andreou, et al., 2010; Gozlan et al., 2020; Spikmans et al., 2020). Ecological consequences include modifications to food web structure (e.g. Britton Davies & Brazier, 2010; Britton Davies & Harrod, 2010) and novel pathogen transmission (Andreou et al., 2012; Sana et al., 2020), and it is often regarded as a pest in lentic systems (Früeder & Pöckl, 2007). This species typically has a suite of life history characteristics that contribute to its success as an invader, being of small body size with short generation time, capable of high reproductive effort and batch spawning (Adamek & Siddiqui, 1997; Rosecchi et al., 2001; Švolíková et al., 2016), with its use of nest male nest guarding posited to increase larval survival (Davies & Britton, 2015b). Recent studies have suggested high plasticity in life history traits, such as somatic growth rates, is apparent following introductions, with initial fast growth when populations are at low density, followed by significantly slower growth post-establishment when populations are at higher abundance (Britton & Gozlan, 2013; Davies & Britton, 2015a). Indeed, population density was the only significant predictor of somatic growth rates across 10 *P. parva* populations covering a latitudinal gradient of 4.0° N, despite there being differences in mean annual air temperatures of approximately 3°C across this gradient that had been considered as an important factor affecting trait expression (Davies & Britton, 2015a). However, there remains considerable uncertainty as to how other life history traits, such as reproductive investment, are expressed in relation to population density, and there is also little information on how these change over the course of a spawning season, given the apparent protracted spawning behaviours of *P. parva* (Gozlan, Andreou, et al., 2010).

Here, the aim was to assess the life history traits of four *P. parva* populations in adjacent ponds at a site in Southern England through regular sampling over a 12 month period. As the populations were of different age (i.e. time since introduction), these provided the potential for testing differences in trait expression between ponds and in relation to their population densities. Selecting adjacent ponds minimised potential latitudinal or temperature effects on the populations, allowing more precise assessment of the density effects on life history traits. Our objectives were to thus assess population differences in life history traits (duration of spawning season, reproductive investment, length and age at maturity, and somatic growth rates) and evaluate any potential causal mechanisms. It was predicted that all populations would display an extended spawning period, as indicated by reproductive effort (as gonado-somatic index) varying between individuals over a prolonged period during spring and summer, with variability in traits between populations according to their abundance.

2 | MATERIALS AND METHODS

2.1 | Site and pond characteristics

The study site was located in Southern England, close to the city of Southampton, being a disused aquaculture site comprising of a number of adjacent small ponds (<400 m^{-2}) in which *P. parva* were present and licensed for temporary holding. Four rectangular ponds were selected for this study, all approximately 400 m^{-2} with depths up to 2 m. In Ponds 1 and 2, *P. parva* had only been present for 3 years prior to sample collection, whereas in Ponds 3 and 4, they had been present for at least 10 years. Ponds 1 and 2 were adjacent to each other, as were 3 and 4, separated by an elevated earth bank of 3 m. The distance between Ponds 2 and 3 was approximately 60 m. The only native fish present in the ponds were very low numbers of three-spined stickleback *Gasterosteus aculeatus* and tench *Tinca tinca*, with *P. parva* being dominant both numerically and by biomass. There were also no hydrological connections between the ponds and so fish were unable to move between them. The ponds also all had extensive beds of submerged macrophytes present throughout the year (e.g. *Elodea* spp.).

2.2 | Fish sampling

Sampling of populations commenced in January 2013 (but with fish capture only from February 2013 due to very low water temperatures in January 2013). Samples were then collected were at least once per month throughout the year (Table 1). Due to the extensive macrophyte beds, sampling was restricted to the deployment of rectangular fish traps that comprised of a circular alloy frame of length 107 cm, width and height 27.5 cm, mesh diameter 2 mm and with funnel shaped holes of 6.5 cm diameter at either end to allow fish entry and hence their capture (Britton et al., 2011). These traps provide representative samples of *P. parva* at lengths above 20 mm (Britton et al., 2011). Each trap was baited with 5 fishmeal pellets of 21 mm diameter and were fished in triplicate in each pond and set in the morning (~09:00) and lifted one hour later. The traps were always deployed in littoral areas and within the macrophyte beds. Following lifting of the traps, all fish were removed, counted, euthanized (anaesthetic overdose; MS-222) and frozen. Counts of the

TABLE 1 Number, mean fork length and length range of *Pseudorasbora parva* captured in monthly samples from Ponds 1–4 between February 2013 and January 2014. All lengths are in mm, with error as standard deviation. '—' indicates no fish captured during the sampling

	Pond 1			Pond 2			Pond 3			Pond 4		
Month	*n*	Mean length	Length range	*n*	Mean length	Length range	*n*	Mean length	Length range	*N*	Mean length	Length range
February	313	34.3 ± 7.5	24–84	—	—	—	—	—	—	—	—	—
March	222	32.4 ± 7.4	15–69	28	46.5 ± 12.4	26–81	57	38.7 ± 6.4	21–57	135	35.8 ± 3.6	27–49
April	93	32.2 ± 8.1	22–58	47	50.0 ± 10	28–83	141	38.2 ± 10.4	23–78	318	35.3 ± 4.2	22–50
May	290	32.5 ± 7.2	20–63	68	48.2 ± 6.6	27–63	281	36.9 ± 8.2	6–84	142	35.4 ± 4.1	27–47
June	232	31.1 ± 5.5	21–52	72	45.2 ± 3.9	30–52	119	37.7 ± 6.5	26–69	100	36.5 ± 3.6	29 – 47
July	6	41.0 ± 10.3	34–61	163	47.8 ± 9.6	28–77	135	41.6 ± 6.6	29–62	84	36.7 ± 4.4	29–62
August	377	31.4 ± 7.2	21–66	117	40.2 ± 10.6	22–71	115	37.8 ± 7.9	22–77	279	36.4 ± 3.6	28–50
September	67	34.2 ± 10.9	24–64	62	45.8 ± 9.1	27–63	136	41 ± 8.0	23–79	23	37.2 ± 4.2	29–48
October	608	36.8 ± 7.7	22–77	30	46 ± 9.5	23–63	20	40.3 ± 12.4	24–69	27	39.6 ± 5.5	30–52
November	122	36.6 ± 7.7	25–67	—	—	—	4	40.8 ± 4.5	37 –47	14	44.8 ± 3.7	39–52
December	7	47.9 ± 7.11	34–63	1	30 ± 0	—	26	36.0 ± 8.7	25–58	36	39.8 ± 5.3	31–52
January	17	35.9 ± 7.0	25–54	—	—	—	31	41.4 ± 5.9	26–54	80	39.64 ± 4.5	31–53

fish enabled calculation of catch per unit effort (CPUE) as a measure of their relative abundance (number of fish per trap per hour; n trap h^{-1}). In addition, the water temperatures of each pond were measured throughout the period of study using Tiny-Tag Aquatic 2 temperature loggers (Gemini Data Loggers, 2021, www.geminidataloggers.com) that recorded temperature every hour. These data were used to calculate the daily mean water temperature per month and the cumulative number of degree-days >12°C, with the latter calculated by totalling the number of degrees above 12°C for each mean daily temperature recording. These temperature data and metrics enabled their effects on the reproductive metrics of *P. parva* to be tested.

2.3 | Data collection and initial analyses

In the laboratory, samples were defrosted, measured (fork length, nearest mm) and weighed (to 0.01 g), before individuals were selected randomly and dissected to identify the sex (immature, male, female). This process continued until a total of 30 female fish had been identified. Between 3 and 5 scales were removed from each fish and used for subsequent age determination using a projecting microscope (×30 magnification). Ovaries were then removed and weighed for female fish, with oocyte diameters then measured using a stage micrometer under a microscope, measuring 20 eggs per individual female.

Ages of fish were categorised as either 1+ or 2+ years (no fish were aged at 3+ years and above, and few were young-of-the-year due to the mesh size of the traps). Sex ratios were expressed as the ratio of male to female fish in samples, and was completed as *P. parva* samples tend to be female dominated in smaller size ranges but male dominated in larger sizes (Gozlan, Andreou, et al., 2010). Reproductive effort (females only) was calculated using the gonado-somatic index (GSI: gonad weight/(body weight − gonad weight)). The length at which 50% of the fish were mature was calculated from the percentage of mature fish in each 5 mm length class using a modification of the formula of DeMaster (1978) as the original formula is based on age classes, so the modification used 5 mm length classes instead (Trippel & Harvey, 1987). For both sexes, a fish was classed as mature when developed gonads could be identified in the body cavity.

2.4 | Statistical analyses

The influence of water temperature was tested on CPUE per pond using a generalized linear model, as the data were not normally distributed (Kolmogorov-Smirnov test, $p < .05$). The dependent variable was CPUE, the independent variable was pond and the covariate was water temperature at the time of sampling. Model outputs were the estimated marginal means of CPUE per pond, their standard error and the significance of differences in mean CPUE according to linearly independent pairwise comparisons with Bonferroni adjustment for multiple comparisons. Sex ratios between male and females were expressed as the ratio of females to males, and tested for the significance of their differences from 1M: 1F using chi-square tests.

The effects of the date of sampling on female GSI were also tested using generalized linear models (GLM), as data were not normally distributed (Kolmogorov-Smirnov tests, $p < .05$, in both cases). In the models for each pond, GSI was the dependent variable, sample date was the independent variable and fish length was the covariate (due to its potential positive influence on GSI). Linear distribution models were used. Reported model results included its overall significance (reporting the Wald χ^2 value and its significance), and the estimated marginal means of GSI per sample date and its associated error (as standard error). The significance of differences in the estimated marginal means per sample date was indicated by linearly independent pairwise comparisons with Bonferroni adjustment for multiple comparisons. A final model was then constructed where peak GSI was the dependent variable, pond was the independent variable and fish length was the covariate. The estimated marginal means for each pond (i.e. mean adjusted values) and their pairwise comparisons indicated the significance of their differences and so also indicated the influence of fish density (as mean CPUE) on these metrics.

Differences in growth rates between the ponds were then assessed by testing differences in length at age 1+ and age 2+ between the ponds in GLMs, where the dependent variable was length at age, pond was the independent variable and sample date was the categorical covariate. Outputs were the overall significance of the model and then the estimated marginal means of length at age per pond, adjusted for the date of capture, and their differences according to linearly independent pairwise comparisons, with Bonferroni adjustment for multiple comparisons. All statistics were completed in SPSS v. 21.0 for Windows (IBM Corp., 2012). Wherever error is expressed around the mean, it is standard error unless otherwise stated.

3 | RESULTS

The generalized linear model (GLM) testing differences in catch per unit effort across the ponds was not significant (Wald χ^2 = 0.84, *df* = 3, *p* = .84), where the effect of temperature as a covariate was also not significant (*p* = .31). Mean CPUE values per pond were 1:116 ± 33; 2:81 ± 23; 3:97 ± 25; and 4:95 ± 22 n trap h^{-1}. The GLM testing the effect of month on fish length was significant (Month: Wald χ^2 = 262.87, *df* = 10 *p* < .01; Pond: Wald χ^2 = 1,285.02, *df* = 3, *p* < .01), with larger fish being captured in July than in other months (Table 1). The *P. parva* in pond 2 (44.40 ± 0.28 mm) were significantly larger than Ponds 1 (33.12 ± 0.16 mm), 3 (37.43 ± 0.23 mm) and 4 (35.49 ± 0.21 mm) (*p* < .01 in all cases).

Across all the analysed samples per pond, the mature fish were male dominated, with sex ratios differing significantly from 1:1 (χ^2, *p* < .05 in all cases; Table 2). Lengths at 50% maturity for males in ponds 1, 2, 3 and 4 were 31.2, 47.0, 30.3 and 32.0 mm respectively; for females, they were 32.2, 47.0, 28.2 and 32.0 mm respectively. Scale ageing revealed all mature fish were at age 1+ years or above.

TABLE 2 Reproductive traits of female *P. parva* in Ponds 1–4. All lengths are in mm with error around mean represented as standard deviation

Pond	Mean oocyte diameter (mm)	Oocyte diameter range (mm)	Sex Ratio (M:F)
1	0.88 ± 0.25	0.20–1.7	1:0.87
2	0.96 ± 0.28	0.30–1.8	1:0.96
3	1.06 ± 0.33	0.30–1.9	1:0.84
4	0.94 ± 0.27	0.30–1.6	1:0.73

There was a significant effect of month on female gonado-somatic index in each pond (GLM: Pond 1: Wald χ^2 = 866.4, *df* = 11, *p* < .01; Pond 2: Wald χ^2 = 456.8, *df* = 8, *p* < .01; Pond 3: Wald χ^2 = 641.3, *df* = 10, *p* < .01; Pond 4: Wald χ^2 = 638.3, *df* = 10, *p* < .01). The effect of length as a covariate was also significant in Ponds 1, 2 and 4 (*p* < .05) but not pond 3 (*p* = .31). Female GSI increased from January, peaked in May and June, and reduced significantly thereafter (Figure 1; Table 3). Values then slowly increased later in the year in preparation for spawning the following year (Figure 1). Across the ponds, there were between 163 and 278 degree days >12°C prior to the post-spawning GSI decline (mean 212 ± 23.9) (Figure 2). The mean monthly temperatures with peak GSI values were between 13.2 and 14.6°C, with higher water temperatures recorded later in the summer (Figure 1). Differences in female peak GSI between the ponds were not significant (GLM: Wald χ^2 = 1.73, *df* = 3, *p* > .05), with mean peak GSI being 18.6 ± 0.9, 20.1 ± 1.1, 19.2 ± 1.2 and 20.1 ± 1.1 in Ponds 1 to 4 respectively (Figure 1).

The oocyte diameters revealed a bi-modal distribution in fish from all ponds in the pre-spawning period (May 2013), with diameters recorded between 0.20 and 1.90 mm (Table 2). Mean oocyte diameters differed significantly between the ponds (GLM: Wald χ^2 = 148.24, *df* = 3, *p* < .01; Table 2); differences were between ponds 1 and 2, 3 and 4; 2 and 3; 3 and 4 and between pond 4 and 3 (pairwise comparisons, *p* < .05), but not between ponds 2 and 4 (pairwise comparisons, *p* > .05) (Table 2).

Mean length at age 1+ was 31.9 ± 0.2; 45.6 ± 0.3; 38.7 ± 0.2 and 36.0 ± 0.2 mm for ponds 1–4 respectively, with mean length at age 2 + being 56.7 ± 1.2; 59.5 ± 0.9; 65.5 ± 1.44 and 48.6 ± 3.1 for ponds 1–4. Bonferroni pairwise comparisons showed significant differences in mean length at age 1+ between all ponds (Wald χ^2 = 1,335.25, *df* = 3, *p* < .01.), with *P. parva* having a significantly greater mean length at age 2+ in Pond 3 (*p* < .01) than all others (Wald χ^2 = 34.739, *df* = 3, *p* < .01). Mean length at age 2+ for fish in Ponds 2 and 4 were not significantly different from those in Pond 1 (*p* > .05).

4 | DISCUSSION

Across the four ponds, there was consistency in the expression of the life-history traits of *P. parva*, with little evidence of substantial and significant differences in the assessed life history traits between the populations. The populations were all male dominated, comprising of individuals that matured at small body sizes and spawned from age 1+ years, and with females that invested heavily in reproduction, at least early in the spawning season. These outputs are relatively consistent with other studies on invasive *P. parva* that demonstrate similar *r*-selected trait expression (Gozlan, Andreou, et al., 2010), a common pattern in invasive fish more generally (Feiner et al., 2012; Fox et al., 2007), but with ages and lengths at maturity that were lower than reported from the native range (e.g. Záhorská & Kováč, 2009). Other studies on *P. parva* in both their native and invasive range have suggested they are a

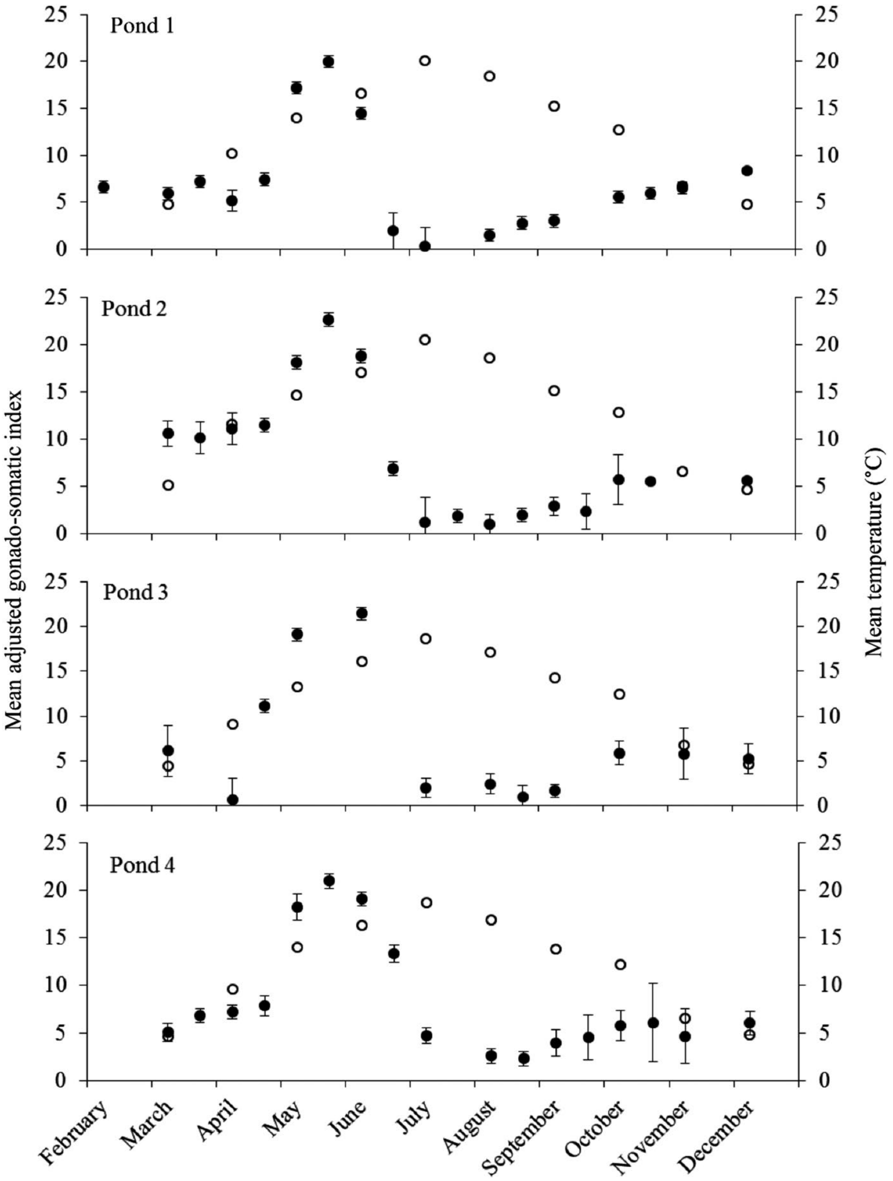

FIGURE 1 Mean monthly adjusted (for fish fork length) gonado-somatic index for Ponds 1–4 with monthly mean water temperatures from February 2013 to December 2013. Where present, bars are standard error and temperature measurement is in °C. ● represents adjusted gonado-somatic index; ○ represents monthly mean temperature

TABLE 3 Pairwise comparisons of mean adjusted (for fish fork length) gonado-somatic index of female *P. parva* between May 2013 and all other months. Mean differences are displayed, with standard error and * denotes significant difference at $p < .05$

May	Month	Pond 1	Pond 2	Pond 3	Pond 4
	February	12.00 ± 0.80*			
	March	11.99 ± 0.67*	9.95 ± 1.46*	13.14 ± 3.10*	14.18 ± 0.92*
	April	11.84 ± 0.77*	8.90 ± 1.04*	9.04 ± 1.07*	12.88 ± 0.93*
	June	5.23 ± 0.77*	7.55 ± 0.89*	−2.21 ± 1.09	3.67 ± 0.91*
	July	18.20 ± 2.11*	18.65 ± 1.09*	17.22 ± 1.34*	15.59 ± 1.09*
	August	16.49 ± 0.66*	18.94 ± 1.10*	17.42 ± 1.17*	17.82 ± 0.90*
	September	15.58 ± 0.84*	17.68 ± 1.29*	17.54 ± 1.10*	16.22 ± 1.41*
	October	12.81 ± 0.65*	14.87 ± 1.44*	13.27 ± 1.62*	14.51 ± 1.66*
	November	12.08 ± 0.80*		13.43 ± 3.09*	15.55 ± 3.11*
	December	10.21 ± 3.60	15.20 ± 4.88	13.97 ± 1.89*	14.26 ± 1.46*

fractional or batch spawning species, having a prolonged reproductive season with the production of young-of-the-year over a number of months (e.g. Gozlan, Andreou, et al., 2010). Here, however, across all populations, there was only one peak apparent in female GSI that occurred in May and June in response to increasing water temperatures (range 13.2–14.6°C in the spawning period) and after approximately 210 degree-days >12°C; GSI significantly declined thereafter, suggesting substantially decreased

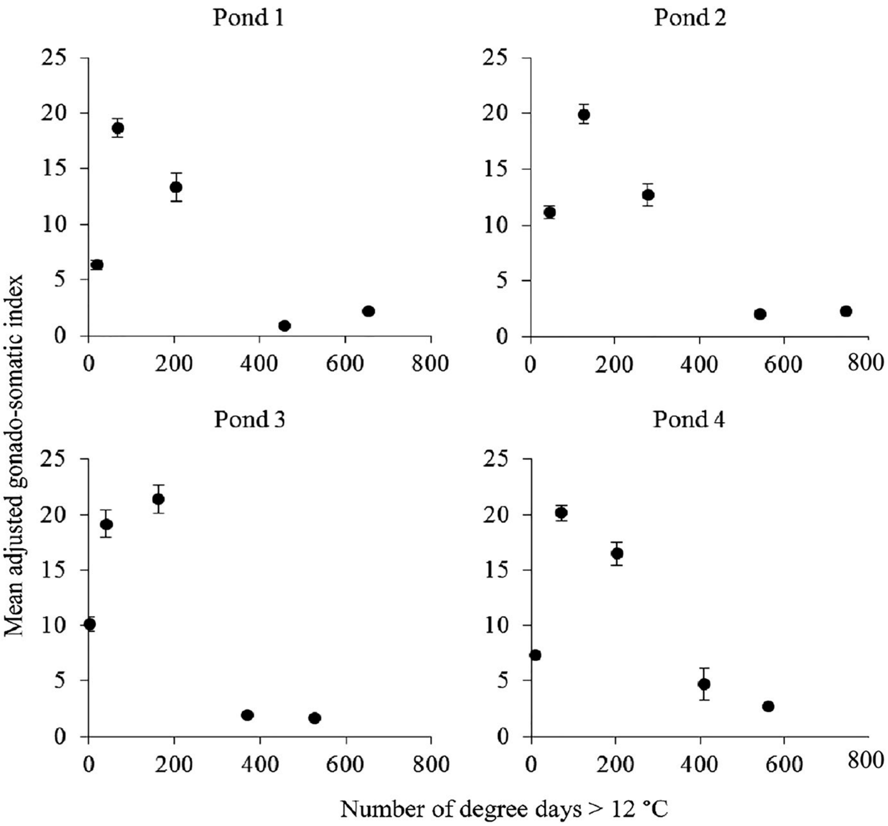

FIGURE 2 Number of degree days greater than 12°C water temperature with mean adjusted gonado-somatic index in Ponds 1–4. Error bars represent standard error

spawning activity. These results suggest these populations had a relatively discrete spawning period that was concluded by June, with this suggestion of a single peak in reproductive effort being contrary to the prediction.

Studies on the plasticity of *P. parva* somatic growth rates have revealed that population density is an important determinant of growth, often having greater effects than temperature (Britton & Gozlan, 2013; Davies & Britton, 2015a). This has been suggested as facilitating *P. parva* establishment as it assists the development and reproduction of newly released propagules early in life, enabling them to overcome population demographic bottlenecks relating to their low density (Britton & Gozlan, 2013; Davies & Britton, 2015a). In the four populations, there was little evidence of high inter-population plasticity in both reproductive and somatic growth metrics, with this consistency in trait expression being an important result. This is because in the study design, the ponds were selected on the basis of their age, with Ponds 1 and 2 being relatively new populations (approximately 3 years since introduction), whereas Ponds 3 and 4 were at least 10 years old. Thus, the rationale of their selection was that the populations in Ponds 1 and 2 would still be establishing, so potentially being at lower abundance when compared to Ponds 3 and 4, and thus were predicted to comprise of faster growing, earlier maturing fish that invested more heavily in reproduction. That this was not apparent relates to their relative abundances; despite the different ages of the populations, catch per unit effort suggested their densities of *P. parva* above 20 mm were not significantly different to each other, suggesting rapid population establishment in Ponds 1 and 2. Thus, their absolute densities were assumed to relatively similar and so insufficient to result in significant plasticity in their life-history traits, with no evidence of any context-dependent differences. Notwithstanding, it is acknowledged that there was considerable temporal variability in the CPUE data in each pond that might have also been related to the location of the individual traps and patchy distributions in *P. parva*, with this variability potentially being a driver of the non-significant differences detected in CPUE between the ponds. Unfortunately, these factors were unable to be quantified in the study and thus their influence on relative abundance remains speculative. It is argued that the use of traps was the only viable method to efficiently capture the *P. parva* samples, given that other capture methods, including micromesh seine netting and electric fishing, unable to be used effectively for these small-bodied fish in weed-infested, small ponds (Britton et al., 2011). However, it is suggested that some caution is used when the CPUE data are used to suggest variability in the absolute density of *P. parva* was low between the four ponds.

These results need consideration in the context of the risk management of invasive *P. parva* populations. Highly invasive across Europe, impacts on native communities include the transmission of a novel pathogen (e.g. Andreou et al., 2012; Sana et al., 2018, 2020) and the detrimental effects of increased inter-specific competition (e.g. Britton, Davies, & Brazier, 2010). In the case of the latter, this might only be apparent at very high population abundances that only occur in disturbed lentic environments, such as angling ponds, where high trophic subsidies from anglers facilitate the production of unnaturally high *P. parva* densities (Britton et al., 2015; Jackson et al., 2013; Tran et al., 2015). The outputs of this study, in conjunction with those of Britton and Gozlan (2013) and Davies and Britton (2015a), suggest that following an introduction of *P. parva* into a new environment, it is likely that the expression of their growth and reproductive traits will enable rapid establishment of a stable population (<2 years) that, where the environment is relatively undisturbed, will then have life-history traits that maintain a relatively stable population size, including spawning events that occur in relatively discrete periods. Consequently, these results suggest that management actions to inhibit the development of their populations in newly invaded environments need to happen soon after their introduction if they are to be effective.

Analyses of the life history traits of invasive fishes tend to be assessed for populations located over broad spatial scales, such as over latitudinal gradients that can act as surrogates for temperature gradients (Cucherousset et al., 2009). These studies tend to show relatively predictable variation in trait expression with latitude; in the Northern hemisphere, slower growth rates and reduced reproductive investment at age tend to occur at higher latitudes (Cucherousset et al., 2009). This pattern has been evident populations of invasive largemouth bass *Micropterus salmoides* (Britton et al., 2010) and pumpkinseed (Záhorská et al., 2017), as well as being weakly evident in common carp *Cyprinus carpio* (Vilizzi & Copp, 2017). In contrast, there has been less focus on identifying consistency in life history trait expression of invasive fish at similar latitudes and where differences between populations, such as in their physical environments and abundances, are minimal. Here, the results demonstrated that there was low variability in the expression of these traits between ponds that differed only in their time since *P. parva* introduction, suggesting that traits such as growth rates and reproductive investment are also predictable across relatively small spatial areas. This indicates that studies investigating patterns at large spatial scales can potentially rely on low replication of populations in specific regions, providing there is low variation in population densities in that region.

In summary, analysis of the life-history traits of these four *P. parva* populations over a 12 month period revealed consistency in the peak of their reproductive season and in the expression of important life-history traits. Their consistency was interpreted as relating to the low variability in relative abundances across the populations, suggesting that at specific densities, aspects of their life-history traits expression are predictable and lack stochasticity. These results thus contribute to increasing knowledge base on invasive *P. parva* in Europe specifically, and small invasive fishes generally, by suggesting that the continuum of life-history trait expression, whilst varying with population density, can be an important predictor of the stability of invading populations.

ACKNOWLEDGEMENTS

We thank the staff of the Environment Agency who contributed to the completion of this work. The views expressed are those of the authors and not their parent organisations.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Raw data are available from the corresponding author at reasonable request.

ORCID

J. Robert Britton https://orcid.org/0000-0003-1853-3086

REFERENCES

Adamek, Z., & Siddiqui, M. A. (1997). Reproduction parameters in a natural population of topmouth gudgeon *Pseudorasbora parva*, and its consequences and food characteristics with respect to sex dissimilarities. *Polish Archives of Hydrobiology*, *44*, 145–152.

Andreou, D., Arkush, K. D., Guégan, J. F., & Gozlan, R. E. (2012). Introduced pathogens and native freshwater biodiversity: A case study of *Sphaerothecum destruens*. *PLoS One*, *7*, e36998. https://doi.org/10.1371/journal.pone.0036998

Bøhn, T., Sandlund, O. T., Amundsen, P.-A., & Primicerio, R. (2004). Rapidly changing life history during invasion. *Oikos*, *106*, 138–150. https://doi.org/10.1111/j.0030-1299.2004.13022.x

Britton, J. R., Davies, G. D., & Brazier, M. (2010). Towards the successful control of the invasive *Pseudorasbora parva* in the UK. *Biological Invasions*, *12*, 125–131. https://doi.org/10.1007/s10530-009-9436-1

Britton, J. R., Davies, G. D., & Harrod, C. (2010). Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: A field investigation in the UK. *Biological Invasions*, *12*, 1533–1542. https://doi.org/10.1007/s10530-009-9566-5

Britton, J. R., & Gozlan, R. E. (2013). How many founders for a biological invasion? Predicting introduction outcomes from propagule pressure. *Ecology*, *94*, 2558–2566. https://doi.org/10.1890/13-0527.1

Britton, J. R., Harper, D. M., & Oyugi, D. O. (2010). Is the fast growth of an equatorial *Micropterus salmoides* population explained by high water temperature? *Ecology of Freshwater Fish*, *19*, 228–238. https://doi.org/10.1111/j.1600-0633.2010.00407.x

Britton, J. R., & Orsi, M. L. (2012). Non-native fish in aquaculture and sport fishing in Brazil: Economic benefits versus risks to fish diversity in the upper River Paraná Basin. *Reviews in Fish Biology & Fisheries*, *22*, 555–565. https://doi.org/10.1007/s11160-012-9254-x

Britton, J. R., Pegg, J., & Gozlan, R. E. (2011). Quantifying imperfect detection in an invasive pest fish and the implications for conservation management. *Biological Conservation*, *144*, 2177–2181. https://doi.org/10.1016/j.biocon.2011.05.008

Britton, J. R., Tran, T. N. Q., & Ruiz-Navarro, A. (2015). Synergistic effects of propagule pressure and trophic subsidies overcome biotic resistance to a non-native fish. *Biological Invasions*, *17*, 3125–3131. https://doi.org/10.1007/s10530-015-0938-8

Cucherousset, J., Copp, G. H., Fox, M. G., Sterud, E., van Kleef, H. H., Verreycken, H., & Zahorska, E. (2009). Life history traits and potential invasiveness of introduced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. *Biological Invasions*, *11*, 2171.

Cucherousset, J., & Olden, J. D. (2011). A conspectus of the ecological impacts of non-native freshwater fishes. *Fisheries*, *36*, 215–230.

Davies, G. D., & Britton, J. R. (2015a). Influences of population density, temperature and latitude on the growth of invasive topmouth gudgeon *Pseudorasbora parva*. *Ecology of Freshwater Fish*, *24*, 91–98.

Davies, G. D., & Britton, J. R. (2015b). Assessing the efficacy and ecology of biocontrol and biomanipulation for managing invasive pest fish. *Journal of Applied Ecology*, *52*, 1264–1273.

DeMaster, D. P. (1978). Calculation of average age of sexual maturity in marine mammals. *Journal of Fisheries Research Board of Canada*, *35*, 862–875.

Feiner, Z. S., Aday, D. D., & Rice, J. A. (2012). Phenotypic shifts in white perch life history strategy across stages of invasion. *Biological Invasions*, *14*, 2315–2329.

Fox, M. G., Vila-Gispert, A., & Copp, G. H. (2007). Life history traits of introduced Iberian pumpkinseed (*Lepomis gibbosus*) relative to native populations: Can differences explain colonization success? *Journal of Fish Biology*, *71*, 56–69.

Früeder, L., & Pöckl, M. (2007). Ecological traits of aquatic NIS invading Austrian fresh water. In F. Gheradi (Ed.), *Freshwater bioinvaders: Profiles, distribution, and threats* (pp. 233–257). Springer Verlag.

Gemini Data Loggers. (2021). Tinytag from Gemini Data Loggers: Robust monitoring. https://www.geminidataloggers.com

Gozlan, R. E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Caiola, N., Cakic, P., Djikanovic, V., Esmaeili, H. R., Falka, I., Golicher, D., Harka, A., Jeney, G., Kováč, V., Musil, J., Nocita, A., Povz, M., Poulet, N., … Robert Britton, J. (2010). Pancontinental invasion of *Pseudorasbora parva*: Towards a better understanding of freshwater fish invasions. *Fish and Fisheries*, *11*, 315–340. https://doi.org/10.1111/j.1467-2979.2010.00361.x

Gozlan, R. E., Britton, J. R., Cowx, I., & Copp, G. H. (2010). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*, *76*, 751–786.

Gozlan, R. E., Záhorská, E., Cherif, E., Asaeda, T., Britton, J. R., Chang, C.-H., Hong, T. O., Miranda, R., Musil, J., Povz, M., Tarkan, A. S., Tricarico, E., Trichkova, T., Verreycken, H., Weiperth, A., Witkowski, A., Zamora, L., Zweimueller, I., Zhao, Y., … Combe, M. (2020). Native drivers of fish life history traits are lost during the invasion process. *Ecology & Evolution*, *10*, 8623–8633. https://doi.org/10.1002/ece3.6521

IBM Corp. (2012). *IBM SPSS Statistics for Windows, Version 21.0*. IBM Corp.

Jackson, M. C., Allen, R., Pegg, J., & Britton, J. R. (2013). Do trophic subsidies affect the outcome of introductions of a non-native freshwater fish? *Freshwater Biology*, *58*, 2144–2153. https://doi.org/10.1111/fwb.12197

L'avrincikova, M., Kovac, V., & Katina, S. (2005). Ontogenetic variability in external morphology of round goby *Neogobius melanostomus* from Middle Danube, Slovakia. *Journal of Applied Ichthyology*, *21*, 328–334. https://doi.org/10.1111/j.1439-0426.2005.00677.x

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. University Press.

Olden, J. D., Poff, N. L., & Bestgen, K. R. (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs*, *76*, 25–40. https://doi.org/10.1890/05-0330

Rosecchi, E., Thomas, F., & Crivelli, A. J. (2001). Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. *Freshwater Biology*, *46*, 845–853. https://doi.org/10.1046/j.1365-2427.2001.00715.x

Sana, S., Hardouin, E. A., Paley, R., Zhang, T., & Andreou, D. (2020). The complete mitochondrial genome of a parasite at the animal-fungal boundary. *Parasites & Vectors*, *13*, 1–12. https://doi.org/10.1186/s13071-020-3926-5

Sana, S., Williams, C., Hardouin, E. A., Blake, A., Davison, P., Pegg, J., Paley, R., Zhang, T., & Andreou, D. (2018). Phylogenetic and environmental DNA insights into emerging aquatic parasites: Implications for risk management. *International Journal for Parasitology*, *48*, 473–481. https://doi.org/10.1016/j.ijpara.2017.11.002

Spikmans, F., Lemmers, P., op den Camp, H. J. M., van Haren, E., Kappen, F., Blaakmeer, A., van der Velde, G., van Langevelde, F., Leuven, R. S. E. W., & van Alen, T. A. (2020). Impact of the invasive alien topmouth gudgeon (*Pseudorasbora parva*) and its associated parasite Sphaerothecum destruens on native fish species. *Biological Invasions*, *22*, 587–601. https://doi.org/10.1007/s10530-019-02114-6

Švolíková, K., Zahorska, E., & Kováč, V. (2016). Unusually high production of oocytes in two invasive populations of topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1846). *Journal of Applied Ichthyology*, *32*, 978–981.

Tran, T. N. Q., Jackson, M. C., Sheath, D., Verreycken, H., & Britton, J. R. (2015). Patterns of trophic niche divergence between invasive and native fishes in wild communities are predictable from mesocosm studies. *Journal of Animal Ecology*, *84*, 1071–1080. https://doi.org/10.1111/1365-2656.12360

Trippel, E. A., & Harvey, H. H. (1987). Reproductive responses of five white sucker *Catostomus commersoni* populations in relation to lake acidity. *Canadian Journal of Fisheries and Aquaculture Science*, *44*, 1018–1023.

Vila-Gispert, A., Alcaraz, C., & García-Berthou, E. (2005). Life history traits of invasive fish in small Mediterranean streams. *Biological Invasions*, *7*, 107–116. https://doi.org/10.1007/s10530-004-9640-y

Vilizzi, L., & Copp, G. H. (2017). Global patterns and clines in the growth of common carp *Cyprinus carpio*. *Journal of Fish Biology*, *91*, 3–40.

Záhorská, E., Balážová, M., Bhagat, Y., & Copp, G. H. (2017). Does latitude drive the phenotypic plasticity of morphological traits in non-native pumpkinseed populations from Europe? *Knowledge & Management of Aquatic Ecosystems*, *418*, 29. https://doi.org/10.1051/kmae/2017021

Záhorská, E., & Kováč, V. (2009). Reproductive parameters of invasive topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1846) from Slovakia. *Journal of Applied Ichthyology*, *25*, 466–469.

How to cite this article: Davies GD, Robert Britton J. Consistency in the life history traits of four invasive *pseudorasbora parva* populations in Southern England. *J Appl Ichthyol*. 2021;37:295–302. https://doi.org/10.1111/jai.14175